

LETTER

Environmental fluctuations can stabilize food web dynamics by increasing synchrony

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Abstract

Natural food webs are species-rich, but classical theory suggests that they should be unstable and extinction-prone. Asynchronous fluctuations in the densities of competing consumers can stabilize food web dynamics in constant environments. However, environmental fluctuations often synchronize dynamics in nature. Using the same ‘diamond-shape’ food web model first used to demonstrate the stabilizing effects of asynchrony in constant environments, we show that weak-to-moderate environmentally induced fluctuations in consumer mortality rates stabilize food webs while disrupting asynchrony. Synchrony actually promotes stability because: (i) synchronous declines in consumer density reduce the maximum abundance of top predators and (ii) resource competition quickly converts synchronous increases in consumer density into synchronous declines. These results are robust to details of food web topology and the implementation of environmental fluctuations. The fluctuation strengths that enhance stability are within the range experienced naturally by many species, suggesting that stabilization via environmental fluctuations is a realistic possibility.

Keywords

Asynchrony, environmental variability, food web, stability, synchrony, weak interaction.

Ecology Letters (2007) 10: 1066–1074

INTRODUCTION

Natural food webs comprise many interconnected species, most or all of which often persist for many generations, making food webs much more stable than predicted by classical theory (May 1973). Explaining this surprising ‘Balance of Nature’ is crucial for both fundamental understanding and predicting responses to anthropogenic perturbations. Recent models and observations suggest that, in constant environments, the densities of competing consumer species will fluctuate asynchronously (McCann *et al.* 1998; McCann 2000; Rooney *et al.* 2006). This asynchrony reduces density fluctuations on adjacent trophic levels by stabilizing the total food supply of predators and the total consumption pressure on resources (McCann *et al.* 1998; McCann 2000; Rooney *et al.* 2006). However, stabilizing mechanisms in natural systems must be robust to the effects of environmental variability. Environmental fluctuations are known to synchronize population dynamics, within species and among different species over large geographical ranges (Moran 1953; Tilman 1996; Ranta *et al.*

1999; Klug *et al.* 2000; Cottingham *et al.* 2001; Engen & Sæther 2005; Royama 2005; Hugueny 2006; Houlihan *et al.* 2007; Vasseur & Gaedke 2007). Understanding how asynchrony impacts the stability of natural food webs requires an assessment of its ability to withstand the synchronizing effects of environmental variability.

To examine food web stability in variable environments we simulated the same four species ‘diamond’ food web previously used to identify the stabilizing effect of consumer asynchrony in constant environments (McCann *et al.* 1998; and see Methods). In this model, a single top predator species P obtains energy from a single resource R via two consumers C_1 and C_2 , creating two distinct energetic pathways (Fig. 1). Most consumers in nature share both resources and predators with other consumers (Williams and Martinez 2000), making this model a useful simplification of many natural food webs. McCann *et al.* (1998) demonstrated that asynchronous fluctuations between the two consumers could arise intrinsically (i.e. in the absence of environmental noise) when one of the consumers is superior at obtaining resources and the predator’s preference is skewed towards the superior

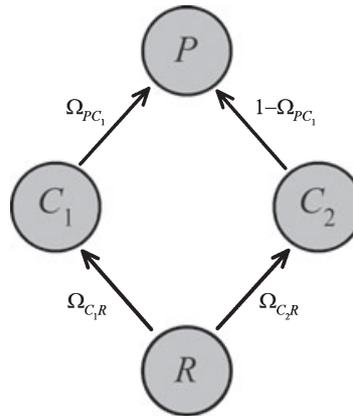


Figure 1 A schematic representation of the food web and its governing differential equation system (modelled after McCann *et al.* 1998). The preference coefficients Ω_{ij} can be manipulated to adjust the strength of a trophic interaction between populations i and j . For the simulations presented in the main paper we set $\Omega_{PC_1} = 0.92$ to generate a weak interaction between the predator P and consumer C_2 . $\Omega_{C_1R} = 1$ and $\Omega_{C_2R} = 0.98$ as in Fig. 2b of McCann *et al.* (1998).

$$\frac{dP}{dt} = -M_P P + \frac{J_P P [\Omega_{PC_1} C_1 + (1 - \Omega_{PC_1}) C_2]}{\Omega_{PC_1} C_1 + (1 - \Omega_{PC_1}) C_2 + C_0}$$

$$\frac{dC_1}{dt} = -M_{C_1} C_1 + \frac{\Omega_{C_1R} J_{C_1} C_1 R}{R + R_{0_1}} - \frac{\Omega_{PC_1} J_P P C_1}{\Omega_{PC_1} C_1 + (1 - \Omega_{PC_1}) C_2 + C_0}$$

$$\frac{dC_2}{dt} = -M_{C_2} C_2 + \frac{\Omega_{C_2R} J_{C_2} C_2 R}{R + R_{0_2}} - \frac{(1 - \Omega_{PC_1}) J_P P C_2}{\Omega_{PC_1} C_1 + (1 - \Omega_{PC_1}) C_2 + C_0}$$

$$\frac{dR}{dt} = rR(1 - R/K) - \frac{\Omega_{C_1R} J_{C_1} C_1 R}{R + R_{0_1}} - \frac{\Omega_{C_2R} J_{C_2} C_2 R}{R + R_{0_2}}$$

consumer. This resulting asynchrony reduces the amplitude of intrinsic fluctuations and further bounds the dynamics from disastrously low densities (McCann *et al.* 1998; McCann 2000).

To determine if the stability achieved by intrinsically generated asynchrony is robust to external environmental impacts, we incorporate environmental fluctuations into the per-capita background mortality rates of consumers. The assumption that environmental fluctuations only affect background mortality rates is realistic for many environmental factors, and simplifies analysis by ensuring that environmental fluctuations do not affect the interaction strengths between species (see Methods). In the simplest limiting case, both consumers experience identical environmental fluctuations. However, in natural systems, species may experience non-identical fluctuations if they occupy different microhabitats, respond to different environmental variables, respond differently to the same environmental variable, or if they exhibit any mix of these possibilities. To address this we also varied the cross-correlation of the consumers' environments (as in Ripa & Ives 2003; see Methods). We demonstrate that regardless of the environmental correlation, consumer species are more synchronized in the presence of environmental fluctuations. Despite this increased synchrony, the food web is more stable (less variable) in the presence of weak or moderate environmental fluctuations than in a constant or highly variable environment. In fact, increased consumer synchrony apparently is crucial to the increased stability generated by moderate environmental fluctuations.

METHODS

The model food web

The dynamics of the four species diamond food web are modelled using standard continuous-time equations in

which resources grow logistically, consumption follows a type II nonlinear functional response, and the consumers and predator experience natural background mortality (Yodzis & Innes 1992; McCann *et al.* 1998; Fig. 1). The model is parameterized so that consumer C_1 is the superior competitor for resources and the preferred prey of the predator (i.e. the 'strong interactor'; Fig. 1, Table 1). Asymmetric competition forces the two consumers to fluctuate asynchronously and preferential predation on C_1 ensures that C_2 is not competitively excluded. The asymptotic dynamic is a stable limit cycle where consumer densities are highly asynchronous.

Implementation of environmental fluctuations and model simulation

We used the standard deviation σ_ξ and cross-correlation ρ_ξ of environmental fluctuations as independent parameters

Table 1 Model parameter values and their descriptions. The consumer mortality rates used in McCann *et al.* (1998) are taken as the medial consumer mortality rates

Parameter	Description	Value
r	Resource intrinsic rate of growth	1.0
K	Resource carrying capacity	1.0
J_{C_1}	Consumer (C_1) ingestion rate	0.8036
J_{C_2}	Consumer (C_2) ingestion rate	0.7
J_P	Predator ingestion rate	0.4
$M_{C_1}(0)$	Medial consumer (C_1) mortality rate	0.4
$M_{C_2}(0)$	Medial consumer (C_2) mortality rate	0.2
M_P	Predator mortality rate	0.08
R_{0_1}	Half saturation constant	0.16129
R_{0_2}	Half saturation constant	0.9
C_0	Half saturation constant	0.5
Ω_{PC_1}	Preference coefficient	0.92
Ω_{C_1R}	Preference coefficient	1.0
Ω_{C_2R}	Preference coefficient	0.98

influencing the mortality rates of consumers C_1 and C_2 . Two series of cross-correlated fluctuations $\xi_1(t)$ and $\xi_2(t)$ were generated by calculating the product of the Cholesky factorization of the 2×2 variance–covariance matrix:

$$\begin{bmatrix} \sigma_\xi^2 & \rho_\xi \sigma_\xi^2 \\ \rho_\xi \sigma_\xi^2 & \sigma_\xi^2 \end{bmatrix} \quad (1)$$

and a $2 \times N$ matrix of random draws from a normal distribution (0,1). For each value of $-1 \leq \rho_\xi \leq 1$ (in discrete steps of 0.01 units), we integrated the food web model (Fig. 1) across a range of σ_ξ beginning from zero and increasing in steps of 0.01 until none of 50 independent replicates persisted. The dynamics of the food web model at $\sigma_\xi = 0$ were identical to those illustrated in Fig. 2b from McCann *et al.* (1998). For each simulation initial densities of the four species were chosen randomly on the uniform interval (0.1,1.0). The food web model was integrated for $N = 50\,000$ time-steps using the fifth-/sixth-order Runge-Kutta-Verner algorithm implemented in the IMSL subroutine IVPRK for FORTRAN 95 (Visual Numerics Inc., 1997).

Any species which dropped below the density threshold of 10^{-6} was considered to be extinct and the simulation was discontinued.

At the beginning of each time-step the instantaneous mortality rates were altered by evaluating the expression:

$$M_{C_i}(t) = M_{C_i}(0) \cdot e^{\xi_i(t)} \quad (2)$$

where $M_{C_i}(0)$ is the medial mortality rate for consumer i and $\xi_i(t)$ are random normal ‘environment’ variables with zero mean, variance σ_ξ^2 , and no temporal autocorrelation (‘white noise’). Temperature and other environmental variables are thought to alter ecological rates via exponential filters such as that in eqn 2 (Gillooly *et al.* 2001; Brown *et al.* 2004; Vasseur & McCann 2005). Exponential filtering also ensures that mortality cannot provide a source of biomass for populations, as could occur with additive environmental stochasticity. Including environmental fluctuations in this manner ensures that the interaction strength (the maximum per capita flow of biomass from species i to species k):

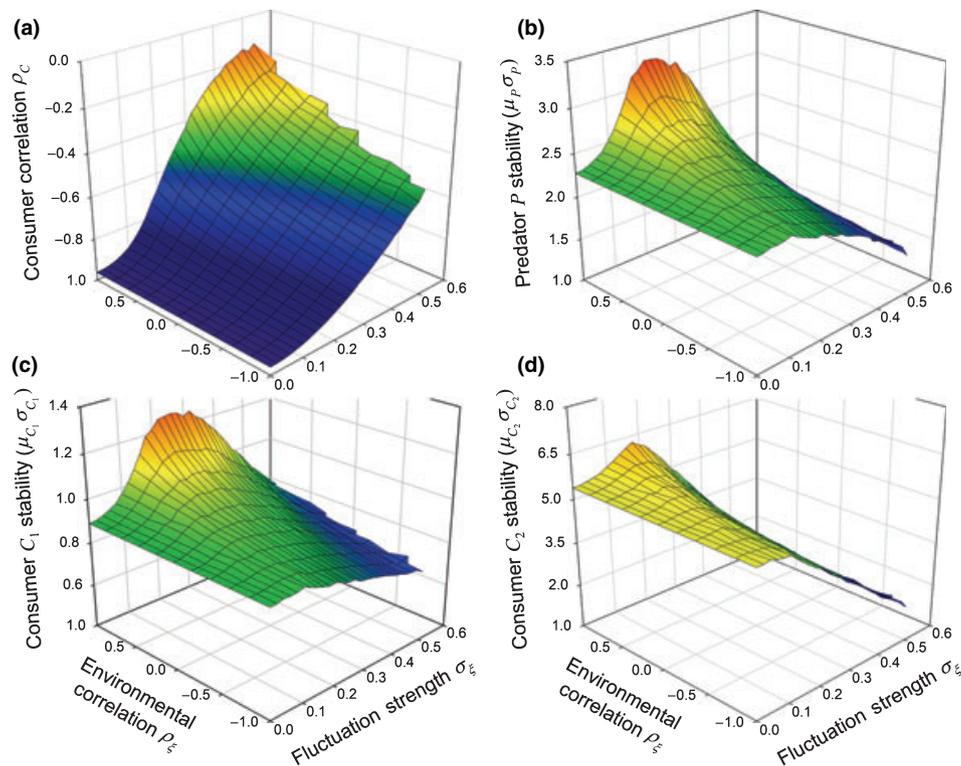


Figure 2 (a) The correlation between consumers C_1 and C_2 and (b–d) the stability (mean/standard deviation, μ_i/σ_i) of the predator and consumers as a function of the standard deviation of environmental noise (σ_ξ), and the correlation between environmental conditions influencing the two consumers (ρ_ξ). Each intersection of grid lines on the contours represent the average value measured from ≤ 50 independent model replicates in which all four species persisted for $N = 50\,000$ time-steps. The surface ends where none of the original 50 replicates persisted. For σ_ξ below the peak in predator stability ($\sigma_\xi \leq 0.24$) up to 4% of simulations were non-persistent. This fraction rose dramatically for $\sigma_\xi > 0.24$ until 100% of simulations were non-persistent at $\sigma_\xi = 0.58$. Mean densities of the four species change very little in response to the environmental fluctuations (unpublished data) indicating that changes in the variance not the mean underlies the results in panels (b–d).

$$I_{ki} = \Omega_{ki} J_k / i_0 \quad (3)$$

(McCann *et al.* 1998) is constant as environmental conditions vary (i_0 is the half saturation density of the functional response; see Table 1).

For the calculation of statistics, we used only the latter 25 000 time-steps of each simulation to ensure that initial transients had subsided. Cross-correlations of consumer densities were calculated as:

$$\rho_C = \frac{1}{N\sigma_{C_1}\sigma_{C_2}} \sum_{t=1}^N (C_1(t) - \mu_{C_1})(C_2(t) - \mu_{C_2}) \quad (4)$$

where μ values indicate the sample mean densities. The stability of each species was measured as the inverse of its coefficient of variation.

Estimating the strength of environmental fluctuations σ_ξ from empirical data

We estimated the strength (standard deviation) of environmental fluctuations σ_ξ observed in empirical systems, to determine if stabilization via environmental fluctuations is a realistic possibility. Few studies report time series of species' natural background mortality rates; we found data for a large number of neotropical tree species (Condit *et al.* 1995), and for zooplankton (Dodson 1972) and phytoplankton (Peperzak *et al.* 2003). Each of these studies provided descriptive statistics for the observed distribution of natural mortality rates. Our model for the incorporation of environmental fluctuations (eqn 2) assumes that, in the presence of normally distributed environmental fluctuations, background mortality rates are distributed log-normally. However, the descriptive statistics provided in the empirical data (e.g. standard deviation) assume a normal distribution. For a normal distribution, 95% of values fall within ± 1.96 SD of the mean. We used this rule to estimate the standard deviation of environmental fluctuations σ_ξ required by our model (eqn 2) to generate a log-normal distribution with an equal frequency of values falling within this range. We then used these estimates of σ_ξ to establish whether the strength of stabilizing environmental fluctuations is in the range observed in natural systems.

RESULTS AND DISCUSSION

Single-species models predict that only positively correlated environmental fluctuations should promote population synchrony (the Moran effect; Moran 1953; Ranta *et al.* 1999; Engen & Sæther 2005; Royama 2005; Hugueny 2006). However, when consumers are coupled by a shared resource and predator, the entire range of environmental correlations (both positive and negative) promotes consumer synchrony (Fig. 2a). Positively correlated environmental fluctuations

promote consumer synchrony in part via classical Moran-type effects (Moran 1953; Ranta *et al.* 1999; Engen & Sæther 2005; Royama 2005; Hugueny 2006). However, consumer synchrony arises in negatively correlated environments from a transient dynamic which behaves very differently than the equilibrium (asynchronous) dynamic in a constant environment. This transient dynamic arises because even negatively correlated environmental fluctuations rarely produce perfectly counterbalanced perturbations to consumer densities; increases or decreases in the density of one consumer are rarely perfectly offset by opposing changes in the density of the other consumer. Therefore, even negatively correlated environmental fluctuations are likely to alter total consumption pressure on the resource. Perturbations to total consumption pressure set up a synchronous transient: decreased (increased) total resource consumption leads to increased (decreased) resource density, followed in turn by a synchronous transient increase (decrease) in consumer densities (e.g. Fig. 3). In the model simulations, and presumably in nature, continually changing environmental conditions enhance the longevity of this synchronous transient state and prevent the system from ever returning to the equilibrium, asynchronous limit cycle. Ironically, the resource competition that generates consumer asynchrony in constant environments (McCann *et al.* 1998; McCann 2000; Rooney *et al.* 2006) is responsible for enhanced synchrony in fluctuating environments (see Appendix S1 in Supplementary Material). Although not all possible perturbations off the limit cycle generate synchronous transients, the synchronous transients dominate the dynamics in fluctuating environments. This result represents a new and highly general mechanism by which environmental fluctuations can synchronize species dynamics, as resource competition is common in nature (Gurevitch *et al.* 1992).

Recent theory suggests that any factor that reduces asynchrony between alternative energy pathways (here C_1 and C_2) should reduce food web stability (Rooney *et al.* 2006). Remarkably, however, stability actually increases in the presence of weak-to-moderate environmental fluctuations (Fig. 2b), even though such fluctuations reduce asynchrony. This contrasts with, but does not contradict, earlier studies (Rooney *et al.* 2006); the stabilizing influence of environmental fluctuations arises in part from a novel mechanism which, at low-to-moderate fluctuation strengths, can supersede other mechanisms. This mechanism arises from the combination of three realistic features of our model: multiple consumer species, fast dynamics of consumers relative to predators and resource competition. Within a region of the limit cycle spanning $c. 5\%$ the cycle period and encompassing the maximal density of C_1 (the consumer which largely drives the stability of the predator P because of the strong C_1 - P interaction), all perturbations off the limit cycle are ultimately stabilizing (Fig. 4a). In this

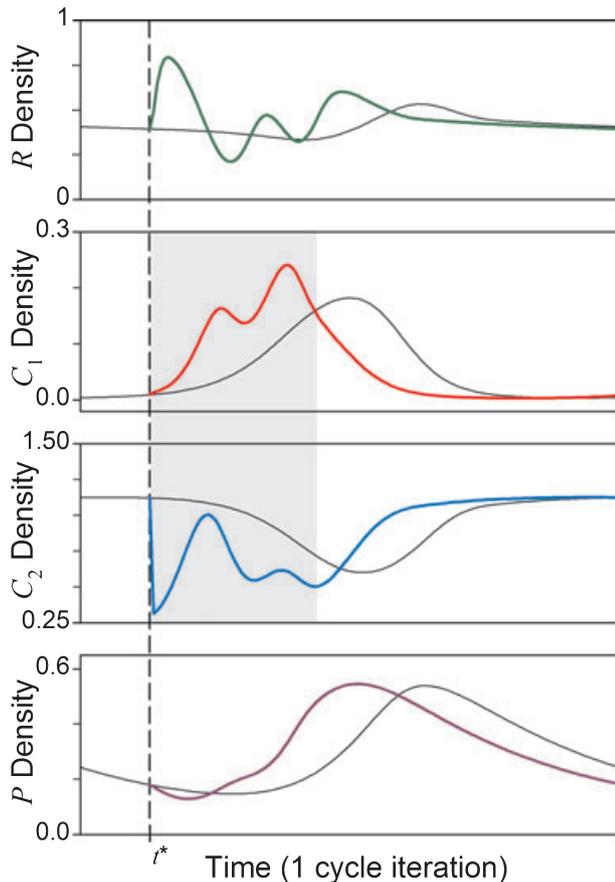


Figure 3 System dynamics following a single strong, asynchronous perturbation [$\xi_1(t^*) = -2, \xi_2(t^*) = 2$] at time t^* (coloured lines) compared with the unperturbed limit cycle (black lines). The asynchronous perturbation to consumers causes resource density R to increase, initiating a synchronous transient response of consumers (shaded region). Following the synchronous transient the system returns to a stable limit cycle which is phase-shifted from the unperturbed system, but where consumer dynamics are again highly asynchronous. Synchronous transients also occur following a perturbation that causes resources to initially decrease (not shown).

region of the limit cycle the predator's density is increasing. Here, an environmentally driven increase in consumer densities quickly reduces resource density but only slightly increases predators (Fig. 4b). In response to resource limitation, both consumers quickly decrease, reducing the predator's apex on the cycle and thus improving its stability (Fig. 4b). As perturbations that decrease consumer density also stabilize the predator by directly slowing the predator's growth during the increasing phase, the ultimate effect of continual random perturbations is an accumulation of stabilizing effects over time. Negatively correlated environments are less stabilizing (Fig. 2b) because environmentally induced increases in one consumer tend to be associated

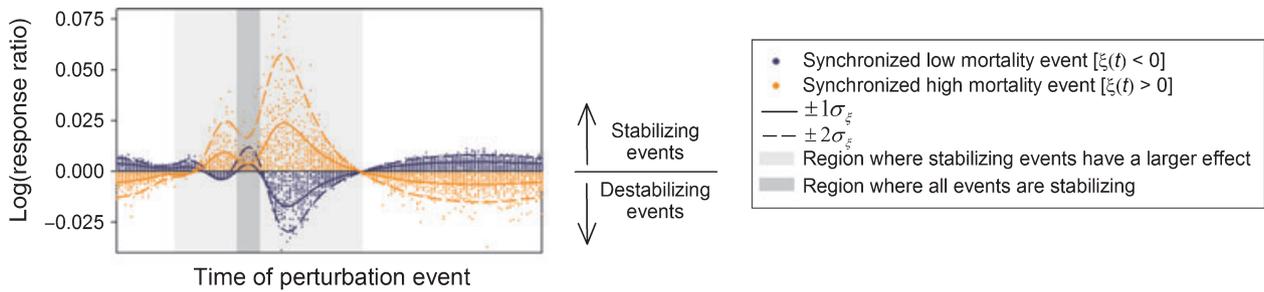
with decreases in the other, producing only a small change in total consumption pressure on the resource and reducing the expression of the synchronous transient. Improved stability in fluctuating environments is manifested both as lower temporal variability (lower temporal variances and coefficients of variation) of C_1 , C_2 and P , and increased minimum densities of P and C_1 (Fig. 4b,c). These latter two species exhibit the lowest minimum densities and therefore experience the highest extinction risk (Fig. 4c).

Although this synchronizing mechanism cannot entirely explain the stabilizing effects of continual perturbations, as with continual perturbations the system never returns to the unperturbed limit cycle, it is clearly an important contributor. In contrast to the counterintuitive effects of weak-to-moderate environmental fluctuations, the effects of strong environmental fluctuations are straightforward: strong fluctuations directly destabilize the system by adding too much variability (Fig. 2b). The nonlinear, unimodal relationship between fluctuation strength and food web stability cannot be explained by previous models which assume small environmental fluctuations and omit biologically realistic nonlinear functional responses (e.g. Ripa & Ives 2003).

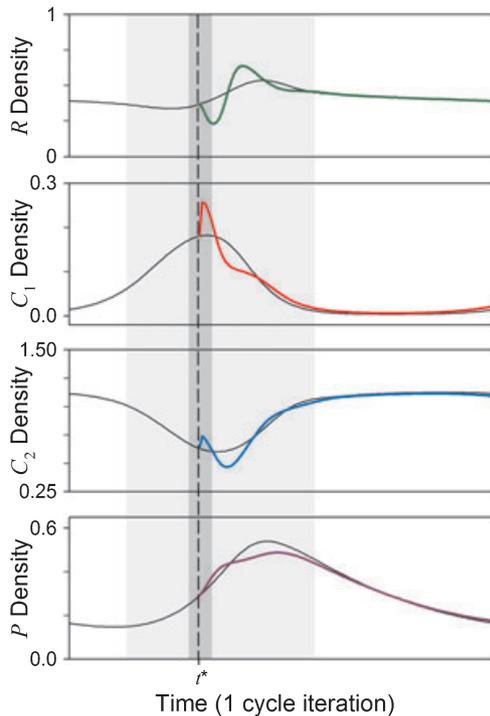
The theoretical results give a qualitative picture of the potential stabilizing effects of environmental fluctuations. Determining whether these effects extend to natural food webs requires an assessment of the natural temporal variability in species' per-capita background mortality rates. These data are sparse in the published literature, but the few available estimates confirm that the degree of variability in mortality rates imposed in our study is biologically reasonable. The variability of natural mortality rate observed in large (> 100 mm in diameter) neotropical trees (Condit *et al.* 1995) equals that generated in our model by mortality fluctuations with $\sigma_\xi \approx 0.48$; for small trees (10–99 mm) the variability of natural mortality rate is equivalent to $\sigma_\xi \approx 0.59$ in our model. These estimates are somewhat larger than those found for *Daphnia* zooplankton (Dodson 1972), $\sigma_\xi \approx 0.37$. For 28 species of phytoplankton (Peperzak *et al.* 2003), the standard deviation of mortality rates because of sinking σ_ξ ranges from ≈ 0.10 to 0.62 (mean: ≈ 0.32). Values of σ_ξ in the empirically observed range of 0.10–0.62 span the range from highly stabilizing to highly destabilizing environments in our model and its variants (Fig. 2b, Appendix S1).

In addition, we can indirectly estimate the value of σ_ξ that would arise from variability in population respiration rate because of temperature variation (e.g. Brown *et al.* 2004). Respiratory losses are a major component of density-independent background loss rates for many species. Using well-established empirical scaling relationships between temperature (T) and respiration rate (Appendix A), one can show that $\sigma_\xi \approx 0.08 \cdot \sigma_T$, where σ_T is the standard deviation of temperature. Thus, in a thermally varying

(a) Relative predator stability following a single, synchronous point perturbation



(b) Transient response to a single synchronous point perturbation



(c) System response to continual synchronous point perturbations

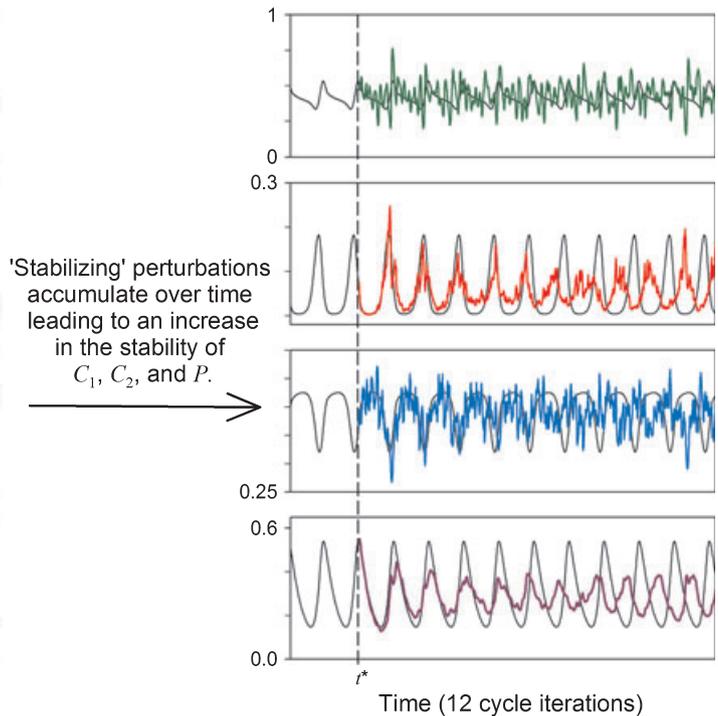


Figure 4 (a) The influence of the timing of a single synchronized perturbation on predator stability as measured by the log(response ratio): the log of the ratio of predator stability in the perturbed and unperturbed systems. Stability (μ_P/σ_P) is measured over one cycle iteration ($c. 147$ time-steps). Each point gives the result of a synchronized ($\rho_\xi = 1$) random perturbation drawn from the distribution which most enhanced predator stability ($\sigma_\xi = 0.24$; see Fig. 2b). Solid and dashed lines give contours for perturbations sized ± 1 and $\pm 2\sigma_\xi$. (b) Transient dynamics of the system in response to a single synchronous, initially destabilizing perturbation at time t^* which occurs in the region of the limit cycle in which all perturbations are ultimately stabilizing. (c) Initiation of continual synchronous, random perturbations ($\rho_\xi = 1$, $\rho_\xi = 0.24$) at time t^* stabilizes the dynamics of C_1 , C_2 and P by reducing variability and by increasing locally minimum densities in C_1 and P .

environment, stability is maximized between $2 \leq \sigma_T \leq 3$ in our model, but extinctions occur readily when $\sigma_T > 5$. Seasonal thermal variability meets or exceeds these thresholds for σ_T in many temperate and most polar environments. Collectively, these empirical estimates of σ_ξ indicate that the stabilizing and destabilizing effects of natural environmental fluctuations may well supersede the stabilizing effects of intrinsic asynchrony.

To determine the robustness of our results we varied a number of assumptions about food web structure and parameter values (including resource productivity, interaction strengths and the strength of resource competition) and the incorporation of environmental fluctuations (demographic rather than environmental noise, and environmental noise affecting all four species). Our results are robust (see Appendix S1 for results from all alternative scenarios).

The addition of environmental fluctuations increases synchrony under every scenario in which consumers C_1 and C_2 compete sufficiently strong. Moderate fluctuation strengths stabilize food web dynamics under every scenario provided that the system is not maximally stable (i.e. exhibits a stable equilibrium point) in the absence of fluctuations.

Diamond-shaped food webs contain a number of important structural attributes of larger food webs, such as resource competition (Gurevitch *et al.* 1992) and alternative energy pathways coupled by species in the upper trophic positions (McCann *et al.* 2005; Rooney *et al.* 2006), making them useful simplifications of more complex food webs. The diamond food web examined here is a common 'motif' or subcomponent natural food webs (Milo *et al.* 2002), and the majority of species in natural food webs occupy intermediate trophic levels and share both resources and predators with other intermediate species (Williams & Martinez 2000). Our model should provide insight into the dynamics of species embedded in this diamond motif. However, natural food webs are much more species-rich and structurally complex than the simple model considered here. Examining the extent to which our results extend to more complex food webs is an important challenge for future work.

There are analogies between the system modelled here and spatial predator–prey systems in which different prey populations occupy different locations and predators move between locations (de Roos *et al.* 1991; Nisbet *et al.* 1993; Jansen 1995; Jansen & de Roos 2000; McCann *et al.* 2005; Rooney *et al.* 2006). Spatially asynchronous fluctuations in prey density and spatial heterogeneity in model parameters (e.g. spatial variation in predator–prey interaction strength) are thought to stabilize spatial predator–prey systems (Murdoch *et al.* 2003). However, the effects of environmental fluctuations on spatial predator–prey systems are largely unexplored. Our results suggest that environmental fluctuations may have surprising effects on the synchrony and stability of spatial predator–prey systems.

Our results reinforce previous work demonstrating that relatively small environmental perturbations can drastically alter the dynamics of nonlinear models (e.g. Bjørnstad & Grenfell 2001; Greenman & Benton 2005). In many instances, this is caused by stochastic resonance, an excitation of the nonlinear system by environmental fluctuations (Wiesenfeld & Moss 1995). Blarer & Doebeli (1999) hypothesized that stochastic resonance might explain insect outbreaks in weakly varying environments. Higgins *et al.* (1997) found that weak environmental fluctuations were sufficient to generate population fluctuations in a stage-structured model of Dungeness crab consistent with catch data. In contrast, we found that weak-to-moderate environmental fluctuations dampen the system's internally generated oscillations, so that the system is less variable in a fluctuating environment.

Environmental fluctuations can generate fundamentally new dynamics by shifting the system close to alternative attractors and repellers in phase space, thereby altering the power spectrum of species' densities (Greenman & Benton 2005; Reuman *et al.* 2006). Spectral analysis reveals that environmental fluctuations cause a reduction in the amplitude of the dominant oscillation of our model, but no change in the frequency (see Figure S9 in Supplementary Material), suggesting that here, environmental fluctuations suppress variability without fundamentally altering the dynamics. While other studies have found that environmental fluctuations can reduce dynamic variability, our results reflect a different and more general mechanism. Desharnais *et al.* (2001) used models and experiments to show that perturbations to a flour beetle population could reduce population variability. However, this result depends on the use of non-random perturbations (every perturbation comprised the addition of the same number of adult females) applied deterministically (i.e. applied only when the system entered one particular, sensitive region of phase space). Orland (2003) demonstrated empirically that externally generated perturbations to densities of a consumer population and its resource could cancel one another out if conducted at appropriate frequencies, leading to less-variable consumer dynamics. In contrast to Desharnais *et al.* (2001) and Orland (2003), we found that realistic, random external perturbations reduce population variability. Further, our results do not arise from high sensitivity (i.e. high local Lyapunov exponent) in certain regions of phase space (results not shown).

Our results show that the role of environmental fluctuations in food web stability should be re-thought: natural food webs may be stable because of environmental fluctuations, not despite them. An important challenge for future work is to more completely identify the mechanisms by which internal feedbacks and external forcing combine to determine food web dynamics. Only by identifying these mechanisms and then quantifying their strength can the surprising stability of natural food webs be explained. This challenge will be difficult to meet. In general, the dynamics of nonlinear stochastic systems are only incompletely understood, because global analytical results are unavailable (Reuman *et al.* 2006). Meeting this challenge takes an added urgency because anthropogenic effects likely will increase future climate variability (Karl *et al.* 1995; Easterling *et al.* 2000).

ACKNOWLEDGEMENTS

We thank E. McCauley, K. McCann, N. Rooney and the referees for valuable comments. This work was supported by NSERC and Alberta Ingenuity fellowships to DAV and by an NSERC Discovery Grant and Alberta Ingenuity New Faculty Award to JWF.

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APPENDIX A: TEMPERATURE-INDUCED FLUCTUATIONS IN MORTALITY RATE (RESPIRATION LOSSES)

Our generalized noise model for background mortality rate perturbations assumes that noise enters the model through an exponential filter, e^{ξ_t} , where ξ_t is a normally distributed random variable with mean $\mu_\xi = 0$ and standard deviation σ_ξ . We wish to understand how the mean and standard deviation of our generalized noise form equates to that which would be generated by temporal variation in environmental temperature (T_t) entering the model via the Boltzmann factor, $e^{E_i(T_t - T_0)/kT_t T_0}$ (Gillooly *et al.* 2001; Brown *et al.* 2004; Vasseur & McCann 2005). From this perspective, background mortality rates can be interpreted as loss rates arising primarily from respiration. If temperature is considered a normally distributed stochastic variable [$\sim \mathcal{WN}(\mu_T, \sigma_T^2)$], we can use expectations to determine the mean μ_T and standard deviation σ_T of temperature by equating expected values for the first and second moments of the two distributions:

$$E[\xi_t] = E[E_i(T_t - T_0)/kT_t T_0] \quad (5a)$$

$$E[\xi_t^2] = E[(E_i(T_t - T_0)/kT_t T_0)^2] \quad (5b)$$

From the expectations: $E[\xi_t] = \mu_\xi = 0$ and $E[\xi_t^2] = \sigma_\xi^2$, we find that

$$\mu_T = E[T_t] = T_0 \quad (6)$$

and

$$\sigma_T^2 = E[(T_t - \mu_T)^2] = \sigma_\xi^2 (T_0^2 k/E_i)^2 \quad (7)$$

Given that the mean activation energy for whole-organism metabolism is *c.* 0.6 eV (Gillooly *et al.* 2001), $k = 8.618 \times 10^{-5}$ eV K⁻¹, and assuming that $T_0 = 293$ K, we find that $\sigma_\xi = 0.081 \cdot \sigma_T$.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Evaluating the robustness of the results to varied assumptions about food web structure and environmental variability (contains text and Figures S1–S8).

Figure S9 Power spectrum of predator density as a function of the strength of environmental fluctuations.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2007.01099.x>

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Editor, Tim Benton

Manuscript received 24 May 2007

First decision made 6 July 2007

Manuscript accepted 18 July 2007