Adaptive Dynamics in the Coral Reefs

In the tropical rain forests or the coral reefs there is a huge diversity of species, and even more species are living in certain places than the environment can keep. A lot of hypotheses were born to explain this pattern at the coral reefs. [1]

One of the first hypotheses was the *Equilibrium hypothesis*, arguing that the species specialise themselves as more as they can adapt to the environment. Nevertheless, the corals do not seem to have been specialised to the degree as required to maintain the observed high diversities at equilibrium. A sharp competition can evolve amongst them. Actually, *the Nonequilibrium hypothesis* is accepted subsequent to Hutchinson's *gradual change hypothesis* as it has been suggested. He noticed a lot of phytoplankton species could coexist despite of the little food (nutriment). This hypothesis is valid only for phytoplankton. In case of the forests, field, and in the coral reefs the *intermediate disturbance hypotheses* is valid.

The competitive exclusion is prevented by *frequent disturbances*. In the coral reef there is a very strong light gradient, which in these light dependent communities allows a potential interaction between growth rate and disturbance.[4]

The diversity of the coral species from 5 m increases reaching 10-20 m and then decreases. This diversity pattern of low diversity near the surface and highest diversity at intermediate depths cannot be explained by any simple physical gradient. Oxygen, temperature, and salinity do not vary sufficiently with depth to be ecologically significant and light decreases exponential. The coral are light dependent because they are in symbiosis with phytoplankton.[5]

The basis assumption of the nonequilibrium paradigm is that competition (for relevant resources such as space, light, plankton, etc.) is intense and if competitive interactions are allowed to proceed to their conclusion, they will usually result in the elimination of most species and dominance by one or few, with an associated reduction in diversity. The factors preventing or slowing this process of the competitive exclusion by slowing the growth rates will make a higher diversity. [7] The fast growing corals cannot allocate so much energy in defence, so they are rather damage by waves (storms, hurricanes) and low tide. Fast growing corals branch and slow growing corals are smaller and massive. (Fig. 1)

Diversity at crest is low where disturbances are so frequent or intense causing the most species cannot survive, and while the lowest under beneath due to competitive displacement disturbances are infrequent.

Fig. 1. Two exemplars of the corals' life strategy: at left there is a fast growing and branching *Acropora* species, at right there is a slow growing and massive *Pavona* species. Both of them is from Red Sea.

Model

The model hereto presented was the target of my examination wherein the conditions of the coexistence and possible way of the evolution having led to this kind of coexistence.

The fast growing corals are the fluctuation dependent strategy and the slow growing coral species are the fluctuation independent strategy. There is a sharp competition between the two strategies, because they deplete the same resource.

Annual growth of the two strategies [6]:

$$N_{(t+1)} = l * N_{(t)} \tag{1}$$

The annual growth rate of the fluctuation dependent (2) and independent strategy (3):

$$\ln l_{1(t)} = e_{(t)} - a(N_{(t)} - K_1) - b(N_{(t)} - K_1)^2 \tag{2}$$

$$\ln l_{2(t)} = -c(N_{(t)} - K_2) \tag{3}$$

$N_{(t)}$ sum of abundance of the two strategies, K_1, K_2 equilibrium densities of strategies 1 and 2 in a stable environment, l annual growth rate, $e_{(t)}$ is an environment fluctuating parameter, which has zero mean $(\overline{e_{(t)}} = 0)$, a,b,c are positive constants. In the two function of the growth rates it is used sum of abundance, because the two strategies are depleting the same resource.

In stable environment two strategies are not able to coexist, because this two strategies exploit a single limiting resource. If $K_1 \rangle K_2$ strategies 1 excludes strategies 2, while if $K_1 \langle K_2$ then strategies 2 excludes strategies 1.

The long-term behaviour of the strategies is determined by the average log growth rates:

$$\overline{\ln l_{1(t)}} = \overline{e_{(t)}} - a(\overline{N} - K_1) - \overline{b(N - K_1)^2} = -a(\overline{N} - K_1) - b(\overline{N} - K_1)^2 - \frac{1}{2} bV(N) \tag{4}$$

$$\overline{\ln l_{2(t)}} = -c(\overline{N} - K_2) \tag{5}$$

where $V(N) = 2\overline{(N - \overline{N})^2}$ is the variance of density. Startegy 2, wich is not directly influenced by environmetal fluctuation in contrast it is affected through density dependence; since log growth rate of strategy 2 is linear function of density, its average is altered only by a change in the average density.

The two strategies are able to coexist in fluctuating environment if: $\overline{N}_1 \langle K_2 \langle K_1$.

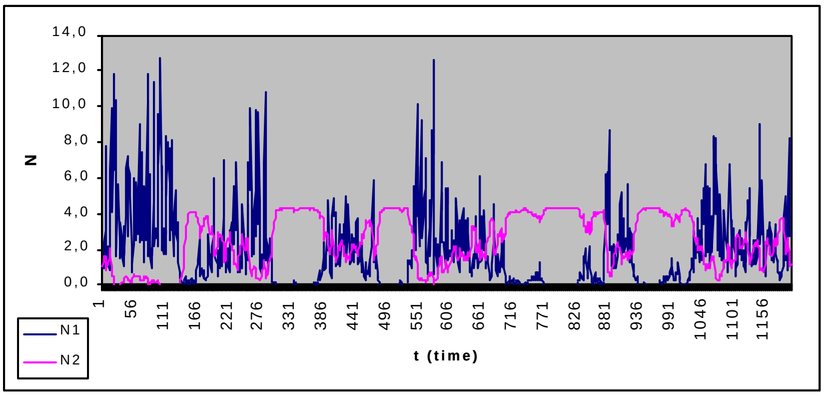

Fig. 2. The volume of strategies is (N) as a function of time (t). N_1: fluctuation dependent strategy, N_2: fluctuation independent strategy. (Initial parameters of value: N_1= 1,0; N_2=1,0; K_1= 4,5; K_2= 4,1; a,c=0,1; b=0,01; -1<e<1)

In nature there are many transitional life forms, not only two strategies. I considered a model in which there is a continuous scale of strategies between the extremes of the previous model. The growth rate depends on the strategy parameter x:

$$\ln l_x(t) = x * x(t) - a(x) * (N(t) - K(x)) - b(x) * (N(t) - K(x))^2 \tag{6}$$

Fluctuation independent strategy: x =0; $\alpha(0)$ = c; $\beta(0)$ = 0; K(0) = K_2.
Fluctuation dependent strategy: x = 1; $\alpha(1)$ = a; $\beta(1)$ = b; K(1) = K_1.

After the numerical analysis of the equations, the plot shows the outcome of simulations started with two different strategies, X1 and X2 present. (Fig. 3) Green dots denote the strategy combinations when the two strategies coexist for long time. In case of blue dots, strategy X1 dies out and strategy X2 wins. Red dots denote the opposite outcome when X1 wins over X2. The main diagonal is the border-line between red and blue: When the two strategies are the same, there are performing equally. Beyond this diagonal, as we can see, the strategies have to be markedly different to be able to coexist. This is something analogous to the niche segregation of the equilibrium theory.

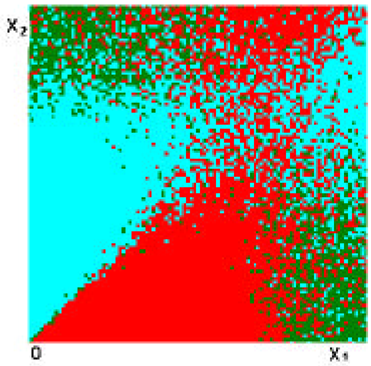

Fig. 3. The competition of two identical strategies: the green colour is indicating the coexistence of the two species. The colour red is indicating the extinction of x_1 and colour blue of the x_2. (Initial parameters of value: N_1= 1,0; N_2=1,0; K_1= 4,5; K_2= 4,1; a,c=0,1; b=0,01; -1<e<1; generation=50 000).

Dynamics of Adaptation

The adaptive dynamics is a mathematical method which connect ecological processes with evolutionary. The adaptive dynamics invasion function of a particular ecological system defines a pairwise invisibility plot (PIP) for resident and mutant strategies. The environment deteriorates with as the population increases, so the population grows reaching the equilibrium density. In this point the growth rate become zero. A new mutant strategy emerges from the equilibrium population of residents. The mutant is rare and the environment determined by the residents. When the invasion function[1] is positive for a particular pair of strategies, the invading mutant may replace the resident. Intersections of the invasion function's zero contour line with 45-degree line it is called singular strategy.

The singular strategy of the PIP has four properties. [2,3] 1. Evolutionary stable strategy: an initially rare mutant cannot invade the resident, so no further evolutionary change is possible. In the PIP the vertical line through the singular strategy lies entirely within a region marked "-" 2. Convergence stable strategy: a mutant can invade the resident strategy, which is closer to the singular strategy. It means that in the PIP there is a "+" region above the diagonal at the left, and below the diagonal on the right of the singular strategy. 3. Invasive ability: a singular strategy can spread in other population when itself it is initially rare. In the PIP the horizontal line through the singular strategy lies entirely in a region marked "+". 4. Mutual invading: if two population: a mutant and resident can mutually invade each other, then monomorphic population can become dimorphic. In the PIP the other diagonal, which is perpendicular to the main diagonal, lies entirely in a "+" region.

The singular strategy is called branching point when it is convergence stable but not evolutionary stable. After the evolutionary branching the two strategies become progressively more distinct.

[1] the logarithm of growth rate in this case

In the examined model there were found evolutionary and convergence stable singular strategy and evolutionary and convergence instable strategy. (Fig. 4)

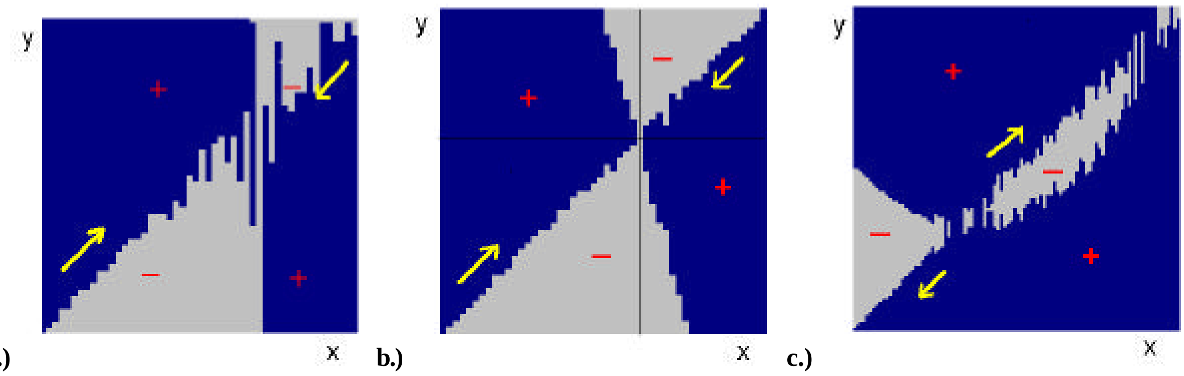

Fig. 4. This pairwise invasibility plots are the results of the numerical analysis of the model. The blue colour is indicating the case when mutant strategy can invade the resident strategy. The grey colour is the case when the mutant strategy cannot invade the resident strategy. The lines show the evolutionary. a.) in case if the alteration of the K_1 equilibrium density to K_2 was linear. It cannot be defined the properties of the singular strategy. b.) the intermediate strategy has advantage. Evolutionary and convergence stable singular strategy c.) the intermediate strategy has disadvantage. Evolutionary and convergence instable strategy.

Conclusions

1. In a stable environment the competitive dominant species exclude the competitive subordinate species, which is associated with reduction in diversity.
2. In fluctuating environment if two species exploit a single limiting resource, they are able to coexist if they follow completely different strategies.
3. The two strategies cannot have monophyletic origin because there was not branching point in the PIPs.

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