LETTER

Early warning signals of extinction in deteriorating environments

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During the decline to extinction, animal populations may present dynamical phenomena not exhibited by robust populations[1,2]. Some of these phenomena, such as the scaling of demographic variance, are related to small size[3–6] whereas others result from density-dependent nonlinearities[7]. Although understanding the causes of population extinction has been a central problem in theoretical biology for decades[8], the ability to anticipate extinction has remained elusive[9]. Here we argue that the causes of a population's decline are central to the predictability of its extinction. Specifically, environmental degradation may cause a tipping point in population dynamics, corresponding to a bifurcation in the underlying population growth equations, beyond which decline to extinction is almost certain. In such cases, imminent extinction will be signalled by critical slowing down (CSD). We conducted an experiment with replicate laboratory populations of *Daphnia magna* to test this hypothesis. We show that populations crossing a transcritical bifurcation, experimentally induced by the controlled decline in environmental conditions, show statistical signatures of CSD after the onset of environmental deterioration and before the critical transition. Populations in constant environments did not have these patterns. Four statistical indicators all showed evidence of the approaching bifurcation as early as 110 days ($\sim$8 generations) before the transition occurred. Two composite indices improved predictability, and comparative analysis showed that early warning signals based solely on observations in deteriorating environments without reference populations for standardization were hampered by the presence of transient dynamics before the onset of deterioration, pointing to the importance of reliable baseline data before environmental deterioration begins. The universality of bifurcations in models of population dynamics suggests that this phenomenon should be general[10–12].

At present, habitat destruction and degradation are the major threats to viability for the majority of globally threatened or endangered bird (1,045), amphibian (1,641) and mammal ($\geq$652) species[13]. The other leading threats to these groups are invasive non-indigenous species, exploitation for human use, emerging infectious diseases and pollution[13]. Each of these causes of extinction is an example of environmental deterioration, the effects of which are expected to be exacerbated by global changes in climate, land conversion and population density[14]. A central problem in the conservation of these species is the timing of interventions and the predictability of extinction[9], but the demographic properties of extinction in deteriorating environments remain poorly understood[15,16] and standard models are almost exclusively concerned with extinction due to demographic and environmental stochasticity and catastrophic events in stationary environments[3,17]. Understanding population dynamics under realistic expectations of future environmental conditions and improving capabilities to predict extinction are therefore priorities for research.

An important but overlooked aspect of environmental deterioration is that changes in environment-driven demographic rates such as reproduction, migration and survival can cause qualitative changes in patterns of population fluctuations. For instance, the same experimental plankton system can have stationary fluctuations, cycles or chaos-like dynamics under different environmental conditions[18,19]. Such qualitative changes in population dynamics are associated with bifurcations in the corresponding models. Although less dramatic, a similar phenomenon occurs in a population that is subject to simple density dependence under conditions which initially cause a positive intrinsic rate of increase (populations rebound when perturbed to small sizes), but that through environmental deterioration eventually declines. This phenomenon is general and occurs in virtually all biologically sensible models, including both discrete-time and continuous-time logistic-like models, and gives rise to a threshold (a transcritical bifurcation) that is a tipping point between a population which will persist and one that necessarily goes extinct.

It has been discovered recently that generic early warning signals may occur that indicate when a tipping point is approaching[10,12,20]. Many such indicators are a result of CSD[10,21,22], a dynamical phenomenon that typically occurs in the vicinity of a phase transition or critical point, including the transcritical bifurcation in the logistic model. CSD refers to the decreasing rate of recovery from small perturbations to a population's expected trajectory in the vicinity of a tipping point. This is seen in the simple logistic model $dn/dt = f(n) = rn(1 - n/k)$, where n is population abundance, t is time, r is the intrinsic rate of increase and k is the carrying capacity, and where the derivative $df/dn = r - 2rn/k$ goes to zero as r approaches $r_c = 0$ from either direction. As a result, small perturbations, such as those caused by demographic stochasticity, may accumulate and persist over time, leading to local increases in variance and autocorrelation as the tipping point is approached[20]. Other early warning signals of an approaching bifurcation include changes in the patterns of skewness[23] and spatial correlation[24]. Just as these statistics have been used to investigate critical transitions in physiological[25], ecosystem[26] and climate system processes[10,27], they should also accompany the process of population decline through environmental deterioration and may therefore provide early indications of population extinction. The generality of CSD in population dynamics has been questioned on theoretical grounds[28], however. Thus, empirical studies are needed to determine whether signals of CSD can indeed warn of impending bifurcations before they occur. Here we present evidence for CSD in experimental populations, showing that the forecasting of population extinction in deteriorating environments is a theoretically achievable possibility.
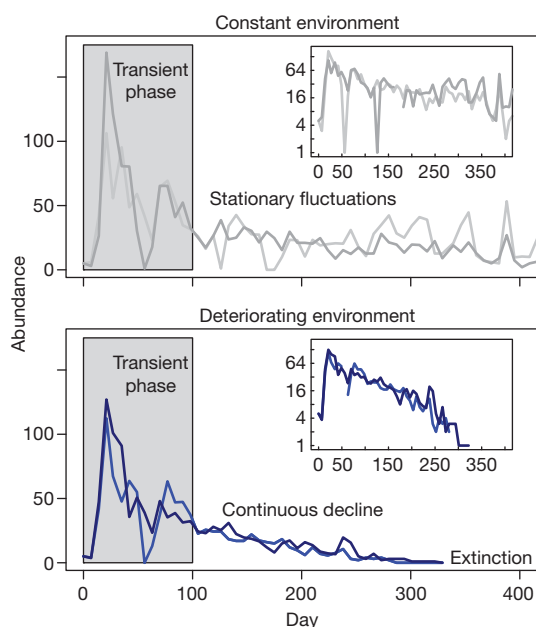
We performed an experiment in which replicate laboratory populations of the cladoceran zooplankton *D. magna* were assigned to deteriorating-environment (treatment) and constant-environment (control) groups (Supplementary Information, appendix I). After an initial period to allow population dynamics to stabilize, populations in the treatment group were subjected to declining levels of food provision. Inspection of time series revealed that virtually all populations had a prolonged ($\sim$100-d) phase of transient dynamics before stabilizing at $n \approx 35$ (Fig. 1). The experiment was terminated on day 416, when the last population in the deteriorating-environment group went extinct. The mean extinction time in deteriorating environments was 297 d (standard error, 16.4 d), and the effect of deterioration on extinction time was

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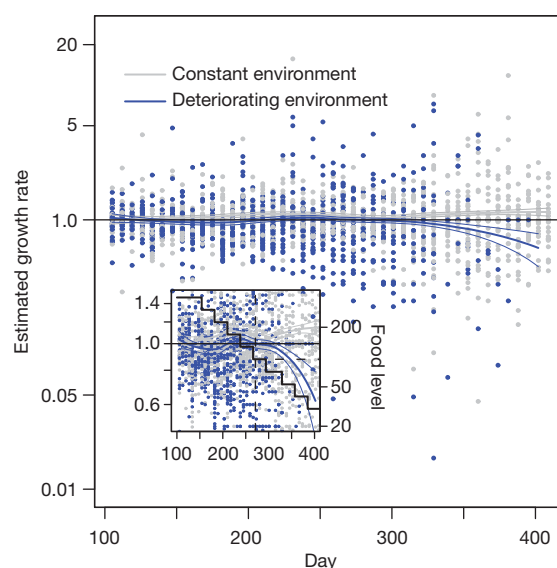
highly significant (proportional hazards regression, $P = 8.4 \times 10^{-9}$; estimated hazard ratio, 14:9). Furthermore, the observed (non-censored) extinction time distribution is noticeably left-skewed (Supplementary Information, appendix II), in contrast to theoretical predictions and previous experimental observations of extinction in constant environments[29].

In the general density-dependent map $n_{t+\Delta t} = n_t \lambda(n_t, \boldsymbol{\theta})$ with nonlinear growth rate λ, a function of the parameter vector $\boldsymbol{\theta}$, the bifurcation occurs at $\lambda(n_t, \boldsymbol{\theta}) = 1$. To locate the timing of this occurrence and relate it to food supply, we first estimated the realized population growth rate in successive intervals for each population using the formula $\hat{\lambda} = (n_{t+\Delta t}/n_t)^{1/\Delta t}$. To diminish the effect of transient fluctuations, observations before day 105 were removed before we estimated population growth rates. A plot of estimated growth rates against time shows that when food is abundant, the realized growth rate is approximately $\lambda = 1$, that is, a steady state corresponding to carrying capacity (Fig. 2), but that it declines precipitously as food is diminished. Interpolation with loess, performed separately for treatment and control groups, shows that the realized growth rate declined past the critical value $\lambda_c = 1$ probably on around day 271 at a food supply rate of 95 μl and no later than day 316 at a food supply rate of 71 μl, and that the threshold was never crossed by populations in the control group (Fig. 2, inset).

To compare the timing of this bifurcation with candidate early warning signals, we calculated four statistical signatures known to indicate the approach to a bifurcation: coefficient of variation[20,30],


Figure 2 | Estimated growth rate versus time for deteriorating-environment and control populations. Deteriorating environmental conditions led to growth rates less than replacement (black line) and eventual extinction. Points are individual estimates corresponding to a pair of successive observations of a particular population. Lines are Loess smooth curves (span, 0.75; thick grey and blue lines) plus/minus standard error (thin grey and blue lines). Results are insensitive to the choice of span in the range [0.6, 1.0]. The inset plot shows the same points over a reduced range to accentuate the downturn in deteriorating environments after day 271, when food levels were 95 μl. The stair plot, corresponding to the secondary y axis, shows actual food supply rate (microlitres of suspended food medium) over time.

Figure 1 | Dynamics of representative populations from an experiment in which extinction was observed under deteriorating and constant conditions. In all populations, a transient phase (grey regions) was observed during which an initial population explosion ('baby boom') was followed by a decline and smaller peak ('echo boom'). Inspection shows this transient period to have ceased by around day 100 in all populations. On day 154, populations in the deteriorating-environment treatment group began to undergo a slow decline in the availability of food while populations in the control group were maintained at the initial level of food supply. Accordingly, in constant-food environments populations settled to a regime of stationary fluctuations, whereas in deteriorating environments the transient phase was followed by a virtually continuous decline. The difference between the stationary fluctuations of the constant-food environments and the continuous decline in deteriorating environments is most evident in the inset panels, where the abundance is plotted on a logarithmic scale and where the continual decline of the population in the deteriorating environment is unmistakable in contrast to the fluctuations in the constant environment.

autocorrelation[30], skewness[23] and spatial correlation[24]. Although there is strong evidence for CSD and the approaching transition in the deteriorating-environment treatment group when populations are considered individually (Supplementary Information, appendix III), the effect is more pronounced in the analysis of the entire experimental ensemble.

To identify the onset of CSD and determine how far in advance the approach to a bifurcation could be detected, we plotted each statistic against time for treatment and control ensembles, marking the estimated time at which the bifurcation was crossed and the times of change in food supply for comparison (Fig. 3). Our main finding is that each of these indicators showed a substantial increase in comparison with constant-environmental controls well before the bifurcation was reached. Furthermore, although each of the four indicators showed evidence of the approaching bifurcation, the effect was most accentuated in the coefficient of variation and skewness.

To determine whether a composite signal (W_1) would provide an earlier and more accurate warning of the approaching bifurcation, we calculated the standardized mean difference between treatments and controls at each date for each statistic, and summed them (Supplementary Information, appendix I). We considered the signal to be unequivocal when its value exceeded its running average by two standard deviations (2σ). Results shown in Fig. 4a demonstrate that in principle a composite index such as this might be used to detect effects of environmental deterioration on population dynamics when compared with dynamics in a constant environment. Because appropriate controls are typically unavailable in non-experimental contexts, we then analysed a composite index that makes use of only the data stream from the deteriorating-environment treatment (W_2; Fig. 4b). This index was more sensitive than W_1 to fluctuations during the baseline period. We conclude that if conditions are not stationary before environmental degradation, the detection of deterioration through CSD may prove to be a formidable challenge if there are not adequate baseline data or reference systems available for calibration.
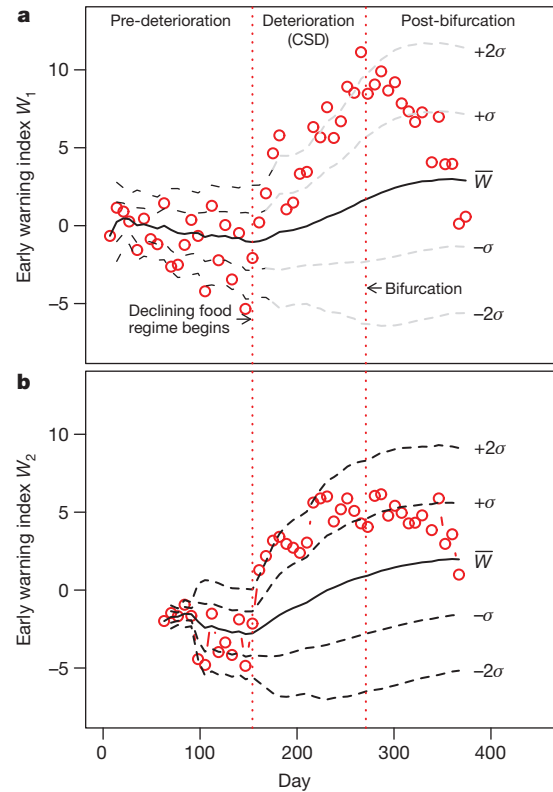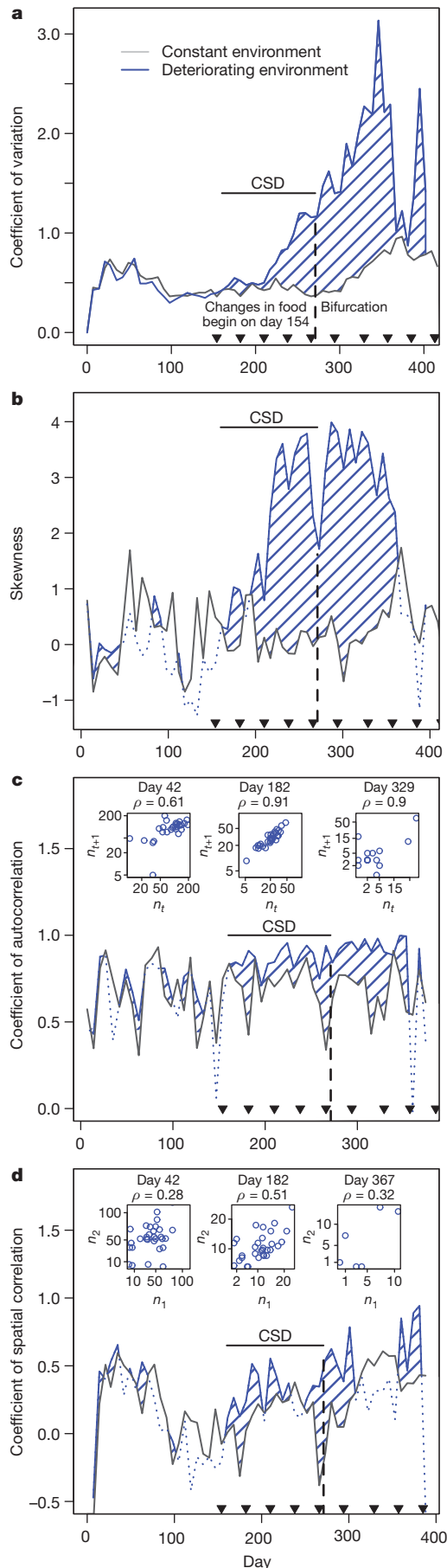
Figure 4 | A composite early warning index comprising all four indicators is highly sensitive to the onset of critical slowing down. a, Time-specific calculations of W_1 when plotted against time show that non-stationary behaviour in population dynamics may be detected within three weeks (where dashed lines change from black to grey) if a 2σ standard is used to trigger a warning and within two weeks if a 1σ standard is used to trigger a warning. The solid line shows the running average of W_1, which will be zero for stationary systems. The index W_1 is based on the standardized mean difference between deteriorating environments and constant reference environments. **b**, For comparison, we also investigated a composite early warning index that depends only on the data stream resulting from chambers in the deteriorating environment treatment (W_2). This index was highly sensitive to fluctuations in the period before the onset of environmental deterioration and never clearly departed from 2σ region. When optimized, however, this index detected critical slowing down as early as one week after the onset of environmental deterioration.

In conclusion, our results show that tipping points in populations can be anticipated. It is not yet clear which early warning signals are most unambiguous and under what conditions. An aggregate measure decreased uncertainty and provided a 2σ level of warning as early as ~8 generations (110 d) before the bifurcation. Forecasting and scenario planning are of increasing importance to environmental policy and decision-making. One significant obstacle to effective forecasting has been the reliance on highly parameterized models that are prone to

Figure 3 | Coefficient of variation, skewness, autocorrelation, and spatial correlation in population size are leading indicators of extinction.
a, Coefficient of variation; **b**, skewness; **c**, autocorrelation; **d**, spatial correlation. The lines show the changes in each measure among populations over time, by treatment, for the duration of the experiment. The hatched regions show the difference between treatment and control populations. The dashed vertical line shows the estimated time at which the transcritical bifurcation occurred and the extinction equilibrium and upper equilibrium switched stability, that is, the critical transition. The period immediately preceding this transition was one of CSD, manifested by increases in each indicator in deteriorating environments relative to control populations. Days on which the feeding regime was changed are indicated by inverted triangles along the x axis. Insets in **c** and **d** illustrate changes in spatial and temporal correlations over time; ρ denotes the correlation coefficient for the designated interval.

mis-specification and may give little or no indication of qualitative changes in system dynamics. Early warning signals based on CSD, by contrast, are model independent and show universal behaviour[10,11]. Given present conservation imperatives, proportionally dwindling resources to study threatened and endangered species, and unprecedented levels of environmental change, understanding the process of extinction in deteriorating environments is central to reversing the processes that result in species extinction and restoring environmental quality while legacy populations remain[14]. Work by us here and by others[12] to detect the occurrence of processes leading to a bifurcation shows that timely intervention may yet be possible even when populations are on the brink of a tipping point.

METHODS SUMMARY

Experiment. Replicate populations of the freshwater cladoceran *D. magna* were evenly divided and randomly assigned to deteriorating-environment ($n = 30$) and constant-environment ($n = 30$) treatment groups. Populations were fed a suspension of freeze-dried blue green alga (*Spirulina* sp.) Populations in each chamber were exhaustively counted in triplicate once per week. Initially, subpopulations were fed 400 µl d^{-1} of the food suspension. Under these conditions, the generation time is approximately two weeks. On day 154, populations in the deteriorating-environment treatment were placed on a regimen of declining food (reduction of 25% per occurrence), with changes at approximately monthly intervals, on days 154, 182, 210, 238, 266, 294, 329, 357, 385 and 413.

Calculation of leading indicators. Early warning signals were calculated at each observation time over the ensemble of populations in each treatment group. The coefficient of variation was calculated as the sample standard deviation divided by the sample mean; sample skewness was estimated as $g_1 = m_3/m_2^{3/2}$, where m_3 is the third central moment and m_2 is the sample variance. The autocorrelation corresponding to each sampling date was calculated as the Pearson's correlation coefficient between the abundance at subsequent sampling times over all extant populations; spatial correlation at each sampling date was calculated as the Spearman's correlation coefficient between the abundance in the two chambers of each microcosm for all extant populations (requiring only one subpopulation to have size greater than zero for the population as a whole to be considered extant).

Calculation of composite indices. To determine whether a composite signal would provide an earlier and more accurate warning of the approaching bifurcation, we calculated the indicators based on the sum of the standardized differences between treatments (W_1) and on the standardized difference from the running average in the experimental treatment only (W_2). See Supplementary Information for details.

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