

LETTERS

High-amplitude fluctuations and alternative dynamical states of midges in Lake Myvatn

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Complex dynamics are often shown by simple ecological models^{1,2} and have been clearly demonstrated in laboratory^{3,4} and natural systems^{5–9}. Yet many classes of theoretically possible dynamics are still poorly documented in nature. Here we study long-term time-series data of a midge, *Tanytarsus gracilentus* (Diptera: Chironomidae), in Lake Myvatn, Iceland. The midge undergoes density fluctuations of almost six orders of magnitude. Rather than regular cycles, however, these fluctuations have irregular periods of 4–7 years, indicating complex dynamics. We fit three consumer–resource models capable of qualitatively distinct dynamics to the data. Of these, the best-fitting model shows alternative dynamical states in the absence of environmental variability; depending on the initial midge densities, the model shows either fluctuations around a fixed point or high-amplitude cycles. This explains the observed complex population dynamics: high-amplitude but irregular fluctuations occur because stochastic variability causes the dynamics to switch between domains of attraction to the alternative states. In the model, the amplitude of fluctuations depends strongly on minute resource subsidies into the midge habitat. These resource subsidies may be sensitive to human-caused changes in the hydrology of the lake, with human impacts such as dredging leading to higher-amplitude fluctuations. *Tanytarsus gracilentus* is a key component of the Myvatn ecosystem, representing two-thirds of the secondary productivity of the lake¹⁰ and providing vital food resources to fish and to breeding bird populations^{11,12}. Therefore the high-amplitude, irregular fluctuations in midge densities generated by alternative dynamical states dominate much of the ecology of the lake.

Although the possibility of alternative states in ecological systems has been recognized for several decades^{13,14}, only recently have good empirical examples been established^{9,15,16}. The most familiar type of alternative states is alternative stable states in which a system has two (or more) stable equilibria, with the system settling to one or the other depending on initial conditions¹⁷. Alternative stable states lead to the possibility that a system may be shifted from one state to another, less favourable, state by a sudden shock or other disturbance, with unfortunate ecological consequences. Once trapped in the new state, undoing the disturbance will not return the system to its original (desirable) state, because the system will remain trapped in the domain of attraction of its new state.

Alternative states, however, need not be stable equilibrium points; they may instead be dynamical structures such as cycles^{18–22}. Here we investigate the possibility of alternative dynamical states, in which one state is an equilibrium point and the other is a high-amplitude stable cycle. Data on the long-term dynamics of the midge *Tanytarsus gracilentus* suggest these alternative states, because they show high-amplitude fluctuations that are not regularly periodic. In most populations in nature and in most simple models, if high-amplitude

fluctuations occur, they occur as fairly regular cycles, with the strong ecological forces that drive the high amplitudes also entraining the dynamics into a stable limit cycle²³.

Tanytarsus gracilentus is the dominant herbivore/detritivore in Myvatn, comprising roughly 75% of the secondary consumers and 66% of secondary production in this shallow, naturally eutrophic lake in northern Iceland¹⁰. As larvae, *T. gracilentus* individuals feed from tubes they construct in the benthic sediment, grazing on both benthic diatoms (algae) and detritus²⁴ consisting largely of dead benthic and planktonic algae, and midge frass. They have two non-overlapping generations per year, with adults forming large swarms around the perimeter of the lake over two 1–2-week mating periods, the first in May and the second in July and early August. In generations with high midge abundance, larvae are limited by food, and adult size decreases for several generations before the population crashes. Detailed statistical evaluation of data on population density, body size and predator abundance suggests that fluctuations in *T. gracilentus* populations are driven by consumer–resource interactions, with midges being the consumers and algae/detritus the resources, as opposed to predator–prey interactions with midges being the prey²⁵.

We have collected data on the abundance of adult midges since 1977 by using window traps at two locations on the shore of the lake²⁶. We have fitted these data to a model constructed to describe the fundamental interactions among midges, algae and detritus (Box 1). In the model, the midge population growth is dependent on density and is limited by the availability of food. Food consists of algae and detritus, which may differ in quality for midges. Algae have density-dependent growth, and detritus is formed from dead algae. In the model, midge populations are allowed to reach densities at which all algae are consumed, at which point the midge population crashes, with the rate of crash being moderated by the presence of detritus, which serves as an alternative food source. A feature crucial to the model is that if all algae are consumed, algal populations can recover through the input of small subsidies from outside the midge–algae–detritus system. These subsidies represent small influxes of algae and detritus into the muddy midge habitat from hard-bottom areas where midges are few. Although we have no direct measurement of this input, much of the algae and detritus in the lake occurs in areas inaccessible to midge larvae, and the hydrological mixing of the shallow lake²⁷ makes influxes of small amounts of this material into the midge habitat a certainty. We added environmental stochasticity to the model as random variation in per capita changes in abundances of midges, algae and detritus. Finally, we fitted the data by using a state-space version of the model²⁸ to incorporate the measurement error that we knew to be significant (Supplementary Methods). Predictions by the fitted model about changes in log (midge populations) from one generation to the next explain 74%

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Box 1 | The midge-algae-detritus model and alternatives

We constructed a midge-algae-detritus model to give a basic description of their interactions, attempting to have a minimum number of parameters that must be estimated from the data. The midge dynamics are

$$x(t+1) = r_1 x(t) \left(1 + \frac{x(t)}{R(t)}\right)^{-q} e^{\varepsilon_1(t)} \quad (1)$$

where $x(t)$ is the abundance of midges in generation t , r_1 is the intrinsic population growth rate, larger values of q produce stronger density dependence, and $\varepsilon_1(t)$ is a normal random variable representing stochastic environmental variability. The dimensionless measure of resource abundance in generation t , $R(t) = y(t) + pz(t)$, is composed of algae, $y(t)$, and detritus, $z(t)$, with the parameter p giving the quality of detritus for midge population growth relative to algae. Because we were interested in dynamics rather than mean abundance, we 'non-dimensionalized' midge densities to produce equation (1) and used a separate scaling parameter K when fitting the model so that the observed $\log(\text{adult midge density})$ equalled $K + \log(x(t))$ (Supplementary Methods). Furthermore, the data showed a distinct seasonal pattern in which spring generations had mean densities 3.4 times higher than summer densities. This might reflect either true differences in survival and/or fecundity between generations or sampling bias due to differences in weather conditions and hence flight activity and catchability. Because we were interested in long-term, multi-generational dynamics, we factored out this consistent seasonal pattern by multiplying summer midge densities by 3.4 before statistical analyses.

Algae dynamics are

$$y(t+1) = \left[r_2 y(t)(1+y(t))^{-1} - \frac{y(t)}{R(t)} x(t+1) + c \right] e^{\varepsilon_2(t)} \quad (2)$$

where r_2 is the algae intrinsic population growth rate and c is the influx of algae from outside the midge habitat. Because we have no data on algae abundance available to midges, $y(t)$ is not observed; therefore, in the model the mean value of $y(t)$ need not be included, and $y(t)$ is dimensionless. The term $[y(t)/R(t)]x(t+1)$ is the amount of resource consumed, $x(t+1)$, scaled by the proportion of that resource which is algae, $y(t)/R(t)$. A key feature of algae dynamics is that midge populations can build to sufficient abundance to consume all algae. When the term for the amount of algae consumed, $[y(t)/R(t)]x(t+1)$,

is greater than the amount produced, $r_2 y(t)[1+y(t)]^{-1}$, we assume that all algae come from influx, so $y(t+1) = c$.

The detritus dynamics are

$$z(t+1) = \left[dz(t) + y(t) - \left(\frac{pz(t)}{R(t)} \right) x(t+1) + c \right] e^{\varepsilon_3(t)} \quad (3)$$

where d gives the retention rate of detritus in the midge habitat. We assume that the influx rate of detritus equals that of algae, and that detritus is produced in proportion to the quantity of algae in the previous generation, $y(t)$. As with algae, if all detritus in the midge habitat is consumed, then $z(t+1) = c$. Because both algae and detritus were not measured, we assumed for estimation purposes that the standard deviations of $\varepsilon_2(t)$ and $\varepsilon_3(t)$ are equal: $\sigma_2 = \sigma_3$.

We compared the midge-algae-detritus model to two additional models. The multidimensional Gompertz log-linear model³⁰ is

$$u_1(t+1) = b_{11}u_1(t) + b_{12}u_2(t) + b_{13}u_3(t) + \varepsilon_1(t) \quad (4)$$

$$u_2(t+1) = b_{21}u_1(t) + b_{22}u_2(t) + b_{23}u_3(t) + \varepsilon_2(t) \quad (5)$$

$$u_3(t+1) = b_{31}u_1(t) + b_{32}u_2(t) + b_{33}u_3(t) + \varepsilon_3(t) \quad (6)$$

where $u_1(t) = \log x(t)$, $u_2(t) = \log y(t)$ and $u_3(t) = \log z(t)$. The Lotka-Volterra model is

$$x(t+1) = r_1 x(t) \exp(-d + b_{12}y(t) + b_{13}z(t) + \varepsilon_1(t)) \quad (7)$$

$$y(t+1) = r_2 y(t) \exp(1 + b_{21}x(t) + b_{22}y(t) + b_{23}z(t) + \varepsilon_2(t)) \quad (8)$$

$$z(t+1) = r_3 z(t) \exp(1 + b_{31}x(t) + b_{32}y(t) + b_{33}z(t) + \varepsilon_3(t)) \quad (9)$$

In equations (7)–(9), three parameters can be removed to non-dimensionalize the equations without changing the observed dynamics of midges; we therefore set $b_{12} = 1$ and $b_{13} = 1$ (assuming that midges benefit from both resources) and $b_{21} = -1$ (assuming that midges reduce algae abundance). As with the midge-algae-detritus model, for both alternative models we fitted the data with a scaling parameter K to factor out mean midge density. Fitting of all three models was performed with a state-space approach factoring in measurement error; see Supplementary Methods for details.

of the variance in generation-to-generation population fluctuations (Fig. 1 and Table 1).

When stripped of environmental stochasticity, the deterministic skeleton of the model shows alternative dynamical states (Fig. 2a). There is a relatively high stable point surrounded by a stable cycle of very high amplitude. The existence of alternative dynamical states pervades the biologically plausible range of parameter values (white

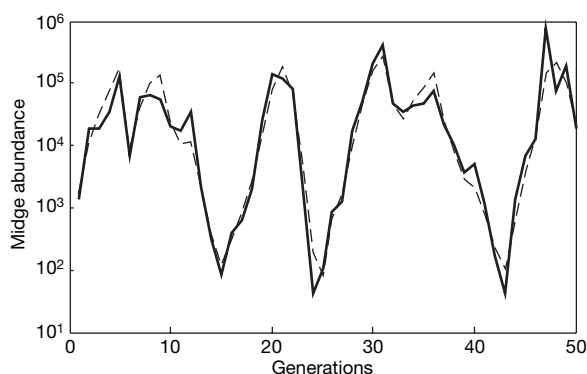


Figure 1 | Population dynamics of *T. gracilentus* in Myvatn. The solid line gives the abundance of midges in each generation, averaged between two traps. The dashed line gives the predicted 'true' (unobserved) abundances from the model given by Box 1 equations (1)–(3) with parameter values estimated by maximum likelihood: $r_1 = 3.873$, $r_2 = 11.746$, $c = 10^{-6.435}$, $d = 0.5517$, $P = 0.06659$, $q = 0.9026$, $K = 9.613$, $\sigma_1 = 0.3491$ and $\sigma_2 = \sigma_3 = 0.7499$.

areas in Fig. 3a), demonstrating that they are a common feature caused by the general structure of the model rather than phenomena requiring unlikely parameter values. In the fully stochastic model, produced by including the level of environmental stochasticity estimated in the fitted model, the population trajectory skips between the domains of attraction of the two alternative states (Supplementary Figs 1–9), for some stretches of time fluctuating around the stable point and for other stretches showing cycles (Fig. 2b). The amplitude of fluctuations is highly sensitive to the rate of influx of resources into the system; as the influx of algae and detritus, c , decreases from 10^{-3} to 10^{-9} , the amplitude increases from less than three orders of magnitude to more than ten orders of magnitude (Fig. 3b). This occurs because lower subsidies (lower values of c) allow midge populations to crash to lower levels before they are saved from extinction by the recolonization of algae. The amount of subsidy needed to save the population is low. The value of c in the model fitted to Myvatn data, $c = 10^{-6.4}$, implies that inputs are six orders of magnitude lower than the abundance of algae at the stable equilibrium point. A full pictorial analysis of the deterministic and stochastic behaviours of the model is given in Supplementary Figs 1–9.

Our midge-algae-detritus model is firmly anchored in biology and fits the data well. The model displays alternative dynamical states and high-amplitude fluctuations over a broad range of parameter values governing the influxes of resources into the system (Fig. 3). This strongly suggests the existence of alternative dynamical states in the real midge system. We obtained further statistical support for alternative dynamical states in two ways. First, the model contains a parameter, q , that dictates the strength of density dependence

Table 1 | Goodness-of-fit measures for the midge–algae–detritus and alternative models

Goodness of fit	Model			Description
	Midge–algae–detritus	Gompertz	Lotka–Volterra	
Number of parameters*	6	9	9	Parameters included in the model deterministic skeleton
–2 LL	156.2	174.7	185.5	$-2 \times \log$ likelihood function
Total R^2	0.98	0.98	0.97	$1 - \text{var } \hat{E}(t) / \text{var } X(t)^\dagger$
Prediction R^2 for $\hat{X}(t+1)$	0.74	0.57	0.38	$1 - \text{var } \hat{E}(t) / \text{var } [\hat{X}(t+1) - \hat{X}(t)]^\ddagger$
Prediction R^2 for $X(t+1)$	0.53	0.39	0.25	$1 - \text{var } \hat{E}(t) / \text{var } [X(t+1) - X(t)]$

See Supplementary Methods for descriptions of measures, and Box 1 for descriptions of the models.

*Number of parameters in the model determining the dynamics. There are six additional parameters in each model for the scaling term K , process variation for midges (σ_1) and algae/detritus ($\sigma_2 = \sigma_3$), and initial densities for midges, algae and detritus.

$^\dagger \hat{E}(t) = X(t) - \hat{X}_p(t)$, where $\hat{X}_p(t)$ is the one-step-ahead prediction of $\log(\text{midge abundance})$ made by models in Box 1.

$^\ddagger \hat{E}(t) = \hat{X}(t) - \hat{X}_p(t)$, where $\hat{X}(t)$ is the one-step-ahead prediction of $\log(\text{midge abundance})$ after being updated by the observed value of $X(t)$ to account for measurement error.

affecting midge growth and reproduction (Box 1). As q decreases and density dependence weakens in the model, the stable point is lost, leaving only the high-amplitude cycle. For the model fitted to the data, the value of q is 0.903, yet the value below which only the high-amplitude cycle remains is 0.737 (Supplementary Fig. 1). We refitted the model to the data constraining q to be small enough for only the high-amplitude cycle to occur, and the fit of the resulting model was statistically significantly worse than the fit with $q = 0.903$ (likelihood ratio test, $\chi^2 = 6.34$, d.f. = 1, $P < 0.012$; see Supplementary Methods). This represents a conservative test because, even for values of q low enough to rule out alternative dynamical states, the stochastic dynamics nevertheless show many of the same characteristics; although the deterministic skeleton of the model does not have alternative states, there is a residual ‘ghost’ that is still detected in the region surrounding the formerly stable point (Supplementary Fig. 9).

As a second line of statistical support, we fitted the data to two additional models and compared the fits with our midge–algae–detritus model (Box 1). We selected the additional models to have flexibility in fitting the Myvatn midge dynamics and yet to be

incapable of producing alternative dynamical states. The first is a three-variable Gompertz (log–linear) model. This model has nine parameters governing the midge dynamics, in contrast with six in the midge–algae–detritus model. Furthermore, we did not constrain the sign of the parameters, so the interactions between the three variables could be positive or negative. Thus, the three-variable Gompertz model represents the most general three-dimensional log–linear model possible, yet because it is log–linear it cannot produce either stable limit cycles or alternative dynamical states. Our second additional model is a two-resource, one-consumer Lotka–Volterra model. Like the Gompertz model, it contains nine parameters governing midge dynamics, and these are fitted only with constraints to guarantee that midges are consumers of the two resource variables. The Lotka–Volterra model can produce stable limit cycles, although it cannot have alternative states. Our strategy was to select additional models that are overparameterized (nine parameters) and thus should have an advantage over the midge–algae–detritus model yet cannot produce alternative dynamical states.

Despite the advantages of the additional models, the midge–algae–detritus model outperformed both of them (Table 1), giving evidence for the plausibility of alternative dynamical states underlying midge population dynamics. Further support for our model comes by applying it to a shorter data set from another shallow eutrophic lake nearby, Lake Vikingavatn (Supplementary Methods). The model fits well, and the parameter estimates are similar to those from Myvatn, with exceptions being explained by characteristics such as lake size.

A striking biological conclusion from the model is the sensitivity of the amplitude of midge fluctuations to very small amounts of resource input, c (Fig. 3); the resource input sets the lower boundary of midge abundance and hence the severity of population crashes. Thus, even though resource input might be six orders of magnitude less than the abundance of resources in the lake in most years, this vanishingly small source of resources is nevertheless critical in setting the depth of the midge population nadir and the subsequent rate of recovery. This sensitivity to resource subsidies might explain changes in midge dynamics that have apparently occurred over the last decades. Although Myvatn has supported a local charr (salmonid) fishery for centuries²⁹, this fishery collapsed in the 1980s, coincident with particularly severe midge population crashes¹¹. Over the same period, waterbird reproduction in Myvatn was also greatly reduced during the crash years¹². These changes might have been caused by dredging in one of the two basins in the lake that started in 1967 to extract diatomite from the sediment. Hydrological studies²⁷ indicate that dredging produces depressions that act as effective traps of organic particles, hence reducing algae and detritus inputs to the midge habitat. Our model predicts that even a slight reduction in subsidies can markedly increase the magnitude of midge fluctuations. Such slight environmental changes can then have seriously negative consequences for fish and bird populations.

Midges are central to the functioning of Myvatn, not only providing food for fish and birds but also representing most of the secondary production in the lake. Our analyses show that the marked, complex midge population dynamics can be explained by alternative

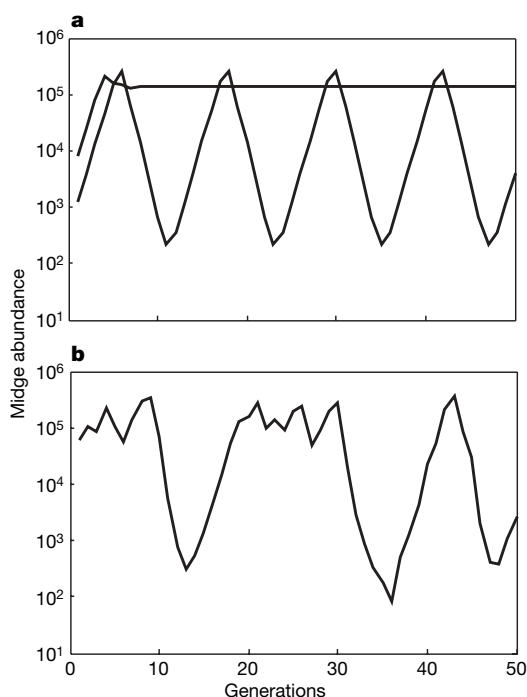


Figure 2 | Simulated dynamics of the model given by Box 1 equations (1)–(3) for 50 generations. a, Dynamics in the absence of environmental stochasticity ($\varepsilon_1(t) = \varepsilon_2(t) = \varepsilon_3(t) = 0$). **b**, Dynamics in the presence of environmental stochasticity. In **a**, two midge population trajectories starting from different initial values are illustrated. Parameter values are equal to those estimated from the data: $r_1 = 3.873$, $r_2 = 11.746$, $c = 10^{-6.435}$, $d = 0.5517$, $P = 0.06659$, $q = 0.9026$, $K = 9.613$; in **b**, $\sigma_1 = 0.3491$ and $\sigma_2 = \sigma_3 = 0.7499$.

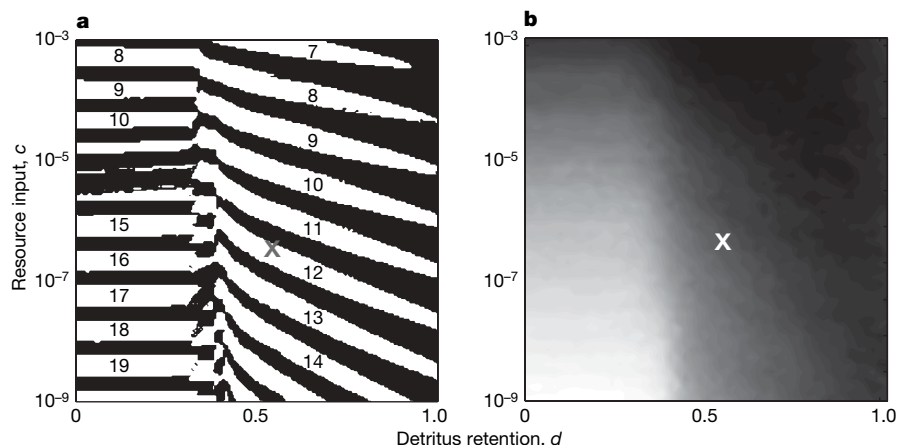


Figure 3 | Dynamics of the midge-algae-detritus model depending on resource input rate, c , and detritus retention, d . **a**, Alternative dynamical states in the deterministic skeleton (black, only a single stable point; white, stable point and stable cycle with integer period labelled). **b**, Amplitude of fluctuations in the stochastic model, with lighter shading

states, with one state a stable point and the other a stable cycle. Alternative dynamical states mean that the character of the dynamics (relatively constant versus cyclic) may change abruptly yet naturally. Moreover, the amplitude of the cycle is highly sensitive to small subsidies of resources into the midge habitat that rescue crashing midge populations. From a conservation perspective, this represents a challenge. Not only are midge dynamics inherently unpredictable, they may also be extremely and unexpectedly vulnerable to small disturbances to the lake.

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corresponding to higher amplitude (black, 10^3 , white, 10^{10}). The crosses mark values estimated from the data. Parameters are $r_1 = 3.873$, $r_2 = 11.746$, $c = 10^{-6.435}$, $d = 0.5517$, $P = 0.06659$, $q = 0.9026$, $K = 9.613$; in **b**, $\sigma_1 = 0.3491$ and $\sigma_2 = \sigma_3 = 0.7499$.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions A.E. and A.G. oversaw the data collection and are responsible for the long-term study on midge dynamics in Mývatn. A.E. and A.R.I. conceived the midge-algae-detritus model, and A.R.I. performed statistical analyses. V.A.A.J. and A.R.I. performed the mathematical analyses of the midge-algae-detritus model.

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