Beyond Catastrophe Theory: Ecological Modelling with Non-Linear Dynamical Systems

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1 Introduction

It is generally assumed that ecological systems will respond gradually to slow changes in their environment, however this has been observed to not always be the case; for example, lake, coral reef and woodland ecosystems shift rapidly between different regimes (Scheffer et al., 2001). In ecology, a **regime** is the characteristic behaviour of an ecosystem; being able to understand, model and even predict abrupt regime changes is an important problem for environmental preservation and agriculture (Rosenzweig, 1971). Regime shifts may occur as a result of perturbations to the environment, such as a volcanic eruption (Almaraz and Green, 2024) or ecosystem overexploitation (Sguotti et al., 2019). When the behaviour of the system changes qualitatively in response to a small change in a parameter, this is called a **bifurcation**; if additionally, the system's state shifts discontinuously, this is a **catastrophe**. The position where this occurs is a **bifurcation point** or **catastrophe point** respectively.

Catastrophe theory and bifurcation analysis offer a route to explain and model discontinuous behaviour using non-linear dynamical systems. By analysing the global and local stability of solutions to the systems, it is possible to classify bifurcations to illuminate the system's behaviour.

In Section 2, we will introduce catastrophe theory, demonstrate its use in ecological modelling and explain some of the criticism it historically provoked. These criticisms were largely addressed by stochastic catastrophe theory, an extension of catastrophe theory (see Section 3.1) which is used in modern ecological applications. We will discuss one of these applications with links to changepoint analysis to demonstrate the potential challenges and opportunities when applying the models to time series data (see Section 3.4). In Section 4, we will delve into how a specific type of ecological model, the Rosenzweig-MacArthur predator-prey model and its extensions, can be used to model complex behaviour, and the possible discontinuous behaviour resulting from these models.

2 Catastrophes and Bifurcations

2.1 Motivating Examples

Example 2.1 (The Cusp Bifurcation and Hysteresis)**.** Consider a response variable y with a control variable x with the following governing equation:

$$\begin{aligned} V(y;x) &= -xy - \frac{3}{2}y^2 + \frac{1}{4}y^4 \\ \frac{\partial y}{\partial t} &= -\frac{\partial V}{\partial y} \\ &= x + 3y - y^3. \end{aligned} \tag{1}$$

For any fixed x, y will evolve to a state where $\partial y/\partial t = 0$; clearly, there will be either one or three real possible solutions satisfying this. These solutions are plotted in Figure 1 for different values of x; specifically, the minima of $V(y,x)$ with respect to y are plotted in black and the maxima in red. The minima are considered **stable states**, since any small random perturbations away from the state due to random chance will result in y returning instead of y diverging, whereas the maxima represent **unstable or inaccessible states** where any random disturbance will cause y to diverge from the state. Assuming the system is currently in a stable state, if x is changed, the current value of y will no longer be an equilibria, so y will evolve to the nearest value which is now a stable equilibria. If we start in the top right of Figure 1, decreasing x will cause only a gradual decline in y until we reach catastrophe point A where $x = -2$ and $y = 2$. Then, if x is decreased further, y will decline precipitately to the lower stable states. After this, increasing x, even beyond the point it originally declined, will not cause y to recover until we reach catastrophe point B, where y will rapidly recover. When it is not possible to predict the state of a system without knowledge of its past evolution, this is called **hysteresis**; Model 1 demonstrates this for $-2 \leq x \leq 2$.

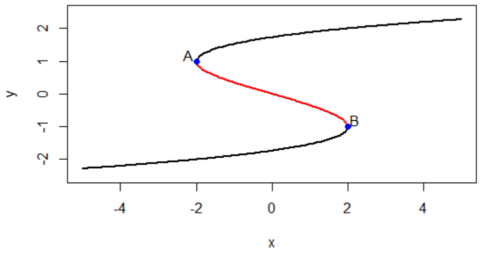


Figure 1: The equilibria of Equation 1 with black representing stable states and red representing unstable states, demonstrating hysteresis for values of $-2 \leq x \leq 2$. A and B are catastrophe points.

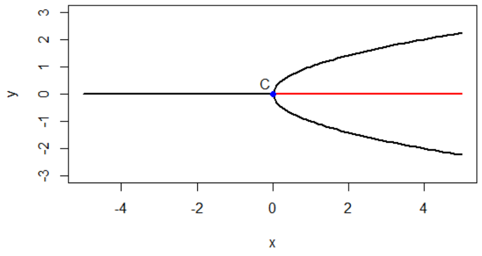


Figure 2: The equilibria of Equation with black representing stable states and red representing unstable states, demonstrating bifurcation occurring at $x = 0$. C is a catastrophe point.

This has important applications for ecological preservation, suggesting that once a catastrophe point has been passed, it may be difficult to reverse the effects of human damage to ecosystems. In the case of coral reef ecosystems, pressure caused by high fishing intensity and increased nutrient load due to changed land-use has dramatically reduced coral reef health; Scheffer et al. (2001) suggests there has been catastrophic shift to a different set of stable states, which will be difficult to reverse.

Example 2.2 (Pitchfork Bifurcation)**.** If the response variable y was modelled as

$$\frac{\partial y}{\partial t} = xy - y^3,$$

then, for all $x \leq 0$, the only stable equilibria is at $y = 0$, but for $x > 0$, the system behaviour will change dramatically, with two possible stable states emerging. This is called a pitchfork bifurcation, and here $C = (0, 0)$ is a catastrophe point.

2.2 Catastrophe Theory

Many natural ecological processes can be modelled as non-linear dynamical systems in the following form:

$$\frac{\partial y}{\partial t} = -\frac{\partial V(y, c)}{\partial y}, \quad c \in \mathcal{R}^n, y \in \mathcal{R}^m.$$

The variable(s) being modelled y are called the **response variable(s)**, and c is one or multiple **control variable(s)** which determine the specific process structure. The system aims to minimise the **potential** $V(y; c)$, so called to draw links between physical systems that minimise potential energy (such as gravitational potential energy). For example, Sguotti et al. (2019) model the biomass of Atlantic cod in this form using the control variables of fishing mortality and sea surface temperature.

Equilibria are states y^* where $\partial V(y^*)/\partial y = 0$, and minima of $V(y, c)$ with respect to y are stable states. Although maxima of $V(y, c)$ with respect to y are equilibria, they are unstable and since almost all physical systems contain an element of randomness which will disturb the state, it is rare to encounter a system in a maximum. Other types of non-stable equilibria include saddle nodes, and, if y is multivariate, centres. Systems may also exhibit stable periodic behaviour; the trajectory of a stable cycle is called the **limit cycle**. Catastrophe points are degenerate equilibria which occur when the Hessian matrix $\partial V(y, c)/\partial y_i y_j$ has zero eigenvalues. At these points, small changes in the control variables can lead to sudden discontinuous behaviour.

Catastrophe theory began as an effort to classify degenerate equilibria and the behaviour of systems at points near the degenerate equilibria. By studying the Taylor expansion of V, Thom (1975) proved there were only seven distinct types of local catastrophe points for any system with four or fewer control variables and any number of response variables. Any catastrophe point can be considered as a “universal unfolding” of a canonical form with one or two response variables, demonstrating the same behaviour. The universal unfoldings of the canonical forms are the seven different families of catastrophe models.

Local bifurcations occur due to changes in the stability of equilibria or periodic orbits as the control variables cross a threshold, as seen in the motivating examples. Local bifurcations are also catastrophes when they involve discontinuous jumps in the response variable between stable states. One further example of a local bifurcation is the **Hopf bifurcation**: this occurs when an equilibrium loses stability and gives rise to periodic orbits where the centre of the cycle is the equilibrium. If the periodic orbits are stable, the Hopf bifurcation is called **supercritical**; otherwise, it is **subcritical**. Since the response variable will not exhibit a discontinuous jump, Hopf bifurcations are not catastrophes.

It is possible to predict local bifurcations through a mechanism called critical slowing down (Shortridge et al., 2024). As the system approaches the bifurcation point, the time for the response variable to return to equilibrium after a perturbation increases.

The **basin of attraction** for a stable solution is the maximal set of states $\mathcal{A}$ such that, if y is initially in $\mathcal{A}$, y will eventually evolve to the solution. The **resilience** of a state can be measured by the area of the basin of attraction (Rakshit and Raghunathan, 2024); if the basin of attraction is smaller, it is more than likely that a random environmental perturbation could lead to the system leaving the basin of attraction and undergoing a regime shift. Scheffer et al. (2001) explores resilience of equilibria in different ecosystems, focusing on how human actions have reduced them, leading to increased risk of regime shifts.

On the other hand, **global bifurcations** are abrupt changes in the qualitative behaviour of the system that cannot be predicted solely from analysing stability and do not exhibit critical slowing down. Global bifurcations often occur when the basin of attractions collide with each other or other stable solutions as parameters change.

2.3 Catastrophe Models

The simplest, and therefore most widely used, catastrophe model exhibiting discontinuous transformations is the **cusp catastrophe model**, which has two control variables and one response variable. It is the universal unfolding of $g(x) = x^4$ and is defined by the following equations:

$$\begin{aligned} V(y;\alpha,\beta) &= -\alpha y - \frac{\beta y^2}{2} + \frac{y^4}{4}, \\ \frac{\partial y}{\partial t} &= -\frac{\partial V(y;\alpha,\beta)}{\partial y} \\ &= \alpha + \beta y - y^3. \end{aligned}$$

Both Example 2.1 and Example 2.2 are simply special cases of this, demonstrating that the cusp catastrophe can exhibit hysteresis and pitchfork bifurcation. With two control variables, the cusp catastrophe model now has curves of catastrophe points where the behaviour of the system changes discontinuously. The surface of equilibria is plotted in Figure 3, and the set of values of the control variables where there are multiple stable states is shaded the floor of the diagram. The α coordinate is called the **asymmetry coordinate**, and determines the skew in the distribution of alternative states across the range of control variables values; the β coordinate is called the **bifurcation coordinate** and determines whether the system is forced into catastrophic bifurcation (Grasman et al., 2009).

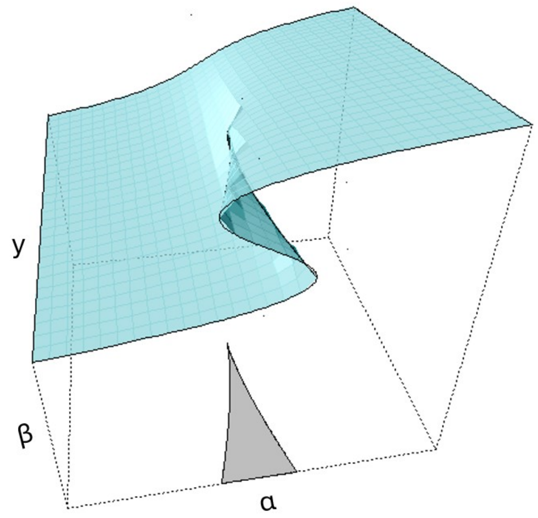


Figure 3: The cusp catastrophe model: the surface of equilibria is marked in blue. The shaded values projected onto the lower plane (the control surface) are the values of α and β where there are multiple steady states and so hysteresis, bifurcation and other non-linear effects may occur. Generated with the R package `cusp` (Grasman et al., 2009).

The **butterfly catastrophe** is a less widely used catastrophe model, which allows for modelling more complex processes; it has four control variables and one response variables. It is the universal unfolding of $g(x) = x^6$ and is governed by:

$$V(y;\alpha,\beta,\gamma,\delta) = -\alpha y - \frac{\beta y^2}{2} - \frac{\gamma y^3}{3} - \frac{\delta y^4}{4} + \frac{x^6}{6},$$

$$\frac{\partial y}{\partial t} = \alpha + \beta y + \gamma y^2 + \delta y^3 - y^5.$$

Parameter estimation for these models presents difficulties, as most parameter estimation techniques are based on minimising the difference between the predictions of the model and the data. However, catastrophe theory is used when there are multiple stable states and thus multiple predictions for the response variable for the same value of the control variables. Additionally, Thom (1975) relies on topological principles of invariance, but goodness-of-fit procedures are not invariant under the transformations allowed in differential topology (Cobb, 1978). Solutions to these issues will be discussed in Section 3.

2.4 Historical Background

Catastrophe theory is a branch of non-linear dynamics first developed by Thom (1975) with wide-ranging applications from economics (Rosser, 2007) to biostatistics (Cobb and Zacks, 1985). Christopher Zeeman promoted catastrophe theory heavily, writing accessible (but not mathematically rigorous) papers that captured public attention, applying it to subjects such as election result forecasting and modelling mental disorders and prison riots (Zeeman and Barrett, 1977).

This led to catastrophe theory becoming highly popular and being applied widely in different fields (Guckenheimer, 1978). Catastrophe theory began to attract criticisms in the late 1970s and it faded quickly from prominence for around twenty years (Rosser, 2007).

Much of the criticism correctly identified improper applications of catastrophe theory. For example, in many applications, particularly in the social sciences, there was arbitrary quantization of control variables which were not meaningfully quantifiable. For example, in order to apply catastrophe theory to model prison riots, (Zeeman and Barrett, 1977, Chapter 13) use "tension" as a control variable, quantified arbitrarily as "sickness plus governor's applications plus welfare visits". Additionally, time was sometimes incorrectly used as a control variable such as in Saunders (1985) which violated the mathematical assumptions of catastrophe theory due to the gradient dynamics (Rosser, 2007).

Finally, there was an over-reliance on qualitative methods; the framework of identifying "catastrophe flags" was a common approach. In Gilmore (1993), nine "catastrophe flags" are discussed; these are qualitative indications that catastrophe modelling is appropriate. The first two of these flags concern the number of equilibria: the system should have multiple stable equilibria; this can be identified if a system displays systematic bimodality, although this could alternatively be an indication of multiple distinct subgroups. In order to have multiple stable states, there must be at least one unstable equilibria; these are identified as values between the stable states that are rarely or never achieved by the system. Other flags include behaviours demonstrated in the examples such as hysteresis, discontinuities in the response variable and divergence. While these qualitative indications are useful in identifying whether it might be advantageous to use a catastrophe modelling framework, Sussmann and Zahler (1978a) correctly argued that quantitive methods are necessary for rigour and to validate the models.

Some other arguments against catastrophe theory were overly broad, with Sussmann and Zahler (1978b) suggesting that misspecification is likely as surfaces can be fitted to any set of points and global forms cannot be verified from local estimates. However this is general problem for fitting models; while naturally care must be taken to not draw inferences from models for points outside the range of the dataset, it is not specific argument against catastrophe theory.

Another criticism was that catastrophe theory relied on deterministic differential equations, whereas real systems will generally include an element of randomness, making it unclear whether catastrophe theory can be applied in practise. However in the next section, we will discuss a stochastic extension to catastrophe theory which solves this issue. This extension also allows a maximum likelihood approach to be used, reducing the reliance of catastrophe theory on qualitative approaches.

Although the name "catastrophe theory" became uncommon in the 1980s, the mathematical ideas persisted as bifurcation analysis. In the 2000s, the critique of catastrophe theory was reevaluated, and stochastic catastrophe theory has been applied recently in ecology and environmental science in Sguotti et al. (2019), Almaraz and Green (2024) and Berk et al. (2021). Overall, catastrophe theory remains a useful tool for modelling dynamic systems in ecology with valid mathematical backing, but one must be cautious not to apply it spuriously.

3 Stochastic Formulations

3.1 Stochastic Catastrophe Theory

In ecological systems, there will typically be an element of randomness, whereas the differential equations in Section 2 describe purely deterministic systems, making it difficult to apply catastrophe theory to real ecological processes. Stochastic catastrophe theory was developed by Loren Cobb and his colleagues (Cobb and Zacks, 1985), (Cobb and Watson, 1980), (Cobb, 1978) and extends catastrophe theory by including a term of idealised Brownian motion and building a framework for making statistical inference. Unfortunately, this framework was not used often until recently, in part due to problems with Cobb and Watson's code, which used poor numerical integration techniques and was sensitive to different starting values (van der Maas et al., 2003).

One alternative attempt to build a framework for statistical inference was GEMCAT (Oliva et al., 1987) and GEMCAT II (Lange et al., 2006), however both iterations of this method use the derivative of the potential function to fit the data, without discriminating between minima and maxima. This is flawed because maxima of the potential function corresponds to inaccessible states, and data being in these states should lead to high error and suggest the model is not well fitted (Wagenmakers et al., 2005b); Cobb's method avoids this issue by using a maximum likelihood approach to fit the parameters of the model.

The governing equation for the stochastic catastrophe model is the following stochastic differential equation:

$$dy = -\frac{\partial V(y;c)}{\partial y}dt + \sigma(y;c)dW_t,$$

where $\sigma^2(y;c)$ is known as the infinitesimal variance and W_t is the Weiner process, or idealised Brownian motion. This has discrete time approximation

$$\Delta y = -\frac{\partial V(y;c)}{\partial y}\Delta t + \epsilon_t \quad \text{where} \quad \epsilon_t \sim \mathcal{N}(0, \sigma(y;c)^2\Delta t).$$

Theorem 3.1 (Kolmogorov Forward Equation for Stochastic Processes (Soong, 1973, Chapter 7))**.** Let x obey the stochastic differential equation

$$dx = m(x;c)dt + \sigma(x;c)dW_t,$$

and define the time-dependent probability density function as

$$f_c(u,t) = \frac{\partial}{\partial u}\mathbb{P}(x(t,c) < u).$$

Then the probability density function for x obeys the *deterministic* partial differential equation

$$\frac{\partial f_c}{\partial t} = -\frac{\partial (m f_c)}{\partial u} + \frac{1}{2}\frac{\partial^2 (\sigma^2(y;c) f_c)}{\partial u^2}.$$

Analogously to deterministic catastrophe theory, if such a probability density exists, the system will evolve to a stationary density where $\partial f_c / \partial t = 0$. Applying Theorem 3.1, this stationary density will occur when

$$\frac{\partial}{\partial u}\left(f_c \frac{\partial V(y;c)}{\partial y} \right) + \frac{1}{2}\frac{\partial^2 (\sigma(y;c)^2 f_c)}{\partial u^2} = 0.$$

This can be solved with typical boundary conditions for a probability density function to give the stationary distribution $f_c^*(y)$ where

$$f_c^*(y) = A\mathrm{exp}\left(\int_{\infty}^{y} \frac{1}{\sigma^2(s;c)} \left(\frac{\partial}{\partial s} \left(2f(s;c) - \sigma^2(s;c)\right) \right) ds \right), \tag{2}$$

and A is a normalising constant. If the infinitesimal variance is constant, the random noise is called **additive** and $\sigma^2(y;c) = \epsilon$. Then (2) can be immediate solved to reveal

$$\log f_c^*(y) = \log A - \frac{2V(y;c)}{\epsilon},$$

and thus there is a one-to-one correspondence between the local maxima of f_c^* and the local minima of V, and they occur at the same values of y. This is unsurprising; since the local minima of V are the steady states which deterministic catastrophe theory would predict the system was in, the highest probability density occurs at these points. Similarly, the unstable maxima has the lowest probability density. The probability density can be used to assess the resilience of a solution, that is, whether stochastic perturbations is likely to change a stable state to an unstable one.

3.2 The Statistical Inference Framework

Once the stationary probability density function has been defined, it allows existing statistical inference frameworks to be used to fit models to data and to test the goodness of fit of a model quantitively. If the potential function and the infinitesimal variance function are both polynomials, then it is possible to derive maximum likelihood estimators from the data for the coefficients of the stochastic catastrophe model (for example, α and β for the stochastic cusp catastrophe model).

Catastrophe models of increasing orders are hierarchically nested: for example, the butterfly catastrophe model differs from the cusp catastrophe model by the addition of two extra control variables as parameters. This means likelihood ratio tests can be done to compare the fit of data to different stochastic catastrophe models. Unfortunately, in many applications, the stochastic cusp catastrophe model is used without considering other stochastic catastrophe models; this is probably due to its relative simplicity and the lack of equivalent R packages to `cusp` (Grasman et al., 2009) for fitting data to other models. Exceptions to this in ecology are Loehle (1989), which applies a butterfly catastrophe model to plant growth with the control variables of precipitation and three variables relating to livestock grazing, and Petraitis and Dudgeon (2015), which suggests a system of corals, seaweeds and algal turfs with three stable states might be a butterfly catastrophe; however neither apply statistical goodness-of-fit tests.

Information criterion approaches can also be done to compare catastrophic models to linear regression and logistic models. While the logistic curve does not have critical points with discontinuous behaviour like catastrophe models, it allows for arbitrarily rapid changes in the response variable and so is the closest non-catastrophic model to catastrophe models. Therefore, Hartelman (1997) suggests that, in order for the cusp catastrophe model to be used, the AIC and BIC should suggest that the cusp catastrophe density is a better fit than the logistic density, and Wagenmakers et al. (2005b) suggests a similar requirement using a Bayesian approach.

3.3 Transformation Invariant Stochastic Catastrophe Theory

If the infinitesimal variance is not constant, the random noise is called **multiplicative**. While additive noise is most commonly used in ecological models, multiplicative noise may be used in population models to model interaction between species and their environment (Spagnolo et al., 2004). In this case, Cobb's framework is less useful. We can rewrite (2) as

$$\frac{d}{dy}(\log f_c^*) = \frac{-1}{\sigma^2}\frac{\partial}{\partial y}(2V + \sigma^2).$$

The stationary points of f_c^* will occur at the roots of $\partial/\partial y(2V + \sigma^2)$; however due to the additional term depending on the infinitesimal variance, these may not be at the stationary points of V, meaning that the points with the highest probability density may not coincide with the steady states predicted. Critically, V and f_c^* may have a different numbers of stationary points. For example, for any polynomial potential, by selecting $\partial/\partial y(\sigma^2)$ to raise $\partial/\partial y(V)$ so all its local minima are above 0, it is possible to find a unimodal stationary probability distribution.

Additionally, the shapes of probability density functions are not invariant under non-linear transformations of the random variable, yet Cobb's method depends entirely on the shape of the probability density function. Non-linear transformations of the response variable may be necessary in experimental settings, for example if it is not possible to directly measure the true variable of interest or if the measurement scale of the response variable is arbitrary. Therefore, it is not sensible to consider the maxima of the stationary probability density function as a stochastic stable equilibrium state in settings with multiplicative noise or where the response variable will require nonlinear transformation (Wagenmakers et al., 2005a).

Instead, Wagenmakers et al. (2005a) proposes a modification Cobb's framework, allowing it to work in these settings. They defined the function

$$I(y) := f^*(y)\sigma(y)$$

which is invariant up to a normalising constant under nonlinear transformations in y, and suggested that statistical inference should be performed using $I(y)$ instead of $f^*(y)$. If $\sigma(y)$ is actually constant, then $I(y)$ is proportional to $f^*(y)$ so stochastic catastrophe theory can be seen as a special case of this framework. Kernel estimation or level crossing methods can be used to estimate $I(y)$ from data.

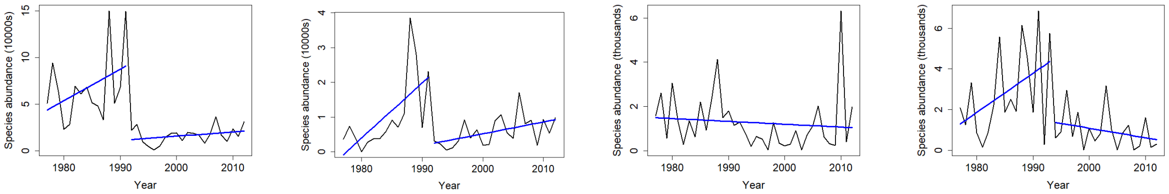
In Spagnolo et al. (2004), autocorrelated or "coloured" noise is used in models of interacting species; this is realistic to ecological settings, as one expects random environmental fluctuations to be correlated over short time frames, even if there is a regime shift. However, neither stochastic catastrophe framework allows for this to be modelled explicitly.

3.4 An Application to Wintering Waterfowl and Links to Changepoint Analysis

By using a stochastic cusp catastrophe model, Almaraz and Green (2024) show that the eruption of Mt. Pinatubo in 1991 caused a decline in the abundance and diversity of wintering waterfowl, which persisted even after the global climate returned to pre-eruption levels, caused by a shift in species densities to an alternative stable state. Demonstrating an ecosystem has undergone catastrophic behaviour, including hysteresis and abrupt shifts between stable states, has important conservation implications and is vital information in evaluating the conservation status of an ecosystem. The authors used 36 years of data (1978-2013) with two population size estimates taken each winter for ten different species of wintering waterfowl.

When looking at time series data which follows a catastrophe model, it is possible to view catastrophe points as changepoints; they are points where the structure of the data changes. In Almaraz and Green (2024), the authors used a variety of techniques such as Bayesian Dynamic Factor analysis and hidden Markov models to look for and demonstrate abrupt and long-lasting shifts in the trend of species density across time before applying the stochastic cusp catastrophe model. They found a shift to a regime with lower levels of wintering waterfowl in 1992; the magnitude of the shift varied between species, with the Common Teal, the Eurasian Wigeon, the Gadwall, the Shelduck and the Graylag Goose all clearly displaying a downwards trend in 1992. Some species followed an alternative trend, with a decline in 1992 followed by slow recovery.

To compare the effectiveness of a changepoint analysis to their approach, and to see if changepoint analysis could be used alongside catastrophe models, I used the Pruned Exact Linear Time (PELT) (Killick et al., 2012) algorithm to look for changes in the regression structure of the data. In order to ensure changes were long-lasting, I required that the minimum time period between changepoints was 5 years. PELT also requires there to be no missing data and expects time series data with equally spaced observations, which did not fit the structure of this data, as there were measurements in December and January for each winter. In order to use PELT, I found the mean estimated abundance for each winter and species; unfortunately, this reduced the amount of information available to the algorithm. In Figure 4, I plot the results for four species. For the Common Teal and Red-Breasted Prochard, the algorithm found a single changepoint in 1992; notably, Almaraz and Green (2024) did not find as strong a trend for the Red-Breasted Prochard. For the Gadwell, Common Pochard, Shoveler, European Wigeon and Pintail, the algorithm succesfully found a single changepoint in the 1990s, however it was later than 1992. However for some species, especially where there was a significant additional recovery period, the algorithm was ineffective; for example, no changepoints were found in the Shelduck, Mallard and Greylag Goose data.



(a) Common Teal (b) Red Brested Prochard (c) Shelduck (d) Gadwell

Figure 4: Fitting a piecewise linear regression structure to the abundance data of wintering waterfowl.

This suggests that changepoint analysis could be a useful tool to use alongside catastrophe analysis to find potential catastrophe points, in particular if changepoints methods are selected better to fit the data structure; unfortunately, there are fewer changepoint packages suitable for detecting changes in trend than changes in mean or variance. However, changepoint analysis cannot be used predictively or to assess causality, as it only uses a statistical model of the data, whereas catastrophe theory introduces a mechanistic model, allowing the possibility of predicting catastrophe points through early warning signals (Shortridge et al., 2024).

After demonstrating abrupt and long-lasting regime shifts, Almaraz and Green (2024) fitted the stochastic cusp catastrophe model to the data using additive noise, in order to test specifically whether the regime shifts between alternative stable states were linked to the disturbance caused by the Mt. Pinatubo eruption. They used information criterion approaches to demonstrate it fitted the data better than logistic or linear models, but did not consider alternative catastrophe models. The control variables were the extension of the flooded area in the Donata wetlands during winter and stratospheric aerosol optical depth, which is a measure of how much sunlight is blocked by particles in the stratosphere.

Another issue faced by Almaraz and Green (2024) was evaluating whether the alternative states were stable; this is a non-trivial problem in ecology, particularly global ecology. A common method in other applications is simply to apply small perturbations to the system and see whether it returns to the equilibrium, for example in El-Rifai et al. (1979), the response variable was the acidity of a membrane, and the authors tested whether the membrane returned to the equilibrium pH after they added substrate and thus whether whether the equilibrium was stable. Obviously, such an approach is impossible when the response variable is the population numbers of waterfowl across a large region. Instead, Almaraz and Green (2024) fitted a regime-dependent extension of the state-space Lokta-Volterra-Ricker model to evaluate the stability of the two regimes they found.

4 Rosenzewig-MacArthur Predator-Prey Models

Predator-prey models have been developed for a long time, starting with the well-known Lokta-Volterra model (Volterra, 1928). In this section, we will first introduce the Rosenzweig-MacArthur predator-prey model and examine its behaviour, before exploring two modern generalisations of this model; in particular, we will focus on how one can model increasingly realistic behaviour with predator-prey models. We will also briefly discuss the ecological and conservation implications.

4.1 The Canonical Rosenzewig-MacArthur Model

A deterministic Gause-style model is given by the pair of non-linear differential equations:

$$\frac{dN}{dt} = f(N)N - g(N)P, \tag{3}$$

$$\frac{dP}{dt} = eg(N)P - mP, \tag{4}$$

where $N \geq 0$ and $P \geq 0$ denote the population densities of prey and predator respectively. The growth rate of prey in the absence of predators is $f(N)$ and in the Rosenzewig-MacArthur model (Rosenzweig and MacArthur, 1963), there is logistic growth given by

$$f(N) = rN\left(1 - \frac{N}{K}\right).$$

The rate of prey consumption per predator is called the functional response and is given by $g(N)$; Holling (1965) derived a number of common choices with ecological backing. A common choice is the Holling type II response with Holling disk parameterisation (Jost et al., 1999) given by

$$g(N) = \frac{aNP}{1 + aqN}.$$

The parameters in both equations are ecologically derived; the parameters m, r, a, q and e are species dependent: they correspond to the predator's natural death rate, the prey's reproduction rate, the predator attacking rate, the predator's handling time for each prey caught, and the food conversion coefficient (the efficiency of the predator in converting food biomass into its biomass) respectively. In this section, we will assume these parameters are constants. Finally, the parameter K is known as the environmental carrying capacity; it is the maximum population of prey that the environment can support in the absence of predators; this will be our control parameter as it is may be changed via habitat destruction or expansion and shifting resource availability.

There are three equilibria: the saddle point extinction equilibria $(0, 0)$, the prey-only steady state $(K, 0)$, and a single coexistence equilibria $(x*, y*)$ found by the non-trivial solution to setting the right hand sides of Equations 3 and 4 to zero. Through analysing the stability of the coexistence equilibria, one find that there are two catastrophe points for the control variable K: $K_1 < K_2$. When $K < K_1$, the prey-only equilibria is globally asymptotically stable, so predators will go extinct from any initial population densities. As $K > K_1$, the coexistence equilibria becomes stable, meaning it can be possible for predators to invade the system if they are introduced to a prey-only environment.

When $K \geq K_2$, the coexistence equilibrium again becomes unstable. However, if the system was previously in the coexistence equilibria, the system will not move to a steady state equilibrium as it will be in the basin of attraction for a limit cycle; instead a supercritical Hopf bifurcation occurs (Figure 5). This effect has been empirically demonstrated to occur in a live predator-prey system with plankton and algae (Fussmann et al., 2000).

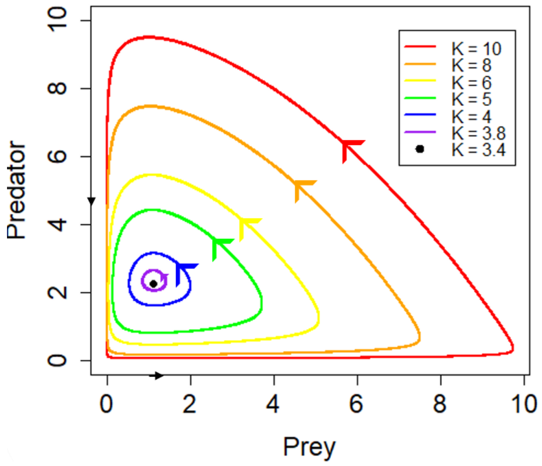


Figure 5: The limiting behaviour of the Rosenzewig-MacArthur model for different values of K and initial population $(0.5, 0.5)$. For $K_1 < K < K_2$, there is a stable coexistence equilibrium. For $K > K_2$, the system displays periodic behaviour with the amplitude of the period increasing as K increases, and also getting closer to the axis. Here $r = 1, a = 0.5, q = 1.2, e = 0.9, m = 0.3$.

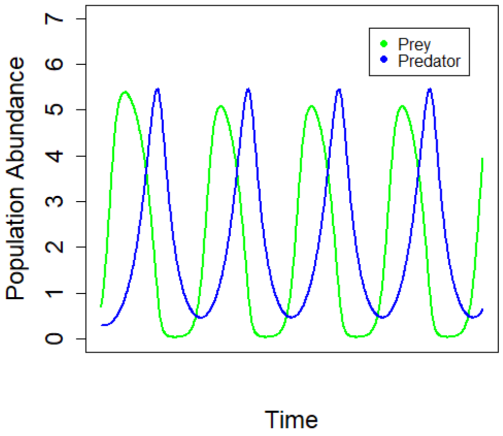


Figure 6: Behaviour of the system in the stable limit cycle solution over time, demonstrating oscillations in predator-prey abundance. Here $K = 6, r = 1, a = 0.5, q = 1.2, e = 0.9, m = 0.3$.

In the periodic solution, when the population of predators is low, the population of prey will increase, thus allowing the growth rate of predators to increase, driving down the population of prey; this occurs cyclically (see Figure 6). The amplitude of the oscillations is determined by K (see Figure 5); as the carrying capacity is increased, the maximum total population increases. However, by considering a stochastic framework, this leads to the paradox of enrichment (Rosenzweig, 1971). Because increasing the amplitude of oscillations leads to the cycle getting closer to the axis and the basin of attraction for the equilibria, random perturbations become more likely to shift the system into the basin of attraction of the equilibria, leading to extinction of one or both species.

4.2 The Allee Effect

The Allee effect is where individual success is dependent on the population size, and occurs in many social species. For example, with smaller population densities, there may be reproductive difficulties and group defence or group hunting may be less effective, meaning each individual is less successful. The Allee effect is called strong if there exists $\theta > 0$ such that the species growth rate is negative for population sizes below θ, so there is a critical survival threshold.

The strong Allee effect in prey has been well studied (Wang et al., 2010). It can be modelled by modifying the prey growth rate to be $f(N) = rN(N - \theta)(1 - N/K)$. Using a linear functional response, Rakshit and Raghunathan (2024) show that the strong Allee effect reduces the resilience of the limit cycle: as θ increases, the basin of attraction for the limit cycle decreases, while simultaneously the amplitude of the cycle oscillations increases. At a threshold (dependent on the other parameters), the limit cycle coincides with the boundary of the basin, leading to a global bifurcation and a regime shift to extinction of both predator and prey. As this is a global bifurcation, critical slowing down does not occur, and new early warning signals need to be developed to predict these regime shifts.

The Allee effect in predators is less well studied (Lu et al., 2024). One approach is to modify the functional response to also be dependent on P; for example Teixeira Alves and Hilker (2017) choose $g(N, P) = (\lambda + aP)N$ for $a, \lambda > 0$. This is logical when the driving factor behind the Allee effect is hunting cooperation, since the per-capita rate of prey consumption will increase as the predator population increases. In the case when the Allee effect is driven by reproduction, Sen et al. (2021) suggests modifying the food conversion rate to be $e\phi(P)$, where $\phi(P)$ is an increasing, de-accelerating function between 0 and 1.

Through analysing this model for three parametrisations of $\phi(P)$, Sen et al. (2021) find qualitatively similar behaviour occuring. Dependent on the parameters of $\phi(P)$, there are between zero and two possible coexistence equilibria, and if there are two coexistence equilibria, one will be stable and one a saddle-point. The addition of the saddle-point coexistence equilibria allows more complex behaviour than the canonical Rosenzewig-MacArthur model. In particular, if the carrying capacity K is increased, leading to the stable coexistence equilibria becoming unstable, unlike in the canonical model, both subcritical as well as supercritical Hopf bifurcations are possible. If a subcritical Hopf bifurcation occurs, this will eventually lead to the system moving into the basin of attraction for the prey-only equilibrium and predator extinction will eventually occur.

Overall, the Allee effect in either prey or predator has been shown to be a destabilising influence, increasing the likelihood of extinctions. However, population abundance inherently has an element of randomness, and so should be modelled with stochastic differential equations. Yu and Ma (2023) explore the setting of stochastic noise in a single species model with an Allee effect, finding that while stochastic noise can stabilise the system, multiplicative noise has a negative effect on population size.

4.3 Spatial Models

So far, we have not considered a spatial component to the models; this is acceptable for small, connected systems but inaccurate otherwise. There are generally two distinct approaches for spatial predator-prey model.

The most thorough approach for spatial predator-prey models is to consider the predator and prey functions to be dependent on spatial location $\mathbf{x}$ as well as time t, and write the governing equations as reaction-diffusion equations; that is, the model becomes:

$$\begin{aligned}\frac{\partial N}{\partial t} &= f(N)N - g(N)P + D_N \nabla^2 N,\\ \frac{\partial P}{\partial t} &= eg(N)P - mP + D_P \nabla^2 P,\end{aligned}$$

where D_P, D_N are matrices which determine the diffusion rates in each spatial direction for the prey and predator respectively. This approach is particularly useful for analysing spatial patterns, called Turing patterns, formed by the predator and prey populations (Owolabi and Jain, 2023).

However, many ecological approaches are simply concerned with overall population numbers of predator and prey, and in particular, predicting or explaining regime shifts. In this case, simpler models can be used. The **patch modelling** approach considers the environment as a set of disjoint patches, where each patch is small enough to ignore spatial effects and there is a dispersal rate for each species between patches. This is particularly valuable for modelling fragmented ecosystems; these may occur naturally, for example if a river divides an ecosystem, however humans are increasing environmental fragmentation through urbanisation and agricultural land use. Lu et al. (2024) explores a patchy extension of the Rosenzewig-MacArthur model with predator Allee effect, with the following model:

$$\begin{aligned}\frac{dN_i}{dt} &= f(N_i)N_i - g(N_i)P_i + (-1)^i d_N(s_N N_1 - N_2),\\ \frac{dP_i}{dt} &= e\phi(P_i)g(N_i)P_i - mP_i + (-1)^i d_P(s_P P_1 - P_2),\end{aligned}$$

where $i, j = 1, 2$ and $i \neq j$. The parameters $d_N, d_p \geq 0$ denote the rate of dispersion from the first patch to the second for the prey and predator respectively, and the parameters s_N and s_P measure the dispersal asymmetry between the two patches for both species. This formulation could be expanded for further patches by considering dispersal rates and the asymmetry for each pair of patches.

With $f(N)$ and $g(N)$ as in the previous section, and $\phi(P_i) = P_i/(b + P_i)$, where b can be considered as the intensity of the Allee effect, Lu et al. (2024) numerically analyse the model to determine there are eight possible steady states. In particular, two stable equilibriums are produced concurrently through saddle-node bifurcations, and they become stable states after subcritical Hopf bifurcations. Compared to the single patch system analysed by Sen et al. (2021), population dispersal leads to more coexistence equilibria and decreases the risk of predator extinction when control parameters are shifted.

Rakshit and Raghunathan (2024) also expanded the Rosenzewig-MacArthur model with strong Allee effects in prey by considering two patches, although they made the simplifying assumptions that predators and prey dispersed at the same rate ($d_N = d_P$) and the dispersal betwen patches was symmetric ($s_N = s_P = 1$). With these assumptions, they demonstrated that a two patch system increases resilience to extinction compared to a single patch system, particularly in situations where a species in one patch is facing extinction due to regime shift. From a conservation perspective, both Rakshit and Raghunathan (2024) and Lu et al. (2024) suggest that connecting fragmented patches through ecological corridors can reduce the risks of species extinction.

5 Discussion

We have discussed the uses and applications of catastrophe theory and bifurcation analysis in ecology, showing how to model discontinuous behaviour and hysteresis, as well as the criticism applications of catastrophe theory provoked for an over-reliance on qualitative methods. Stochastic catastrophe theory responded to this criticism by allowing quantitative goodness-of-fit tests to be applied and this work is still relevant, as seen in the recent application to wintering waterfowl. Transformation invariant stochastic catastrophe theory extends stochastic catastrophe theory, enabling the quantitative framework to be used more accurately in settings with multiplicative noise and where the response variable requires non-linear transformation; unfortunately, currently, all applications of stochastic catastrophe models in ecology assume additive noise. Future ecological studies using stochastic catastrophe theory should consider whether multiplicative noise would be a more accurate model and use the invariant function $I(y) = f^*(y)\sigma(y)$ instead of the density function for parameter estimation. Stochastic catastrophe theory could also be developed to allow the modelling of autocorrelated or “coloured” noise.

An important type of ecological model is the predator-prey model; we have explored modelling complex systems including spatial components and Allee effects in either species. Developing and analysing these models to remove simplifying assumptions and model more realistic behaviour is an active area of research; other recent adaptations include modelling the fear effect in prey and cannibalism in predators (Diz-Pita and Otero-Espinar, 2021). Research could also be done into systems with simultaneous Allee effects of different strengths in both predator and prey. Another area of research concerns modelling more than two interacting species in food webs or whole ecosystems (Northfield et al., 2017).

There is ample scope to apply stochastic catastrophe models of higher order than the cusp catastrophe, allowing systems to be modelled with more response or control variables. Often deterministic models of population dynamics are used in ecology, whereas stochastic models are more realistic and could offer insights into the probabilities of regime shifts; for example, a stochastic framework leads to the paradox of enrichment and Spagnolo et al. (2004) finds that noise can induce new spatiotemporal patterns. Stochastic population dynamics for a single species were also explored in Takimoto (2009) with the application of determining early warning signs for regime shifts in a population from low to high abundance for invading populations, however further research is needed on finding early warning signals for global bifurcations in predator prey systems (Rakshit and Raghunathan, 2024). In systems with abrupt regime shifts and multiple stable states, stochastic catastrophe models with two response variables could be used to model predator-prey systems, allowing further development of early warning signs.

Finally, if time series data is fitted to a stochastic catastrophe model, there are links to changepoint analysis, because abrupt shifts in a system's behaviour can be described as changepoints; research could be conducted to compare the results of changepoint analysis and stochastic catastrophe theory for different data structures. However, unlike catastrophe theory, changepoint analysis cannot be used predictively or to assess causality, as it doesn't use a mechanistic model.

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