

10 How Many Levels Are There? How Insights from Evolutionary Transitions in Individuality Help Measure the Hierarchical Complexity of Life

Carl Simpson

How the vast range of spatial and temporal scales on which biological processes interact and relate to each other is a fundamental problem in evolutionary biology. The standard solution was given by Darwin and formed the core of the modern synthesis. Observed processes of organisms interacting with their environment (which includes other organisms) produce all the patterns at all spatial and temporal scales. From this perspective, biology is uniformitarian, patterns at all scales are thought to be caused by the observable local processes. Unfortunately, observations at large scales do not seem to be reducible to local patterns in all cases. The most critical of these observations are those transitions in evolution known as evolutionary transitions in individuality (Buss 1987; Maynard Smith and Szathmary 1995; Michod 1999). What occurs during these transitions is the passing of the dominant fitness components from one level of organization to a higher, more inclusive level, and with it new levels of organization, evolution, and ecological interaction emerge. That is to say, as the new level of individuality emerges, we find new agents that not only have fitness values, the fitness of these new agents dominates the evolutionary trajectory of them and their components.

From the view of some standard theory, these transitions are impossible. The lowest levels of selection are thought to always dominate because of higher heritability, shorter generation times, and other factors that seem to stack the cards in favor of the lowest levels. Yet, the transition from individuated cellular to well-individuated multicellular life occurred approximately sixteen times in largely unrelated groups (Bonner 2001; Maynard Smith and Szathmary 1995), and that from individuated multicellular life to partially individuated colonial or social life occurred multiple times in ten animal phyla (Wilson 1975). That may not seem like a lot considering those occur over 4.6 billion years and among countless other origination events, including the origin of life, but though these events are rare, they also seem to be patterned: Often these transitions occur in clusters of independent events like during the Cambrian Explosion. Clearly, these are not just statistical possibilities.

Since the modern synthesis, only conceptual work on the hierarchical nature of life has tried to explicitly incorporate the diversity of processes at the varying spatial and temporal scales in which organisms live and evolve. Curiously, all the hierarchies are rigid, having

only a few discrete levels of fixed rank. And there are often two hierarchies, one for organisms and one for their interactions. There are the replicator/interactor hierarchy (Hull 1980), the replicator/vehicle hierarchy (Dawkins 1982), the genealogical/ecological hierarchy (Eldredge 1985; Eldredge and Greege 1992), the codical/material hierarchy (Williams 1992), and the fraternal/corporate hierarchy (Queller 2000). It is curious, at least when viewed with a desire to unify phenomena, that when hierarchy theory encounters biology, it splits its effort. After all, the level both hierarchies have in common is the organism.

Because the majority of work on hierarchies did not realize the importance of the major transitions, most existing hierarchies are themselves static, unevolving, and synchronic. After Buss (1987), we know that any hierarchy must be diachronic and evolvable. The emergence of new hierarchical levels during a major transition explicitly allows for the hierarchy as a whole to evolve over time (Buss 1987; Maynard Smith and Szathmary 1995; Michod 1999). But while theories of the major transitions are dynamic, they have not tried to incorporate ecology and evolution, which leaves the dual hierarchies, flawed as they may be, as the only hierarchy that takes ecology seriously.

Buss's notion that individuality is derived can teach us an additional lesson about the emergence of new levels. Individuality is derived, but poorly individuated organisms are still common today, yet they can themselves undergo additional major transitions. The sponges and cnidarians provide the best examples. Though they originated over a period of more than 550 million years, only a few lineages have increased their internal integration, but never as much as a simple bilaterian. Yet, both form aggregations and have many colonial species. Is a sleaze of sponges or a coral colony at the same level as colonial or social groups that evolved from highly individuated organisms such as social insects or mammals? There is no clear answer, but individuality itself cannot be the sole criterion for a new level. The hierarchical levels included in the major transitions and transitions in individuality seem to be only those that are highly derived, where it is easy to distinguish between levels.

These problems with current concepts in hierarchy and the major transitions do not allow us to answer some important questions about the hierarchical history of life: How many levels are there now and how many have there been in the past? Over time, we presume that the number of levels only increases cumulatively from the primitive prokaryotic level, through the eukaryotic, multicellular levels, and finally to the colonial level. But the levels in this list are independently derived many times with no constraint on what level the ancestor was at. The levels on this list also ignore ecological levels. A measure of the hierarchical complexity over time should include all types of levels.

Three phases can be identified in transitions in individuality. The aggregate phase is the least individuated, the group phase intermediately individuated, and the individual phase is the most. Each phase is characterized by a dominant fitness component. Differential expansion is the component associated with aggregates, differential persistence is associated with groups, and differential reproduction is characteristic of paradigm individuals. Evolu-

tionary transitions to more individuated phases require the accumulation of additional fitness components, but new levels are attained once the expansive component of fitness is attained. This allows us to know that organisms in each of the three phases of individuality are at the same level if they share a common ancestor.

The aggregate phase has never been considered important in major transitions, but turns out to be essential in the emergence of a new level of selection. The recognition of the aggregate phase allows for the precise identification of a new level and is general enough to incorporate both ecological and genealogical levels as aggregates of organisms from any number of species.

Transitions in Individuality

The View from Current Theory

Transitions in individuality occur when a lineage of organisms of a particular hierarchical level of organization evolves such high integration among organisms that the aggregations eventually become individuals at a new higher level. An explanation of transitions in individuality must describe the emergence of a new level and the subsequent individuation at that level.

It is generally understood that the major challenge a lineage faces when undergoing a major transition in evolution involves the emergence of fitness at a new level (Michod 1999; Okasha 2006). Traditionally, fitness in this context is taken to be reproductive-output measurable by the number of offspring produced. If a new level of fitness is the number of offspring groups produced by a group, it is easy to see how difficult it would be for selection among groups to operate: The number of descendent groups would be tiny compared to the number of offspring produced by constituent organisms. This seems to limit the efficacy of high levels of selection to very particular circumstances, the most important being a decrease in reproductive effort at the lower level (Wade 1978; and see Rice 1995, for other interesting examples).

There is more to fitness than the production of offspring. At the very least, there is also differential viability, or persistence, since some organisms live longer than others. Sometimes living longer allows the organism to produce more offspring, but more importantly, the frequencies of phenotypes in the future are affected just by the existence of long-lived organisms. Michod and collaborators (Herron and Michod 2008; Michod 2006, 2007; Michod et al. 2006; Michod and Herron 2006; Roze and Michod 2001) developed models showing that a simple trade-off between cell reproduction and viability in Volvocacean algae can contribute to a successful transition in individuality—as is indicated by the presence of a germline in the derived colonial members like *Volvox*.

Fitness in Michod's models is the product of viability and fecundity. The fitness of a single cell may be quite low if it specializes in reproduction or viability at the expense of

the other. Each cell has a life history describing its partition of fitness into reproductive and viability components. The colony as a whole has a large number of cells with variation in their life histories. In Michod's model the fitness of the colony, w , can be greater than the average fitness of cells (\bar{w}_p , subscripts are explained in table 10.1) if the covariance between each constituent cell's commitment to growth (v) and reproduction (b) is less than zero. Michod defines colony level fitness as $w = \bar{w}_p - \text{cov}(v, b)$ (Michod 2007).

Michod's model requires that somatic cells tend not to undergo cell division, which in plants and Volvocaceans is what is observed. However, this model does not generalize to animals. At the organismal level, animals have a huge range of somatic cell types that can produce germ cells even after they undergo considerable cell division (Buss 1987; Nieuwkoop and Sutasurya 1981). At the colonial level, clonal growth and sexual reproduction commonly co-occur. Animals have undergone transitions in individuality from cellular to multicellular as well as from multicellular to colonial levels at least fifteen times. It seems that at least half of the examples of transitions in individuality do not satisfy Michod's requirement that $\text{cov}(v, b) < 0$.

In animals, cell division is critical for developmental differentiation and growth. Animals seem to happily ignore the theoretical difficulties with the emergence of a new level of fitness, they are all highly individuated at the organismal level with apparently high fitnesses at the cellular and organismal level. To illustrate the issue, an individual of the cnidarian *Hydra* has 121 cells of 15 types (Bell and Mooers 1997) and a large number of offspring. The dog *Canis familiaris* has $10^{13.7}$ cells and 99 cell types (Bell and Mooers 1997), and on average 42 offspring across 7 litters, assuming 6 puppies a litter. An animal starts its life with a single cell and ends with potentially trillions of cells. Almost simultaneously new offspring can be produced, but the number of successful offspring can be orders of magnitude lower than the numbers of cells. Cell division and organismal reproduction are clearly decoupled.

Since the majority of transitions in individuality occur in animals, first from single cellular to multicellular transitions in the origin of the Metazoa, and subsequently in a number of colonial transitions in a number of animal phyla, we must understand how reproduction can evolve at a new level. A complex trait like reproduction to evolve requires the prior emergence of other components of fitness at the high level.

Expansion Is a Third Component of Fitness

Though it is not widely known, significant conceptual work on levels of selection has been done by Leigh Van Valen since the early 1970s, though with a much different focus than standard multilevel selection theory. As a consequence of trying to understand the implications of the Red Queen's hypothesis, Van Valen (1976) proposed a very general interpretation of fitness; fitness is best understood as the amount of energy an evolutionary entity controls that is available for expansion. This energy could be quantified as the number of reduced

carbon atoms available for oxidation, or the number of calories stored in an organism's tissue. For example, an organism controls some amount of energy from food sources, some of which is used to repair damaged tissues, the remainder can be used either to grow or to produce offspring. The expansive energy is that which can be used for growth or reproduction.

To see how the notion of expansive energy is useful, we can translate it to a more traditional counting-based notion of fitness where fitness is the number of individuals an organism produces. But what is an individual? The problem is that biological individuality corresponds roughly to how countable a type of organism is. Not all organisms are countable. Some, like snails, come in roughly the same size and have a discreet boundary, so that it is easy to understand what we mean by ten snails. But most sessile organisms in the marine benthos and a wide variety of plants are poorly individuated solitary and colonial organisms that can be of almost any size (see Clarke, this volume, for a discussion of plants in the context of transitions). A single large bryozoan colony can easily contain as many zooids as one hundred smaller colonies. What, then, do we mean by ten bryozoan colonies? Harper (1977) proposed counting genetic individuals called genets or alternatively counting physically defined modules called ramets. So ten bryozoan colonies would consist of ten genets, and the number of ramets would be equal to the number of zooids in all the colonies. The numbers of genets and ramets are essentially estimates of expansive energy. If an organism produced no offspring, instead spending all its expansive energy on growth (which includes clonal reproduction), the number of ramets would be directly proportional to expansive energy (in units of calories, for example). Alternatively, all expansive energy could be used for the production of offspring. The number of genets would be directly proportional to the expansive energy.

The expansive energy notion of fitness allowed Van Valen (1976) to distinguish three components to fitness: differential expected expansion (or growth), differential expected persistence (or viability), and differential expected multiplication (or fecundity). All three can change the frequencies of traits in a population over time. They are standard values, so that even if one does not accept the energy notion of fitness itself, the importance of these three components can be understood in standard theory.

The Three Phases of Transitions in Individuality

Conventionally, the fitness of a biological entity is the product of its reproductive output (multiplication) and its viability (persistence) (Michod 2007). But this notion of fitness is inadequate for understanding transitions in individuality, because in the earliest phase, nothing like reproduction in the usual sense occurs. Nor does the most primitive aggregate persist in any obvious way, because they may continuously break apart and form anew. In fact, the traditional fitness components are themselves built at each new level of

individuality (as is individuality itself) (Buss 1987). A more fundamental notion of fitness is required (Van Valen 1976), which includes three components: expansion, persistence, and multiplication. In this more general sense, an entity that expands more than another is more fit. A bamboo that covers a field by sending out clonal runners is more fit than one that consist of only a single shoot. Likewise, a bristlecone pine alive for thousands of years is more fit than another lasting a century.

In the following subsections I use a multilevel expansion of Sean Rice's (2008) stochastic derivation of the Price equation (Frank 1998; Hamilton 1975; Okasha 2006; Price 1972; Rice 2004) to describe multilevel evolution during the three phases of transitions in individuality. Rice's stochastic equation is useful because it treats phenotypes and fitness as random variables, which allows us to describe evolution prior to the origin of reproduction in the new whole, when random fragmentation predominates. Treating both fitness and phenotype as random variables, we can describe how both the phenotype and number of offspring depend on the size of the propagules formed in addition to the phenotype and size of the parent. In other words, the offspring of a parent with a specific phenotype will be very different phenotypes depending on the number and size of offspring produced. This contrasts with the standard Price equation, where the parent can produce only a set number of offspring of a particular type as a function only of its own phenotype.

The form of a hierarchical expansion of the stochastic Price equation is similar to other multilevel expansions (Frank 1998; Hamilton 1975; Okasha 2006; Price 1972; Rice 2004). It is most similar to the version of Arnold and Fristrup (1982) developed for studying species selection, however, because by recognition of expansion, a clear distinction between the multiplication of parts and the multiplication of wholes is possible.

Damuth and Heisler (1988) distinguish between multilevel selection type 1 and type 2, where either multiplication is of members of a whole (MLS 1), or multiplication of the wholes themselves occurs (MLS 2). Although they intended to clarify the differences between species selection and group selection, it has become clear that the key to understanding major transitions is understanding how MLS 1 evolves into MLS 2 (Okasha 2006). An understanding of the evolution of reproduction using the multilevel stochastic "Rice equation" allows us to understand how MLS 1 can transition into MLS 2 (table 10.1).

The basic form of the Price equation tracks the change over time in the mean of a trait in a population ($\Delta\bar{\phi}$). The mean trait value changes due to selection and changes that occur during the process of reproduction, including a lower level of selection. Selection is described by the covariance between fitnesses, w , and traits, ϕ : ($\text{cov}(w, \phi)$). Changes due to other processes can be summarized by the expected change in traits between offspring and parent ($\phi^o - \phi = \bar{\delta}$), weighted by the fitnesses associated by those traits, $E(w\bar{\delta})$. Adding the values of those two terms and scaling them by the average fitness (\bar{w}) describes the change in the mean trait value over time. The basic single level Price equation is

Table 10.1

Symbols and notation for the hierarchical expansion of Rice's (2008) stochastic version of the Price equation.

Level	Symbol	Meaning
Whole	N	Population size
	ϕ	Phenotype of a whole
	ϕ^o	Mean phenotype of a whole's offspring
	δ	$\phi^o - \phi$
	$\hat{\delta}$	Expected mean value of δ in the population
	m	Reproductive output of a whole
	v	Persistence (viability) of a whole
	w	Demographic fitness of a whole; equal to mv
	\bar{w}	Expected demographic fitness in the current environment
	Ω	$\frac{w}{\bar{w}}$ conditional on $\bar{w} \neq 0$
	E	Expansive fitness of a whole; equals $n_g \bar{w}_p$
	Parts	n_g
ϕ_p		Phenotype of a part
ϕ_p^o		Mean phenotype of a part's offspring
δ_p		$\phi_p^o - \phi_p$
$\hat{\delta}_p$		Expected mean value of δ_p in the population
w_p		Demographic fitness of a part
\bar{w}_p		Expected demographic fitness of parts within a whole
Ω_p		$\frac{w_p}{\bar{w}_p}$ conditional on $\bar{w}_p \neq 0$
\bar{w}_p		Average fitness of parts across all groups

$$\Delta \bar{\phi} = \frac{1}{\bar{w}} [\text{cov}(w, \phi) + E(w\bar{\delta})] \tag{10.1}$$

Rice's stochastic version has one additional variable, Ω , which is equal to w/\bar{w} , where w is the fitness of an individual and \bar{w} is the average fitness of the population; Ω is conditional on $\bar{w} \neq 0$. Variables with a hat, that is, $\hat{\delta}$ and $\hat{\Omega}$, indicate the expected value of the random variable in question. Variables with a bar are the average values of those variables. The stochastic Price equation (Rice 2008) is

$$\Delta \bar{\phi} = \text{cov}(\phi, \hat{\Omega}) + \text{cov}(\hat{\delta}, \hat{\Omega}) + \overline{\text{cov}_i(\delta, \Omega)} + \bar{\delta} \tag{10.2}$$

Equation 10.2 contains two more terms than equation 10.1. The first, $\text{cov}(\hat{\delta}, \hat{\Omega})$, measures the covariance between expected fitness and the expected difference between parent and offspring. This term will be positive if offspring with high expected fitness are consistently different from their parents. The covariance is calculated over the entire population. The

second additional term, $\overline{\text{cov}(\delta, \Omega)}$, measures the covariance between the number of offspring a single parent produces and the difference between offspring and parent. This term will be nonzero if the number of offspring an individual produces is related to the phenotypes that are produced. Several biological processes could be described by this term, including “offspring-size/clutch-size tradeoffs” (Charnov and Ernest 2006), and importantly for transitions in individuality, any relationships between propagule size and offspring phenotype.

The term, $\bar{\delta}$, is the average difference between ancestors and descendents. Many processes can be incorporated into the value of this term, but importantly, evolution at a lower level of selection directly effects $\bar{\delta}$. Since the difference between ancestors and descendents can be taken over any time interval, $\bar{\delta}$ takes the same form as $\Delta\bar{\phi}$, but with selection and other processes occurring at a lower level; $\bar{\delta}$ itself can be described by some form of the Price equation (Arnold and Fristrup 1982; Frank 1998; Hamilton 1975; Okasha 2006; Rice 2004; Simpson 2010). The form underlying the Price equation describing $\bar{\delta}$ depends on the type of group level reproduction that is occurring. In the primitive case, there is no group reproduction per se, but each group (or patch) may have its own inherent rate of population growth. Assuming that selection and mutation are the only sources of change within groups, and that group phenotypes and group growth rates are random variables, $\bar{\delta}$ equals

$$\bar{\delta} = \text{cov}(\phi_p, \widehat{\Omega}_p) + \bar{\delta}_p \quad (10.3)$$

The covariance term measures the effects of selection, while $\bar{\delta}_p$ measures the average difference between parent and offspring members. The variable Ω_p is the ratio between the group-specific growth rate, \bar{w}_p , and the growth rate of the whole population of groups, \bar{w}_{p_i} .

The expected change between ancestors and descendents ($\hat{\delta}$) is also needed in two terms in the equation 10.2. The importance of this value increases during the later phases of transitions because the expected offspring values depend on the mechanisms that produce offspring. Rice (2008) also provides a form of his equation written as the expected change in mean phenotype ($\Delta\hat{\phi}$), which is incorporated in a hierarchical expansion, by noting that $\Delta\hat{\phi} = \hat{\delta}$ and recursively expanding:

$$\hat{\delta} = \text{cov}(\hat{\phi}_i^o, \widehat{\Omega}_p) + \overline{\text{cov}(\phi_i^o, \Omega_p)} + \bar{\delta}_p \quad (10.4)$$

During evolution through the three phases of transitions, $\hat{\delta}$ becomes increasingly important because its values are deeply coupled with the mechanism of emerging level reproduction.

Substituting equation 3 (but not equation 10.4, for clarity) into equation 10.2 gives the full hierarchical expansion. Where the term $\hat{\delta}$ occurs, equation 10.4 can be substituted. The terms are shifted vertically to visually indicate their level of operation. We can identify selection at the level of wholes, interaction between the behavior of the parts during the reproduction of the wholes (where wholes and parts interact), and evolution among parts. The change in group phenotype over time is given by

$$\begin{array}{l}
 \text{whole} \qquad \qquad \text{wholes and parts interact} \qquad \qquad \text{parts} \\
 \Delta\bar{\phi} = \text{cov}(\phi, \hat{\Omega}) \\
 \qquad \qquad \qquad + \text{cov}(\hat{\delta}, \hat{\Omega}) + \overline{\text{cov}(\hat{\delta}, \Omega)} \\
 \qquad \qquad \qquad \qquad \qquad \qquad \qquad \qquad \qquad + \text{cov}(\phi_p, \hat{\Omega}_p) + \bar{\delta}_p
 \end{array} \tag{10.5}$$

Remember that the form of this multilevel description is constant throughout evolution during the three phases. Each term takes on new values as the mechanism of reproduction of wholes evolves. The first phase begins when organisms aggregate in some way.

Phase I: The Aggregate Phase

Despite the unfamiliarity of expansion as a fitness component, it is a direct reflection of the conventional components of the fitness of the members when viewed from the level of the aggregate or group. Indeed, differential expected expansion of aggregates changes the frequencies of members in a population in just the same way as differential multiplication of the members of the aggregates does; the only difference is the focal level (figure 10.1). The standard theory assumes that the average fitness of members (\bar{w}_p) is equal to the fitness of the group (w) (Frank 1998; Okasha 2006; Rice 2004). I find that definition difficult to accept because fragmentation of an aggregation (multiplication at the higher level) is independent of the reproductive output of the members, even in primitive examples. It is more parsimonious to treat the average member fitness, \bar{w}_p , as what it is—the population growth rate. In the expansive framework, expansive aggregate-level fitness (E) equals the average member fitness (\bar{w}) multiplied by the group size (n_g): $E = n_g \bar{w}_p$. Of course, these two definitions of group-level fitness are mathematically similar. The important aspect to remember is that, by equating the average fitness of members with the expansive fitness of aggregates, we do not assume that the aggregates themselves produce descendent *aggregates*, only that the aggregates themselves change in size or extent.

Okasha (2006) made a similar conceptual distinction following Damuth and Heisler (1988). He identifies two classes of group-level fitnesses: collective fitness and particle fitness. Particle fitness is the number of offspring constituent *particles* a collective aggregate produces, and collective fitness is the number of *collectives* a collective produces (which Okasha calls collective fitness₁ and collective fitness₂, respectively). During the aggregate phase of transitions, aggregates have only particulate fitness (collective fitness₁). Viewed from the focal level of members, the change in frequencies of types can be driven by any of the three fitness components among members (fitnesses at the member level could be a combination of fitness₂ and fitness₁ from the level below). Moving up, so that the focus is on the aggregate level, selection among aggregates appears to be driven only by the expansive component of fitness, their differential changes in size. At the focal level of wholes,

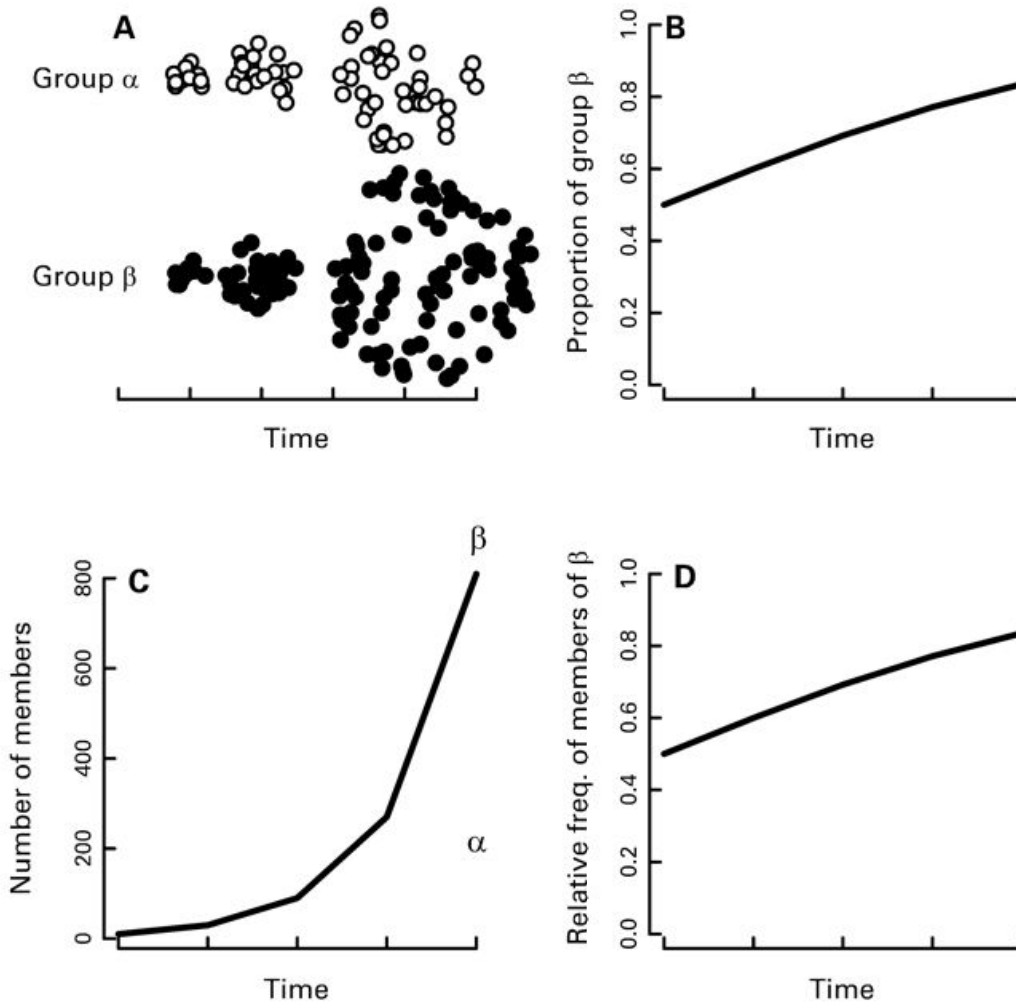


Figure 10.1

The expansive component of fitness is the change in size of units at the focal level. From a hierarchical perspective, differential expansion is caused by differential multiplication of constituent units. Panel A illustrates a hypothetical example of evolution by differential expansion. Group α expands at a lower rate than group β . Over time, there is a greater proportion of group β in the environment, as shown in panel B. The number of members of type α and β is tracked in panel C. The change in frequency of type β members shown in panel D matches the change in proportion of group β in the environment shown in panel B.

the expansive fitness is its change in size, while the demographic fitness of the whole is the differential multiplication and persistence of wholes.

The more traditional demographic fitness of aggregates (collective fitness, or fitness₂), w , is the product of the reproductive output (m) of collectives and their persistence (v), so that $w = mv$. In the aggregate phase, aggregate-level reproduction does not occur at all, or at best it is not systematic. If no reproduction occurs, m , the reproductive output at the aggregate level, is equal to zero and w is also equal to zero. There must be some viability, so v can never be equal to zero. If aggregate viability were equal to zero, they would have no staying power, instantly disaggregating. In the aggregate phase, I assume v follows a uni-

form distribution, so there is variation in how long each aggregate can last, but that variation is not correlated with anything. Because $m = 0$, w also equals zero. If there is some degree of fragmentation, I assume it is uncorrelated with the phenotype of the aggregates. By noting that $\text{cov}(x, y) = \beta_{x,y} \text{var}(x)$, we can see that if both the variance in reproductive output is zero (where $\Omega = 0$) and the aggregate phenotype and aggregate reproduction is uncorrelated (e.g., m has a uniform distribution), all three covariance terms involving Ω in equation 10.5 will equal zero because $\beta_{\phi, \Omega} = 0$.

When the first three terms of equation 10.5 that contain Ω , are also equal to zero, we can see that the change in mean group phenotype is governed exclusively by the evolution within groups:

$$\begin{aligned}\Delta\bar{\phi} &= \text{cov}(\phi, \hat{\Omega}) + \text{cov}(\hat{\delta}, \hat{\Omega}) + \overline{\text{cov}(\delta, \Omega)} + \text{cov}(\phi_p, \widehat{\Omega}_p) + \bar{\delta}_p \\ \Delta\bar{\phi} &= 0 + 0 + 0 + \text{cov}(\phi_p, \widehat{\Omega}_p) + \bar{\delta}_p \\ \Delta\bar{\phi} &= \text{cov}(\phi_p, \widehat{\Omega}_p) + \bar{\delta}_p\end{aligned}\tag{10.6}$$

All that is required in the aggregate phase is for membership in an aggregate of other organisms to have an effect on fitness, positive or negative, so that there is a nonzero covariance between the aggregate trait and the fitness of members. There seems to be no limit on the components of the aggregate. Other species or conspecifics could influence the fitness of others in an aggregate. Therefore, the aggregate phase may be quite common in nature. If, in a patch of ground, earthworms till the soil particularly well so that the vegetation grows lush, giving the earthworms more to feed on, all organisms in the patch benefit. If the members of the productive patch then reproduce more than members of other patches, even with random and independent dispersal members of the productive patch will increase over the landscape. In this example, aggregate phenotype is productivity, which all members contribute to in their own way.

Phase II: The Group Phase

It is important to recognize that the fitness components that characterize the three phases are not mutually exclusive. A lineage entering into the group phase does not require natural selection by expansive fitness to be turned off. On the contrary, transitions between the three phases occur by the *accumulation* of new components of fitness.

In the aggregate phase described earlier, the persistence and multiplication components of fitness have no selective traction because their variation is uncoupled from the phenotypes of the aggregates. However, once some aspect of aggregate-level phenotype (e.g., frequencies of types of members) become correlated with persistence or viability, so too does multiplication, and only the causal connection between the multiplication component of fitness and phenotypes is initially absent; the multiplication component sorts (Vrba and

Gould 1986), but it does not select, because phenotypes do not directly cause the number of offspring.

Members of groups can directly influence the viability or persistence of groups in any number of ways. A classic example is the alarm calls in squirrels; despite the high cost to the individual making the call, more group members survive, and therefore the group as a whole persists longer if the number of altruists is high (Sherman 1985). Any arbitrary function of the phenotype $f(\phi)$ could conceivably specify the actual relationship between persistence and phenotype.

Groups themselves do not form offspring per se, but they can fragment and form new groups by fission. Primitive groups must divide by fission if they divide at all, and the details of group fission have consequences for the efficacy of selection. We can understand the potential for evolution in such groups by modeling group reproduction as random sampling without replacement from finite parental colonies. A group reproduces by forming small propagule groups consisting of random subsets of the members.

Consider a group with N members. Beneficial traits occur in this group at a proportion, q , and the number of members in a propagule derived from that group is n , its propagule size. The number of members of that propagule that are beneficial, either altruistic or not, is equal to k/N . In the group are a total of j defectors, occurring at a frequency of $1 - q$. The probability of the offspring consisting of exactly k members of type q , given their proportion in the parent and the size of the propagule follows the hypergeometric probability:

$$Pr(k; n) = f(k; N, m, n) = \frac{\binom{j}{k} \binom{N-j}{n-k}}{\binom{N}{n}} \quad (10.7)$$

Equation 10.7 gives the probability that the resulting propagule has the phenotype k/n , independent of its viability. Figure 10.2 illustrates reproduction by random sampling for the case where $k = n$. The probability of forming a propagule with all members of type k is highest when the propagule size is equal to 1.

If the viability of the propagule (v) is a function of the proportion of beneficial members in the propagule (k/n), so that $v = f(k/n)$, and the minimum viability for a propagule occurs if it contains at least k members of the beneficial type in a frequency greater than or equal to a threshold $X \cdot n$. The probability of producing a viable offspring with the phenotype k is

$$Pr(k; n) = \frac{\binom{j}{k} \binom{N-j}{n-k}}{\binom{N}{n}} \cdot f\left(\frac{k}{n}\right) \quad (10.8)$$

The probability of producing a viable offspring of any viable type ($k \geq X \cdot n$) is

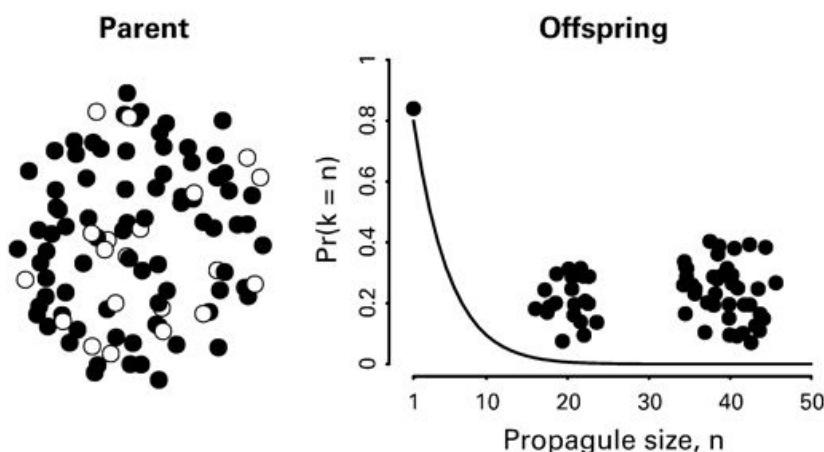


Figure 10.2 Group-level reproduction is modeled as sampling without replacement. Here, I show the probability of producing an offspring where all members of a founding propagule of size n are fixed for a particular trait. The number of propagule members containing the trait is equal to k . The probability of producing offspring that contains only members with the trait is equal to $\text{Pr}(k = n)$. If frequency of the traits in the population is equal to p , then the maximum value of $\text{Pr}(k = n)$ occurs when n equals 1 and is equal to p . In this example, p in the parent equals 0.8; members containing the trait are black. Members that don't are gray.

$$\text{Pr}(X \cdot n \leq k \leq n) = \sum_{k=X \cdot n}^n \left[\frac{\binom{j}{k} \binom{N-j}{n-k}}{\binom{N}{n}} \cdot f\left(X \leq \frac{k}{n} \leq 1\right) \right] \quad (10.9)$$

Three factors influence the probability of forming a viable offspring: propagule size (n), tolerance for deleterious members (measured by the range of phenotypes that are viable: $X \cdot n \leq k \leq n$), and the magnitude of the viability function ($f(k/n)$). When there is high tolerance for deleterious members ($X \cdot n$ is much smaller than n) and the variation in viability is low, then the probability of producing a viable offspring is high, no matter what the propagule size (figure 10.3, B and E). When X is large, the probability of producing a viable offspring decreases as propagule size gets larger (figure 10.3, B and E). Things get interesting when the effects of viability are stronger. Figure 10.3 H shows the effects of a monotonic fitness function (figure 10.3 G) on the probability of producing a viable offspring. Larger propagule sizes always lower the probability of producing a viable offspring because the highest viability is found in phenotypes that are uniformly of type k . When propagules have only one member, the chance that a propagule is fixed for k is the highest.

Of the three important parameters, propagule size has the greatest effect on the probability of forming viable offspring. Moreover, propagule size directly influences the total number of possible offspring a group can form. Since propagules are formed by fission, the maximum number of propagules a parent group produces, i , occurs when the propagule size is 1. The number of offspring decreases as a function of the propagule size (n). When

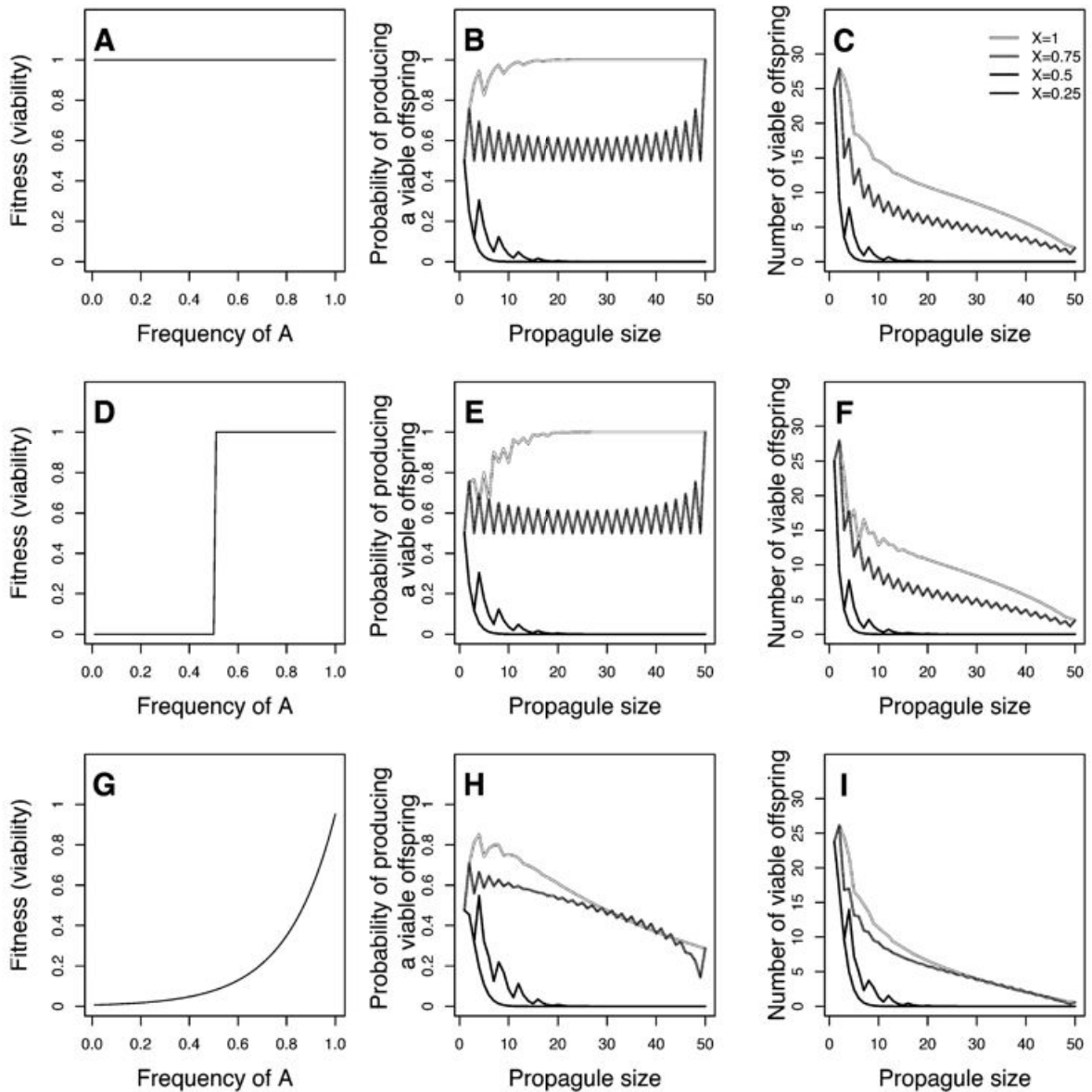


Figure 10.3

The demographic fitness of a group is a function of the viability function, the probability of forming a viable offspring by random sampling of the parent group, and the maximum propagule size of an offspring. Here, I explore various combinations of the three influences on fitness for a parent group consisting of fifty members, half of which are deleterious ($j = 0.5$), and the other half are beneficial. The viability of offspring propagules is a function of the frequency of beneficial members in the propagule and shown in panels A, D, and G. The probability of producing a viable propagule is plotted in the center column (panels B, E, and H), the panel in each row is for the viability function in the same row. The probability of forming a viable offspring depends on the tolerance of deleterious members, which can range from a quarter ($X = 0.25$) to none of the propagule ($X = 1$). The legend in panel C applies to all center and right column panels. Panels C, F, and I show the demographic fitness of parent groups and is the product of the probability of producing a viable offspring and the expected number of offspring with uneven partitioning, given the maximum propagule size.

Table 10.2
The enumerated partitions of a group with five members

5	4	3	3	2	2	1
	1	2	1	2	1	1
			1	1	1	1
				1	1	
						1

the formation of propagules is random, any size propagule can form; parent groups may produce offspring of a variety of propagule sizes. Parent groups are partitioned into offspring. The number of possible partitions becomes quite large even if the size of the parent group is small. A group of ten members can be partitioned in forty-two different ways. A group with five members can be partitioned into propagules in seven ways, shown in table 10.2.

Maximum propagule size can be considered to be the maximum number of members in a particular partition. In the case in table 10.2, there are two possible partitions for a propagule size of 3: 3,2 and 3,1,1, consisting of two and three offspring, respectively. In this example, when maximum propagule size is 3, the average number of offspring is 2.5.

I calculated the average number of offspring for a group from a direct enumeration of the partitions of a group consisting of fifty members for each propagule size between one and fifty. Alternatively, even partitions can be made of a group, where the group is split into as many propagules as possible of the same size. The number of offspring (*i*) is given by the number of members, *N*, and the propagule size, *n*:

$$i = \frac{N}{n} \tag{10.10}$$

As there are often several ways to partition a group with the same maximum propagule size, the partitioning estimate gives a larger expected number of offspring than an even partitioning of equal-size propagules given by equation 10.10 (figure 10.4).

Propagule size is also important because it directly affects the multiplication component of group-level fitness. The multiplication component of group-level fitness is the actual number of viable offspring produced by a parent group and is determined by the product of equations 9 and 10, assuming offspring with constant propagule size:

$$Pr(X \cdot n \leq k \leq n) = \sum_{k=X \cdot n}^n \left[\frac{\binom{j}{k} \binom{N-j}{n-k}}{\binom{N}{n}} \cdot f\left(X \leq \frac{k}{n} \leq 1\right) \right] \tag{10.11}$$

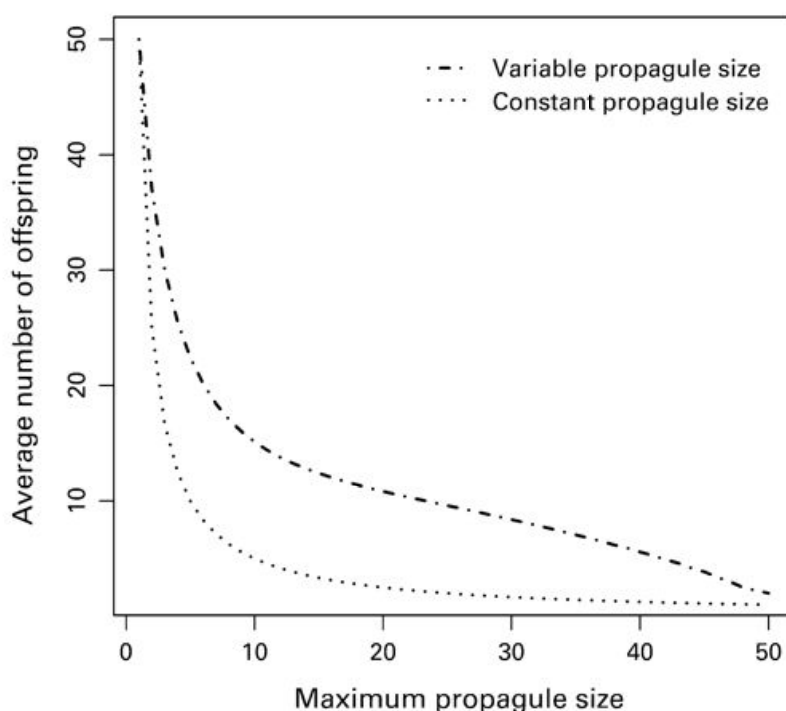


Figure 10.4

Propagules can be formed either by partitioning the parent into propagules with variable numbers of members or by subdividing the parents into propagules with constant numbers. Variable propagule size is achieved by partitioning the offspring into all possible sized propagules, given a maximum propagule size. The maximum propagule size contains the largest number of members. All possible partitions were enumerated for a parent with fifty members. The average number of offspring is calculated from the average number of offspring with the same maximum propagule size. (See table 10.2 and the worked example in the text.) The number of offspring produced, i , when propagule sizes are constant among offspring is given by N/n , where N is the number of members in the parent, and n is the propagule size.

Figure 10.3 (panels C, F, and I) shows the expected group-level fitness as a function of the maximum propagule size when partitioning is variable. As expected, when maximum propagule size is small, the number of offspring is much higher.

Importantly, even if there is no tolerance for deleterious members in a propagule (where $X = 1$), intolerant groups will still have comparable fitness to very tolerant groups. Further, if the partitioning of groups into propagules is actually unspecified, the majority of partitions include a large number of single-member propagules. Since possessing small propagules results in such strong sorting, those traits that are possible to inherit with a single propagule will rapidly increase in frequency.

The model of reproduction outlined earlier shows how group-level reproduction and the change in phenotypes during the reproduction process are tightly coupled, leading to non-zero values in two additional covariance terms in the stochastic Price equation (equation 5). Recall that the term $\text{cov}_i(\hat{\delta}, \Omega)$ describes the average covariance between the number and phenotypes of the offspring of a single parent. Small propagules increase the numbers of offspring, w , so Ω is also affected by propagule size. If a parent group has a phenotype with mixed members, small propagules will have the effect of segregating the members, so

that propagules will tend to consist of only one type. Since propagule size influences both fitness and phenotype, $\text{cov}_i(\hat{\delta}, \Omega)$ will be positive. The among-group covariance between the change over reproduction and fitness, $\text{cov}(\hat{\delta}, \hat{\Omega})$, will also be positive because of variation in propagule size. Since propagule size is initially unspecified, the group phenotype is uncorrelated with number of offspring, the first term in equation 5, $\text{cov}(\phi, \hat{\Omega})$ consequently equals zero.

Evolution in the group phase, as characterized by equation 5, is influenced by the evolution among members and the interaction between the reproduction of groups and the emerging group-level fitness within and among groups:

$$\begin{aligned} \Delta\bar{\phi} &= \text{cov}(\phi, \hat{\Omega}) + \text{cov}(\hat{\delta}, \hat{\Omega}) + \overline{\text{cov}_i(\delta, \Omega)} + \text{cov}(\phi_p, \hat{\Omega}_p) + \bar{\delta}_p \\ \Delta\bar{\phi} &= 0 + \text{cov}(\hat{\delta}, \hat{\Omega}) + \overline{\text{cov}_i(\hat{\delta}, \Omega)} + \text{cov}(\phi_p, \hat{\Omega}_p) + \bar{\delta}_p \\ \Delta\bar{\phi} &= \text{cov}(\hat{\delta}, \hat{\Omega}) + \overline{\text{cov}_i(\hat{\delta}, \Omega)} + \text{cov}(\phi_p, \hat{\Omega}_p) + \bar{\delta}_p \end{aligned} \tag{10.12}$$

The two key features of the group phase are differential viability of members with respect to the group and random fragmentation of groups. Both features can be expressed in a large number of ways. Members can either be inviable or cheaters, both of which negatively affect the group as a whole. Random fragmentation is more variable still. There are two ways that propagule membership can form. The simplest is direct fragmentation, so that a single organism can be a member of multiple groups over its life. For example, buffalo herds can temporarily fragment and reassemble with no evolutionary significance, or stromatolite colonies can fragment. Additionally, propagule members can be produced by the same mechanism as other members are, either by cell division, asexual reproduction, or sexual reproduction, as long as any group member could be a parent.

Phase III: The Individual Phase

Again, there are no discrete boundaries between phases. The advantages of a small propagule are many: It increases the ability to maintain rare beneficial traits by isolating them from deleterious traits and it increases the multiplication component of group-level fitness. As long as the ability of the group to divide is maintained, groups can expand before a further bout of reproduction occurs. If expansion is too slow, further reproduction by the group will produce fewer offspring. So the evolution of a small propagule size necessitates a change in the relative generation times between groups and members, because many generations of parts may be needed to expand the group sufficiently for the group to reproduce without a loss in fitness. Even though the rapid multiplication of parts unfortunately increases the risk of deleterious mutants originating, a small propagule successfully purges those mutants.

The benefits of small propagules are not limitless. A consequence of the evolution of a small propagule size is a uniformity in members. It is commonly expected that a division

of labor among group constituents benefits the group with the increased efficiency that the ability to perform multiple tasks simultaneously allows (Bonner 2001; Harvell 1994). If a division of labor is to arise among constituents, it must contend with the constraints the random reproduction of the group imposes. Any variation within a group after its founding by a small propagule or by differentiation must be easily reversible to a totipotent state. Otherwise not all variants can be inherited. The limit on inheritance of variation and the overall uniformity of groups produced by group-level selection constrains the evolution of division of labor. Only the origin of specified reproductive members will break the constraint imposed by group-level selection, opening the door to extensive division of labor. The deviation from unbiased random sampling distinguishes evolution in the third phase of transitions.

In the hypergeometric model of reproduction outlined in the previous subsection, the expected phenotype of a propagule, $\hat{\phi}'$, is equal to nk/N . Members of type k and other types all have the same probability of being sampled. Fisher's noncentral hypergeometric distribution allows for different sampling probabilities for each member type and would be appropriate to substitute into equation 11 in place of the hypergeometric. However, if propagule size is already small and the group generation times are already long compared to those of the members, nonrandom reproduction can no longer be modeled by a sampling process.

Instead, it is the partitioning of life history into growth and reproduction that is important to the evolution of individuals. An individual controls a finite amount of energy, ψ , in which some fraction is used for maintenance ($\varepsilon(\psi)$).

The rest, equal to its expansive fitness, can be further partitioned into growth ($\pi(\psi)$) or reproduction ($1 - \pi(\psi)$). The efficiency of reproduction is given by, η_r . The reproductive output of an organism with a given growth strategy is equal to (Baudisch 2008)

$$m(\psi) = (1 - \pi(\psi))^{\eta_r} \varepsilon(\psi) \quad (10.13)$$

A wide range of partitioning strategies are possible, from almost constant growth to a phase of rapid growth followed by only reproduction. It may seem strange that such variety in life-history strategy affects reproductive output. Many organisms have unlimited growth, but all real examples, from sponges to coral colonies, reproduce, each spawning millions of gametes into the oceans. Equation 13 describes reproduction as the fraction of energy not used for growth or maintenance. Only if $\pi(\psi)$ and $\varepsilon(\psi)$ are zero could reproductive output be maximized, so in individuals that grow continuously at a high rate, the actual energy expenditure on offspring will have to be low. Even if each offspring is cheap, so that η_r is high, it is important to remember that $m(\psi)$ is only the multiplicative component of fitness. A huge selective filter occurs in the settlement of corals, dramatically increasing the number of juvenile recruits only when the percentage of gravid corals is close to 100 percent (Hughes et al. 2000). Therefore, extremely low values of the persistence component of fitness v could be quite common. Since w is the product of m and v , the demographic

fitness of corals and sponges can be quite low. But since the overall fitness includes expansive and demographic components, those individuals that focus on growth can still have high fitness.

The first covariance term in equation 10.5 finally takes on a value. The phenotype of the individual can directly influence fitness, both by growth and directly, so $\text{cov}(\phi, \hat{\Omega})$ has a nonzero value:

$$\Delta\bar{\phi} = \text{cov}(\phi, \hat{\Omega}) + \text{cov}(\hat{\delta}, \hat{\Omega}) + \overline{\text{cov}(\delta, \Omega)} + \text{cov}(\phi_p, \hat{\Omega}_p) + \bar{\delta}_p \quad (10.14)$$

Organisms and colonies in the individual phase are common. All metazoan organisms are in the individual phase because the organisms themselves are reproductive. However, organisms vary in their degree of individuality. Variation in individuality is correlated with the degree to which reproductive members are determined in the organism (Simpson in review). Three different grades of individuality are well known: the poorly individuated cellular grade (Hyman 1940) with largely somatic embryogenesis (Buss 1983, 1987; Nieuwkoop and Sutasurya 1981), intermediately individuated tissue grade organisms (Hyman 1940) with a mix of epigenetic and preformistic germ specification (Buss 1983, 1987; Nieuwkoop and Sutasurya 1981), and highly individuated organisms of the organ-system grade (Hyman 1940), also with a mix of epigenetic and preformistic germ specification (Buss 1983, 1987; Nieuwkoop and Sutasurya 1981).

Evolution and Ecology Within Transitions in Individuality

The expansive and demographic fitness components are clearly associated with different life-history strategies that determine ecological specialization. Organisms that have a significant component of expansive fitness specialize in growth and the occupation and control of space. Corals, bryozoans, sponges, and a number of plant groups have a large expansive component of fitness. Evolution in snails and other motile organisms with approximately determinate growth is dominated by the demographic mode of fitness. It is difficult to describe examples of *organisms* that have only an expansive component of fitness, because there are none, at any level. But recognizing the expansive component of fitness has the benefit of allowing the boundedness of entities be undefined. (The conceptual issues of boundedness in hierarchical levels is well reviewed in section 2.1 of Okasha 2006.) Trait groups, patches, or other aggregations can all change in their spatial extent. A coral colony, a coral reef, as well as a reef community type can all expand in their spatial extent and density of occupation, even if they don't all possess a reproductive capacity.

Because the persistence and multiplication of aggregates is random (following a uniform distribution, for example), the aggregate phase may seem to be rare since many processes that would generate more elaborate underlying stochastic distributions are common. Several physical factors, however, may limit the potential multiplication and differential persistence of aggregates. The most important of these is the relative size of the aggregate compared to

the total habitable area. If an aggregate (think of a highly dispersed trait group) covers nearly the same area as the possible habitat, there can be no net multiplication. No dispersal is possible because there is nowhere new to go. But when aggregates are small relative to the potential habitable area, no purely geometric limits on multiplication exist.

Even with the natural limits, the aggregate phase of transitions in individuality could well be the most diverse phase in terms of the number of distinct aggregates and the number of independent transitions. This is because aggregates require only a context where a set of organisms experience an increase of demographic fitness. It is possible for communities of all scales to satisfy this criterion. Wilson (1980) explored this basic phenomenon in general, but interest has waned, I believe, because the mechanism suffers from an inability to form adaptations of any complexity. Natural selection always leads to adaptation (Van Valen 2009), but natural selection that is primarily expansive has adaptive limits, even within organisms.

The limits to adaptation are imposed mainly by the mechanisms that produce variation between aggregates. All variation within and among aggregates is produced by the constituent organisms, even if the aggregate is at a much higher level. New variants can be expressed within a single aggregate if the potential for aggregate-level multiplication is low, or in a descendent aggregate if multiplication is common. Since the potential for multiplication is largely controlled by the size of the aggregate relative to the habitat area, small aggregates should have a greater potential to differ from each other. Large aggregates will be so few that what variation does occur will generate little selective effect among aggregates.

Of course, in most aggregates, variation is often deleterious, and so the evolutionary pathway tends to pass through the three phases of transitions if the level of adaptations is to increase. But in those aggregates that are composed of multiple species, there is a natural source of preexisting variation, offering an alternative path of a sort to division of labor. Multispecies communities, if they multiply to some degree, have the trouble that members disperse separately, so the heritability of community structure is low.

Coordinated dispersal is fairly common in coral reef communities in the form of multi-species mass spawning (Harrison et al. 1984). It is common for the spawning of one organism to induce spawning in others nearby, resulting in all members of all species spawning simultaneously (Strathmann and Fernald 1987). This means that even if communities are assembled randomly (e.g., Hubbell 2001), any coordinated timing in reproduction will lead to a higher chance of a community reassembling.

The demographic openness of coral reef communities varies according to spatial scale and member dispersal ability (Knowlton and Jackson 2001). At the local scale, reef-dwelling species with larvae that don't disperse well are demographically closed; all members of those types originate locally. Other member species with planktonic larvae can disperse well enough, so that most members are derived from elsewhere and therefore demographically open. At larger scales, the limits of larval dispersal bound communities

(Caley et al. 1996). Historically, reef-building corals, which are mostly colonial, have been observed to have higher extinction rates than the largely solitary reef-dwelling corals (Simpson and Kiessling 2010). As a consequence of these higher extinction rates, large-scale diversity-stability relationships are observed (Simpson and Kiessling 2010).

A single species is a member of aggregates at each of the spatial scales, from locally to larger scales. Each of the scales can be a level of aggregation in its own right. Natural selection is possible at any one of these levels, but I suspect its efficacy is limited by the conflicts among multiple levels. The existence of multiple simultaneous levels of aggregation can undermine patterns so that no consistent patterns are observed as studies cross spatial scales (as described in Jablonski 2008). Any successful coordination among the members of an aggregate will therefore often not translate to other constituent or subsuming levels of aggregation. One way to think about this is in terms of constraints. In multispecies communities, there is no way to channel variation in such a way that optimal solutions to conflicting problems can be found.

Even with all the problems with adaptive community evolution outlined earlier, some multispecies communities have overcome them. The origin of eukaryotes by symbiosis and lichens are the most striking examples, but there are countless other examples of symbioses (Moran 2006) that would qualify as aggregations. In lichens, fragments of the thalus can disperse both the fungal and algal bionts (Budel and Scheidegger 1996; Honegger 1998; Walser 2004).

The origin of eukaryotes is special, partly because these organisms become the building blocks of so much diversity. Mostly, though, they are the clearest example of a multispecies aggregation—that due to the internalized nature of their aggregations—and have solved the problems associated with dispersal and covariation that are inherent in aggregations. Their small size means that they do not face a geometric limit to their reproductive capacity. For example, growth and division of mitochondria can be linked with cell division. Integration is high enough that, in metazoans, strange cross-level effects are common. One interesting example is that mitochondrial genes are integral to the functioning of programmed cell death (Danial and Korsmeyer 2004) in metazoans.

Aggregates and the Number of Hierarchical Levels

The ease with which ecological hierarchical levels fit into the aggregate phase suggests that it may not be necessary to distinguish ecological and evolutionary hierarchies after all. The hierarchy of ecological interactors—organisms, avatars, local ecosystems, and regional ecosystems (Eldredge and Greege 1992)—can now be seen as a terse list of some common levels of aggregation (figure 10.5). The ecologically organized units are potential, or incipient, higher-level evolutionary individuals. Spatial and temporal scales vary continuously, but a new level does not occur at each scale. Instead, levels correspond to spatial and temporal scales *where dynamics occur*. These are many, but they are not all equal.

Level of organization	Multi-organismal level	<i>Regional ecosystem</i> <i>Local ecosystem</i> <i>Avitars</i> Demes Wolf pack Fish School Slezee of Sponges	Human society Squirrel colony	Clade Species Ant colonies
	Multicellular level	Stromatolites Social bacteria	Colonial ciliate	Sea Urchin Snail Volvox Dictyostelium
	Cellular level			Single-celled Eukaryotes Prokaryotes
		Aggregate phase	Group phase	Individual phase
Phase of transition				

Figure 10.5

The three phases of transitions can be mapped to the hierarchical level of organization. Groups of organisms at various levels of organization can aggregate into new levels. With the right conditions, the aggregations can evolve high degrees of individuality by entering new phases of transitions. Ecological and evolutionary members of the dual hierarchies (e.g., Eldredge and Greege 1992) are mapped equally well into this table. Levels in the ecological hierarchy are shown in *italics*, while levels in the geneological hierarchy are shown in **bold**. Solitary, social, and colonial organisms can occur in any cell, and examples are plotted in normal text. Limits on the adaptive evolution of communities keep them from entering the group and individual phases to a great extent, so they tend to fill up the aggregate phase. The vertical positioning of each is based on the level of organization and further ranks are the qualitative rank order according to spatial and temporal scale. The phase of transitions is based on the dominant component of fitness as estimated by the proportion of the entity that is dedicated to reproduction (Simpson 2009b).

It is possible that we can observe this heterogeneity in meta-analyses of scale in ecological processes. Often, small-scale local patterns do not predict observations made at larger scales (reviewed in Jablonski 2007). From the view I argue for here, each new scale is a potential new level. The level status is attained only when something about the context of the scale leads to an increase in expansive energy of the members. The energetic criteria is important because there is—at least to a first approximation—a limit to the energy available (Van Valen 1976). This limitation in energy is what drives dynamics: Evolution, like economics, is driven by scarcity.

The difficulty in identifying a new level is also due to the lack of clear differences in rank. A coral reef community in the Caribbean may not share precisely the same rank as one in the Red Sea. From a strict constitutive hierarchy view, both are at the same level because they consist of a set of organisms. But because of dispersal and the spatial arrangement of habitable area, the Caribbean reefs are closed demographically, consisting of endemic species, and therefore have a different evolutionary potential from reefs of comparable size in the Red Sea. Those Red Sea reefs are connected by dispersal to the rest of the Indo-Pacific, and so the important scale that determine dynamics is much larger than that of the Caribbean reefs. The rank of the Caribbean level of selection is lower than that for the Red Sea and Indo-Pacific together, because the Caribbean consists of a set of reefs, whereas the Red Sea consists not only of its constituent reefs but also of members from other geographic provinces. This lack of clear boundaries between levels has always been used as an argument against hierarchy. I hope we have learned from Buss (1987), and the three phases of transitions discussed earlier, that when new levels emerge they may not be clearly demarcated; nonetheless, they do occur.

Recognition of the importance of aggregates makes the distinction between scale and hierarchy that Jablonski (2007) and others have advocated even more important. Scale, of course, is just an arbitrary metric. But such hierarchical levels tend not to consist of individuals in the biological sense (where the whole is well bounded, countable, and multiplies). The conceptual difficulty in distinguishing scale and hierarchy is present because they are largely correlated. Jablonski (2007) makes the distinction by recognizing that levels have the characteristics of philosophical individuals, because the constituents of a level are connected in some way. I believe my focus on dynamics and energy control accomplishes the same thing, with a focus on what drives evolution.

Perhaps the complex picture of countless levels, both emergent and individuated, can be best illustrated with the example of humans. One of the key differences between the major transitions in evolution of Maynard Smith and Szathmáry (1995) and the evolutionary transitions in individuality of Michod (1999) is in their treatment of humans, human culture, and language. Maynard Smith and Szathmáry (1995) say that, once language occurs, everything changes and a new level of evolution is attained. Michod (1999) is more specific; the new level must be that of human groups. But these don't have the status of full individuals. One of the only steadfast rules of hierarchy is that rates of change decrease as

you ascend levels in the hierarchy (Salthe 1985, 1993).¹ If the evolution at group level occurs in humans, the rate of change should be slow relative to morphological change. Human culture does just the opposite. The rate of cultural change is much faster than subordinate levels.

If there is significant group-level evolution, large numbers of groups would be required, so how many human groups are there? This question is surprisingly difficult to answer. Humans can be partitioned into groups based on cultural, religious, linguistic, political, geographic, genetic, subcultural, and other possible ways to criteria. But a partition on one criterion will rarely match partitions on others because humans naturally belong to several groups. Instead of giving up and saying there are no groups, we can recognize that a multitude of groups coexist, with each at a potentially different level because of differences in the scale of inclusiveness. Each group will vary in its components of fitness, as will other subordinate and subsuming groups. And the directions of selection may not coincide. This is the same situation as we find in ecological hierarchies. Effectively, an infinite number of levels exists in the interstices between obvious organizational levels. The obvious levels, like integer numbers, are those that have proceeded through to the individual phase of transitions—cellular, multicellular, and multiorganismal (colonial or social).

The path a lineage takes through the phases of transitions is not fixed, but determined by ecology. Expansive fitness, though it straddles levels, can be a potent component of high-level fitness because it directly contributes to the ability to control and occupy space. Whole animal phyla, like the bryozoans, are dedicated to this mode of life, and so are those only partially individuated at both the organismal and colonial levels (Simpson in review). The existence of multiple adaptive peaks that represent particular ecological life-history strategies also means that there is no way to be stalled midtransition (Stearns 2007), even if transitions are not instantly complete.

New aggregates constantly form and most probably dissipate before they attain a significant amount of expansive fitness. Even in *Volvox*, incipient levels can be observed, when a colony contains within itself three generations of offspring. Deciding whether *Volvox* is an alga with parental care or a colony of colonies is not as important as recognizing that even here we can see how levels of aggregations spontaneously arise. The raw material for entering into another aggregate phase of transitions is already present.

Even in the early fossil record, between 2.6 to 2.3 billion years ago, we can see complex spatial structuring in stromatolitic reef complexes (Grotzinger 1989), and even if the stromatolites are not biogenic themselves (Grotzinger and Knoll 1999), the spatial structure would still influence the life in these reef complexes.

Once ecology occurs, there is no upper limit on the potential hierarchical complexity of life. Of course, the first life forms had ecology. The only limits are on the potential for those levels and degrees of aggregations to evolve. Since the origin of life, it seems that the hierarchical complexity of life has always been infinite. What we think of as the transitions in

individuality, and an increase in hierarchical complexity, are only instances where the individual phase has been reached.

Acknowledgments

Many thanks to Brett Calcott and Kim Sterelny for organizing an exciting and successful meeting. I am grateful to Eva Karner and Werner Callebaut at KLI for the wonderful experience at Altenberg. Thanks to Dan McShea and Wolfgang Kiessling for commenting on this paper and to Dave McCandlish and Lauren McCall for discussing many of the ideas in this paper with me. This work was funded by the Cambridge-Templeton Foundation, grant # 1038 to D. McShea.

Note

1. This rule seems to work in both physical and evolutionary hierarchical systems. Geological processes continuously change the surfaces and possibly the internal structure of planets while the basic organization of the solar system changes considerably more slowly. The number of types of ant colonies, if measured by patterns of social organization is dwarfed by the number of ant species. Although not conclusive, this pattern suggests that the evolution of colony types is much slower than the evolution of organismal traits. Variation in rate of change across levels is largely a consequence of a many-to-one relationship between lower-level parts and the whole.

References

- Arnold, A. J., and K. Fristrup. (1982). The theory of evolution by natural selection: A hierarchical expansion. *Paleobiology* 8(2): 113–129.
- Baudisch, A. (2008). *Inevitable Aging?: Contributions to Evolutionary-Demographic Theory*. Demographic Research Monographs 4. Berlin: Springer.
- Bell, G., and A. O. Mooers. (1997). Size and complexity among multicellular organisms. *Biological Journal of the Linnaean Society* 60(3): 345–363.
- Bonner, J. T. (2001). *First Signals: The Evolution of Multicellular Development*. Princeton, NJ: Princeton University Press.
- Budel, B., and C. Scheidegger. (1996). Thallus morphology and anatomy. *Lichen Biology* 37–64.
- Buss, L. W. (1983). Evolution, Development, and the Units of Selection. *Proceedings of the National Academy of Sciences* 80(5): 1387–1391.
- Buss, L. W. (1987). *The Evolution of Individuality*. Princeton, NJ: Princeton University Press.
- Caley, M. J., M. H. Carr, M. A. Hixon, T. P. Hughes, G. Jones, and B. A. Menge. (1996). Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics* 27: 477–500.
- Charnov, E. L., and S. K. M. Ernest. (2006). The offspring-size/clutch-size trade-off in mammals. *The American Naturalist* 167(4): 578–582.
- Damuth, J., and I. L. Heisler. (1988). Alternative formulations of multilevel selection. *Biology and Philosophy* 3(4): 407–430.
- Danial, N., and S. Korsmeyer. (2004). Cell death critical control points. *Cell* 116(2): 205–219.
- Dawkins, R. (1982). *The Extended Phenotype: The Gene as the Unit of Selection*. San Francisco: Freeman.

- Eldredge, N. (1985). *Unfinished Synthesis: Biological Hierarchies and Modern Evolutionary Thought*. New York: Columbia University Press.
- Eldredge, N., and M. Greege. (1992). *Interactions: The Biological Context of Social Systems*. New York: Columbia University Press.
- Frank, Steven A. (1998). *Foundations of Social Evolution*. Princeton, NJ: Princeton University Press.
- Grotzinger, J. P. (1989). Facies and evolution of Precambrian carbonate depositional systems: Emergence of the modern platform archetype. In P. Crevello, J. Wilson, J. Sarg, and F. Read (eds.), *Controls on Carbonate Platform and Basin Development*. Society of Economic Paleontologists and Mineralogists Special Publication 44: 79–106.
- Grotzinger, J. P., and A. H. Knoll. (1999). Stromatolites in Precambrian carbonates: Evolutionary mileposts or environmental dipsticks? *Annual Review of Earth and Planetary Sciences* 27(1): 313–358.
- Hamilton, W. D. (1975). Innate social aptitudes of man: An approach from evolutionary genetics. In R. Fox (ed.), *Biosocial Anthropology* (pp. 133–155). New York: Wiley.
- Harper, J. L. (1977). *Population Biology of Plants*. New York: Academic Press.
- Harrison, P., R. Babcock, G. Bull, J. Oliver, C. Wallace, and B. Willis. (1984). Mass spawning in tropical reef corals. *Science* 223(4641): 1186–1189.
- Harvell, C. D. (1994). The evolution of polymorphism in colonial invertebrates and social insects. *Quarterly Review of Biology* 69(2): 155–185.
- Herron, M., and R. Michod. (2008). Evolution of complexity in the volvocine algae: Transitions in individuality through Darwin's eye. *Evolution* 62(2): 436–451.
- Honegger, R. (1998). The Lichen symbiosis—What is so spectacular about it? *Lichenologist* 30(3): 193–212.
- Hubbell, S. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton, NJ: Princeton University Press.
- Hughes, T. P., A. Baird, E. Dinsdale, N. Mutschaniwskyj, M. Pratchett, J. Tanner, and B. Willis. (2000). Supply-side ecology works both ways: The link between benthic adults, fecundity, and larval recruits. *Ecology* 81(8): 2241–2249.
- Hull, D. L. (1980). Individuality and selection. *Annual Review of Ecology and Systematics* 11: 311–332.
- Hyman, L. H. (1940). *The Invertebrates: Protozoa through Ctenophora*. New York: McGraw-Hill.
- Jablonski, D. (2007). Scale and hierarchy in macroevolution. *Palaeontology* 50(1): 87–109.
- Jablonski, D. (2008). Biotic interactions and macroevolution: extensions and mismatches across scales and levels. *Evolution* 62(4): 715–739.
- Knowlton, N., and J. B. C. Jackson. (2001). The ecology of coral reefs. In J. F. Bruno, M. D. Bertness, S. D. Gaines, and M. E. Hay (eds.), *Marine Community Ecology* (pp. 395–422). Sunderland, MA: Sinauer.
- Maynard Smith, J., and E. Szathmáry. (1995). *The Major Transitions in Evolution*. San Francisco: W.H. Freeman.
- Michod, R. (2006). The group covariance effect and fitness trade-offs during evolutionary transitions in individuality. *Proceedings of the National Academy of Sciences* 103(24): 9113–9117.
- Michod, R. (2007). Evolution of individuality during the transition from unicellular to multicellular life. *Proceedings of the National Academy of Sciences* 104(suppl 1): 8613.
- Michod, R. E. (1999). *Darwinian Dynamics: Evolutionary Transitions in Fitness and Individuality*. Princeton, NJ: Princeton University Press.
- Michod, R. E. (2001). Cooperation and conflict in the evolution of multicellularity. *American Zoologist* 41(6): 1526–1526.
- Michod, R. E., Y. Viosat, C. A. Solari, M. Hurand, and A. M. Nedelcu. (2006). Life-history evolution and the origin of multicellularity. *Journal of Theoretical Biology* 239(2): 257–272.
- Moran, N. (2006). Symbiosis. *Current Biology* 16(20): 866–871.
- Nieuwkoop, P. D., and L. A. Sutasurya. (1981). *Primordial Germ Cells in the Invertebrates: From Epigenesis to Preformation*. New York: Cambridge University Press.
- Okasha, S. (2006). *Evolution and the Levels of Selection*. Oxford: Oxford University Press.
- Price, G. R. (1972). Extension of covariance selection mathematics. *Annals of Human Genetics* 35(4): 485–490.

- Queller, D. C. (2000). Relatedness and the fraternal major transitions. *Philosophical Transactions: Biological Sciences* 355(1403): 1647–1655.
- Rice, S. H. (1995). A Genetical Theory of Species Selection. *Journal of Theoretical Biology* 177(3): 237–245.
- Rice, S. H. (2004). *Evolutionary Theory: Mathematical and Conceptual Foundations*. Sunderland, MA: Sinauer.
- Rice, S. H. (2008). A stochastic version of the Price equation reveals the interplay of deterministic and stochastic processes in evolution. *BMC Evolutionary Biology* 8: 262.
- Roze, D., and R. E. Michod. (2001). Mutation, multilevel selection, and the evolution of propagule size during the origin of multicellularity. *American Naturalist* 158(6): 638–654.
- Salthe, S. N. (1985). *Evolving Hierarchical Systems: Their Structure and Representation*. New York: Columbia University Press.
- Salthe, S. N. (1993). *Development and Evolution*. Cambridge, MA: MIT Press.
- Sherman, P. W. (1985). Alarm calls of Belding's ground squirrels to aerial predators: nepotism or self-preservation? *Behavioral Ecology and Sociobiology* 17(4): 313–323.
- Simpson, C. (2010). Species selection and driven mechanisms jointly generate a large-scale morphological trend in monobathrid crinoids. *Paleobiology* 36(3): 481–496.
- Simpson, C., and W. Kiessling. (2010). The role of extinction in large-scale diversity-stability relationships. *Proceedings of the Royal Society B: Biological Sciences* 277: 1451–1456.
- Simpson, C. (in review). The evolution of division of labour.
- Stearns, S. (2007). Are we stalled part way through a major evolutionary transition from individual to group? *Evolution* 61(10): 2275–2280.
- Strathmann, M., and R. Fernald. (1987). *Reproduction and Development of Marine Invertebrates of the Northern Pacific Coast: Data and Methods for the Study of Eggs, Embryos, and Larvae*. Seattle: University of Washington Press.
- Van Valen, L. M. (1976). Energy and evolution. *Evolutionary Theory* 1(7): 179–229.
- Van Valen, L. M. (2009). How ubiquitous is adaptation? A critique of the epiphenomenist program. *Biology & Philosophy* 24: 267–280.
- Vrba, E. S., and S. J. Gould. (1986). The hierarchical expansion of sorting and selection—sorting and selection cannot be equated. *Paleobiology* 12(2): 217–228.
- Wade, M. J. (1978). Critical review of models of group selection. *Quarterly Review of Biology* 53(2): 101–114.
- Walser, J. C. (2004). Molecular evidence for limited dispersal of vegetative propagules in the epiphytic lichen *Lobaria pulmonaria*. *American Journal of Botany* 91(8): 1273–1276.
- Williams, G. C. (1992). *Natural Selection: Domains, Levels, and Challenges*. New York: Oxford University Press.
- Wilson, D. S. (1980). *The Natural Selection of Populations and Communities*. Menlo Park, CA: The Benjamin/Cummings Publishing Company.
- Wilson, E. O. (1975). *Sociobiology: The New Synthesis*. Cambridge, MA: Belknap Press of Harvard University Press.