

# Organic-matter loading determines regime shifts and alternative states in an aquatic ecosystem

Jennie Sirota<sup>a</sup>, Benjamin Baiser<sup>b</sup>, Nicholas J. Gotelli<sup>c</sup>, and Aaron M. Ellison<sup>b,1</sup>

<sup>a</sup>D. A. Sirota, B. Baiser, N. J. Gotelli, and A. M. Ellison, *Journal of Ecology*, 2013, 101, 1054-1065; doi:10.1111/1365-2745.12102; <sup>b</sup>A. M. Ellison, *Journal of Ecology*, 2013, 101, 1054-1065; doi:10.1111/1365-2745.12102; <sup>c</sup>N. J. Gotelli, *Journal of Ecology*, 2013, 101, 1054-1065; doi:10.1111/1365-2745.12102; <sup>d</sup>A. M. Ellison, *Journal of Ecology*, 2013, 101, 1054-1065; doi:10.1111/1365-2745.12102; <sup>e</sup>A. M. Ellison, *Journal of Ecology*, 2013, 101, 1054-1065; doi:10.1111/1365-2745.12102

<sup>f</sup>A. M. Ellison, *Journal of Ecology*, 2013, 101, 1054-1065; doi:10.1111/1365-2745.12102; <sup>g</sup>A. M. Ellison, *Journal of Ecology*, 2013, 101, 1054-1065; doi:10.1111/1365-2745.12102; <sup>h</sup>A. M. Ellison, *Journal of Ecology*, 2013, 101, 1054-1065; doi:10.1111/1365-2745.12102; <sup>i</sup>A. M. Ellison, *Journal of Ecology*, 2013, 101, 1054-1065; doi:10.1111/1365-2745.12102

Slow changes in underlying state variables can lead to “tipping points,” rapid transitions between alternative states (“regime shifts”) in a wide range of complex systems. Tipping points and regime shifts routinely are documented retrospectively in long time series of observational data. Experimental induction of tipping points and regime shifts is rare, but could lead to new methods for detecting impending tipping points and forestalling regime shifts. By using controlled additions of detrital organic matter (dried, ground arthropod prey), we experimentally induced a shift from aerobic to anaerobic states in a miniature aquatic ecosystem: the self-contained pools that form in leaves of the carnivorous northern pitcher plant, *Sarracenia*

approaching tipping point (22–24). These studies revealed that signals of a tipping point could be detected as early as eight generations before a transcritical threshold was crossed (22), that systemic stochasticity could reduce the signal-to-noise ratio in early-warning indicators of tipping points (23), and that fold bifurcations in system dynamics occurred as a catastrophic threshold between different system states was crossed (24). Although consistent with

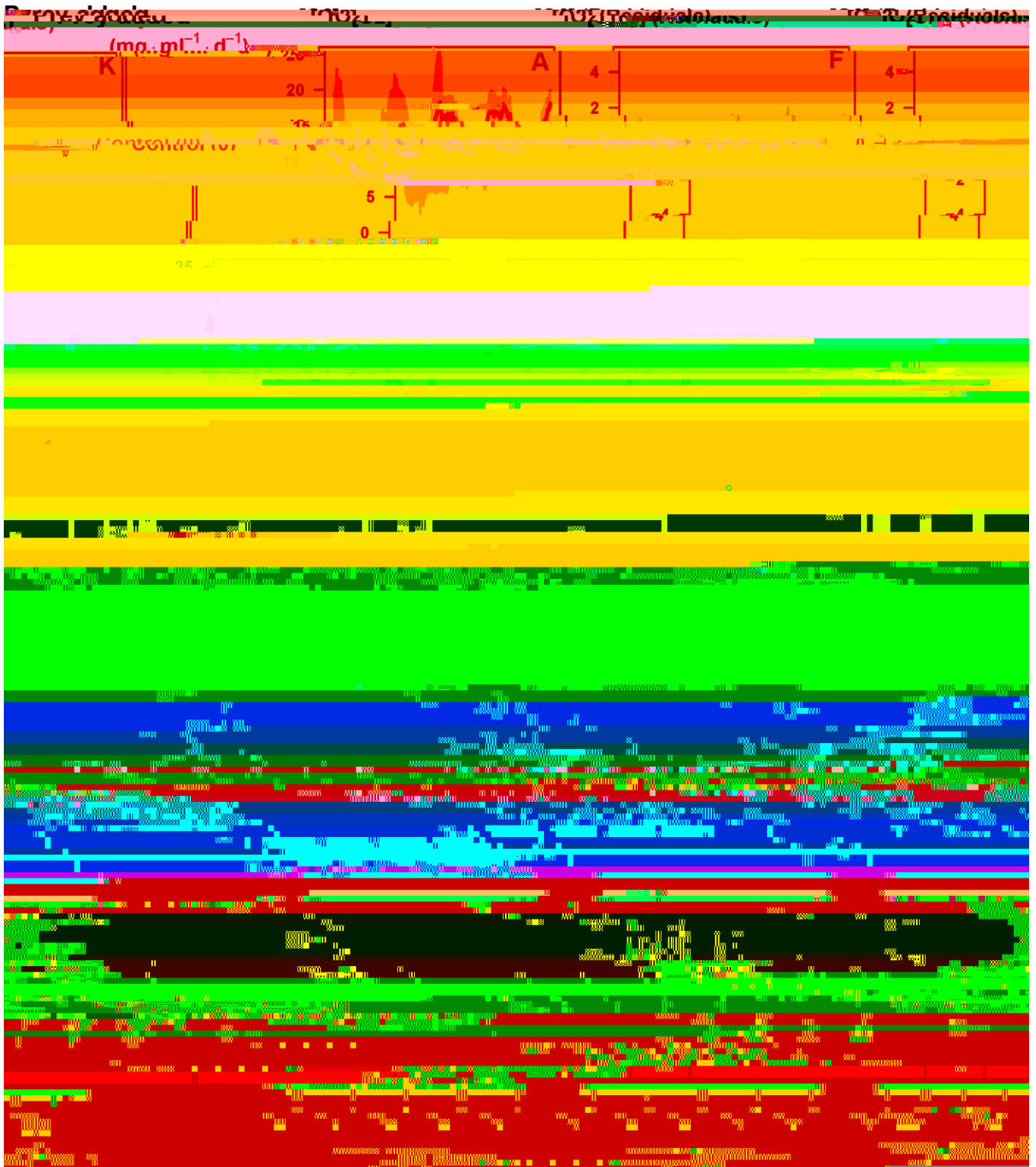


Fig. 1. A)  $n$  (m.g. ml<sup>-1</sup> d<sup>-1</sup>) vs. time (days) for  $Sarracenia$  population. The data points (black) are fitted by the model (red line). The parameter values are  $\lambda = 20.95 \pm 1.26$ ,  $\mu = 0$ ,  $\sigma = 0.125$ ,  $\tau = 0.25$ ,  $\beta = 0.5$ ,  $\gamma = 1.0$ . B)  $n$  (m.g. ml<sup>-1</sup> d<sup>-1</sup>) vs. time (days) for different parameter values (A-E). C)  $n$  (m.g. ml<sup>-1</sup> d<sup>-1</sup>) vs. time (days) for different parameter values (F-J). The 95% confidence interval (CI) is shown in grey. D)  $n$  (m.g. ml<sup>-1</sup> d<sup>-1</sup>) vs. time (days) for different parameter values (K-O). The 95% CI is shown in grey. The x-axis represents time in days, and the y-axis represents population density.

regime shift [ $\mu_{(5)} = 3.76$ ;  $P = 0.007$ ; compare colored box plots in Fig. 3]. A statistically stronger, but qualitatively similar, result was found in the  $1.0 \text{ mg}\cdot\text{mL}^{-1}\cdot\text{d}^{-1}$  prey-addition treatment: all three statistical moments were higher, and the temporal trend in  $[\text{O}_2]$  was significantly more negative, before the regime shift than after it [mean,  $\mu_{(5)} = 7.28$ ;  $P < 0.001$ ; variance,  $\sigma_{(5)}^2 = 5.46$ ;  $P = 0.001$ ; skewness,  $\mu_{(5)} = 4.93$ ;  $P = 0.002$ ; slope,  $\mu_{(5)} = 3.39$ ;  $P = 0.01$ ]. We note, however, that these patterns do not necessarily indicate CSD. Deterministic dynamics could cause manipulated microecosystems to simply diverge further from the controls, leading to an increase in variance that would be unrelated to CSD. Thus, evidence for CSD would be better identified from analysis of individual time series or of replicate time series within each treatment (A, B, C, D).

The relationship between  $[\text{O}_2]$  and light available for photosynthesis—the primary driver of O



... (14). Br a ...  
... (7), ...  
... (SI Appendix, F. 16) ...  
... (7); ... C D ... (SI  
Appendix