LETTER

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Alternative stable states explain unpredictable biological control of *Salvinia molesta* in Kakadu

Shon S. Schooler[1], Buck Salau[2], Mic H. Julien[1] & Anthony R. Ives[3]

Suppression of the invasive plant *Salvinia molesta* by the salvinia weevil is an iconic example of successful biological control. However, in the billabongs (oxbow lakes) of Kakadu National Park, Australia, control is fitful and incomplete. By fitting a process-based nonlinear model to thirteen-year data sets from four billabongs, here we show that incomplete control can be explained by alternative stable states[1–4]—one state in which salvinia is suppressed and the other in which salvinia escapes weevil control. The shifts between states are associated with annual flooding events. In some years, high water flow reduces weevil populations, allowing the shift from a controlled to an uncontrolled state; in other years, benign conditions for weevils promote the return shift to the controlled state. In most described ecological examples, transitions between alternative stable states are relatively rare, facilitated by slow-moving environmental changes, such as accumulated nutrient loading or climate change[5,6]. The billabongs of Kakadu give a different manifestation of alternative stable states that generate complex and seemingly unpredictable dynamics. Because shifts between alternative stable states are stochastic, they present a potential management strategy to maximize effective biological control: when the domain of attraction to the state of salvinia control is approached, augmentation of the weevil population or reduction of the salvinia biomass may allow the lower state to trap the system.

Awareness and concern about the ecological consequences of alternative stable states is growing as more examples have been identified[1,5,7–9]. In many examples, the alternative states are very stable, so that in the absence of an extraordinary perturbation, the system remains at its 'natural' state. Concern arises because states can change abruptly even when the environmental drivers responsible for the change occur gradually; if the ecological system is perturbed by a slow-moving driver, the system may remain largely unchanged until it reaches a threshold catastrophe and abruptly shifts to another state[1]. At present, there is a theoretical enterprise to identify the early warning signs of these abrupt shifts[10,11]. Equally disturbing, once the shift occurs the system will show hysteresis[1]; even if the environmental perturbation were reversed, the system would stay at its new state, inhibiting the ability of managers to repair the system to its desired state[12].

Ecological systems, however, are subjected to stochastic and cyclic perturbations, and if alternative states are weakly stable and perturbations are large enough, then shifts between states may be routine[1,13]. Alternative stable states may thus generate underlying forces that govern the stochastic dynamics of the system, leading to complex and seemingly irregular, eruptive behaviour. In fact, it may be difficult to identify the alternative stable states, yet at the same time be difficult to understand the dynamics of the system without first identifying that alternative stable states exist.

Salvinia molesta, a South American aquatic plant, is one of the most widespread and environmentally, economically and socially destructive invasive plant species. Since 1939, it has invaded lake and river systems in tropical and subtropical habitats around the world[14]. Its success is owing to its ability to double in biomass every 3–4 days, and to regenerate vegetatively even after severe damage or drying[15,16]. It is capable of forming dense mats up to 1-m thick that make waterways unnavigable and displace aquatic organisms[14]. Nonetheless, highly successful biological control is often provided by the salvinia weevil (*Cyrtobagous salviniae*, Curculionidae) that since 1980 has been introduced into most regions where salvinia has invaded[17]. The salvinia weevil is a strict specialist on salvinia; adults feed on growing meristematic tissue (buds), whereas larvae tunnel through vascular tissues[14], which together often lead to marked reductions in salvinia with no additional expenditure of resources[14,17].

Salvinia invaded Kakadu National Park in 1983[16], and the salvinia weevil was released later that year[18]. Although the weevils rapidly established and successfully controlled salvinia for several years, in 1988–1990 salvinia resurged to form thick mats. This led to an intensive research project conducted by the Australian Commonwealth Scientific and Industrial Research Organization (CSIRO) in Kakadu[18] and the establishment of a long-term monthly sampling program (Fig. 1). Unlike lake systems that experience continuously successful biological control of salvinia, the Kakadu billabongs are subjected to annual flooding that flushes salvinia downstream, mixing it among billabongs within the same floodplain. Floods also translocate salvinia to and from the billabongs and moist terrestrial sites; salvinia persists in these terrestrial sites during the dry season, sometimes at high biomass, where it has a refuge from the strictly aquatic weevils. Salvinia also occurs in the understory of grasses that grow over water along billabong edges where it is partially protected from both flooding and weevils[14]. Thus, whereas the billabongs of Kakadu are highly perturbed, salvinia has refuges against both flooding and weevils from which it can reinvade open water.

Fieldwork during 1991–1994 led to the following hypothesis for the failure of continuous biological control. When salvinia is at low density, it has relatively high nitrogen content and high growth rate. Salvinia is thus highly susceptible to biological control, and the many developing

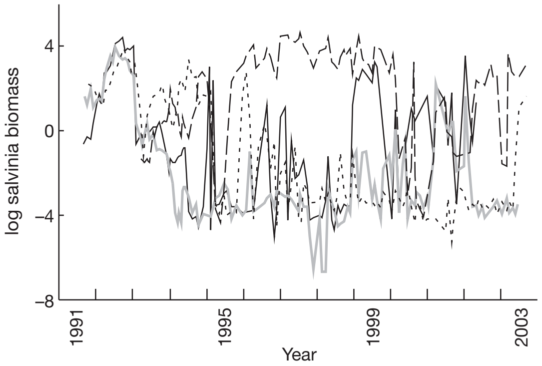

Figure 1 | Log biomass of salvinia in four Kakadu billabongs. Grey line shows data for Jabiluka, dashed line for Minggung, black line for Jaja and dotted line for Island. The vertical axis is scaled to have mean zero across all billabongs.

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[1]CSIRO Ecosystem Sciences, Long Pocket Laboratories, Indooroopilly, Queensland 4068, Australia. [2]Department of the Environment, Water, Heritage, and the Arts, Kakadu National Park, Jabiru, Northern Territory 0886, Australia. [3]Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706, USA.

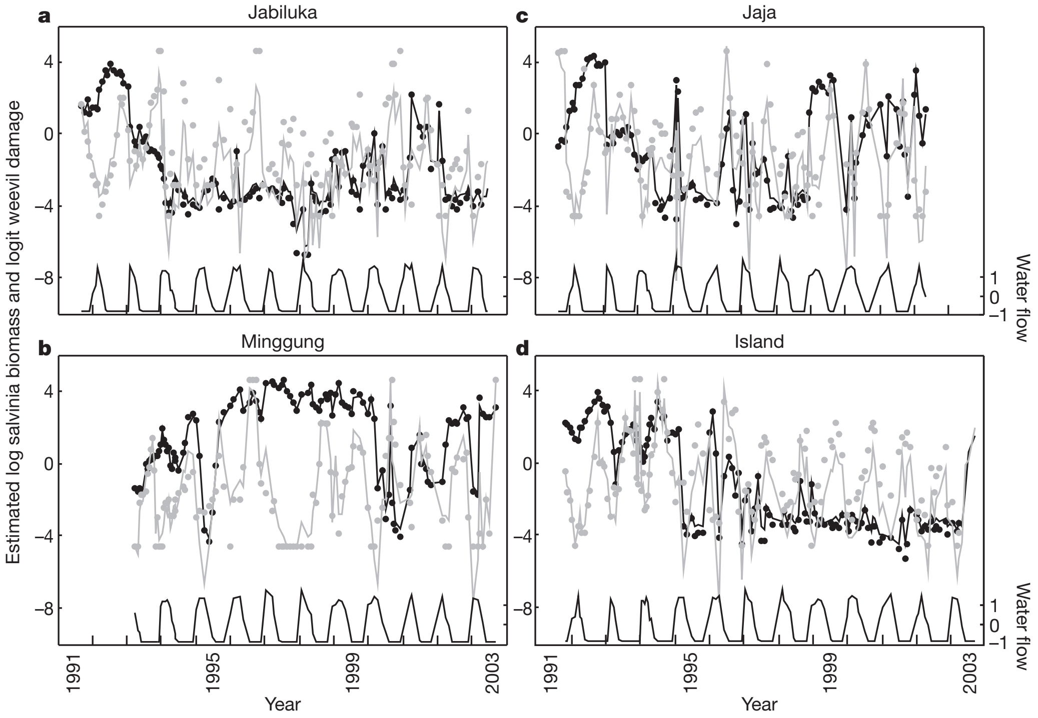

Figure 2 | Fitted model to log salvinia biomass (black) and logit weevil damage (grey) for four billabongs. a–d, Dots give the raw data, and lines give the updated values from the Kalman filter (Box 1). Data and fitted model are standardized to have mean zero across all billabongs. The log water flow measured at monitoring stations in each drainage is given by the line at the bottom of the figure and is standardized to have mean zero and variance one (note different axis).

buds support high weevil numbers[19]. Conversely, when salvinia is at high density, growth rates are relatively low, and new buds are scarce. In this condition much of the plant biomass occurs as vegetative, non-meristematic tissue often piled high above the water surface. This salvinia is much less suitable for weevils and is thus difficult to control. Although not stated as such, this is a hypothesis of alternate stable states determined by the growth state of salvinia: a low biomass state maintained by weevil attack, and a high biomass state that has escaped weevil control. As found in other cases of alternative stable states, the salvinia–weevil system involves a species that has distinct life forms[1,20] and a herbivore that can potentially lose control of its food plant[21,22].

Standard analyses of the time-series data from the four billabongs reveal none of the dynamical hallmarks of successful biological control: there is little evidence that weevil damage is associated with declines in salvinia biomass (Supplementary Information). Further, changes in salvinia biomass between monthly samples are characterized by frequent small steps and occasional large jumps, indicating that nonlinear processes are driving salvinia dynamics (Supplementary Information). Therefore, we built a nonlinear model from what we know about the biology of the system (Box 1). Briefly, the model assumes that salvinia biomass is divided into two categories, one with copious buds that is vulnerable to weevils and the other that is not, with the proportion represented by these two categories depending on total salvinia biomass[18]. The growth of salvinia biomass depends on the amount of vulnerable tissue. Weevils attack this vulnerable tissue non-uniformly, so that attacks can be aggregated among buds. The population growth rate of the weevils depends on the amount of salvinia biomass damaged. There is net migration of salvinia into billabongs from external areas or the grass understory along billabong edges, and mortality/flushing of both salvinia and weevils that depends on the water flow through the drainages. There is also stochastic variation that affects the per capita growth rates of both salvinia and weevils, and this variation can increase with increasing water flow. The latter property accounts for possible increases in unpredictable flushing or filling of billabongs with salvinia or weevils during flood events. The model fits the data well, with most parameters showing statistically strong effects on the observed dynamics (Fig. 2 and Supplementary Information).

Key biological insights from the fitted parameter values of the model include the following (Table 1). The proportion of salvinia biomass in the category that is invulnerable to weevil attack, g, is generally high, ranging from $g_{\mathrm{min}} = 0.91$ to $g_{\mathrm{max}} = 0.94$, which is consistent with weevils attacking meristematic tissues (adults) and vascular tissue (larvae). Flooding events reduce the abundance of weevils ($d_{\mathrm{w}} < 0$), yet have little net effect on the mean abundance of salvinia ($d_{\mathrm{s}} = 0$). However, flooding events increase the variability in sample-to-sample fluctuations in salvinia biomass ($\sigma_{\mathrm{s2}} > 0$; see Table 1). These two patterns could be caused by flooding events moving salvinia among billabongs, between billabongs and surrounding land, and from the grass understory into open water; this would simultaneously increase the variance in salvinia

Table 1 | Estimates from the best-AIC fitting model of the biologically relevant parameters

Parameter	Value	Description
g_{min}	0.91	Minimum weevil-invulnerable tissue
g_{max}	0.94	Maximum weevil-invulnerable tissue
b_1	5.41	Salvinia morphology inflection point
b_2	385.7	Slope of morphology change at b_1
a	0.09	Weevil attack rate
k	3.38	Aggregation parameter for weevils
c	0.94	Weevil reproduction scale parameter
m	0.0085	Salvinia net immigration
v	0.79*	Salvinia self-regulation form parameter
d_{s}	$0^{\dagger}$	Change in salvinia with water flow, $\delta_{\mathrm{s}}(z_t) = d_{\mathrm{s}}\, z_t$
d_{w}	–0.24	Change in weevils with water flow, $\delta_{\mathrm{w}}(z_t) = d_{\mathrm{w}}\, z_t$
σ_{s1}	0.21	Salvinia process error, var.$\{\varepsilon_{\mathrm{s}}(z_t)\} = (\sigma_{\mathrm{s1}} \exp(\sigma_{\mathrm{s2}}\, z_t))^{\dagger}\tau_t$
σ_{s2}	0.35	Water flow effect on salvinia process error
σ_{w1}	0.42	Weevil process error, var.$\{\varepsilon_{\mathrm{w}}(z_t)\} = (\sigma_{\mathrm{w1}} \exp(\sigma_{\mathrm{w2}}\, z_t))^{\dagger}\tau_t$
σ_{w2}	$-0.08^{\ddagger}$	Water flow effect on weevil process error

AIC, Akaike information criterion. The model without alternative stable states ($g_{\mathrm{min}} = g_{\mathrm{max}}$, $b_1 = b_2 = 0$) has a ΔAIC of 48.76 and provides a statistically significantly inferior fit to the data (${\chi_3}^2 = 52.76$, $P \ll 0.001$). For the model, $R^2 = 0.73$ and 0.38 for log salvinia biomass and logit weevil damage, respectively. All values are statistically significant by likelihood ratio tests except as follows. *Not different from 1 (ΔAIC = 1.08). †Not different from 0.01 (ΔAIC = 1.82). ‡Not different from 0 (ΔAIC = 1.86).

biomass and cause a net reduction of weevil abundance as salvinia colonizes billabongs from weevil-free refuges.

Existence of the alternative states requires the proportion of salvinia biomass in the category vulnerable to weevil attack to change with salvinia biomass; if the model is constrained so that this proportion does not change ($g_{\min} = g_{\max}$), then alternative stable states are impossible, and the fit of the model is statistically significantly reduced (likelihood ratio test, $\chi_3^2 = 52.76$, $P \ll 0.001$). This provides strong support for the existence of alternative stable states. In three of the billabongs, the system spends time in the domains of attraction to both stable states, whereas Minggung has generally high salvinia abundance and rarely occupies the domain of weevil control (Fig. 3). We fit the model assuming that the underlying processes were identical across all billabongs. The poor salvinia control in Minggung could be due simply to the stochastic nature of the dynamics, by chance never staying long in the region of weevil control. There may be other differences between Minggung and other billabongs that we cannot identify, although such differences are not required to explain the observed dynamics.

Owing to the annual flooding events and high stochasticity in the system, the fit of the model relies not only on the existence of alternative stable states, but also the transient dynamics of the corresponding deterministic model. Although the deterministic model gives alternative stable states when the logarithm of water flow is fixed at its mean value, when the log water flow is fixed at one standard deviation below its mean, there is only a single stable point, and when fixed at one standard deviation above its mean, the weevil is eliminated from the system (Supplementary Information). Therefore, as the water flow regime fluctuates through its annual cycle, the alternative stable points alternately disappear; a possible, although still incomplete, description is that there are two alternative, environmentally forced cycles that have separate domains of attraction (Supplementary Fig. 8). Nonetheless, the 'ghost' of the boundary between stable points still affects the transient dynamics of the system[6,23,24]. An added complexity is that the dynamical forces around the two alternative stable states differ. In the domain of attraction to the state with high salvinia biomass, changes in biomass are slow compared to changes in weevil damage, as illustrated by the deterministic trajectories of the model (Fig. 3). This allows salvinia biomass to dynamically wander between high and moderate values. The domain of attraction to the lower stable state contains trajectories that tend to approach the stable point through increases in both salvinia biomass and weevil damage, causing a positive correlation between these two variables. All of these dynamical patterns contribute to the strength of fit of the model to the data.

Our analyses point to possible opportunities to foster biological control of salvinia at Kakadu. For many examples of ecological systems with alternative stable states, the stability of the states makes transitions between them ecologically difficult and operationally challenging from a management perspective[8,12]. The Kakadu billabongs, however, are highly stochastic and experience periodic flooding, giving a window of opportunity to shift the system between states[25,26]. Even for Minggung, where biological control has been ineffective, the system occasionally jumps into the domain of attraction to the lower state of salvinia control. This occurs towards the end of the dry season after weevil populations recover from depression during flooding. If weevil control could be augmented at this time by inoculating Minggung with infested salvinia from other billabongs, the system could be captured in the lower domain of attraction. An alternative strategy would be to chemically or mechanically reduce salvinia as it is recovering from a flushing event, thereby allowing weevils more time to exert control. There is no guarantee that these strategies would work the first, the second, or even the third try. However, our theoretical demonstration that this lower state probably exists for Minggung should give hope for repeated attempts. Although alternative states are generally thought to present severe management challenges, when they are identified and understood, they may also present management solutions[8,27].

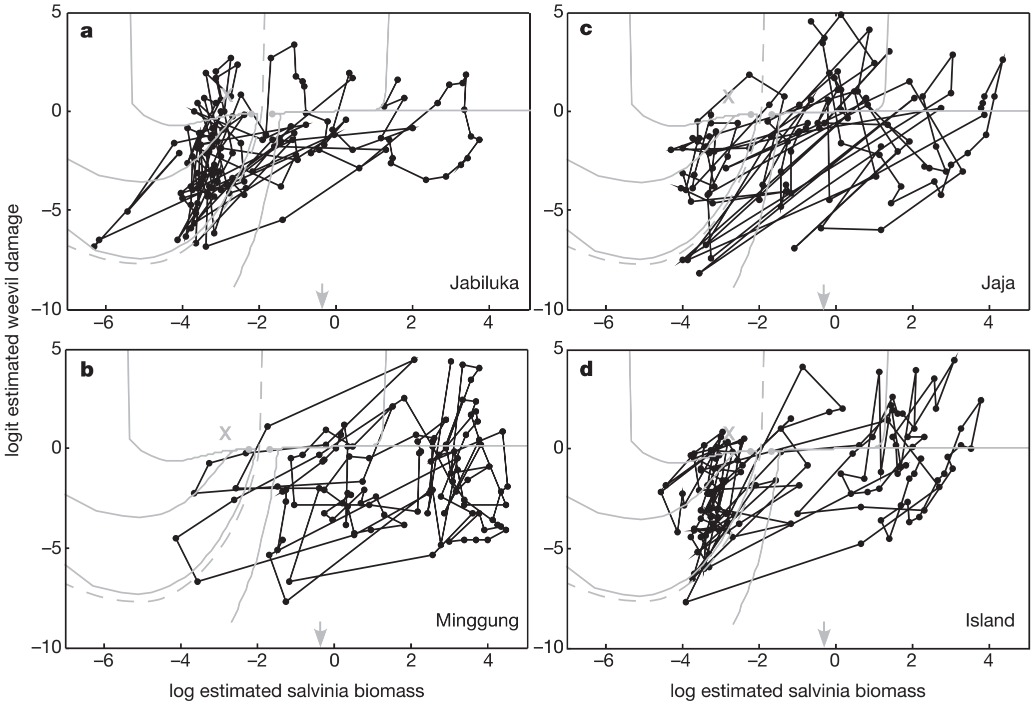

Figure 3 | Phase portraits of logit weevil damage against log salvinia biomass for the four billabongs. a–d, Values have been standardized to have mean zero across all billabongs. Plotted trajectories (black dots and lines) are updated values fitted to the data, thereby smoothing the data to account for measurement error (Box 1). The dashed grey line divides the domains of attraction to the two stable points, marked with grey dots, and example deterministic trajectories are included (solid grey lines) when the drainage water flow is fixed at its mean value, the time step between samples is assumed to be $\tau = 8.83$ days, and there is no stochasticity in the model. The grey cross gives the equilibrium abundance of salvinia when there is no stochasticity and the log water flow is fixed at one standard deviation below its mean value. The grey arrow gives the deterministic abundance of salvinia in the absence of weevils which occurs when the flow rate is one standard deviation above its mean value (Supplementary Information).

BOX 1:

Salvinia–weevil model

We fit a single model to the data simultaneously for all four billabongs, thereby assuming that their dynamics are governed by the same processes. The model has a nonlinear state–space form[28], with one set of equations describing the biological processes driving the dynamics and the other describing the sampling used to generate the data. Both process and measurement equations contain stochastic elements, with process error encapsulating environmental variation and measurement error describing any deviations between the 'true' state of the process variables and the data.

The process equations are:

$$x_{t+1} = \left\{ \left[x_t g(x_t) + x_t (1 - g(x_t)) e^{r\tau_t} (1 + (1 - g(x_t)) x_t)^{-v} (1 - p_t) \right] \right.$$
$$\left. \exp(\delta_s(z_t)) + m\tau_t \right\} \exp(\varepsilon_s(z_t))$$
$$y_{t+1} = \{ c x_t (1 - g(x_t)) e^{r\tau_t} p_t \exp(\delta_w(z_t)) \} \exp(\varepsilon_w(z_t))$$

where x_t and y_t are the salvinia biomass and weevil abundance at time t, $p_t = 1 - \left(1 + \frac{a\tau_t y_t}{k(1 - g(x_t)) x_t} \right)^{-k}$ is the proportion of susceptible salvinia attacked by weevils assuming that the distribution of attacks is given by a negative binomial with aggregation parameter k, and τ_t is the time interval between model iterations (averaging 8.83 days). The function $g(x_t)$ gives the proportion of salvinia biomass in the category invulnerable to weevil damage. $g(x_t)$ follows an inverse-logit function with minimum and maximum values $g_{\min}$ and $g_{\max}$, inflection point where $x_t = b_1$ and slope at the inflection point given by b_2. The input variable z_t is the log water flow measured at monitoring stations in each drainage, and $\delta_s(z_t)$ and $\delta_w(z_t)$ give the response of salvinia and weevil survival rates dependent on water flow.

The measurement equations are:

$$X_t^* = X_t + \log(g(e^{X_t})) + C + \alpha_s$$
$$W_t^* = \mathrm{logit}(p_t) + \alpha_w$$

where $X_t = \log x_t$ is the 'true' log salvinia biomass from the process equations, X_t* is the observed log salvinia biomass assuming that only the invulnerable category is sufficiently dense to occur in visual sampling, and W_t* is the logit of the observed weevil damage. The constant C is an overall scaling term for salvinia biomass, because the process equations are non-dimensional. The random variables α_s and α_w give measurement error, with α_s assumed to have a Gaussian distribution with mean 0 and variance σ^2_{ms}, and α_w assumed to have a quasi-binomial distribution with variance $\left(\frac{1}{n} + \sigma^2_{\mathrm{mw}} \right) \frac{1}{p_t(1 - p_t)}$; if $\sigma^2_{\mathrm{mw}} = 0$, this would be the variance under a binomial distribution with a sample size of n, but to allow greater-than-binomial distribution, we also estimated σ^2_{mw}.

The model was fit using an extended Kalman filter to estimate the likelihood function[28]. The Kalman filter is an iterative algorithm in which the 'true' population sizes and estimates of their uncertainties are projected forward using the model. When an iteration coincides with a sample point, the true population sizes are updated using the observed values and the estimates of the measurement error; if the measurement error is small, then updating pulls values closer to their observed values. The model values plotted in Figs 2 and 3 are these updated values. The parameter r, the intrinsic rate of increase of the salvinia, was set at 0.08 per day as determined by extensive experiments at Kakadu (M.H.J., unpublished data). Backwards model selection was performed to find the best-fitting model, and the best-fitting model was confirmed with forward selection. Likelihood ratio tests were used to assess the statistical significance of key variables. Model parameters are described in Table 1, and detailed descriptions of the model and fitting procedure are given in the Supplementary Information.

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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 M.H.J. developed the initial hypothesis explaining the partial success of salvinia biological control and designed the CSIRO sampling program at Kakadu. B.S. managed the Kakadu sampling program, and S.S.S. and B.S. assembled the data set. S.S.S. and A.R.I. designed the overall concept of the project reported here, and A.R.I. performed the analyses.

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