Appendix 3.4

The following material is Appendix 3.4 for Chapter 3 of: Fowler, C.W. 2009. Systemic Management: Sustainable Human Interactions with Ecosystems and the Biosphere. Oxford University Press

1 Selective extinction, speciation, and evolution for two categories

As in Appendix 3.3 we can consider N_1 and N_2 to be the number of species in two categories. The rate at which species evolve from the first category to the second is p_1N_1, and from the second to the first it is p_2N_2. With the effects of speciation through replication included, species are added at the rate of r_1N_1 for the first group and r_2N_2 for the second. Let d_1N_1 and d_2N_2 be the extinction, or species-level death rates for the two groups, respectively. With all elements of selective extinction, speciation and evolution included, the respective rates of change for each group will be

$$dN_1/dt = r_1N_1 - d_1N_1 - p_1N_1 + p_2N_2$$

and

$$dN_2/dt = r_2N_2 - d_2N_2 - p_2N_2 + p_1N_1$$

Assuming that the two groups neither grow to infinite numbers of species nor suffer complete extinction, but instead achieve some form of an equilibrium, the rates of change can be considered zero. This assumption allows study of the nature of the balance achieved (even if in reality such an equilibrium is dynamic). At such an equilibrium the ratio of one category (N_1) to the other (N_2) can be determined. The ratio can be called ρ ($\rho = N_1/N_2$).

Under these conditions

$$dN_1/dt = \rho r_1 - \rho d_1 - \rho p_1 + p_2 = 0$$

and

$$dN_2/dt = r_2 - d_2 - p_2 + \rho p_1 = 0$$

From these equations it is possible to solve for ρ as a function of the "per-capita" (per-species, relative, or "instantaneous") rates involved. This allows the determination of the ratio of species in one category to that of the other for an idea of how the various rates contribute to the relative abundance of the two groups. Several of these expressions (all of which must be simultaneously true) are:

$$\rho = p_2/(p_1 - r_1 + d_1)$$
$$\rho = (p_2 - r_2 + d_2)/p_1$$
$$\rho = (d_2 - r_2)/(r_1 - d_1)$$
$$\rho = -(r_2 - d_2 - 2p_2)/(r_1 - d_1 - 2p_2)$$

Note that the first two expressions are analogous to that obtained in Appendix 3.3. They are ratios of the species-specific rates at which species are exchanged between categories but modified by the replication and extinction rates. The next-to-last expression is a ratio of the differences between these two species-specific rates for each group.

With six variables (the per-species rates) that must meet the condition of balance, any one can be chosen to be determined by the other five. For example,

$$r_1 = (d_1(r_2 - d_2) + p_1(r_2 - d_2) - p_2d_2)/(r_2 - d_2 - p_2)$$

There are similar equations for each of the other five variables.

The example of asexual (represented by N_1) versus. sexual reproduction (N_2) can be used to examine the implications of the interactions and balance of all the processes of selective extinction and speciation in these equations. For rates that apply over a given time span, and for a particular (here, hypothetical) physical environment, we can pick values

for the respective rates to see what the resulting ratio of asexual to sexual reproducers would be. Arguments pertaining to selective extinction support a higher rate of extinction for asexual species than sexual species. Thus, the extinction rate for the sexual species can be chosen as 0.1 and that for the asexual species can be a multiple ($x > 1$) of the sexual species' rate. Arguments involving selective speciation would lead to the choice of values for r_2 that are greater than r_1. Also r_2 must be larger than d_2 to replace those lost to the asexual category through pseudo-extinction.

For this example the following values were chosen to illustrate the principles at play in the balance achieved:

$$r_1 = 0.05, \quad r_2 = 0.105$$
$$d_1 = xd_2, \quad d_2 = 0.1$$
$$p_1 = 0.001 \quad p_2 = ((r_2 - d_2)(r_1 - d_1 - p_1))/(r_1 - d_1)$$

Because evolutionary theory predicts shift away from the sexual category (i.e., more often than not, owing to the costs of sexual reproduction to individuals; endnote 30, Chapter 3), we want values of p_2 that are larger than those of p_1. In this example the values of p_2 are consistently about five times as great as those of p_1, varying from 0.00510 to 0.00501 (compared to 0.001 for p_1) for x between 1 and 5.

For the values of the rates making up the selective extinction and speciation tabulated above, the ratio ρ is 0.1 if the extinction rates are equivalent. This ratio falls markedly as the extinction rates of the asexual species increases.

Although this model suffers from the inadequacies of all models of living systems, it illustrates the way the observed ratio of asexual to sexual species may be maintained by selective extinction and speciation.[1] Even when evolution tends to transform species in opposing directions, the other elements of selective extinction and speciation can counterbalance the effects to produce observed ratios.

Note

1. Keep in mind that for some kinds of species (i.e., accounting for another characteristic) the ratio may be reversed (e.g., for very small-bodied species).