
Appendix 3.2

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1 Evolutionary contributions to the formation of species-level patterns (frequency distributions)

Extinction has only defined the groups: it has by no means made them....

—Charles Darwin

This appendix further develops the concept that patterns among species are simply natural phenomena that emerge from the complexity both of the systems within which they occur and of which they are composed. Chapter 2 began consideration of *what* is involved in this explanatory complexity, with examples including the abiotic environment, and the evolutionary processes of natural selection, speciation and extinction, and ecological mechanics. Chapter 3 continued that process. This appendix elaborates through consideration of *how* the mechanics of evolutionary processes, particularly speciation and extinction, contribute to species-level patterns and, in fact, may be the most important contributing factors.

The bulk of what are presented here are hypothetical examples to explore the effects of extinction and speciation to include the evolution of species (the latter involving natural selection as it acts on individuals, genes, and gene combinations). These processes are examined in their contribution to the formation of species-level patterns, particularly as frequency distributions among single and multiple species characteristics. Early sections compare the effects of selectivity or nonselectivity in one or more evolutionary process. A later section describes how

some species characteristics compensate for others to reduce the risk of extinction for a particular species. The structure and function of ecosystems and other species groups are then described as the result of selective extinction and speciation, in concert with all other contributing factors (Fig. 1.4)—the emergence of ecosystems involves evolution at various levels. Another section highlights the relative importance of evolutionary changes, particularly selective extinction and speciation, in the formation of frequency distributions.

1.0 Evolutionary development of species-level patterns (frequency distributions)

When considering the extinction, speciation, and evolution of species, the ways species function within ecosystems is as important as their morphology (the cornerstone of taxonomy). The function of species includes their coevolutionary interactions (“...life is a dense web of genetic interactions...”; Lederberg 1993). From an evolutionary/ecological perspective, species may be classified according to characteristics independent of pedigree or taxonomic relationship to other species. In other words, they may be placed in categories based on measurements like those of the species distributions shown in Chapter 2. Characteristics such as body size, trophic level, geographic range, metabolic rates, population variability, population size, and generation time are shared by all species, just as are their taxonomic links. Among higher trophic levels selectivity in consumption (e.g., selectivity by size or sex) are measurable characteristics regarding interspecific interactions.

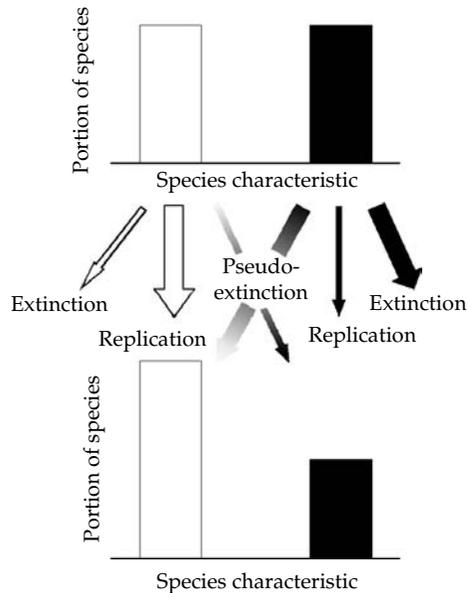
Limits to variation among species are key to the information in each species-level pattern. These limits are observable in the form of frequency distributions—often “bell” curves with tails

representing declines in the number of species each side of a mode. In this section, the influence of extinction and speciation in the formation of frequency distributions is described using hypothetical examples, illustrated graphically. The purpose here is to show how selective extinction and speciation combine in a trial-and-error process to produce examples of sustainability among species.

This section begins by illustrating how selective extinction and speciation (coupled with the microevolution involved in speciation) influence frequency distributions for a single species-level characteristic. This requires making the unrealistic assumption that individual characteristics affect evolutionary processes independently. In nature, the simultaneous actions of selectivity along multiple dimensions create a complex of factors that contribute to the formation of species frequency distributions. Examples seen in the following are presented for patterns resulting from two or more interacting evolutionary factors in an effort to better understand this complexity. Such examples are an oversimplification of nature but reveal critical insights. Other examples further illustrate the interplay of evolutionary processes, showing how extinction, speciation, and/or evolution may be selective for some species characteristics and non-selective for others.

1.1 Effects on relative abundance of two groups for one species-level characteristic

Species of any group (set, or sample) can be divided into subsets represented by bars corresponding to the portion of the sample they represent (Appendix 1.3, Fowler and Perez 1999). Examples were shown in Chapters 1 and 2 where we begin to see first approximations of probability distributions of practical utility in implementing Management Tenet 5 (Chapter 1). Species that can be divided into two categories for a single species-level characteristic can be treated the same way, as shown in Appendix Figure 3.2.1. The species-level characteristic in this illustration is generic but could apply to a specific case (e.g., one group might be species that reproduce sexually and the other asexually, or one might be of high trophic level and another low, on each side of an arbitrary midpoint).



Appendix Figure 3.2.1 The effects of selective extinction and speciation on the relative number of species in two categories of one species-level characteristic (see Table 3.1). Relative, not absolute, rates are indicated by the width of the bars on the arrows. Over a unit of time, the group represented by the white bar on the left of the top panel experiences more cladogenic replication. The group on the right (black bar) experiences more extinction and pseudoextinction (i.e., loss through anagenesis). After the combined effects of this selectivity (bottom panel), the group of species on the left outnumber those on the right.

The top panel of Appendix Figure 3.2.1 represents the starting point of a hypothetical set of species divided into two groups with the same number of species in each group. Selective extinction, as shown in this example, removes a greater fraction of those on the right than those on the left. If extinction were acting alone, the result would be a redistribution of the relative numbers of species so that the group on the left would be a larger portion of the total; the number of species on the left would change to outnumber those on the right. By contrast, nonselective extinction (which would be shown by arrows of equal width on the right and left of a graph like Appendix Fig. 3.2.1) would not, on the average, change the relative numbers of species. Each species would have the same probability of extinction and the same¹ fraction of each group of species would, on average, suffer extinction.

Extinction, however, is only part of what determines relative species numbers. Speciation is also involved. This includes species replication² as shown by the vertical arrows between the panels of Appendix Figure 3.2.1. The species in the category on the left have a higher species-level replication rate than those on the right. Some speciation may include anagenesis but with insufficient change to move to a different category. In the absence of extinction or anagenic interchange, the category with the highest replication rate would eventually be represented by the larger (and growing) fraction of the total number of species (which itself would be increasing).

Species-level dynamics also include anagenesis or evolution to change category (pseudoextinction). In Appendix Figure 3.2.1 such a change is illustrated by the central diagonal arrows. The number of species in the category that loses a larger fraction of its (new) species to the other category exhibits a relative decline (black bar again becomes smaller than the white bar). The portion of species in each category changes as a consequence of the impact of such selective anagenesis. However, anagenic change can result in an equilibrium in such a model. This can happen because the growing category eventually contributes enough to the smaller category to make up for the latter's loss, now in absolute numbers of species (Appendix 3.3).

The relative magnitude of contributions by extinction, replication, and evolution differ over time and in regard to species characteristics, but they are simultaneous processes (Table 3.1). Equilibria³ achieved in the resulting frequency distribution of species thus contribute to the formation of ecosystem properties. In Appendix Figure 3.2.1 this is exemplified by the relative portion of species in each of the two categories.

The combined effects of all three processes (extinction, species replication, and evolutionary or anagenic change) illustrated in Appendix Figure 3.2.1 result in relative⁴ growth of the group on the left and decline in that on the right. The growth of species numbers on the left is an example of the expression of the interplay of these processes in Combination 1 (Table 3.1). The relative effects of extinction and anagenesis are positive by contributing to an increased portion of species. These effects

are reinforced by cladogenic replication. The loss of species in the group on the right is an example of Combination 4 wherein the negative effects of anagenesis and extinction are reinforced by selective replication. The replication rate (vertical arrows) of the group on the left is larger than the extinction rate for the same group. The extinction rate of the group on the right is larger than on the left. Finally, the rate of conversion of species from the group on the right to that on the left is the larger of the two anagenic exchange rates. Clearly, the number of combinations of potential rates is infinite, as are the outcomes, even though the options fall into the eight categories of Table 3.1.

One set of combined dynamics is noteworthy. If the extinction rates of two groups of species (as in Appendix Fig. 3.2.1) are quite different but equal to the replication rates in each case, the *differences* between extinction and replication rates are zero for each group. Consequently, there would be a larger turnover among species for a group with larger extinction and replication rates (expressed as relative rates or probabilities, not absolute numbers), but species numbers would not change. Species numbers would depend on the level at which speciation and extinction are in balance. It is possible, for example, that high speciation rates would be characteristic of a group with low species numbers. For purposes of illustration we can make the unrealistic assumption that we have a case wherein there is no effect from ecological mechanics and no incremental changes contributed by extinction or replication. In such cases, the ratio of species numbers between two categories would depend only on the exchange between them via evolution (i.e., anagenesis, Appendix 3.3)⁵.

An enigma in modern biology is the preponderance of species that reproduce sexually⁶ because sexual reproduction is so costly to individuals.⁷ The observed abundance of sexually reproducing macroscopic species is easily explained by the effects of selective extinction and speciation⁸ (Fowler and MacMahon 1982, Appendix 3.4). This entails the combined effects of a variety of rates of extinction and replication, all in combinations with evolution that puts a drain on sexual reproducers. Such dynamics demonstrate the hierarchical potential for selective extinction and replication

to override natural selection among individuals in anagenesis. This is especially true in Combinations 6 and 7 of Table 3.1, but also other combinations when the rates are high enough for the combined effects of cladogenesis and extinction to overpower anagenesis.

1.2 Patterns from combined selective processes (single dimension)

What are the options for the dynamics in more complex situations? The example above (Appendix Fig. 3.2.1, and Appendices 3.3 and 3.4) consists of a discrete categorization of species into two groups for one characteristic. As seen in Chapter 2, most species-level characteristics are not discrete categories but involve continuous variables (e.g., body size, metabolic rates, and population variability). The spectrum of observed values for each such characteristic may be divided into numerous segments or categories (“bins” of values). As in patterns represented by the histograms of Chapter 2, a bar can be used to graphically represent the number or portion of species in each category or subdivision (Appendix 1.3, Fowler and Perez 1999).

The portion of species (as well as raw species numbers, or percentages of totals) can thus be represented in a frequency distribution in a variety of ways, even continuously, as probability distributions (Fowler and Perez 1999). The added complexity seen in such cases involves the fact that for categorized groups, anagenic change can move species in either direction from any category or point. A mix of such processes occurs and involves a large variety of contributing factors, some with directional bias. The direction in which a particular species may evolve is thus not a simple matter; the probability that it will evolve in a particular direction can be considered a product of all contributing factors.

Thus, each group of species along a continuum experiences extinctions, replication, exchanges with the group above (to the right in graphs like those of Chapter 2), and exchanges with the group below (to the left). As we now know, replication processes may be subdivided into three categories:

1. Species that remain unchanged.

2. Species that multiply through cladogenic splitting without sufficient anagenic change to leave a defined group.

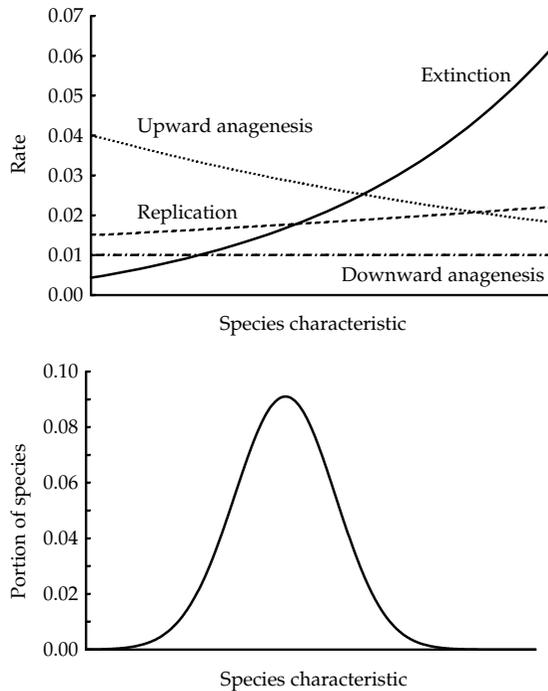
3. Species that exhibit enough change in one or more of their other characteristics (i.e., in the categories for a different measure or dimension) to become new species. A species may stay at the same trophic level, for example, but become a new species on the basis of change in another attribute, such as body size.

1.2.1 Processes in combination

One way of seeing the combined processes of selective extinction, selective replication, and selective anagenic evolution is shown in Appendix Figure 3.2.2. This would be an example of the ways a particular combination of the rates involved might reflect the effects of a hypothetical environment on a hypothetical set of species. This graph shows the combination of dynamics affecting species in their distribution across a spectrum of single-dimension measurements (e.g., any of those of the single-characteristic species frequency distributions in Chapter 2). In the top panel of this figure, each of the four processes is represented: extinction, replication, and anagenesis in two directions.

The only process of Appendix Figure 3.2.2 that is not selective is downward anagenesis (the fraction of species that will evolve smaller values of the hypothetical characteristic). This process, downward anagenesis, occurs at a rate that is independent of the exhibited characteristic.⁹ The line is flat. By contrast, selectivity occurs in the upward anagenesis of the example in Appendix Figure 3.2.2 because this evolutionary process happens more often among species low in the spectrum (to the left) than those higher in the spectrum (on the right). Species in this example evolve predominantly toward higher values (i.e., toward the right),¹⁰ faster for species low (left) in the range than for those to the right.

To ensure correct interpretation of similar graphs later in this appendix it is helpful to relate to a specific set of species within the spectrum of the species-level characteristic. Appendix Figure 3.2.2 shows a case where, for a specified period of time, 0.5% of the species exhibiting the smallest measure of the characteristic (i.e., those species at the far left)



Appendix Figure 3.2.2 Selective extinction and speciation depicted in a hypothetical example. This example shows selectivity in both extinction and speciation across a continuous measure of a species-level characteristic. Here, extinction and multiplicative replication increase with increases in the species-level characteristic, and upward anagenesis decreases. Downward anagenesis is nonselective (completely so if it remains unchanged above and below the segment of species level measure represented by the abscissa). Overall, anagenesis tends to be upward in this example because the probability of upward anagenesis is greater than that for downward anagenesis for the entire range. All apply only within the range shown. Three of the four processes are selective because the rates (relative rates reflecting probabilities) at which they occur are correlated with the magnitude of the species-level characteristic.

will go extinct; 1.0% of these species will evolve to exhibit even less of the characteristic (downward anagenesis); 1.5% will replicate to produce similar species; and 4.0% will evolve toward greater measures of the characteristic (upward anagenesis). These are the rates used in the matrix in Appendix 3.5, just as are the other rates shown in the top panel, corresponding to the other measures of the characteristic. Repeated application of these rates in the matrix model of Appendix 3.5 generates the distribution shown in the lower panel.

The core of selectivity in extinction and speciation involves two components:

1. The rates, or probabilities, of extinction and speciation change across the range of each species-level characteristic.
2. The specific nature or shape of the curves exhibiting the selectivity vary among physical and biotic environments.

Evolution through processes that include natural selection among individuals are selective as expressed in selective anagenesis. The postulates of selection among species presented in Chapter 3 are graphically exemplified by the top panel of Appendix Figure 3.2.2. Included are the selective evolutionary processes involved in anagenesis. All apply as assumed for a hypothetical unspecified environment and, in reality, would change as environments change. Selective extinction, speciation, and evolution can also be represented in the form of mathematical models. The model described in Appendix 3.5¹¹ was used to produce this and similar graphs of this appendix with different sets of assumed or hypothetical parameters (rates) as shown in the top panels of the graphs.

The bottom panel of Appendix Figure 3.2.2 shows the frequency distribution or relative abundance of species expected to result from the selectivity of extinction, speciation, and evolution exhibited in the top panel, when they are assumed to be the only contributing factors.¹² This distribution is the balance of the interactions of all three processes (four when upward and downward anagenesis are counted separately, Appendix 3.5). In this example, species tend to be most numerous in the central part of the spectrum of possibilities. This is explained by the tendency for extinction to be greater than replication at the upper end of the range (upper panel), thereby preventing the buildup of species toward the right. Species that form in the low end tend to evolve toward the higher end more rapidly than they are replaced by replication. This prevents the buildup of species toward the left end of the spectrum. Thus, the interplay of the eight combinations of interacting forces from Chapter 3 changes continuously across the spectrum of the species level characteristic.¹³

Appendix Figure 3.2.2 demonstrates the necessity of including selectivity as part of the species-level dynamics involved in the formation of species-level patterns. This figure illustrates the influence of such selectivity as it might contribute to the structure and functioning of ecosystems as assembled from species affected by these processes. Arguments restricted to consideration of individual-level selection might consider species frequency distributions to be purely fortuitous, although speciation processes, especially any anagenic trends, might not be ignored. In this example, based on natural selection among individuals alone, one would expect most species to be at the high end of the spectrum, primarily through the effects of upward anagenesis. Although the predominant direction of evolution tends to be in that direction for all categories of species, it would be more so for species at the low end of the range for the hypothetical species-level characteristic shown in Appendix Figure 3.2.2. Species at the high end tend to replicate into similar species more rapidly than at the lower end.

However, the magnitude of extinction rates at the higher (right) end are enough to prevent the accumulation of species that might be expected on evolutionary arguments alone, or for that matter, pure diffusion as a random process. Consideration of the effects of any of the other processes alone can be equally misleading. Selective extinction, speciation, and evolution in combination integrate all of the evolutionary dynamics contributing to the formation of patterns (e.g., frequency distributions) among species. These are dependent on the environment in which they occur, including the biotic environment of other sets of species to which they are exposed.¹⁴ As stated before, these evolutionary dynamics contribute to the formation of patterns among species. This happens in combination with the contributions of ecological mechanics. The latter includes immigration and emigration of species through changes in their geographic ranges. Such dynamics have their consequences by adding species to, or removing species from, any relevant geographically defined set of species.

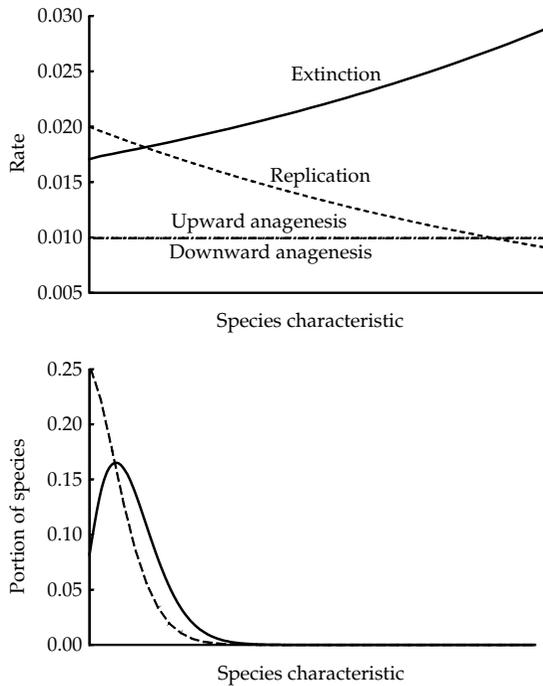
1.2.2 Further examples

More hypothetical examples of selectivity in extinction and speciation are helpful in understanding

patterns among species and how these processes contribute to the characteristics of any set, group, or collection of species. Models such as that of Appendix 3.5 can be used to explore these processes and, simultaneously, appreciate both the potentials and limitations of such models. Although each example below focuses on one hypothetical species-level characteristic, it is important to remember the variety of real characteristics over which these species-level dynamics and distributions occur (Table 2.1); each example reflects the effects of both a hypothetical physical environment and the dynamics of internal biotic forces (exogenous and endogenous factors).

The next example demonstrates selectivity restricted to extinction and replication through cladogenesis. Appendix Figure 3.2.3 illustrates selective extinction and speciation wherein extinction increases and replication decreases while neither form of anagenesis is selective in relation to the hypothetical species-level characteristic. In this example, both forms of anagenesis are nonzero, and equal, so that species change position only through nondirectional diffusion along the axis of the species-level characteristic. This demonstrates the ways that the characteristics of the set of species (i.e., not the individual species) within a species frequency distribution can evolve in ways where extinction and cladogenesis override anagenesis or the effects of natural selection among individuals.¹⁵

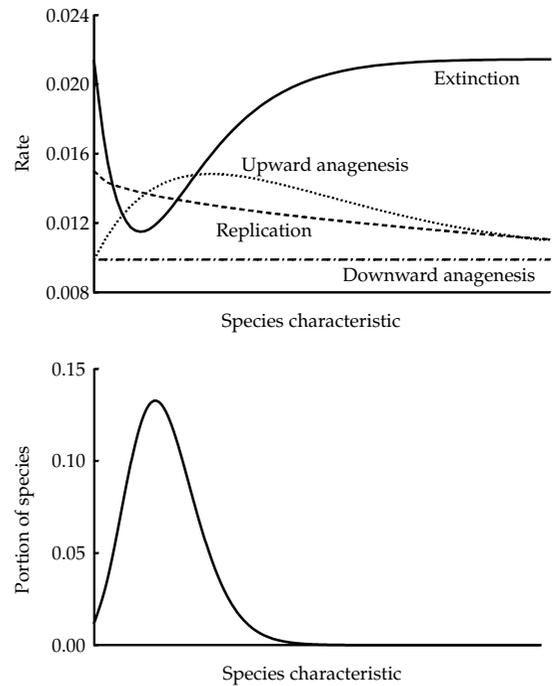
This combination in this example results in the accumulation of most species at the lower end of the scale (lower panel, Appendix Fig. 3.2.3). The pattern is represented as a product of equilibrium conditions.¹⁶ In nature, such a pattern would be seen as a collection of species tending toward such an equilibrium that would be dynamic and influenced by a multitude of other factors. Before achieving equilibrium most sets of species and the ecosystems assembled from them are faced with new environmental conditions that eventually result in a different equilibrium, often before it is achieved. The projected endpoints of such evolution keep changing as continuously “moving targets” of the evolutionary process. When environmental changes are of a magnitude that is not beyond the capacity for change in the dynamics among species (some of which result in extinction



Appendix Figure 3.2.3 A hypothetical set of selective extinction and speciation processes (top panel) and the resulting species frequency distribution (bottom panel), assuming no effects of ecological mechanics. Only extinction and replicating speciation are selective within the spectrum shown. The dashed line for the species frequency distribution is the distribution resulting from no anagenesis beyond the limits of the graph to the left (a zero measure of the species-level characteristic). The solid line represents the case wherein downward anagenesis results in extinction at the same extreme (extinction would be a step function at zero where all species go extinct).

of all species in particular categories), patterns emerge. Species-level characteristics representing adaptations in response to environmental fluctuation may develop patterns that themselves show change over long time scales as cases where there is only the potential for pattern otherwise.¹⁷

One aspect of the example in Appendix Figure 3.2.3 is important in applying the methods laid out in Appendix 3.5. The lower end of the spectrum represents an endpoint of possibilities. There are at least two options. One option is that species evolve to the lower extreme and go extinct. Another option is that species stop evolving in that direction. The first drains species from the collection. The second



Appendix Figure 3.2.4 A hypothetical set of selective extinction and speciation processes with selective upward anagenesis (top panel) and the resulting species frequency distribution (bottom panel). Downward anagenesis occurs but is not selective over the range shown.

terminates evolution, resulting in an accumulation of species. Both are forms of selectivity that apply only to the species at that extreme. In this example the results of both options are shown.

Another hypothetical example of selective extinction and speciation is presented in Appendix Figure 3.2.4. Species near the lower end of the scale suffer extinction quite rapidly. At the upper end of the scale, and beyond an intermediate minimum, extinction rates achieve another maximum. The production of new species through replication is high for species at the low end of the scale. Selective upward anagenesis is higher for species in the intermediate ranges of the characteristic. Trends in evolution toward larger values of the characteristic decline with such increases. Downward anagenesis occurs but not selectively.

This example may¹⁸ roughly approximate some of the qualities of species dynamics regarding body size. Tiny species approaching the molecular

level in body size may suffer extinction quite rapidly owing to their simplicity and lack of options in adaptive strategies. With increasing size, extinction rates may reach a minimum above which the increased generation time, and other problems or risks associated with body size, might lower the evolutionary rate and increase the extinction rate. New species produced through replication may occur quite rapidly for the molecular-sized species.¹⁹ The selective upward anagenesis, for example, would account for Cope's rule (Cope 1885, 1896, LaBarbera 1989, Newell 1949). Trends in evolution to larger body size decline with size as the potential evolutionary rate declines.

As illustrated in the examples presented above, a variety of patterns can occur. Appreciation of this variety can be aided by exploring such examples with alternative forms of selectivity. This can, for example, involve various sets of parameters in a model such as that of Appendix 3.5. Such experience helps clarify the effects of the combination of dynamics and takes advantage of one of the useful aspects of modeling exercises.²⁰ It must be kept in mind, however, that the resulting examples (e.g., those shown in the lower panels of Appendix Figs 3.2.2 through 3.2.4) represent situations assumed to be in equilibrium. Care must be taken in drawing more than general conclusions about such illustrative use of mathematical models because, as with all such models, the complexity of reality is beyond such oversimplification. These models, for example, do not directly account for ecological mechanics; specifically, emigration and immigration of species to any particular set of species that might be defined in geographic space are not included.²¹

In reality, the shape of the curves representing selective extinction and speciation (top panels of Appendix Figs 3.2.2 through 3.2.4) would be habitat-specific to include the effects of the environment, including those factors that exert their influence through ecological mechanics. The shape of the selectivity curves is also dependent on the numbers of species in addition to their characteristics. Diversity dependence (rates that also depend on total species numbers) may be more than a simple function of total numbers of species; it may also involve a complex function of not only species richness but also the characteristics

of their emergent pattern(s). This would be comparable to the influence of age distribution and genetic composition on density dependence in population dynamics. Thus, we need to appreciate the influence of selective extinction and speciation, but recognize that the complexity of ways they can operate are beyond representation by simple mathematical models such as those shown here (i.e., beyond comprehension but not to be ignored as part of reality).

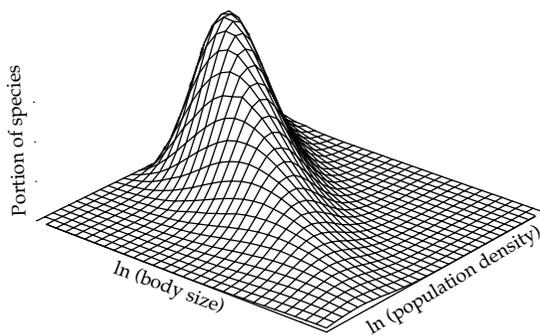
One element of understanding that emerges from the above is the fact that, in many cases, natural selection at the species level works in concert with the results of natural selection at the individual level. This conclusion is inherent in much of the literature listed in the citations of Chapter 3. The dynamics leading to balances among the opposing forces (especially of Combinations 2, 5, and 6 of Table 3.1) involve production of species by natural selection (primarily among individuals) that are then subject to the effects of selective extinction and speciation. The carving away of species by extinction is particularly prominent in Combinations 5 and 6 when extinction rates are high enough to prevent the accumulation of species produced by evolutionary processes acting within species.

1.3 Patterns among species in two dimensions

As is obvious, and illustrated in Chapter 2, patterns in species numbers occur in relation to multiple species-level characteristics. The caveat of "everything else being equal" was an underlying assumption in the simplistic single-character examples presented above and the single-dimension examples in Chapter 2. It is possible to gain some insight into how the dynamics of species are influenced by more than one of their characteristics simultaneously.

As above, consideration of two dimensions must proceed knowing that the probability of extinction or speciation is related not just to the characteristics of any particular species, but to the combined influence of all contributing factors. Nevertheless, it is instructive to proceed with the exploration of examples to better understand at least some of the dynamics behind species interacting in two-dimensional space. Expressed in terms of

the dynamics of groups of species, the fraction of a group expected to go extinct or to speciate depends on the combined effects of all their characteristics. In other words, the shapes of the selectivity curves of the top panels of Appendix Figures 3.2.2 through 3.2.4 would vary in relation to other species-level characteristics. Appendix Figure 3.2.5 shows an example of a species frequency distribution along two continuous characteristics similar to several from Chapter 2, particularly the frequency distribution for body size and population density (both in log scale). In the corner of the distribution represented by species with small bodies and low densities, a high extinction rate might prevent the accumulation of species owing to the vulnerability of species with small body size to environmental variability.²² Their population variability could make them subject to higher extinction rates at low population densities. On the other hand, species in the corner represented by dense populations of large bodied species would be subject to a number of limitations.²³ Lack of resistance to parasitic and predatory species that would evolve to take advantage of the biomass at such population size might lead to extinction. Anagenic pseudoextinction would occur if evolution led to lower population densities to solve such problems. Coevolution of defense mechanisms by resource species could lead to an insufficient energy base to support such



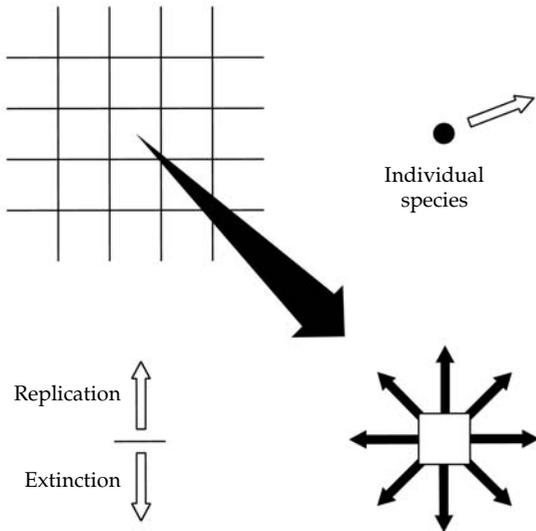
Appendix Figure 3.2.5 A smoothed or fitted frequency distribution of species within two continuous species-level characteristics. For example, this might represent the portion of species or species numbers in an ecosystem (or other sample), distributed over adult body size and population density (x and y axis, in log scale).

densities. Moreover, there are risks of extinction by loss of resource species caused by high consumption rates. Predators consuming large quantities of prey may risk the consequences of extreme interaction strength identified in food web work (e.g., de Ruiter *et al.* 1995, May 1981a).

The selective extinction and speciation curves that would result in distributions like Appendix Figure 3.2.5 might be similar to those in Appendix Figure 3.2.4, with the selectivity curves dependent on body size. A cross-section of the volume shown in Appendix Figure 3.2.5 could be taken at a specific population density. Such a cross-section would represent species numbers by body size at that density and would have a shape like the lower panel of Appendix Figure 3.2.4.

As in the case of a single characteristic, the distribution of species over the surface defined by both dimensions in Appendix Figure 3.2.5 depends on the balance among the various interacting rates, with such balances often highly susceptible to environmental influence.²⁴ However, the simultaneous effects of such selectivity for two characteristics show its effect within a species-level pattern wherein exchange of species involves rates of anagenesis in any direction.

The simultaneous dynamics of speciation and extinction for such a case are shown in Appendix Figure 3.2.6. The grid represents the plane below a surface like that of Appendix Figure 3.2.5. Each square represents a category of species classified simultaneously for two species-level characteristics. Such categories can experience anagenetic evolution that would carry an individual species into any of the neighboring categories, as shown in the lower right of this figure. An individual species, represented on the surface defined by the two dimensions, can evolve in an infinite number of directions in that plane (instead of only one of two directions along a single dimension). In other words, the vector of evolution within two dimension can carry an individual species in any direction. As in all cases, replication and extinction contribute and remove species. This is shown in the lower left of Appendix Figure 3.2.6 as an end-view of any one of the squares from the grid; the upward arrow represents an increase in species numbers and the downward arrow represents a decrease.



Appendix Figure 3.2.6 Extinction, speciation and evolutionary change involving two species-level characteristics. The measure of one characteristic (dimension) is represented by the abscissa of the grid, the other by the ordinate. An individual species can evolve in any direction in this grid (single species represented by the black circle) and more collectively by the square surrounded by arrows. In the third dimension, replication adds to the numbers in any square and extinction removes them (shown by the end-view of a square in the lower left).

Selectivity, as in earlier examples, consists of rates that are dependent on the position of species, now in the two-dimensional space. Directional evolution alters the rates of change in anagenesis so that, for the group (species in any bounded category), the majority of species evolve one way. Such bias can include directional evolution in both characteristics as represented by the single species in the upper right of Appendix Figure 3.2.6. Selectivity determines how often such change occurs, as dictated by the characteristics of the species. Two-dimensional frequency distributions like that shown in Appendix Figure 3.2.5 result, in part, from a balance among rates combined with stochastic and historical influences of the environment.

The potential shapes of frequency distributions for two characteristics can be infinite, just as in the simpler case of a single dimension. What we see in nature represents a finite set of such options.

Appendix Figure 3.2.5 shows a generalized representation of species numbers distributed over population density and body size. Similar graphs could be constructed to represent the frequency distribution of species over other combinations such as trophic level and population variability. Selective extinction would prevent the accumulation of species that exhibit both high trophic level and high population variability. The frequency distribution for this combination of species-level characteristics probably would be similar to that for trophic level and generation time. Most species are expected to show low population variance and low trophic level.

Species numbers can be represented and studied in a variety of combinations of two characteristics. Just a dozen characteristics would reveal over 60 patterns (Table 2.1) like those of Appendix Figure 3.2.5, each with a different shape.

1.4 Frequency distributions for more than two dimensions

In reality, ecosystems are, in part, products of all species characteristics that are influential in determining rates of replication, extinction, and anagenic change. A consideration of selective extinction and speciation for more than two characteristics is necessary to appreciate the complexity of ontogenetic processes behind species-level patterns and their contributions to the structure and function of ecosystems. This complexity translates to the impossibility of ever completely explaining any particular distribution. What we see in nature is the emergent; that is, the things that can be characterized and shown graphically are products of complexity (Fig. 1.4). Graphic representation of such distributions is difficult for three dimensions and nearly impossible for more, as was noted in Chapter 2.

One way of illustrating the density of species within a species-level pattern in two dimensions was shown in Chapter 2 (e.g., Fig. 2.29), wherein each point represents a species so that the density points are indicative of the density of species. The relative density of points varies in the different regions of such graphs. This kind of graphic presentation can be extended to three dimensions

such that each axis represents a species-level trait and each point represents a species in relation to the measure of each of its characteristics (e.g., Fig. 2.34). In this example, the distribution is an approximation of that expected for species plotted according to their population variability, population density, and body size. Few species exhibit large body size in combination with high population variability, and high population density. Most are small-bodied species with intermediate population density and variability. No species occur with very low population variability, such that the cloud of points in Figure 2.34 is suspended in space.

Consideration of species frequency distributions as in the previous hypothetical example (Appendix Fig. 3.2.5) is a step toward understanding the “morphology” of species-level patterns (and thereby ecosystems), each as made up from populations reflecting the characteristics of a particular set of species. It also demonstrates that in spite of the potential for variety, such distributions show limits and can be evaluated through comparisons over time, among ecosystems and taxonomic groups, and across space. Although great variety in the form of species frequency distributions is obvious, limits are set by a variety of factors, including the selectivity of speciation and extinction.²⁵ Such limits exemplify hierarchical constraint (Ahl and Allen 1996, Campbell 1974, O’Neill *et al.* 1986, Wilber 1995). The complexity of natural collections of species becomes increasingly apparent as one realizes that these patterns occur in multi-dimensional space (each species in its own niche) that cannot be presented graphically.

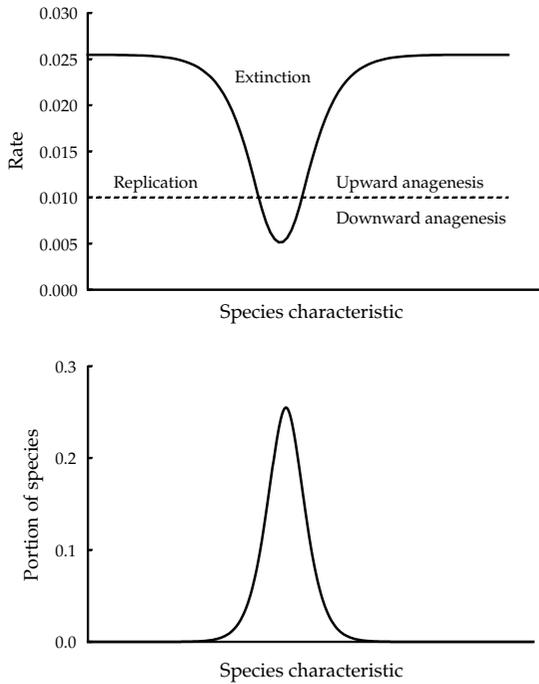
1.5 Patterns: complexity

Graphic representation of selective extinction, speciation, and evolutionary rates allows for a clear distinction to be made between selectivity and nonselectivity in these processes. Nonselective processes are independent of species-level characteristics; process and characteristic are not correlated (even when the characteristic is that of an ecological process). This is exemplified by the flat line representing the probability of downward anagenesis in Appendix Figure 3.2.4.

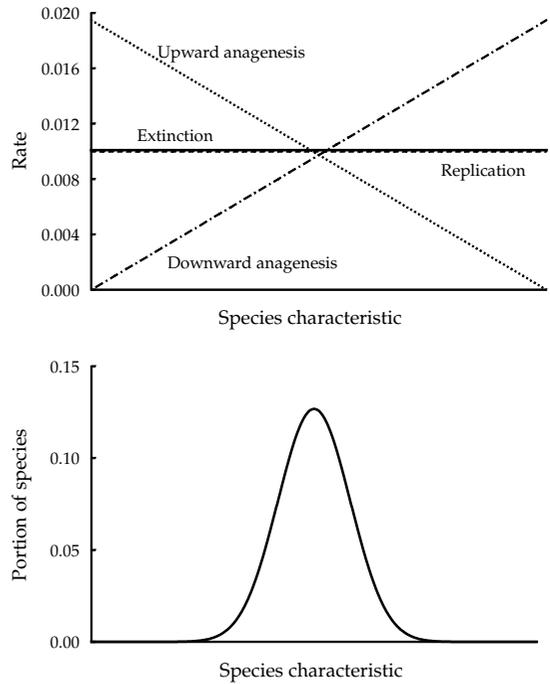
However, it should never be forgotten that selective extinction and speciation are occurring for characteristics other than those being observed in any one specific frequency distribution, regardless of the number of characteristics involved. Some evolutionary processes may be more closely related to a particular species-level characteristic than another. Theoretically, changes may be confined to only the indirect effects of processes or characteristics involving other factors. In the end, such distinctions are more important for identification and understanding the complexity of processes involved than explaining outcome.²⁶ This is because species frequency distributions of the same shape can result from a variety of selective extinction and speciation dynamics and, of course, other contributing factors (Fig. 1.4). However, additional hypothetical examples, as given below, can further illustrate the distinction.

Appendix Figure 3.2.7 shows an example in which speciation rates are nonselective; extinction alone is selective. There is no directional component to anagenic change; evolution both upward and downward is equal so the lines are superimposed. Cladogenesis, in this example, is also nonselective but occurs at a rate high enough to prevent extinction from draining species numbers to zero. Because extinction is the only process in Appendix Figure 3.2.7 that is selective, the frequency distribution in the lower panel is entirely determined by this process. Species accumulate in the vicinity of the species-level characteristic where the extinction rate is at its minimum. The effects of ecological mechanics are ignored in this illustration, but not to be forgotten, as in other examples presented in this appendix.²⁷

Ecological mechanics are also ignored (at least not considered directly) in Appendix Figure 3.2.8, where the frequency distribution of species is determined only by selective anagenesis, because extinction and cladogenic replication occur nonselectively. Selective anagenesis tends to remove species from the higher and lower regions of the range of the species-level characteristic and concentrate them toward the middle. As with all frequency distributions among species (species-level patterns), when this happens, evolution tends to concentrate species in this region as a form of “evolutionary



Appendix Figure 3.2.7 A hypothetical set of selective extinction and nonselective speciation processes (top panel) and the resulting species frequency distribution (bottom panel). Both forms of anagenesis and replicating cladogenesis are not selective and equivalent over the range shown but can easily involve other characteristics of the species involved.



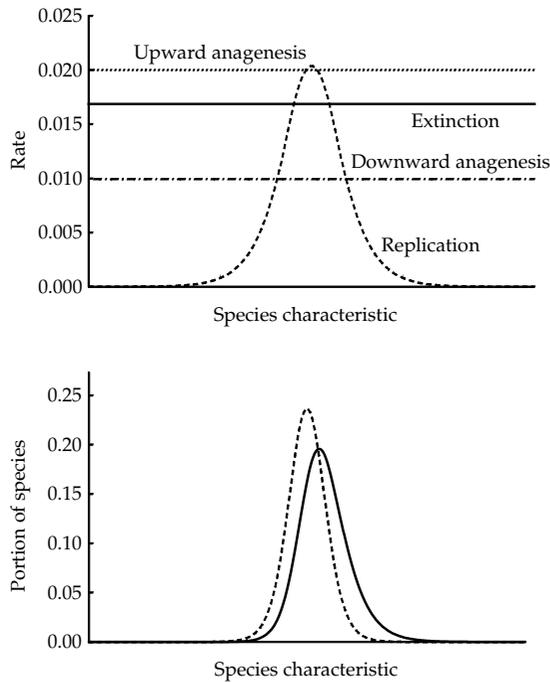
Appendix Figure 3.2.8 A hypothetical set of extinction and selective speciation processes that are not selective (top panel) and the resulting species frequency distribution (bottom panel). Both forms of anagenesis are selective. Replicating cladogenesis and extinction are not selective and nearly equivalent over the range shown.

stable strategy" (ESS, or a kind of Nash equilibrium, Nash 1950a,b) with consequences for species frequency distributions and the ecosystems drawn from them.

A combination of dynamics of Appendix Figures 3.2.7 and 3.2.8 would further reinforce a concentration of species such as shown in the bottom panels of each figure. Such may be the case for density dependence (Fig. 2.21) if anagenic evolution and selective speciation reinforce each other for an ecosystem-level ESS, especially if cladogenesis is relatively nonselective.

In contrast, the species frequency distribution of Appendix Figure 3.2.9 is the result of a hypothetical situation in which only replication (i.e., cladogenesis) is selective. Nonselective extinction removes species along the entire spectrum and species tend to concentrate where they are most rapidly generated by replication.

Directional speciation is influential when upward and downward anagenesis are independent of the species-level characteristic but occur at different uniform rates. This can influence both the shape and position²⁸ of the species frequency distribution. The lower panel of Appendix Figure 3.2.9 shows two frequency distributions. The solid line corresponds to the rates depicted in the panel above. The broken line shows the frequency distribution if the two forms of anagenesis are identical in magnitude to the downward anagenesis in the panel above (i.e., both 1% per unit time). The only difference between the two cases is that the rates of anagenesis differ from each other in one case (solid line in lower panel) but not the other (dashed line in lower panel); neither is selective. For the case in which upward anagenesis is greater than downward anagenesis (solid curve in lower panel), the species frequency distribution is shifted upward



Appendix Figure 3.2.9 A hypothetical set of nonselective extinction and selective speciation processes (top panel) and the resulting species frequency distribution (bottom panel). Both forms of anagenesis are completely equivalent over the range shown. Extinction is nonselective while replicating speciation is selective. The species frequency distribution shown by the solid line in the bottom panel corresponds to the conditions depicted in the top panel. The broken line corresponds to the case wherein both forms of anagenesis are equal to the downward form above.

(to the right) and is wider, compared to the case wherein both are the same.

Collectively, the hypothetical examples of this section show that the nature of species frequency distributions can be significantly influenced by any one of the processes of selective extinction and speciation acting without selectivity in the others. In reality, of course, selectivity involves a huge variety of combinations. Selective speciation alone may be one of the more influential factors in producing some of the patterns observed in nature, while others may have their origins influenced more by selective extinction, or selective evolution (anagenesis). In some cases the species represented in any particular ecosystems may have achieved an equilibrium or balance among

such forces (including nonevolutionary forces). It is likely that the collections of species in natural ecosystems are tending toward such balances as conditions change in their physical environment. This may occur without achieving equilibrium before a new set of conditions comes into play, giving rise to a “moving target” regarding what might ultimately be an equilibrium. Therefore, the observed distributions can only approximate equilibrium conditions, including those resulting from change. To the extent that they occur, such equilibria, or observed patterns, would be the ecosystem-level counterpart of an ESS (or Nash equilibria, Nash 1950a,b) at the species level.²⁹

2.0 Risk compensation in selective extinction

The risk of extinction for an individual species is related to all of its characteristics. Each characteristic either heightens or alleviates risk according to the influence of the species’ environment. For example, a large-bodied species may be at less risk of extinction than a small-bodied species in the same habitat when we consider only its lower population variability (Fig. 2.30). A species at a high trophic level may be at less risk of extinction than one at a low trophic level if we ignore trophic level and consider only geographic range. However, there is tradeoff among risks. Thus, two species may have nearly identical total risks through the tradeoff associated with their different characteristics.

Although the composite risks of extinction for species may thus be quite similar, no two species are expected to face identical risks of extinction. The shape of frequency distributions largely result from limits imposed by the combined effects produced by the risks of extinction for each characteristic. Thus, a species with high population variability, long generation time, high trophic level, small range size, and multiple interspecific dependencies would be unlikely to persist long before extinction. Such a combination would entail risks so high that they could not be overcome through low risk for another trait. Risks are multiplicative, possibly a contributing factor behind the log-normal nature of many patterns in nature (Limpert *et al.* 2001).³⁰

Thus, the risk of extinction contributes to determining the configuration or shape of species-level

patterns, much like a container determines the shape of its fluid or gaseous contents but with limits that are observed to be “fuzzy”. Any diffusion in the process of evolution (or ecological mechanics) results in ever-increasing variability, producing “pressure” against such limits. The boundaries or edges of species frequency distributions are not so sharp or well defined as those established by a container, but are nevertheless real as constraints or limits. These limits, set in part by species being “trimmed away” through extinction, are crucial in finding what is abnormal for systemic management (Fowler and Hobbs 2002).

Thus, a set of species fits within limits defined by macroevolutionary constraints as do the sets of individuals making up species (e.g., Slobodkin 1986). Beyond these boundaries, species often experience increasingly higher risks, including extinction. Evolutionary development that carries species to such combinations of characteristics results in extinction.³¹ Some characteristics cannot evolve owing to constraints from within (intrinsic limits); e.g., infinite life span or carbon-based protoplasm in a carbon-free environment are impossible. Bounds are also influenced by the environment and evolutionary limits on the speciation and evolutionary processes. Evolutionary processes, including selective extinction and speciation, can create only with the raw materials at hand. A species with a trophic level of ten cannot evolve in an ecosystem inhabited by species with trophic levels otherwise confined to six and below.

The “clouds” of species in the multidimensional spaces formed by species characteristics (e.g., Fig. 2.34) represent a counterpart of the niche concept for individual species. The shape and position (form) of these distributions varies from habitat to habitat. Again using the metaphor of a container, the pattern of species characteristics is limited by factors that include the environment. For example, size, measured as biomass, or diversity dependence is limited by factors such as solar radiation and precipitation. For some characteristics, species undergo selective extinction and speciation to conform to the limits set by the environment. For other characteristics, species tend to converge in spaces offering minimum risk for the individuals. Within these dynamics, convergent evolution at all levels

can occur to result in similar strategies in similar settings. As is the case for Nash equilibria in general (Nash 1950a,b), what works at all levels of biological organization is represented in frequency distributions that account for complexity in general (Fig. 1.4).

In the central portions of these clouds of species, where most species are located, extinction risks are likely to be roughly comparable from species to species. They experience the effects of the “tradeoff principle” noted by Rosenzweig (1995). These central locations may include species of quite different combinations of other characteristics. For example, several species may be quite similar to each other in body size, trophic level, and geographic range, but very dissimilar in population variability and numbers of prey species consumed (i.e., different from those characteristics in which the cloud is being viewed). Some combinations of factors contributing to structure and form in frequency distributions among species may even lead to an internal structure; these would be exemplified by bands or strata of species of varying concentrations within species clouds like that of Figure 2.34 (e.g., Holling 1992; note the modes of Appendix Figs 2.1.1, 2.1.12, and Fig. 2.22 of Chapter 2).

Evaluating extinction risk (e.g., for endangered species) is complicated by the tradeoff among combined sources of risk. For the same reason, it is difficult to discover patterns in selective extinction and speciation in the palaeontological record. We are lucky to have comparisons that cover sufficiently broad ranges of species-level characteristics to produce at least a few cases where selectivity is empirically observed, for example those cited in Chapters 2 and 3.

3.0 Ecosystem structure and function

The frequency distributions exemplified by the graphs in this appendix and Chapter 2 represent structure for the sets of species they represent. Various sets of species are represented in ecosystems and the patterns they exhibit are influenced by a large number of factors (Fig. 1.4) that include selective extinction and speciation (Fowler and MacMahon 1982). From the point of view of selective extinction and speciation, measures of

predator-prey relationships (e.g., Figs. 2.6 and 2.7) or any other species characteristic cannot be the principal focus, nor can any one be ignored. All are important in exactly the way they are important in nature and are reflected by the related frequency distributions (Fig. 1.4, Belgrano and Fowler 2008).

We are dealing here with what species frequency distributions are, what they represent, and how they originate. Thus, interactions among species based on materials and energy dynamics (i.e., ecological mechanics) receive no more *a priori* importance than those based on information dynamics exemplified by genetic/evolutionary interaction (e.g., coevolution, Jordano 1987, Thompson 1982). Ecosystem structures based on pollination, seed dispersal, chemical communication, behavior, or vector transmission (e.g., parasites and diseases) also emerge as patterns. Metabolic rates of the various species represented in an ecosystem contribute to its energy dynamics. The metabolic pattern among species contributes to the overall metabolic dynamics for the ecosystem. Species of different metabolic rates occur in different population densities and therefore make different contributions to the total. These are accounted for in the frequency distributions of species by density. Temporal variability is accounted for, in part, by the frequency distribution of population variation. The total is an emergent integration of the effects of selective extinction and speciation over all species-level characteristics, combined with other factors such as the effects of ecological mechanics.

In dwelling on selective extinction and speciation restricted to species-level characteristics, we cannot forget the processes of selective extinction and speciation as influenced by the abiotic environment. As has been mentioned repeatedly, the shapes of real-world selectivity curves (and resulting frequency distributions) are influenced by both the physical and biotic environment. The shapes of the curves that we observe in research are certain to be influenced to some degree by short-term dynamics as well as a variety of other factors, including sampling and other statistical error.

In the popular focus on biodiversity, total number of species is seen as an important characteristic of ecosystems. Total numbers represent but one measure of an ecosystem represented by the area

or volume within species frequency distributions (e.g., the volume under the surface of Appendix Fig. 3.2.5 if it were presented in raw numbers instead of portions of a total, or the volume of the cloud in Fig. 2.34). Perhaps more important is the composition of species, or their distribution in multidimensional space, in an ecosystem, as reflected in the shapes of species-level patterns. No species-level characteristic should be forgotten, each being specific to its physical environment.³² The habitat specificity of such species collections leads to standards of reference in evaluation of ecosystems (e.g., their integrity, Karr 1990, 1991, 1992, and status, Rapport 1989a,b).

The focus of this appendix is more conceptual than applied or empirical. To undertake a complete, reductionistically exhaustive, study of patterns and their formation is impossible for two reasons. First, the number of combinations of groups of more than two factors together increases by orders of magnitude (Table 2.1). The practical impossibility of any serious consideration of all such combinations is clear when the number of species characteristics exceeds a dozen or so. The handful of species characteristics studied so far is only the beginning of the potential number of characteristics that may be the focus of future studies. Recognition of more species-level characteristics (e.g., polyploidy, Masterson 1994, Orr 1990, Rosenzweig 1995) will continue to reveal the complexity of life at the ecosystem level of organization. Because of this complexity, models such as that in Appendix 3.5 are merely tools to understand and appreciate, but never to fully represent, the complexity of ecosystems and their dynamics.

Second, we are only beginning to understand selectivity in extinction and speciation for currently recognized species-level characteristics. The time scale of these dynamics is often orders of magnitude longer than human life spans and the processes are of a complexity only touched upon by palaeontological sciences.

4.0 Relative importance of contributing processes

The main objective of this appendix is to emphasize that among all the factors that contribute

to the formation of species frequency distributions, evolutionary processes cannot be ignored. Importantly, they are not ignored when we use the patterns emergent from such processes to guide management. These include evolution through natural selection among individuals, among species, or among groups of either. Extinction is further emphasized because the risks of extinction are especially important in management.

Having made this point, an important argument can be posed as a claim that is, and will continue to be, subject to debate in scientific circles. The argument makes two assertions; both pertain to understanding the formation of species frequency distributions and both have practical implications. These assertions are:

- That the formation of species frequency distributions may be more influenced by selective extinction and speciation than by the evolution of species themselves, involving natural selection among individuals.
- That the combination of evolutionary processes probably are much more important than ecological dynamics and mechanics in the formation of species frequency distributions. In other words, both species- and individual-level selection are more important than the nonevolutionary factors.³³

While these assertions are relevant as scientific issues, they are relatively unimportant to management. We can use species frequency distributions as they represent natural variability whether or not we understand, or can agree about, how they arose.³⁴ The actual importance of such contributing factors is inherent in the empirical information (Fig. 1.4). Origins and explanations should be debated (e.g., see Hubbell 2001) but not to the exclusion of utility.

Why should we expect that selective extinction and speciation are so important? The argument is basically one of hierarchical constraint (e.g., Ahl and Allen 1996, Allen and Starr 1982, Bateson 1972, Burns *et al.* 1991, Buss 1988, Koestler 1978, Mayr 1982, McNeill 1993, O'Neill *et al.* 1986, Orians 1990, Salthe 1985). Very simply, selection at the species level occurs across the effects of selection at the individual level and ecological mechanics and,

furthermore, places limits on what is allowed both in microevolution and mechanical dynamics.

Consider nonevolutionary factors first. If the population of a species varies because of seasonal variation in the physical environment (e.g., fluctuations in temperature, rainfall, or radiation), it is experiencing the effects of ecological mechanics. Both population level (numbers) and population variation are influenced by such mechanics in the short term. However, species with characteristics that resist these kinds of influences, and have reduced population variability as a result, are at an advantage over species that have not adapted. On average, the adapted species experience less risk of extinction from population variation than those vulnerable to the effects of ecological mechanics that result in variation in population numbers. Overall, the stress of mechanical dynamics results in adaptation among species just as the stress of ultraviolet radiation results in adaptation to survive its effects among individuals.

The same argument can be made for biotic mechanics. For example, species that experience population variation from predator/prey interactions are, on average, more subject to extinction than species with less variation from these causes. Some species are expected to survive the extinction risks of variation by virtue of characteristics that make them less vulnerable than those with characteristics that lead to predator/prey cycles. As a result, the effects of biotic mechanics in the formation of species frequency distributions are expected to be dominated by the evolutionary effects of selective extinction and speciation. When mechanically induced characteristics pose risk of extinction, extinction tends to win.

Now consider evolution through natural selection within species, exemplified by cases in which there is variation in the heritability of directional anagenesis.³⁵ Natural selection will occur at the species level between species with heritable evolutionary trends and species having characteristics that resist trends. One or the other will be favored. Which comes to predominate depends on whether the trends lead to increased or decreased risk of extinction (Combinations 5 and 6 of the interactions described in Chapter 3, Table 3.1). For example, at the species level, characteristics have

selective advantage if they avoid or prevent evolution toward larger body size when increasing body size leads to greater risk of extinction. Vulnerability through limited evolutionary plasticity results in the extinction of species that do not possess such characteristics. An exoskeleton that prevents insects from attaining large size, for example, may make them less vulnerable to extinction than species with endoskeletons that allow large size. The result would be what we see: larger numbers of invertebrate species than vertebrates.

These arguments are not meant to reject contributions to the formation of species frequency distributions from nonevolutionary factors and microevolution. They are presented here only in superficial form, but they cannot be ignored. At this point in the history of science, many will consider the idea no more than a hypothesis. However, to the extent that these arguments have substance, nonevolutionary factors are little more than sources of short-term variation for individual measurements of species in regard to their position within species frequency distributions and varying risks of extinction. As such, the argument is meant to emphasize the need to account for the risk of extinction, including our own, in our decision making. This happens in the use of patterns to guide management which avoids the abnormal.

Notes

1. The fraction would never be exactly the same because of stochastic differences due to the complexity of process involved. They would be the same only averaged over time in the case of no long-term trend—a situation which may be rare.
2. From here forward the term replication will be used to refer to cladogenesis in which no change in category occurs (but for which there would be an increase in species numbers). It is thus analogous to birth rates at the population level and represented by the size of arrows in Appendix Figure 3.2.1. Related processes include the simple continued existence of a species in a category and species in a category which undergo anagenesis but of a form that is either (a) insufficient to change categories or (b) for an unrelated species-level measure that gives rise to a new taxonomic designation. The latter processes apply to crude rates that carry species forward in time and the multiplicative factors generated in the models of this appendix (to include the replication rate).
3. Because actual (especially constant) equilibria are rare in nature and entirely relative to time scale, the concept may better be characterized as one of a tendency toward equilibrium in tracking or following changing environmental conditions. It is important to distinguish the equilibria one might expect based on a model from empirically observed patterns as tendencies that emerge from the complexities of natural circumstances.
4. The term “relative” refers to the fact that one is smaller or larger than the other regardless of the absolute numbers involved in their total. This way both groups could be growing or declining in absolute numbers but one more so than the other. This would result in changes in the ratio of the number of species in one group to that of the other making the comparison relative.
5. This paragraph counters any tendency to conclude that cases with high speciation are cases in which species numbers must be high (or the reverse, to conclude that because species numbers are high speciation rates must be high).
6. The effect of body size must be accounted for here. Among the microscopic species of bacteria, viruses, etc., asexual reproduction may predominate.
7. See endnote 30, Chapter 3.
8. The combined elements of extinction, speciation and evolutionary change are not always presented together but as Eldredge (1985) says: “Sex prevails at least in large measure because it creates stable, extinction-resistant entities in nature”. The simplicity of the explanation provided by selective extinction and speciation is often expressed in similar simple statements but other works spell out the process in more detail (e.g., Blackman 1981, Buss 1988, Eldredge 1985, Gould and Eldredge 1977, Maynard Smith 1983, 1988, Stanley 1975b, 1990a, Vrijenhoek 1989).
9. If these situations are related back to Table 3.1, we see a gradation from combination 2 on the left side of Appendix Figure 3.2.2 to combination 5 on the right. In the middle, corresponding to the peak accumulation of species, is combination 1 wherein species are supplied by replication and anagenesis from below at a rate that (in combination) is not overshadowed by extinction as fast as in cases further to the right.
10. Thus, anagenesis in this example is stochastically directional because it proceeds predominantly (but not exclusively) in one direction.
11. Such models become the basis for ecosystem modeling as based on a genetic view of species frequency distributions involving species sets from which ecosystems are assembled. Such models would be expanded, in

principal, to the many dimensions that apply as species-level characteristics and would involve the coevolutionary aspect of each species in its effect on the others (including the reciprocity). This is to be compared to ecosystem modeling based primarily on ecological mechanics typical of conventional ecosystem science.

Models of selective extinction and speciation exhibit a parallel with models in the study of populations. This parallel concerns the methodology of continuous versus discrete variables. The approach, often attributed to Lotka (1939, e.g., Goodman, 1981), considers population birth rates and mortality as continuous functions of age. Frequency distributions of individuals by age (age distributions) are also treated as continuous. This approach in population studies is analogous to Slatkin's (1981) for species groups wherein species characteristics are treated continuously. The method applied to species groups in Appendix 3.5 is analogous to that of Leslie (1945, 1948) for populations, with discrete groups in each case. Age-groups of populations and categories of species are considered discrete. Both Slatkin's approach and that in Appendix 3.5 capture the basic elements of species dynamics and allow for exploration of the ways selective extinction and speciation might be realized for any particular characteristic of species.

Such models differ from population models (except for models of geographic distribution) in that models of selective extinction and speciation are diffusion models (Slatkin 1981). In reality, the rates of evolution, speciation, and extinction are often likely to depend on species numbers in specific categories (character-specific diversity dependence) such that the respective rates are also functions of the species number at the corresponding level of the species-level trait.

12. Specifically, the values shown in the graph are 40 points connected by a smoothed line. The 40 points were determined by application of the procedure detailed in Appendix 3.5 using the parameter values shown in the top panel. The lower panel of this graph (and other similar graphs in this appendix) thus represent the distribution of species at an assumed equilibrium. In nature, the dynamics of the abiotic environment and other factors can be expected to prevent achievement of this precise form. It would not be surprising to find close approximations as frequency distributions track their environment as dynamic Nash equilibria (see endnote 29 of Chapter 3, and Fig. 1.4).

13. Keep in mind that these examples are to demonstrate the mechanics of selective extinction and speciation abstracted from the effects of ecological mechanics (especially current effects of human influence, and species-level movement as changes in geographic range that

would be experienced as species-level immigration/emigration by ecosystems).

14. This is parallel to embryological development. It reflects both the effects of external environments as well as internal interactions. In the embryological development of individuals, some tissues influence the growth of neighboring tissues and together are responsive to environmental circumstances exogenous to the organism.

15. This might be viewed as a set of cases wherein the eight combinations in Table 3.1 are reduced to four because anagenesis is without effect. The remaining combinations would involve the pairs 1 and 7, 2 and 8, 3 and 5, plus 4 and 6.

16. Again, found by the procedure described in Appendix 3.5 as with all the following examples.

17. Thus, we again see potential for order out of chaos consistent with the views of Prigogine (Prigogine and Stengers 1984). The stress of such change would eventually be expected to result in selective pressures to which ecosystems would respond with solutions found in species-level selection.

18. The use of the term "may" here and elsewhere relates to the examples as hypothetical examples. But it also relates to the stochasticity, complexity and uncertainty that will always exist in explanatory sciences reduced to the elements focused on by each field of science. In Chapters 4, 5, and 6, this will be revisited as basis for precautionary approaches to management.

19. Each mutation produces a new strain. Owing to the lack of sexual reproduction such mutations cannot be incorporated into the genetic code of any but the direct descendants of the parents with the mutations. Due to the short generation time for the tiny species such strains may accumulate mutations to further diversify at a rapid pace. Although this presents a taxonomist's nightmare, it does represent rapid evolution and a cladogenic-like diversification regarding species-level characteristics.

20. These models might go so far as to include components which generate the shapes of the rate curves of the upper panels of graphs in this appendix as functions of environmental conditions (the abiotic influence on selectivity). In any case, the models shown in this appendix are simple enough to be exercised using ordinary spreadsheet software. In no case is a model the reality it represents, but is helpful in understanding and appreciating the reality of the kinds of dynamics involved.

21. If, over evolutionary time, a species adapts in such a way as to promote geographic relocation, it is much like a "mutation" at the species level (among a set of species). This kind of dynamic can result in changing total species numbers, as well as numbers within any specific category, of a species-level pattern.

22. See the discussion of Figure 2.19 and references such as Gaston and Lawton (1988a,b), Hanski (1990), Pimm (1991), and Sinclair (1996) regarding population variability and body size.

23. The literature (e.g., Brown and Maurer 1987) regarding correlations between population density and body size should be consulted for a wide variety of explanations (and possible biases) for this relationship. Some of these were noted in Chapter 2.

24. It is within such balances, especially when they are caused by small differences in rates, that small environmental influences may have large effects. These would be the equivalent of "butterfly effects" in determining outcomes expressed in the patterns we observe (e.g., Bateson 1979, Gleick 1987, Koehl 1989 and Pennycuik 1992).

25. The limits set by extinction are easily understood in that characteristics that guarantee extinction (especially instantaneous extinction) will not exist.

26. Some processes (like extinction) may more rapidly respond to environmental forces than others so the importance of recognizing each component is not lost.

27. The ecological mechanics of conventional ecosystem models involve parameters that determine the interactions represented among populations, the density dependence of each population, and give rise to model behavior that includes population variation. This chapter and appendix deal with the evolution of such 'parameters' in the real world and the evolution of emergent behavior (or other characteristics) thus subject to higher level evolutionary processes through selective extinction and speciation. In this sense, selective extinction and speciation are among the processes that would be part of the answer to questions regarding the origin, existence, and relative frequencies of parameters within conventional ecosystem models.

28. As an ecosystem characteristic, the mean of species-level features is thereby influenced, when the set of species involved are determined by their cooccurrence in a geographic area.

29. Evidence for equilibria in species numbers, lack of evolutionary change (also referred to as stasis) and other forms of equilibria are discussed by Eldredge (1991), Stanley (1989), Webb (1987), Willims (1992), and Wright (1945). Evidence for ecosystem-level convergent evolution is seen in the similarity among ecosystems in similar habitats (e.g., deserts, rain forests, lakes, etc.). These are Nash equilibria in the sense that the advantages for both the species and its individuals play into their formation; anything disadvantageous for either will not work.

30. This is explained by the multiplicative nature of the probability of surviving independent risk. Risks of such magnitude cannot be mitigated through low risk

attributes that are unrelated, such as sexual reproduction. However, in probabilistic terms, if such a species exists it would be expected to reproduce sexually (as well as to exhibit low risk of extinction from all of its other characteristics).

31. This would be exemplified by Appendix Figure 3.2.4 wherein upward anagenesis carries species to extinction. It can be argued that dynamics of this type (not necessarily this specific example but all combinations of types 5 and 6, Table 3.1) are more common than not ('evolutionary suicide,' 'evolution to extinction,' or 'Darwinian extinction'; Dobzhansky 1958, Parvinen 2005, Potter 1990, Rankin and López-Sepulcre 2005). Virtually all species produced by natural selection at the level of the individual have gone extinct.

32. Saying that such things should not be forgotten is not equivalent to saying that they should be included in conventional models. The latter is impossible; in the end, it is impossible to include everything in man-made models owing to complexity. Urging that they not be forgotten is merely a matter of restating the need to be sure that they are accounted for, especially insofar as it relates to management (Management Tenet 3, Chapter 1).

33. It should be noted that this would imply that conventional ecosystem models largely miss their mark in representing ecosystems. It is not an argument that ecological mechanics are not part of what happens in ecosystems, only an argument that the patterns in ecosystem structure and function (including ecological mechanics) as we observe them are more heavily influenced by natural selection than as direct products of the mechanics alone.

34. What is being said here is simply that we can adhere to the principle of management dictating that we should maintain components of ecosystems within their normal ranges of natural variability (Tenet 5, Anderson 1991, Apollonio 1994, Christensen *et al.* 1996, Fowler and Hobbs 2002, Francis *et al.* 1999, Fuentes 1993, Grumbine 1994, Holling and Meffe 1996, Mangel *et al.* 1996, Moote *et al.* 1994, National Marine Fisheries Service Ecosystem Principles Advisory Panel 1998, Pickett *et al.* 1992, Uhl *et al.* 2000, Wood 1994) without understanding or explaining the variability. This statement is not meant to say that understanding is unimportant. For example, understanding what is normal and what is abnormal is critically important, as is understanding the matter of patterns representing the factors that contribute to their emergence (Fig. 1.4).

35. An example might be the heritability of features that either resist or promote the evolution of asexual reproduction. Early sexually reproducing species might have been divisible into two groups, those with greater range

of options to evolve asexual reproduction than those (the other group) that had heritable characteristics that tended to resist reversion to asexual reproduction.

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