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Spruce Budworm

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Abstract

This Paper will examine the interaction between the spruce budworm and the balsam fir forests in eastern Canada. As outlined in their 1978 paper, Ludwig, Jones, and Holling take into consideration the intrinsic growth rate of the budworm, with carrying capacity and predation affecting the population growth.

1. Introduction

The spruce budworm is a very destructive native insect in the northern spruce and fir forests of the Eastern United States and Canada. Outbreaks of the spruce budworm are a natural part of the cycle of events associated with the maturing of the balsam fir. While the budworm feeds on a variety of plant species, the balsam fir is the hardest hit. Predators tend to keep the budworm population in check. However, periodic outbreaks of budworm populations can effectively wipe out an entire forest. The catastrophe theory of budworm outbreaks predicts that major infestations occur as the result of a cusp-catastrophe event. In this situation populations jump from negligible to epidemic levels.

In 1978 D. Ludwig, D.D. Jones, and C.S. Holling performed a qualitative analysis of the spruce budworm and its affects on the balsam fir forests. The article 'Qualitative Analysis of Insect Outbreak Systems' appeared in The Journal of Animal Ecology.

2. Insect Outbreak Model

Ludwig et al. began with the assumption that the budworm population N is governed by the logistic equation

$$\frac{dN}{dt} = r_B N \left(1 - \frac{N}{K_B}\right) \tag{1}$$

Where r_B is the birth rate of the budworm and K_B is the carrying capacity of the forest. The carrying capacity is related to the density of the foliage.

The growth of the budworm population is negatively affected by predation, therefore the equation governing the population becomes

$$\frac{dN}{dt} = r_B N \left(1 - \frac{N}{K_B}\right) - p(N) \tag{2}$$

The rate of predation $p(N)$ depends on the budworm population. When budworm populations N are high predators are very active. Predators are birds. For small population densities predators tend to seek food elsewhere.

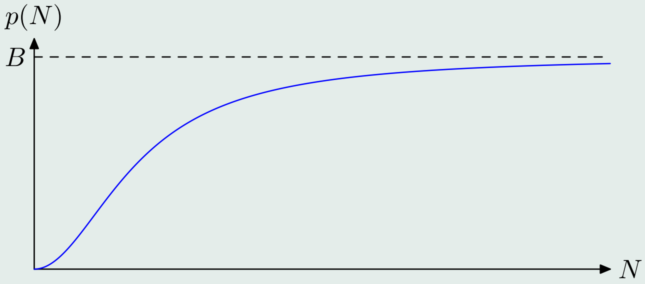

Figure 1: Graph of $(BN^2)/(A^2+N^2)$.

Biological studies show that when budworm populations are low, the rate at which predators eat the budworms is minimal but as budworm populations increase, the rate at which predators eat the budworms slowly increases until a critical value is reached. Beyond this critical value predation is close to its saturation point. Ludwig needed a function that would exhibit the behavior of predation and came up with

$$p(N) = \frac{BN^2}{A^2+N^2} \tag{3}$$

where A and B are positive constants. As seen in Figure 1 this function at N real close to zero predation is minimal. As $N \to \infty$ predation grows until it reaches saturation.

Ludwig then concludes that the budworm population is goverened by

$$\frac{dN}{dt} = r_B N\left(1-\frac{N}{K_B}\right) - \frac{BN^2}{A^2+N^2} \tag{4}$$

To further examine this saturation effect we will look at $p(N)$ and simply use the first derivative test to see where the function is increasing or decreasing.

$$p'(N) = \frac{(A^2 + N^2)(2BN) - (BN^2)(2N)}{(A^2 + N^2)^2} \tag{5}$$

Simplify the numerator.

$$p'(N) = \frac{2BN((A^2 + N^2) - N^2)}{(A^2 + N^2)^2} \tag{6}$$

This gives us

$$p'(N) = \frac{2A^2BN}{(A^2 + N^2)^2}. \tag{7}$$

Because A and B are assumed positive, our function $p(N)$ is always increasing.

Next, use the second derivative test to check for concavity and to find the point of inflection.

$$p''(N) = \frac{(A^2 + N^2)^2 2A^2B - 2A^2BN2(A^2 + N^2)2N}{(A^2 + N^2)^4} \tag{8}$$

Combine like terms and factor the numerator.

$$p''(N) = \frac{2A^2B(A^2 + N^2)((A^2 + N^2) - 4N^2}{(A^2 + N^2)^4)} \tag{9}$$

This simplifies to

$$p''(N) = \frac{2A^2B(A^2 - 3N^2)}{(A^2 + N^2)^3}. \tag{10}$$

To find the roots of this function set $A^2 - 3N^2 = 0$. This will give us the inflection point of $p(N)$. This critical value is the point beyond which the rate predation is changing with respect to N is slowing.

$$A^2 - 3N^2 = 0 \tag{11}$$

$$3N^2 = A^2 \tag{12}$$

$$N^2 = \frac{1}{3}A^2 \tag{13}$$

$$N = \pm\sqrt{\frac{1}{3}A^2} \tag{14}$$

Populations are always positive so

$$N = \sqrt{\frac{1}{3}}A \tag{15}$$

Our critical value for N_c is $\sqrt{\frac{A}{3}}$. As seen in Figure 2 N_c is an approximate threshold value and acts as a switch. For values below N_c predation is somewhat slow and for values above N_c predation becomes much greater. This rate continues to increase until there are so many budworms that birds have their fill begin to search for food elsewhere.

Now let's consider the equation that Ludwig suggests governs the budworm population.

$$\frac{dN}{dt} = r_B N\left(1 - \frac{N}{K_B}\right) - \frac{BN^2}{A^2 + N^2} \tag{16}$$

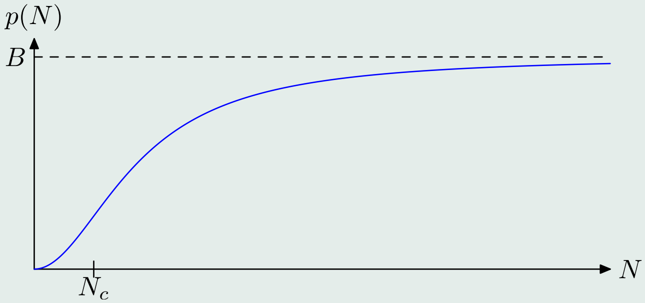

Figure 2: The population value N_c is an approximate threshold value. for $N < N_c$ predation is small, while for $N > N_c$ it is switched on.

This equation has four parameters, r_B, K_B, B and A. The parameters A and K_B have the same dimensions as N (budworms), r_B has dimension time^{-1}, and B has the dimensions of budworms per unit time.

Before analyzing the model we should express it in nondimensional terms. By scaling we no longer have to concern ourselves with units and it greatly simplifies the process. We introduce nondimensional quantities by

$$u = \frac{N}{A}, \; r = \frac{Ar_B}{B}, \; q = \frac{K_B}{A}, \; \tau = \frac{Bt}{A} \tag{17}$$

Let's note here that

$$\frac{dN}{dt} = \frac{dN}{du} \cdot \frac{du}{d\tau} \cdot \frac{d\tau}{dt} = A \cdot \frac{du}{d\tau} \cdot \frac{B}{A}. \tag{18}$$

Therefore,

$$\frac{dN}{dt} = B\frac{du}{d\tau}. \tag{19}$$

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Substituting $N = uA$ and $dN/dt = B du/d\tau$ in (16) gives us

$$B\frac{du}{d\tau} = r_B uA\left(1 - \frac{uA}{K_B}\right) - \frac{Bu^2A^2}{A^2 + u^2A^2}. \tag{20}$$

Dividing through by B gives us

$$\frac{du}{d\tau} = \frac{r_B uA}{B}\left(1 - \frac{u}{K_B/A}\right) - \frac{u^2}{1+u^2}. \tag{21}$$

And finally substituting $q = K_B/A$ and $r = Ar_B/B$ in (21) gives us

$$\frac{du}{d\tau} = ru\left(1 - \frac{u}{q}\right) - \frac{u^2}{1+u^2}. \tag{22}$$

Now our differential equation has only two parameters r and q which are just numbers and u is also just a number. In order to further analyze this model we must find the steady states, or equilibrium points of this equation. We will do this by setting $du/d\tau = 0$ in (22).

$$0 = ru\left(1 - \frac{u}{q}\right) - \frac{u^2}{1+u^2} \tag{23}$$

It is easily seen that $u = 0$ is one solution. The other solutions must satisfy

$$r\left(1 - \frac{u}{q}\right) = \frac{u}{1+u^2} \tag{24}$$

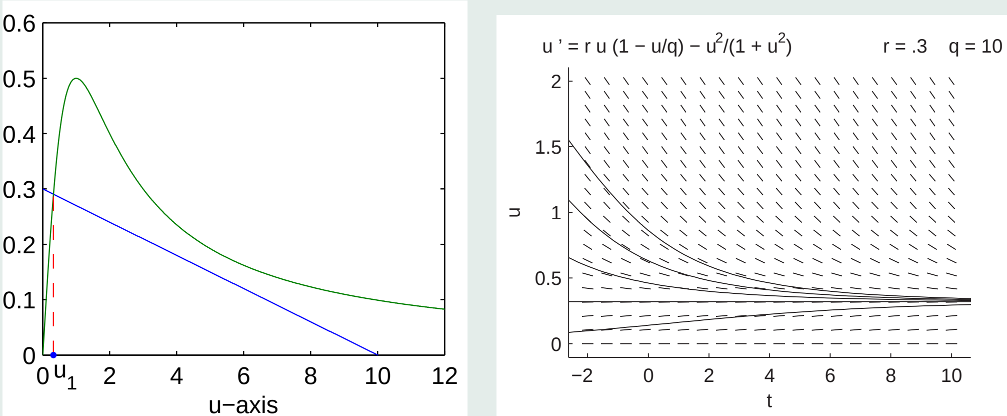

Figure 3: There is a stable equilibrium point at u_1.

3. Steady States

In order to determine the existence of solutions of (24) we will simply graph the left hand side which is a line and graph the function on the right. Where the graphs intersect are the equilibrium points. After performing this operation it is obvious that for a certain fixed q we can have one, two, or three equilibrium points.

Figure 3 shows that for a fixed q and a sufficiently small r there is one steady state solution at u_1. A **dfield** graph is utilized to show that u_1 is a stable equilibrium point.

Figure 4 shows that as r increases there is a point of tangency at u_2. In **dfield** note that u_2 is a semi stable equilibrium point. This is a point of bifurcation, the

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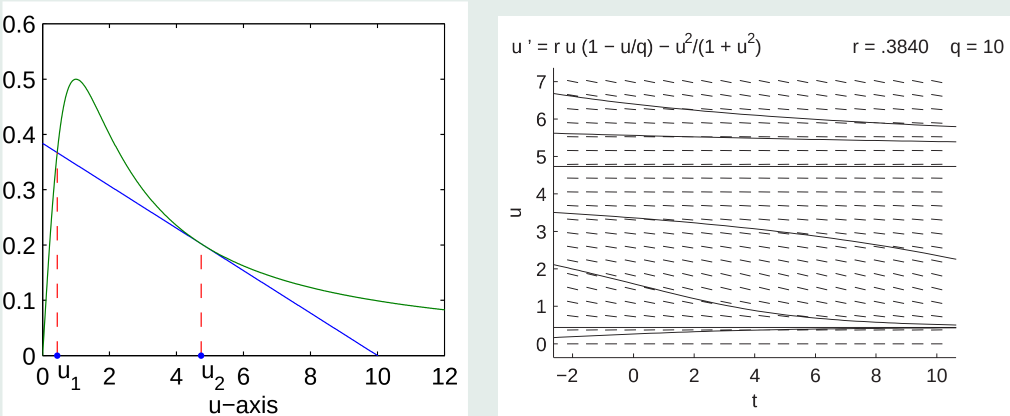

Figure 4: As r increases we have a semi stable equilibrium point at u_2 and a stale equilibrium point at u_1

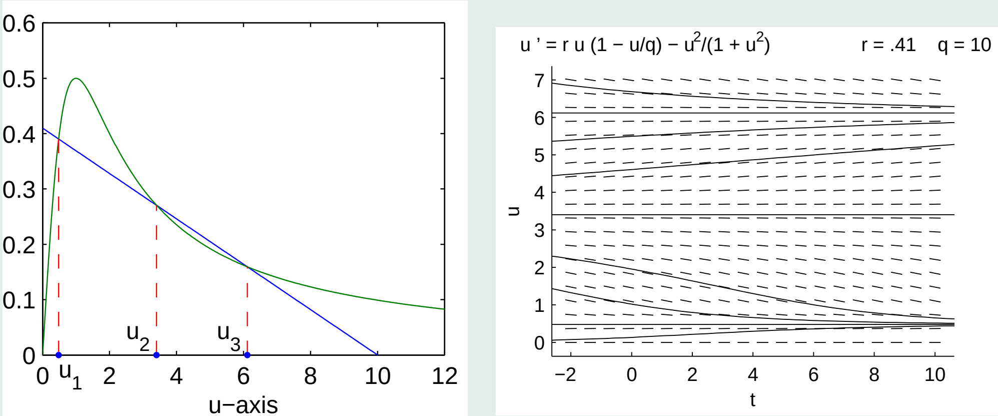

Figure 5: Stable equilibrium point at u_1, unstable equilibrium point at u_2, and a stable equilibrium point at u_3.

significance of which we will discuss later.

In Figure 5 we increase r further and have three steady state solutions. Once again we use **dfield** to show that u_2 is an unstable equilibrium point while u_1 and u_3 are stable.

In Figure 6 we continue to increase r and see that u_1 and u_2 are moving closer together. When these two points coalesce into one we will have another bifurcation.

In Figure 7 we see that u_1 and u_2 have become a single point of tangency. As seen in the **dfield** graph this is a semi stable equilibrium point.

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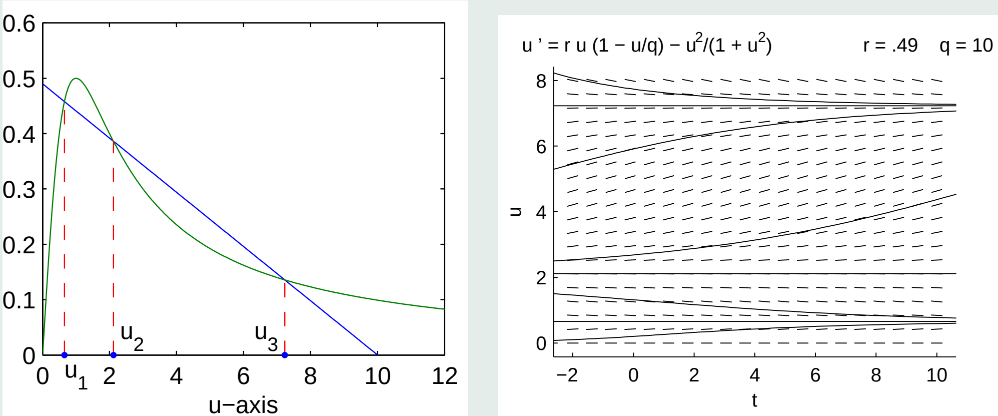

Figure 6: As r increases u_1 and u_2 move closer together.

4. Bifurcation

At this time it is obligatory to explain the significance the bifurcations that occur in this model. Creating a graph in rq-space will enable us to see with much more clarity the behavior of the budworm population as it rises and falls. We will see in this section this model exhibits a hysteresis effect. We will also witness a cusp catastrophe. Figures 4 and 7 show that points of tangency happen when

$$r\left(1-\frac{u}{q}\right)=\frac{u}{1+u^2}, \tag{25}$$

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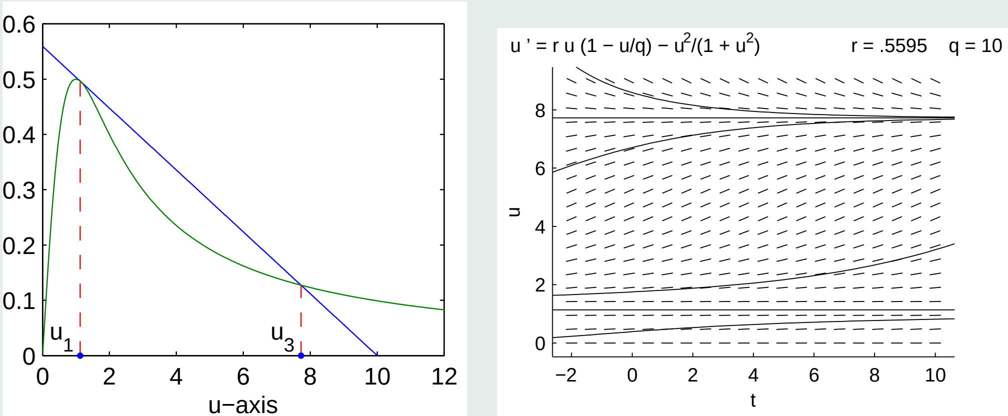

Figure 7: Increasing r u_1 and u_2 have coalesced into one semi stable equilibrium point.

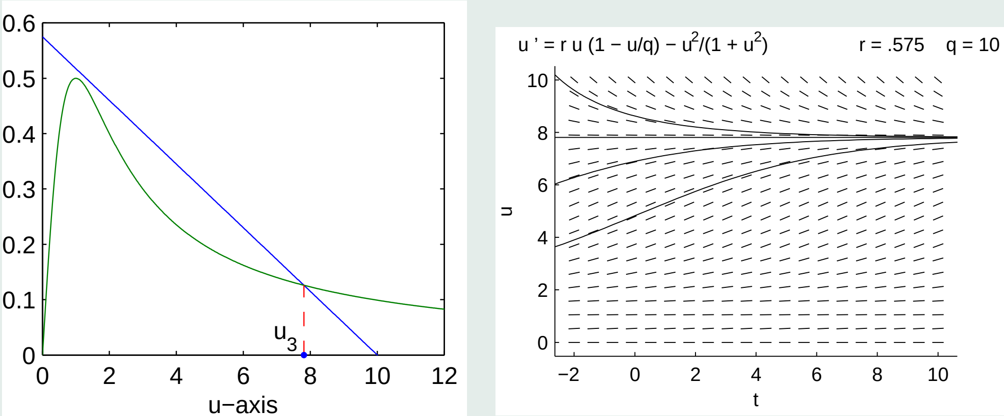

Figure 8: One stable equilibrium point at u_3.

and because the tangent lines at these points must have the same slope

$$\frac{d}{du}\left\{r\left(1-\frac{u}{q}\right)\right\}=\frac{d}{du}\left\{\frac{u}{1+u^2}\right\}. \tag{26}$$

In order to define parametrically, in terms of u, the bifurcation curve in the rq-space we must first perform the differentiation of (26). rewriting (26) gives us,

$$\frac{d}{du}\left\{r-\frac{r}{q}\right\}=\frac{d}{du}\left\{\frac{u}{1+u^2}\right\} \tag{27}$$

Differentiating both the left and right hand side gives

$$-\frac{r}{q}=\frac{(1+u^2)-u(2u)}{(1+u^2)^2}. \tag{28}$$

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Combining like terms in the numerator gives

$$-\frac{r}{q} = \frac{1-u^2}{(1+u^2)^2}, \tag{29}$$

and multiplying by q yields the result

$$r = q\frac{u^2-1}{(1+u^2)^2}. \tag{30}$$

Now substituting this result back into equation (25)

$$q\frac{u^2-1}{(1+u^2)^2}\left(1-\frac{u}{q}\right) = \frac{u}{1+u^2} \tag{31}$$

Distributing q and multiplying through by $(1+u^2)^2$ gives

$$(u^2-1)(q-u) = u(1+u^2). \tag{32}$$

Performing the multiplication on the left and distributing the right,

$$u^2q - u^3 - q + u = u + u^3. \tag{33}$$

Combining like terms,

$$(u^2-1)q = 2u^3. \tag{34}$$

And finally dividing by (u^2-1) shows us that

$$q = \frac{2u^3}{u^2-1}. \tag{35}$$

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Substituting q into (30) gives us

$$r = \frac{2u^3}{u^2-1} \cdot \frac{u^2-1}{(1+u^2)^2}. \tag{36}$$

The (u^2-1) terms cancel leaving

$$r = \frac{2u^3}{(1+u^2)^2}. \tag{37}$$

This gives us a graph in rq-space. See Figure 8. In figure 10 we see two perspectives of the behavior of the budworm population as r increases. What we see here is a hysteresis effect as we move along the path $ABCD$. In the region that lies between the points A and B there is one stable equilibrium point. This is exactly the behavior produced by our numerical solver in figure 3. As r increases to B we have a second semi stable equilibrium point. This is exactly the behavior produced by our numerical solver in figure 4. Further increasing r to the region that lies between the points B and C there are three equilibrium points, this analysis is supported by the graphs in Figure 5. When the r value reaches C we once again see two equilibrium points, this is confirmed by the graphs in figure 6. In the region between C and D we once again see one equilibrium point, we see this very behavior in Figure 7.

The interpretation of these graphs are very important. We are told that when budworm populations reach a certain level a huge population explosion occurs. Once again following the path $ABCCD$ we see this huge jump. The affects of this jump are very hard to reverse. Following the path $DCBBA$ we see that the distance traveled from D to B is much longer than the path from A to C. This

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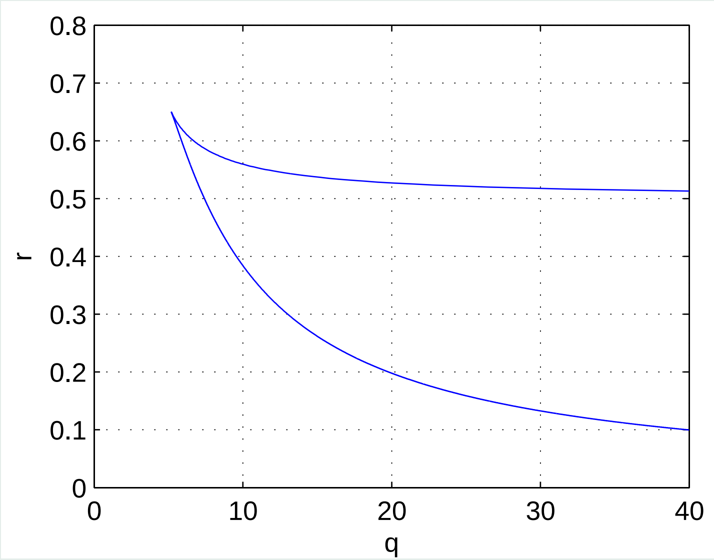

Figure 9: Graph of rq-space.

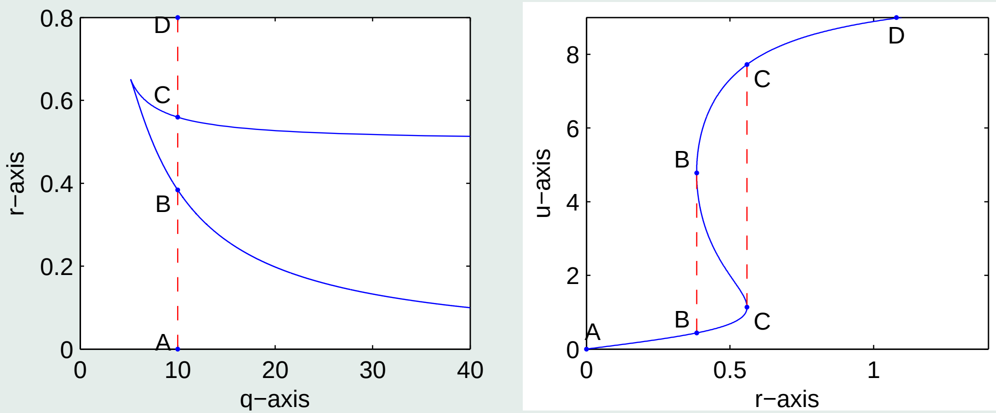

Figure 10: Path of r in rq-space.

means that it takes much longer for budworm populations to recede from high levels than it takes for them to reach them.

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