

LETTER

Are patterns of density dependence in the Global Population Dynamics Database driven by uncertainty about population abundance?

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Abstract

Density dependence in population growth rates is of immense importance to ecological theory and application, but is difficult to estimate. The Global Population Dynamics Database (GPDD), one of the largest collections of population time series available, has been extensively used to study cross-taxa patterns in density dependence. A major difficulty with assessing density dependence from time series is that uncertainty in population abundance estimates can cause strong bias in both tests and estimates of strength. We analyse 627 data sets in the GPDD using Gompertz population models and account for uncertainty via the Kalman filter. Results suggest that at least 45% of the time series display density dependence, but that it is weak and difficult to detect for a large fraction. When uncertainty is ignored, magnitude of and evidence for density dependence is strong, illustrating that uncertainty in abundance estimates qualitatively changes conclusions about density dependence drawn from the GPDD.

Keywords

Density dependence, GPDD, observation error, time series.

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INTRODUCTION

Density dependence in population growth rates is a fundamental concept for ecological theory as well as for population management. Estimating density dependence in wild populations has, however, proved challenging. Ideally, density dependence in growth rates should be estimated directly from the effects of density acting on the traits contributing to population growth. Given current progress in statistical methods for jointly analysing data on both population size and demographic traits (Besbeas *et al.* 2005), and with long-term population studies involving demographic data becoming increasingly common, this approach holds a bright future. However, the number of such studies is currently limited and they only cover a rather narrow range of taxa. Long-term time series on population abundance are more common and can be used to estimate density dependence in population growth rates. Under this approach, density dependence is defined as a general tendency of per capita growth rates to decrease when population size is large and increase when it is small, and is identified as a statistical pattern not tied to any specific biological mechanism (Wolda & Dennis 1993).

It was noted early that estimates and tests of density dependence based on regressing log transformed current observed population size, y_t , on previous log transformed observed population size, y_{t-1} , are sensitive to uncertainty in the observations (St-Amant 1970; Kuno 1971; Itô 1972; Slade 1977). Similar concerns were aired about estimates from fisheries models of stock-recruitment data (Ludwig & Walters 1981; Walters & Ludwig 1981). Uncertainty inflates the Type I error rate of tests for density dependence (Shenk *et al.* 1998) and tends to bias estimates towards stronger density dependence if dynamics are under-compensatory and towards weaker density dependence if dynamics are over-compensatory (Benson 1973). Bulmer (1975) devised two tests for density dependence taking the time series nature of the data into account. One of those was designed to be robust

against uncertainty about population size and has been shown to perform better than density dependence tests ignoring uncertainty in estimates of population abundance (Shenk *et al.* 1998). Simple procedures to correct for effects of uncertainty such as the SIMEX method have been suggested (Solow 1998; Freckleton *et al.* 2006) but typically require that the variance of the uncertainty about population size is known. A more direct approach to account for uncertainty is provided by state space models, first used for modelling population dynamics in the fisheries literature (e.g. Mendelssohn 1988; Sullivan 1992). State space models in these cases consist of a model of a population dynamical process combined with a model of the uncertainty in the abundance estimates, sometimes termed observation, measurement or sampling error, and may be used to estimate the variance of this uncertainty as well as to filter out its effects (de Valpine & Hastings 2002; Calder *et al.* 2003; Buckland *et al.* 2004; Dennis *et al.* 2006). Estimates derived from state space models tend to have smaller bias than estimates ignoring uncertainty about population abundance, but can also have large variances (Knappe 2008), and the statistical properties of even simple state space model estimators are not fully understood (Dennis *et al.* 2006; Lebreton 2009).

The Global Population Dynamics Database (GPDD), containing over 5000 time series on population abundances obtained from various forms of population surveys, has provided an opportunity for ecologists to explore population dynamical patterns over a wide range of taxa (Inchausti & Halley 2001). Analyses using data in the GPDD have focused on, e.g., extinction risks (Fagan *et al.* 2001; Inchausti & Halley 2003; Brook *et al.* 2006), population cycles (Kendall *et al.* 1998; Murdoch *et al.* 2002) and effects of weather (Knappe & de Valpine 2011) but, arguably, the studies stirring the most attention as well as debate have addressed population regulation and density dependence. These have explored patterns in the shape of density dependence (Sibly *et al.* 2005; Polansky *et al.* 2009) and in the strength of regulation and density dependence (Brook & Bradshaw 2006; Sibly *et al.* 2007;

Ziebarth *et al.* 2010). Conclusions have been contradictory with Ziebarth *et al.* (2010) in contrast to Sibly *et al.* (2007) reporting only weak population regulation and Brook *et al.* (2006) reporting ubiquitous density dependence. None of these studies explicitly accounted for uncertainty in abundance estimates. It has, however, been argued that uncertainty may be responsible for some of the conclusions drawn by Brook & Bradshaw (2006; Lebreton 2009), that they provide a potential caveat of the analyses of Sibly *et al.* (2005; Reynolds & Freckleton 2005) and in general, that uncertainty may explain the dynamic patterns seen in the GPDD time series (Akçakaya *et al.* 2003; Holmes *et al.* 2007).

The aim of this study was to examine the strength of and evidence for density dependence in the GPDD while accounting for uncertainty in population abundance estimates. The extent to which estimates of density dependence are affected by including vs. omitting uncertainty in the models depends on the underlying population dynamics (Benson 1973; Freckleton *et al.* 2006) and on the degree of uncertainty in the abundance estimates. Hence, despite knowing that uncertainty, if ignored, will bias tests and estimates of density dependence, the magnitude of the bias cannot be assessed unless the dynamical parameters as well as the variance of the abundance uncertainty are estimated. The effect of uncertainty about population abundance on estimates of density dependence in the GPDD is therefore unclear *a priori*. The strength of evidence for density dependence taking uncertainty into account and the impact of uncertainty on estimation is studied here for the first time in the GPDD and, more generally, across a large number of real ecological time series covering a wide range of animal taxa.

MATERIAL AND METHODS

We analysed 627 time series with population indices obtained from the GPDD (NERC Centre for Population Biology 1999). Data sets were filtered out from the database by removing harvest and non-index based data, data sampled at non-annual intervals and time series taking less than 15 unique values. Among the 627 remaining time series, the number of observations per series has a median of 23 and ranges from 15 to 157 (Figure S1 in Appendix S2). The identities of the individual data sets analysed are given in Appendix S1.

We use the stochastic Gompertz population model to analyse the strength of density dependence in the data. The model is defined through

$$N_{t+1} = N_t \exp(a - b \log N_t + \varepsilon_t)$$

where N_t is population density or size in year t , a is an intercept, b is a measure of the strength of density dependence and ε_t is normally distributed process error with mean zero and standard deviation τ . By log transforming the population abundance and putting $x_t = \log N_t$ this simplifies to

$$x_{t+1} = a + (1 - b)x_t + \varepsilon_t = a + cx_t + \varepsilon_t \quad (1)$$

where $c = 1 - b$ is the lag 1 autocorrelation of the log transformed population abundance when the process is stationary. The model has a stationary distribution only when $|c| < 1$. The stationary distribution of the log transformed population size is normal with mean $a/(1 - c)$ and variance $\tau^2/(1 - c^2)$, giving a log normal stationary distribution for the population size. When c is equal to 1 ($b = 0$), the process is density independent, and on the log scale is a Gaussian random walk with drift given by a .

Uncertainty in population abundance estimates is modelled with a log normal distribution in such a way that log transformed population abundance estimates y_1, \dots, y_T are given by

$$y_t = x_t + \eta_t, \quad (2)$$

where $\eta_t \sim N(0, \sigma^2)$ (Dennis *et al.* 2006). Four variants of the model defined by (1) and (2) were fitted to each data set; a full model with both uncertainty about population abundance and density dependence denoted by SSG (state space Gompertz), a model with uncertainty about population abundance, but no density dependence (c fixed to one) denoted SSRW (state space random walk), a model with density dependence, but no uncertainty about population abundance (σ^2 fixed to zero) denoted G (Gompertz) and a model with neither uncertainty about population abundance nor density dependence (c fixed to one and σ^2 fixed to zero) denoted RW (random walk).

All models were fit through numerical maximisation of the log likelihood computed using the Kalman filter implemented in R (R Development Core Team 2010). The Kalman filter was initiated by assuming a wide prior distribution on the initial state centred around the first observation, $x_1 \sim N(y_1, 10)$. For each model and data set the numerical maximisation (using the BFGS algorithm implemented in the optim function) was repeated for 50 random starting values to ensure that we found the global optimum (Dennis *et al.* 2006).

The maximum likelihood (ML) estimate of c under the state space model with uncertainty about population abundance (SSG) will be denoted \hat{c}_{SSG} and the ML estimate under the model without uncertainty about population abundance (G) will be denoted \hat{c}_G . It should be noted that the estimates \hat{c}_G are biased for c in small samples even if there is no uncertainty about population abundance. Under stationarity, the bias amounts to $E(\hat{c}_G) - c = -(1 + 3\delta)/T + O(1/T^2)$ (Kendall 1954). This first-order bias is non-negligible for most ecological time series and will tend to assign stronger density dependence to shorter time series, if the dynamics are under-compensatory. To uniformly limit the bias to less than 0.1, say, one needs a time series of at least length 40. The magnitudes of small sample biases of \hat{c}_{SSG} are not known in general, but it is reasonable to assume they may be equally non-negligible (Staudenmayer & Buonaccorsi 2005; Dennis *et al.* 2010).

To investigate the effect of uncertainty in population abundance estimates on tests for density dependence we used the likelihood ratio statistic for the null hypothesis $c = 1$ against the hypothesis $c \neq 1$. That is, we used the maximum log likelihood values ℓ_{SSG} , ℓ_{SSRW} , ℓ_G and ℓ_{RW} obtained from the numerical optimisations and computed the two test statistics $LLR_{SSG} = -2(\ell_{SSRW} - \ell_{SSG})$ and $LLR_G = -2(\ell_{RW} - \ell_G)$. The null distributions of the test statistics were approximated by parametric bootstrapping. For each time series and test, 100 data sets were simulated using the parameter estimates from the RW and SSRW model-fits that were then fitted to the respective models to obtain the likelihood ratio statistics and approximate P -values. This was a relatively low number of bootstrap replicates, but was adequate for our purposes and was computationally feasible. The reason for bootstrapping the likelihood ratio test statistic is that it does not follow the usual asymptotic Chi-squared approximation as the null hypothesis gives non-stationary dynamics (Dennis and Taper 1994; Dennis *et al.* 2006). We also investigated model selection methods by using BIC and AICc to compare between density dependent and density independent models, either accounting for uncertainty in the observations (SSG vs. SSRW) or ignoring uncertainty (G vs. RW).

Hypothesis tests only indicate the evidence for density dependence within each data set. Considering the full distribution of P -values, strength may be borrowed across data sets to obtain stronger inference about the proportion of density dependent time series. One way of doing so is a key component of the false discovery rate (FDR) method of Storey (2002) which aims at estimating the maximal proportion of data sets that could be density independent. This method builds on the fact that P -values are uniformly distributed under the null hypothesis. By assuming that all large P -values come from data sets under the null hypothesis, an upper bound for the total fraction of data sets that satisfy the null hypothesis can be obtained (Storey 2002). However, since bootstrap P -values from density independent simulations turn out to be not quite uniform, we transformed them to be uniform using their own empirical distribution function. We then applied the same empirical distribution function to the real data P -values, before estimating the bound. Both, the FDR procedure and our empirical P -value adjustment can be interpreted as making the results more conservative: we obtain lower bounds on the fraction of density dependent data sets.

As small sample biases and several other statistical properties of maximum likelihood estimators for state space models are unknown, the methods used here might not give an accurate view of the strength of density dependence across data sets. We therefore simulated two sets of mirrored time series to get a picture of how parameter estimates would have been distributed if all populations were governed by either density independent dynamics or weakly density dependent dynamics. For each real time series, we thus simulated two series, one with uncertainty about population abundance, but no density dependence and the other with uncertainty about population abundance and all data sets weakly density dependent via ϵ set to 0.8. The parameters for the simulation of density independent data were based on the estimates obtained from fitting the models to the real data, i.e. the SSRW estimates, and for the density dependent data on a separate fit of the real data with ϵ fixed at 0.8. The time series were simulated with the same length and with missing data in the same places as the corresponding real data. The simulated data were then analysed in the same way as the real data by fitting all the models SSG, SSRW, G and RW and computing BIC and AICc values and bootstrap tests.

RESULTS

The time series may be divided into two categories; data sets for which the state space model (SSG) and the Gompertz model (G) give identical estimates of density dependence due to the estimate of the variance of the uncertainty about population abundance falling at the boundary ($\sigma^2 = 0$), and data sets where $\hat{\epsilon}_{SSG}$ and $\hat{\epsilon}_G$ differ. Of the 627 data sets analysed, around 236 (38%) belong to the first category and 391 (62%) to the second (using a numerical threshold of 0.01 for the standard deviation of the uncertainty about population abundance being effectively zero, Figure S2 in Appendix S2). The absolute value of the differences between $\hat{\epsilon}_{SSG}$ and $\hat{\epsilon}_G$, representing the differences between point estimates of density dependence accounting for and ignoring uncertainty, range from 0 to 1.09. In general, for any particular data set $\hat{\epsilon}_{SSG}$ tends to be farther away from 0 than $\hat{\epsilon}_G$ (Fig. 1). In terms of strength of density dependence, this means that state space model estimates tend to indicate weaker strengths than the Gompertz estimates if the Gompertz estimates indicate under-compensatory density dependence and stronger strengths if the

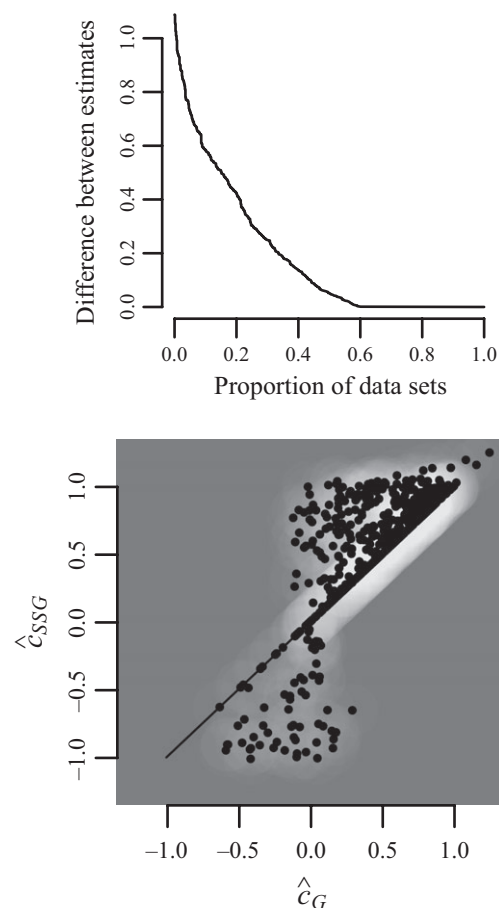


Figure 1 The top panel shows the proportion of data sets for which the absolute value of the difference in strength of density dependence between accounting for and ignoring uncertainty is larger than the value on the x-axis. For example, for around 20% of the data sets the difference between the estimates is larger than 0.5. The bottom panel shows pairwise comparisons of estimates of ϵ under the state space model (SSG) and Gompertz model (G). The identity line is drawn for reference.

Gompertz estimates indicate over-compensatory dynamics. If the Gompertz estimates indicate close to perfectly compensatory dynamics ($\epsilon = 0$), state space model estimates may push estimates in either direction. These results may be understood as the consequence of noise in abundance estimates reducing the lag 1 autocorrelation of the dynamics. The lag 1 autocorrelation of the observations y_t is (under stationarity) $\frac{\epsilon}{1 + (1 - \epsilon^2)\sigma^2/\tau^2}$ which has an absolute value smaller than $|\epsilon|$ and reduces to ϵ when $\sigma^2 = 0$. Intuitively, by filtering out noise, the state space model will therefore tend to restore autocorrelation to the hidden dynamics.

Despite a large proportion of boundary estimates, the distribution of $\hat{\epsilon}_{SSG}$ across all data sets is clearly very different from and predominantly right shifted compared with the distribution of $\hat{\epsilon}_G$; similar patterns are seen for the simulated data sets (Fig. 2, Figure S3–S5 in Appendix S2). Compared with the simulated density independent data, the distribution of state space model estimates $\hat{\epsilon}_{SSG}$ for the real data is left shifted indicating existence of density dependent data sets (Fig. 1, Figure S6 in Appendix S2). A similar comparison between $\hat{\epsilon}_{SSG}$ for the real and simulated density dependent data shows that the distribution for the real data contains a few more

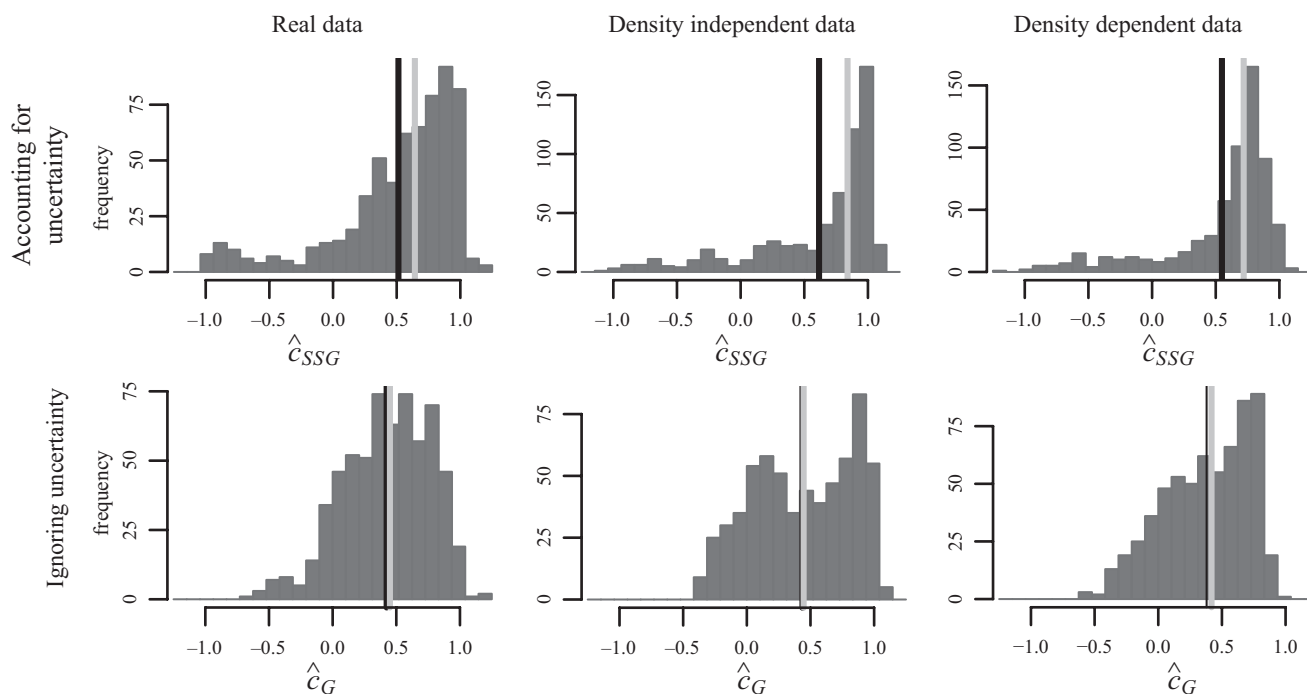


Figure 2 Histograms of estimates of ϵ accounting for uncertainty (top panels) and ignoring uncertainty (bottom panels) for the real data (left panels), simulated density independent data (middle panels) and simulated density dependent data (right panels). The means of the estimates across all data sets are indicated by black lines and the medians by grey lines.

data sets indicating density independence or very weak density dependence, but also a few more data sets indicating stronger density dependence (Fig. 2, Figure S7 in Appendix S2).

Bootstrap tests for density dependence not accounting for uncertainty suggest that the majority (56%) of data sets are density dependent at the 5% level (Table 1, Fig. 3). Accounting for uncertainty about population abundance, only 16% of the tests turn out significant. The simulated density independent data illustrate that Type I errors are inflated to 50%, if uncertainty is not controlled for. When accounting for uncertainty, the Type I error rate is close to nominal, but the distribution of P -values deviates slightly from the expected uniform distribution in that there are fewer large values than anticipated (Fig. 3). The average power across all data sets for detecting density dependence at $\epsilon = 0.8$ while controlling for uncertainty is 20% at the 5% level, under the parametric bootstrap test (Table 1). Similar to hypothesis testing, model selection using BIC or AICc shows a strong tendency to indicate density dependence, even when it is not present, if uncertainty in abundance estimates is ignored (Table 1).

Using the distribution of P -values to estimate a lower bound for the proportion of density dependent data sets suggest that at least 45% of the data sets are density dependent, when uncertainty is accounted for (Table 1). The same estimate when ignoring uncertainty indicates that nearly all (94%) data are density dependent.

DISCUSSION

We have shown that uncertainty in population abundance estimates and small sample effects are capable of qualitatively changing inference drawn about density dependence from population time series data in large scale, multi species studies. Ignoring the possibility

of uncertainty in abundance estimates, one may come to the conclusion that, when data sets are analysed individually, density dependence is present in 56% of the 627 GPDD populations using bootstrap tests and 76–80% using model selection (Table 1). Similar evidence for density dependence (50% and 64–70% respectively) could arise from density independence combined with noisy observations. The proportion of data sets that individually suggest density dependence is reduced to 16% with bootstrap tests and 34–38% with model selection, when uncertainty in abundance estimates is accounted for. Analysing the evidence for density dependence across all data sets suggests that at least 45% of the time series are to some degree density dependent (or in other ways incompatible with a random walk model; Wolda & Dennis 1993) when uncertainty is accounted for, and 94% when it is not (Table 1). Part of the weaker support for density dependence should be attributed to a decrease in power when estimating the amount of uncertainty in abundance estimates. Point estimates, however, also show a different picture with a much larger portion of time series estimated as nearly density independent or weakly density dependent, when uncertainty is accounted for.

Are patterns in density dependence seen in the GPDD, when not accounting for density dependence, in fact driven by uncertainty in abundance estimates, as suggested by Akçakaya *et al.* (2003) and Holmes *et al.* (2007)? A definitive answer to this question would require more precise estimates of the variance of the uncertainty about population abundance than that provided by the state space models. To obtain such estimates information that is not available in the GPDD would be needed. Nevertheless, our results suggest that uncertainty in abundance estimates may to a large degree be shaping the pattern of strength of density dependence estimated from the data and are certainly capable of

Table 1 Proportion of real and simulated data sets showing support for density dependence or density independence under significance tests and model selection while accounting for (SSG) or ignoring uncertainty (G). All simulated data contain uncertainty about population size unless the corresponding variance estimate for the real data is zero

	Lower bound for proportion of density dependent data sets (%)	Significant density dependence tests at the 5% level	BIC support for density dependence (BIC(DD) + 2 < BIC(DI))	BIC support for density independence (BIC(DI) + 2 < BIC(DD))	AICc support for density dependence (AICc(DD) + 2 < AICc(DI))	AICc support for density independence (AICc(DI) + 2 < AICc(DD))
Real data, SSG fit	45%	16%	34%	14%	38%	12%
Simulated density independent data, SSG fit	(0%)	5%	18%	33%	21%	24%
Simulated density dependent data, SSG fit	54%	20%	44%	9%	48%	9%
Real data, G fit	97%	56%	76%	3%	80%	1%
Simulated density independent data, G fit	76%	50%	64%	11%	70%	6%
Simulated density dependent data, G fit	100%	63%	82%	0%	84%	0%

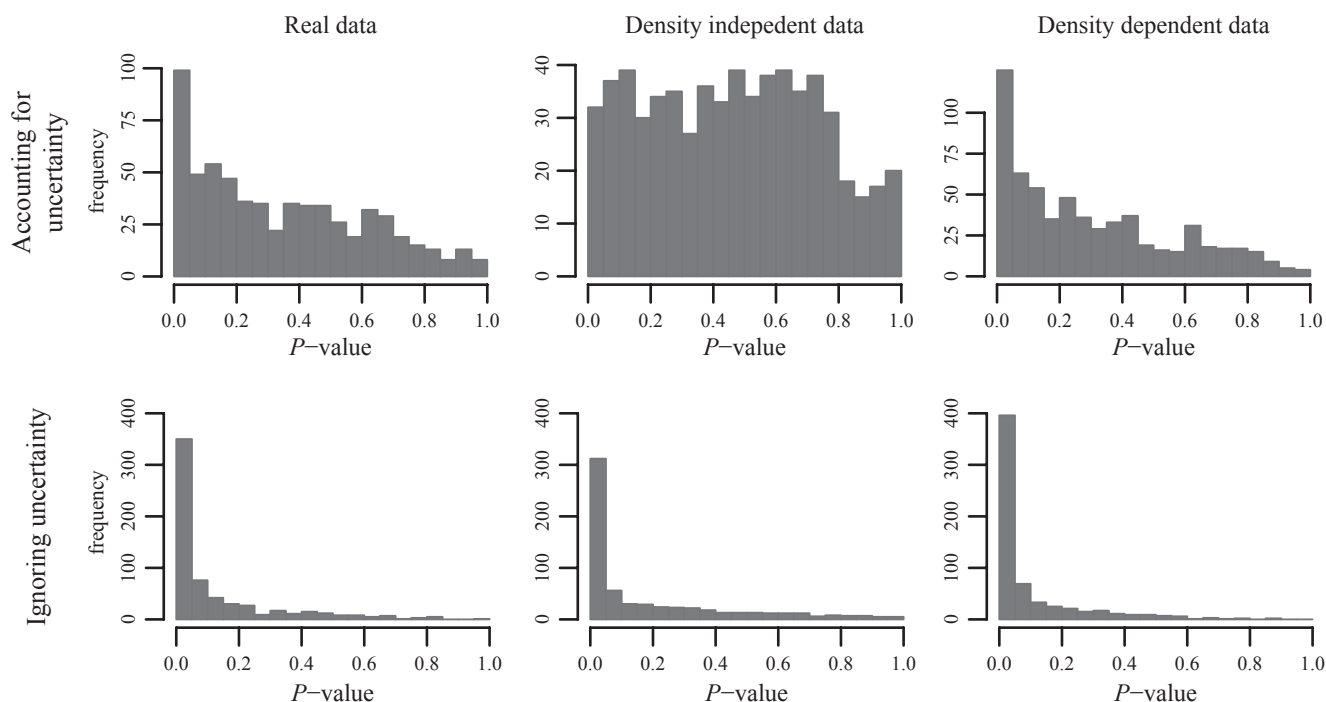


Figure 3 Histograms of bootstrap P -values based on accounting for uncertainty (top panels) and ignoring uncertainty (bottom panels) for the real data (left panels), simulated density independent data (middle panels) and simulated density dependent data (right panels).

driving qualitative conclusions derived from them. It is in this respect interesting to compare our results to previous analyses of density dependence in the GPDD. One should bear in mind that different studies have used different criteria for selecting subsets of the data, and that inference methods have varied. In making comparisons, complete agreement among the results of those studies should therefore not be expected. Brook & Bradshaw (2006) found significant density dependence at the 5% level for 33–50% of their time series (depending on the test used) and support for density dependence using best model BIC for 66% of the time series. The time series and methods used here provide even stronger indications of density dependence, when uncertainty is ignored. In the light of our results, one might therefore ask

whether their conclusion would have been upheld if uncertainty about population abundance had been controlled for (Lebreton 2009). Sibly *et al.* (2007) suggested strong regulation in the GPDD. On the other hand, our results are similar to the results found by Ziebarth *et al.* (2010) in that both our studies suggest that regulation may be weak in many of the data sets in the GPDD. Our explanations differ however, due to the different starting points taken. Ziebarth *et al.* (2010) argued that the qualitative difference found between their study and Sibly *et al.* (2007) was due to them analysing on average longer time series and incorporating lagged density dependence. Our results show that ignoring vs. accounting for the possibility of uncertainty about population abundance alone can give rise to similarly diverging conclusions. In

theory, the two approaches could be combined, but would call for caution about the estimability of model parameters given the short length of many GPDD series.

Analysing a large collection of widely diverse data within a limited modelling framework by necessity involves several potential caveats. Without attempting to provide an exhaustive list, we will here discuss those we find could be most important to consider. First, as noted above, it is difficult to assess how precise abundance estimates in the GPDD are. Separating uncertainty in abundance estimates from process error based on a univariate time series is notoriously difficult, and estimates of the variance of the uncertainty tend to be imprecise. Point estimates of the variance in the observations suggest coefficients of variation (CV) that are high for several data sets (the CV is larger than 0.5 for 23% of the data sets, Figure S2 in Appendix S2). Our results may underestimate the effect of uncertainty for many data sets. About 40% of the variance estimates representing abundance uncertainty are at the boundary (equal to zero) for the SSG model, but all data sets not corresponding to a complete census must contain some amount of uncertainty. It may seem tempting to apply model selection criteria to determine whether or not to include uncertainty about population abundance in the final model, but this is not likely to work well in practice (Knape *et al.* 2011). On the contrary, as even small amounts of uncertainty can lead to undesirable biases (Lebreton 2009) it is advisable to include it in all models under a model selection scheme, if there are reasons to assume that they may be present in the data. Second, uncertainty about population abundance and lagged density dependence can give rise to similar autocorrelation structures (Ziebarth *et al.* 2010). It is therefore conceivable that lagged density dependence could be picked up as uncertainty in our parameter estimates. Third, an auto-correlated environment affecting the dynamics of a population may give rise to a density dependent pattern in a population time series even if the effect of the environment is not density dependent (Maelzer 1970; Solow 1990). This will cause density dependence to be over-estimated if the environment is negatively auto-correlated and under-estimated if it is positively auto-correlated. Fourth, Gompertz models have log-linear population dynamics. This might provide a decent first-order approximation for many populations, but not for populations undergoing strongly non-linear dynamics. Non-linearities could lead to parameter estimates being biased in directions and with magnitudes that are not known. However, the model for density independence used for hypothesis testing would also serve as a null model for several non-linear population models, in which case an incorrect alternative model might reduce power, but would not inflate Type I error rates. Bayesian point estimates for our GPDD data under a Ricker model also leave our main conclusions unaffected (Appendix S3). Fifth, it can be debated to what extent the GPDD is representative of ecological time series in general (Inchausti & Halley 2003). The GPDD pertain to a wide range of species, but the collection of data is unbalanced in several ways. For example, the number of data sources is significantly smaller than the number of species and some studies account for a large proportion of time series across several species. It is further difficult to assess the general quality of the time series.

CONCLUSIONS

The dramatic effect that uncertainty can have on the dynamics of population abundance time series is a serious obstacle for our understanding of large-scale patterns in density dependence in

population growth rates. Unfortunately, there is no known easy way around the problem. When the amount of uncertainty in population estimates is unknown, as is the case for the GPDD, the best approach currently available is to fit a state space model in an attempt to quantify the errors. For the lengths of time series typical in ecology, precision and power is relatively low using this method. This low power combined with the strong bias caused by uncertainty in abundance estimates leads to diverging inference about density dependence from the collection of time series when accounting for relative to ignoring uncertainty in the estimation procedure. The strong support for density dependence in the time series is reduced to the point that the majority of the data sets might be nearly density independent.

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AUTHORSHIP STATEMENT

JK performed analyses and wrote the first draft of the manuscript. PdV contributed to revisions of text and methods.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Main IDs of the GPDD data sets analysed.

Appendix S2 Additional figures.

Appendix S3 Robustness of point estimates to linear dynamics assumption.

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