Appendix 3.5

The following material is Appendix 3.5 for Chapter 3 of: Fowler, C.W. 2009. Systemic Management: Sustainable Human Interactions with Ecosystems and the Biosphere. Oxford University Press

1 Selective extinction and speciation in numerous categories

The case of numerous categories of species along a single dimension can be represented by dividing up the range of values for a species level characteristic in a number of adjoining categories. We can then let the number of species in the i-th category be N_i (and, of course, the portion of species in the i-th category is $N_i/\Sigma N_j$). The index i (or j for the sum) extends from 1 at the lowest end of the spectrum over which the categories of species are spread, up to n at the highest end. As in the cases represented in Appendix 3.4, changes in number in the i-th category result from: (1) pseudo-extinction of its own numbers, (2) evolution of species originating in other categories to contribute species to the i-th category, along with (3) replication and (4) extinction within the category. Two rates of pseudo-extinction must be distinguished in this example because species will be evolving in both directions. Those from above can be represented by $a_{i+1}N_{i+1}$ and those from below by $b_{i-1}N_{i-1}$ from the $i-1$ and $i+1$ categories, respectively. It is assumed that the time unit chosen for application of these equations is small enough to avoid anagenic change that carries a species across a category into a second (from category i to $1 + j$, where $j > 1$, although this can happen in nature and models to account for it can be constructed). This helps keep the model being developed as simple as possible.

Now, the rate of change for the i-th group can be expressed by:

$$dN_i/dt = r_iN_i - d_iN_i - a_iN_i - b_iN_i + a_{i+1}N_{i+1} + b_{i-1}N_{i-1}$$

For purposes of illustration, species characteristics in this chapter were divided into 40 categories, each with its own rates of replication, extinction, and anagenic exchange. With computers these equations can be dealt with using numerical methods. But another approach is satisfactory for finding equilibrium frequency distributions, especially in cases of very small changes (e.g., 3% changes per unit time, or less). This approach consists of a transition matrix that can be implemented on spreadsheet software.

The categories of species can be considered as members of a vector of n numbers:

$$\begin{matrix} N_1 \\ N_2 \\ . \\ . \\ . \\ N_{i-1} \\ N_i \\ N_{i+1}. \\ N_{n-1} \\ N_n \end{matrix}$$

The matrix that represents the dynamics of the collection of species in these n categories can then be represented as functions of the rates specified as above. The elements of the diagonal of the matrix are multiplicative crude rates such that hidden in them is the survival of species to be carried forward from one unit of time to the next in the same category (i.e., those species that experience insufficient anagenic change to move to a different category and that do not go extinct). This matrix is

$$
\begin{matrix}
e^{r_1-d_1-a_1-b_1} & 1-e^{-b_2} & 0 & 0 & \cdots & 0 & 0 & 0 & 0 \\
1-e^{-a_1} & e^{r_2-d_2-a_2-b_2} & 1-e^{-b_3} & 0 & \cdots & 0 & 0 & 0 & 0 \\
0 & 1-e^{-a_2} & e^{r_3-d_3-a_3-b_3} & 1-e^{-b_4} & \cdots & 0 & 0 & 0 & 0 \\
\vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\
0 & \cdots & 1-e^{-a_{i-2}} & e^{r_{i-1}-d_{i-1}-a_{i-1}-b_{i-1}} & 1-e^{-b_i} & 0 & 0 & \cdots & 0 \\
0 & \cdots & 0 & 1-e^{a_{i-1}} & e^{r_i-d_i-a_i-b_i} & 1-e^{-b_{i+1}} & 0 & \cdots & 0 \\
0 & \cdots & 0 & 0 & 1-e^{-a_i} & e^{r_{i+1}-d_{i+1}-a_{i+1}-b_{i+1}} & 1-e^{-b_{i+2}} & \cdots & 0 \\
\vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\
0 & 0 & 0 & 0 & 0 & \cdots & 0 & 1-e^{-a_{n-1}} & e^{r_n-d_n-a_n-b_n}
\end{matrix}
$$

Under most circumstances, each time the vector of species numbers is multiplied by the matrix the species numbers change. Over time (i.e., repeated application of the matrix, assuming its parameters do not change—an unrealistic simplifying assumption) the frequency distribution of species begins to approach a constant form. Such distributions are exemplified in the bottom panels of Appendix Figures 3.2.2–3.2.4 and 3.2.7–3.2.9. But as changes in frequency distribution occur, changes also occur in the total number of species; species numbers within each category change as does the total among them. Eventually, both the frequency distribution of species and the rate of change in species numbers become constant. In the terminology of matrix algebra, the frequency distribution takes on values determined by the principal eigenvector and the rate of change is determined by the principal eigenvalue. The latter is a scalar (λ) that can be multiplied by the number of species in each element (N_i) determined by the eigenvector to obtain the number at the next time interval.

The value of such a matrix model is the ability to explore the effects of a variety of different selective extinction and speciation regimes. The nature of dynamics in both species numbers and in achieving characteristic distributions is important. Questions regarding the speed with which equilibria are established and which forms of selective dynamics are most efficient in rapidly approaching equilibria can be addressed. Knowledge regarding species-level characteristics that exhibit such dynamics can be used to hypothesize which ecosystem level characteristics are likely to be most robust and which most sensitive to stress.

In the application of the above matrix for illustrations in this chapter (especially those of Appendix 3.2), species numbers were assumed to have experienced some form of limitation to their numbers. Thus, one form of equilibrium was assumed. It was a form of diversity dependence to establish a means of avoiding the result of no species, and the result of an infinite number of species. This was done through adjusting all extinction rates by a constant (i.e., leaving the selectivity unaltered). Rates used to produce illustrations for this chapter were therefore chosen so as to represent equilibria as explained below.

A "brute force" method of finding the dominant eigenvalue and corresponding eigenvector of a "species dynamics matrix" is to simply apply the matrix to a vector of species numbers repeatedly. Through this iterative approach, both the eigenvalue and eigenvector emerge simultaneously. To prevent species numbers from increasing to unmanageably large or small levels during such iterative procedures, the total is readjusted after each iteration without disturbing the distribution (i.e., the same fraction of the total remains in each category). After having determined the eigenvalue of an original matrix, the values of this matrix can then be adjusted so that a new matrix is formed

with an eigenvalue of 1 (condition of no net change in species numbers).

In adjusting a matrix to make its eigenvalue be equal to 1, all elements of the matrix are divided by the eigenvalue of the original matrix. This preserves the values of each element in relationship to the others as each one is changed by the same factor. The elements above and below the diagonal contain only the rates of anagenesis (pseudo-extinction) that are always changed from the original values in making this adjustment. Thus,

$$1 - e^{-a_i'} = \frac{1 - e^{-a_i}}{\lambda},$$

where a_i' is the new value of a_i and similar equations apply to the values above the diagonal. The diagonal elements, however, are functions of all four types of dynamics (replication, extinction, and anagenesis both downward and upward: $r_i - d_i - a_i - b_1$). But the rates of anagenesis $(-a_i - b_i)$ are determined by the changes in the off-diagonal elements.This means that changes in replication and extinction are necessary to achieve an eigenvalue of 1—the situation needed to achieve the condition of no change in species numbers. The difference between these two rates $(r_i - d_i)$ must be adjusted to accomplish this end because the rates of anagenesis are already determined by the off diagonal elements. This leaves freedom of choice for which rate (speciation or extinction) to change and by how much. For the examples shown in the graphs of this chapter, the rates of extinction were adjusted to achieve these conditions; the rates of speciation were left as originally chosen.

To explore the effects of various regimes of selective extinction and speciation as shown in Appendix 3.2, hypothetical relationships between each rate and measures of the species level characteristic were chosen. These have the same shapes but different values from those presented in the top panels of the figures. Iterative solutions for the principal eigenvalues and vectors were determined. The eigenvalue was used to adjust the original matrix, as described above, thus determining final values for the four processes of selective extinction and speciation. These are the numbers presented in the top panels of the figures. This process preserves the distribution in extinction and speciation rates over the range of the chosen species level properties. In other words, the selectivity of selective extinction and speciation are unchanged in this process. Thus, in all cases, the rates shown in the top panels of the graphs of Appendix 3.2 represent those that resulted in the distribution shown in the lower panels after making the adjustments described above.

In choosing rates for the matrix above, and the time unit over which the matrix applies, care must be taken to avoid evolution that, in reality, carries species across more than one category. The matrix, as described above, is based on an important assumption. As mentioned above, it is assumed that the species-level characteristic is not one that exhibits "jumping" from one character category to another by skipping a number of intermediate categories.

Species characteristics such as geographic range, or population variation, violate this assumption. These situations can be dealt with by probabilities or rates in the matrix that are off the diagonal by more than one element (such as in stage matrices as applied in the study of insect population dynamics). This would not be necessary for many characteristics. Such elements would contain values corresponding to the probability that a species would, for example, undergo cladogenesis of an independent character and split to divide its range so as to form two species. These would have ranges that would both be smaller than that of the original. This would be an example of relatively dramatic "mutation" at the species level compared to the more nearly continuous evolutionary changes as traditionally understood. Any character that experiences the more sudden changes would be represented by off-diagonal elements.

Other similar models may be constructed (e.g., see Slatkin 1981). Their construction and use in exploring the dynamics described in this and the last chapter is encouraged as learning exercises and research tools. It is mandatory, however, that the models never be perceived as anything other than tools for enhanced understanding (they are not the systems they represent).