While mathematics for its own sake is certainly exciting and beautiful, we should not forget that it is important in a wide range of fields. For example, you might be surprised by the variety of mathematical models and problems arising from the study of biology and ecology. Lord Robert May is a scientist who made important contributions to this field.

Robert May was born 1938 in Sydney. He studied mathematics and theoretical physics at Sydney University and his PhD thesis focused on superconductivity. In 1959 he left Australia for a post-doctoral position in the Division of Engineering and Applied Physics at Harvard University, before returning to the University of Sydney in 1962. He soon became interested in ecology, specifically animal population dynamics, and took up a Professorship in the Biology Department at Princeton in 1973. In 1988, May moved to Britain and became a Professor at Oxford University and a fellow of Merton College.

May studied population dynamics, the relationship between complexity and stability in natural communities, infectious diseases, and biodiversity. Especially through his application of mathematical techniques and background as theoretical physicist, he could contribute to major developments in population biology. He also was involved in the development of theoretical ecology.

Over the years May received numerous awards for his work. In 1996 he was knighted for services to Science. May was also Chief Scientific Adviser to the UK government from 1995 to 2000 and president of the Royal Society from 2000 to 2005.

Mathematics and Ecology

At this point you might wonder exactly which kind of mathematics was part of Robert May’s work. I am sure you know that many processes in nature can be described by mathematical models. In ecology, a simple example is the study of seasonally breeding populations, whose generations do not overlap.

A relationship between $X_t$, the size of the generation $t$, and $X_{t+1}$, the size of generation $t + 1$, may be expressed as $X_{t+1} = F(X_t)$, where $F(X)$ is some function. Quite often a smooth function is chosen. This is then called a first order difference equation. Studies of the dynamical properties of these models usually involve the observation of stability of equilibrium solutions with respect to small disturbances. May published multiple texts in this field, in particular the article "Simple mathematical models with very complicated dynamics" gives a nice summary of results.

One such function, studied in detail and popularized by May, is the so called Logistic map

$$X_{t+1} = rX_t(1 - X_t),$$

where $r$ is some parameter with $0 < r \leq 4$, and $X_t \in [0, 1]$. Then $F(X) = rX(1 - X)$ only takes values inside $[0, 1]$. Now $F$ is an increasing function in $(0, 0.5)$ and a decreasing function in $(0.5, 1)$. So for $X_t \in (0, 0.5)$ a larger value of $X_t$ corresponds to a larger size of the next generation, say due to reproduction. Note that the value of $X_{t+1}$ is proportional to $X_t$. Further, if $X_t \in (0.5, 1)$, then $X_t$ increases while $X_{t+1}$ decreases, say due to starvation.

As the parameter $r$ increases, the dynamic properties of $F$ change drastically. It is a good example to show how complex behaviour arises even from very simple models. Here I want to present some interesting properties of the logistic map.
Fixed Points

An equilibrium value \( X^* \) of \( F \), a so called fixed point, satisfies \( F(X^*) = X^* \). Then each generation has the same size. In the case of the logistic map, there is a fixed point at \( 0 \) and the fixed point in \((0, 1)\) is given by \( X^* = (r - 1)/r \), provided that \( r > 1 \).

Now we might be interested in the behaviour of the model if the starting population has a size close to (but not equal to) this fixed point, that is, we consider small disturbances about \( F \) of \( X^* \), the value of \( X_t \) will tend to \( X^* \) as \( t \to \infty \). (This can be shown easily using techniques covered in first year Analysis at university). On the other hand, if \( |F'(X^*)| > 1 \) no such behaviour is guaranteed and the fixed point is unstable.

Now note that \( F'(X^*) = r(1 - 2X^*) = 2 - r \) since \( X^* = (r - 1)/r \). So we have a stable fixed point \( X^* \) if and only if \( 1 < r < 3 \). Further consider the fixed point \( 0 \) and suppose \( r < 1 \). Then \( X_{t+1} = rX_t(1 - X_t) < rX_t = r^2X_{t-1}(1 - X_{t-1}) < r^2X_{t-1} < \cdots < r^{t+1}X_0 \) and \( X_t \to 0 \) as \( t \to \infty \) for all \( X_0 \). Hence \( 0 \) is a stable fixed point for \( r < 1 \).

Cycles

We already noted above that for \( r > 3 \) the fixed point \( X^* \) is unstable. We can observe very interesting dynamical properties as \( r \) increases further.

Define \( F^{(k)}(X) = F(F(...(F(X))...)) \) to be the function obtained by applying \( F \) \( k \)-times to \( X \). \( X^*_k \) gives a cycle of length or period \( k \) if \( F^{(k)}(X^*_k) = X^*_k \), and further \( F^{(j)}(X^*_k) \neq X^*_k \) for \( j \in \{1, \ldots, k - 1\} \). We can find such cycles by looking for fixed points of \( F^{(k)}(X^*_k) \). If we are given some cycle of period \( k \), \( X^*_k \), then we can also determine its stability by considering the derivative of \( F^{(k)} \). As before, we have stability for an absolute value less than \( 1 \) at \( X^*_k \). So, as \( r \) increases, any cycle that was originally stable will become unstable.

The logistic map and many other similar maps have a very interesting property: Once a cycle of period \( 2^k \) becomes unstable, two new stable cycles of period \( 2^{k+1} \) will appear. As \( r \) increases further, these cycles become unstable, and four stable cycles of period \( 2^{k+2} \) appear, and so on. Such a sequence of doublings is also known as period doubling cascade. In a bifurcation diagram, shown on the last page, we can easily observe this phenomenon. The diagram shows the stable cycles of the logistic map for given values of \( r \). However, it should be noted that it also includes cycles of lengths which are not powers of \( 2 \).

Chaos

So far, we have only discussed cycles of period \( 2^k \), but there may also be cycles with an odd period. In particular, the first 3-cycle of the logistic map appears when \( r \approx 3.8284 \).

Tien-Yien Li and James Yorke showed a very surprising result: Say \( f \) is a continuous function mapping from an interval \([a, b]\) back to \([a, b]\). If \( f \) has a 3-cycle it also has a cycle of period \( n \) for any positive integer \( n \), and further, there are initial points for which we do not even have asymptotically periodic behaviour. For such initial points the behaviour seems to be entirely chaotic. One example of such a function is our logistic map \( F \).

For the logistic map May further noted that there will always be an uncountable number of cycles of integral period and an uncountable number of aperiodic solutions for \( r \) greater or equal to \( 3.8284 \), the value at which the first 3-cycle occurs. Interestingly, given a specific \( r \), there will also always be a unique stable cycle attracting almost all initial points. You might ask what this means in more precise terms. Say the initial point of this unique cycle is \( Y_0 \) and \( Y_t = F^{(t)}(Y_0) \) is the size of generation \( t \). \( Y_{t+k} = Y_t \), where \( k \) is the period of the cycle. Then for almost any initial point \( X_0 \), \( X_t \) will be arbitrarily close to \( Y_t \) for sufficiently large \( t \), though there are also uncountably many points for which this is not true.
We see that even simple functions like \( F(X) = rX(1 - X) \) have interesting properties. May summarized it like this in his article "Simple mathematical models with very complicated dynamics":

"... the very simplest nonlinear difference equations can possess an extraordinarily rich spectrum of dynamical behaviour, from stable points, through cascades of stable cycles, to a regime in which the behaviour (although fully deterministic) is in many respects "chaotic", or indistinguishable from the sample function of a random process."

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\text{References} \\
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