9 The Reintegration of Biology, or 'Nothing in Evolution Makes Sense Except in the Light of Ecology'

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Introduction

'Nothing in biology makes sense except in the light of evolution', said Theodosius Dobzhansky in an address to the American Society of Zoologists.[1] Dobzhansky was arguing for the continued importance of organismal biology — including evolution — amid fascination with the increasingly prolific discoveries of molecular biology concerning DNA and its function within the cell. How does the perennial biological tradition studying 'how things are' sit with the Darwinian study of 'how things came to be this way'? Dobzhansky would no doubt be pleased to see the prominent place held by the notion of evolution in 21st century culture, and also reassured to know that many of today's general biology textbooks give prominence to the theory of evolution by means of natural selection. He would also be pleased to know about the new light being shed on genetic correlates and drivers of evolutionary change in molecular biology, including developments in the

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study of epigenetics. But questions continue to be asked about what kind of scientific artefact evolutionary theory is, and to a large degree the challenge of relating evolutionary biology to molecular biology remains as grand now as it was then. Dobzhansky might be saddened at the continued decline in the teaching of systematics and taxonomy in leading universities and at what is probably a growing imbalance between coverage of molecular versus organismal biology at undergraduate level. Shedding light from evolution into studies of biochemistry, molecular genetics and cell physiology, and helping students appreciate the relationships between them, is perhaps as challenging as ever.

The idea we explore in this chapter is that the biological discipline of ecology is fundamental to the relationship between evolution and the rest of biology. Thus, we explore a three-way relationship between ecology, evolution and biology. We argue that evolution and ecology need to be taken as mutually interdependent, and that biology as a whole will benefit from a reintegration. Although ecology and evolution are parts of biology in its broad sense, we will use 'general biology' to mean the rest of the biological sciences apart from these two — and especially cellular and molecular biology. Ultimately, we ask what a more ecological version of biology — a reintegrated biology — might look like.

The Senses of Ecology and Evolution

Some initial light can be shed by looking at the range of meanings of the terms 'ecology' and 'evolution'. Our first term was coined by Ernst Haeckel, a friend of Charles Darwin, in 1866. From its Greek roots, 'ecology' literally means 'study of home', and it has always been used scientifically to describe the study of living organisms at home in their environments. This includes the interactions of individual plants and animals with other individuals that are closely related, as well as with members of other species; it extends from mutually beneficial relationships through to predation and parasitism. It also includes interactions of organisms with their non-living environments (like the atmosphere) and partially-living environments (like soil). Ecological science also considers patterns of organisms across space and how they change through time. In this way, as we move from timescales that can easily be studied in an ecological survey or monitoring programme towards timescales long enough for lineages to undergo changes in their characteristics, ecological science blends into its neighbour, evolutionary science.

We will look in more detail at the characteristics of scientific ecology below, but for now we will note two other meanings that have been derived from the scientific sense. First, 'ecology' is sometimes used to refer to a system of interactions among any kind of agents, as when economists talk of the ecology of a financial system. This seems to be a simple analogy, drawing upon the richness of ecological science in describing complex relationships among individuals — which need not be organisms. Second, in popular use 'ecology' has come to evoke political movements for sustainable living and environmentally responsible practices. In this ethical sense it is more often used as an adjective, 'ecological' being similar to 'green' in phrases such as 'the green movement'. This usage, which dates back to the 1970s, reflects how the study material of ecological science is under threat. Like archaeologists and anthropologists, ecologists study a diversity of things that can't be recovered if they are lost. 'Ecology' as a term, then, turns out be pregnant with wider meaning. It can provide a scientific analogy for other areas of thought, and it can point to a popular movement that transcends scientific study.

'Evolution' has just as diverse a range of meanings. Sometimes it is used simply to mean 'gradual development' or 'progressive change', as when we speak of the evolution of a language. In popular culture, 'evolution' can also stand for a materialistic view in which everything has gradually developed through natural processes out of previously-existing matter and energy in a grand cosmological history. Then there is the narrower scientific sense of evolution as a biological theory for the origin of species. Charles Darwin, in his culture-shaping book *The Origin of Species*,[2] suggested that the differences between biological species are not absolute but only a matter of degrees of continuous variation, disputing the classical view that species were real distinct types. And the more popular materialistic worldview resonates in some ways with Darwin's interest to show how the origin of biological diversity could be explained by laws of nature, just as ongoing planetary motion can be explained by laws of physics. This vision led to Darwin's most significant contribution to biological thought, and the central meaning of evolution. The process of evolution by natural selection, as envisaged by Darwin and his contemporary Alfred Russel Wallace, is one in which, as living things produce offspring that differ from their parents, certain changes progressively accumulate over many generations. This is evolution as a phenomenon, and gives its name to evolution the scientific theory.

In the rest of this chapter we will look in more detail at the scientific senses of 'ecology' and 'evolution' and their relationships with the rest of biology. What kinds of theories and principles are we dealing with? As we address this, we will uncover some intriguing and perhaps unexpected characteristics of the structure of science, as well as some fascinating idiosyncrasies about the biological sciences.

An Integrative View of Science: Law and Order

In order to account for the diversity of the different scientific activities that make up biological research, we need a broad definition of science. Science is commonly defined in terms of knowledge, in line with its etymological root, but this is at once too restrictive and too broad. It is over-restrictive because definitions of 'knowledge' are themselves subject to debate, as are questions of how 'true' or 'real' scientific concepts can be. At the same time, it is too broad because large swathes of 'knowledge' do not seem to be scientific: memories, acquaintance and tacit knowledge, for example. Instead, in line with our integrative approach, let's try the following: science is the human endeavour to describe the hidden rational order of the cosmos. 'Cosmos' is from the Greek word for order, which is appropriate enough, as we do indeed start with a conviction that the world is orderly and then seek to specify that order with increasing precision. From physics to sociology and from astronomy to linguistics, scientific work involves formal description of regular order: things like constant relationships, underlying structures and general systems that seem to recur across space and time. This is why scientific knowledge is often useful for prediction, explanation and devising new technologies: one place and time can be treated much like another once we discern some underlying order.

This simple description of science allows us to say what the diverse fields of ecology, evolution and biology have in common, and to outline their characteristic differences. First of all, ecology tends to be a search for order where there may appear to be none: in the apparent disorderliness of our natural environment and the haphazard encounters of organisms with each other. Ecological order sometimes yields to mathematical description only when ecologists try zooming out to observe large enough areas: it is characteristically a spatial science. Evolutionary science, on the other hand, is more like an attempt to order diverse categories of organisms by reconstructing their family trees on the basis of scientific reasoning — that is, by reasoning from other kinds of order. Evolutionary order refers to a past far beyond living memory but one that can be hypothetically reconstructed and ordered using other sciences such as genetics and geology. It is about zooming out, as it were, across different spans of past time so as to put the diversity of observed life forms into a meaningful order: typically what we call a phylogeny. Finally, we come to general biology. It is of course somewhat crude to lump the rest of biology together, but for present purposes we may portray biology as a search for layers of order and their interrelations as they contribute to the functioning of organisms (see the chapter by Leyser and Wiseman). This is at least sufficient to draw contrasts with ecology and evolution. In brief, we are suggesting that ecologists search for order by looking at different spatial scales, evolutionists find order in scientific hypotheses about the past, while other biologists, confronted with a great deal of order at the outset, describe how different levels of order relate to each other in the functioning of living organisms.

The biological sciences as a whole are a rich and diverse set of disciplines, practised by people with a wide range of interests and skills.

Order is a helpful term, but we need to dig a little deeper into the philosophical roots of the sciences to articulate an overarching perspective that will help us to reintegrate biology. If science is about describing the rational order of the cosmos as accurately as possible, it should be possible to say something about how biological 'order' can be described 'accurately', and what is meant by 'rational' here. We don't simply mean placing items in order by speculation or whim! One important and traditional notion that can take us further is that of laws: scientific laws, and laws of nature. Several important features of these concepts will help us think about reintegrating biology.

First, laws have figured prominently in the discourse of the natural sciences at least since Johannes Kepler,[3] who described a set of laws of planetary motion. Scientific laws have long been conceived of as laws of nature: inviolable prescriptions for how things must, and always do, happen, given certain conditions. Laws therefore allow us to make deductions: in the appropriate conditions, a certain phenomenon will occur. The conditions can be very stringent or even perhaps impossible, such as 'if there is no friction', 'if colliding bodies are perfectly elastic' or, in biology, 'if the environment is constant' (no weather! — Implausible but achieved by creating laboratory conditions), for example.

A second feature of scientific laws is that they are often stated in mathematical terms, as equations. This entails precision, and is one of the senses in which science may be said to describe a 'rational' order. This is especially interesting because the correspondence between mathematical structures and the material world has sometimes evoked surprise in scientists. Maths is developed from intuitions and axioms that do not refer to physical systems, so it seems remarkable when a piece of maths turns out to be applicable and useful for understanding a physical or biological system. In biology, we may think of the occurrence of numerical sequences such as the Fibonacci sequence when the numbers of repeating units in an organ are counted, like scales in a pinecone (other examples will be mentioned when we discuss laws in ecology in the next section). The 'unreasonable effectiveness of mathematics' for the sciences, as Eugene Wigner called it,[4] implies an order of correlation among different aspects of reality, and different sciences. The applicability of simple mathematical laws to scientific problems, and similarly of physical analyses to living organisms, and of biological approaches to psychological problems — such discoveries as these all contribute to the excitement of the scientific project of describing a rational order in the cosmos.

A third important point concerns the provisionality of scientific laws. For example, while Galileo's law of inertia has stood the test of time and is now better known as Newton's First Law of Motion, his law of planetary motion conflicted with Kepler's laws and has not been retained.[3] Scientific laws, clearly, are not beyond revision or rejection, and cannot be assumed to be real laws of nature. There is a large philosophical debate as to whether any law that a scientist might describe can refer to a real law of nature, as well as the question of how scientists could be sure of this. But it is clear that scientific views are subject to revision. This should come as no surprise in view of their speculative nature. Newton posited his laws of motion as universally applicable throughout all space and time despite his never having left the Earth and without being a time-traveller! These laws were duly celebrated and widely taught as laws of nature until Albert Einstein's theory of General Relativity relativised them as mere approximations to the results of laws described in terms of curved space-time. This is typical of the fate of scientific laws through history: they may be superseded, yet mostly survive major theoretical changes without being rejected outright. Now from our perspective early in the 21st century, Einstein's laws seem to be correct, having been validated to high precision by numerous experiments and observational tests — but the lesson we must learn from history, and perhaps intuition, is that scientific laws are always provisional. They seem to express laws of nature, but nature has a habit of proving more subtle than scientists expect.

We shall look at the scientific nature of ecology in more detail in the next section, but here we briefly consider the scientific characteristics of evolution. The principle of natural selection is that individuals whose traits make them more likely to survive to reproduce and then reproduce more successfully eventually leave more descendants, thus contributing more to successive generations, than those individuals with other characteristics. To have evolution by natural selection, it is necessary that traits subject to such selection are heritable — otherwise the mechanism is reset at each generation and nothing fundamentally changes — and that novel variation in selected traits continues to arise — otherwise change will cease or move in cycles. Understood in this way, evolution is the scientific study of regular processes occurring in the natural world in such a way as to produce certain kinds of patterns — or order — in the diversity of living organisms. It is important to note that we refer to evolution here as a process, and natural selection as a principle: neither are laws in the strict sense of empirical descriptions of either necessary or contingent order from which deductions can be made. Darwin might be thought to have discovered a law of biological evolution on the template of the laws of physics, as Haeckel suggested in applying Emmanuel Kant's phrase 'a Newton of the blade of grass' to Darwin. Indeed Darwin himself perhaps hinted at such an ambition in the closing sentence of the Origin of Species, which is worth quoting for its eloquent subtlety:

> There is grandeur in this view of life, with its several powers, having been breathed originally into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most varied have been, and are being, evolved.[2]

But what law of nature did Darwin propose, if any? He refers earlier in the book to 'one general law, leading to the advancement of all organic beings, namely, multiply, vary, let the strongest live and the weakest die'.

This doesn't fulfil the standard notion of scientific laws outlined above: it does not allow predictions to be deduced and there is no conceivable way it could be falsified. Rather, it stands as a rule or algorithm that neatly summarises the principle of evolution by natural selection. In fact, we argue below that the scientific character of evolutionary science does not rest on any evolutionary laws but on the way in which it is situated in the context of other areas of biology — especially ecology.

This discussion of scientific laws is important because such laws appear in the different biological sciences in some contrasting ways — which together build up an integrated picture of biological order. We now need to look at the case of ecology.

Ecology and Its Laws

One of the striking things about today's science of ecology is just how successful ecologists have been at finding relationships between a diverse array of things that aren't easily measured or can't be detected by our senses at all. This is a facet of ecologists' search for order where naively we would see chaos. It is perhaps one of the reasons, incidentally, why ecology is under-appreciated in secondary education, since it is often necessary to use statistical techniques to interrogate large amounts of data before this order can be seen. Most ecological experiments cannot be done in a laboratory, nor are they particularly theatrical; rather they require data to be gathered from large geographical areas and/or long time-periods. But ecology is a science coming of age as ecologists appreciate the scope for unifying principles and theories. We are also becoming bolder in proposing laws.

We can begin with the numerical patterns that describe population dynamics. First comes the recognition that there are populations of individual animals and plants whose members interact with each other in a given region, such that changes in the size of these populations over time might show some kind of patterns. What size of region we should look at and how to sample it is one of the principal ecological challenges, but a fruitful answer to such challenges is revealed by the ability to describe numerical relationships between the size, or density, of a population from one season to the next, or between the size of a population of one species and that of another with which it interacts. Such descriptions have given rise to a class of laws known as density-dependence relationships. These laws generally take the form of simple mathematical models into which approximate numbers can be fitted to make sense of any particular situation, so they are not often useful for making precise predictions about the abundance of a species at a given time and place. Nevertheless, it was a crude precursor of such laws that inspired Darwin's theory of natural selection. Thomas Malthus' *An Essay on the Principle of Population*[5] pointed out that the numerical powers of increase of a human population were consistent with a geometric law which is clearly not fulfilled: if it were, the population size would increase at every generation by the average number of children born over the lifetime of each adult. Malthus suggested that the population growth would instead be limited by the food supply, which he whimsically suggested might be increased by a fixed amount at each generation. He contemplated a population growth rate that we would now describe as density-independent, and posited instead one that is density-dependent, constrained by the current density with respect to the food supply.

Another broad area of ecological laws is spatial laws. Spatial ecology has roots in the 19th century but took off following the suggestion that large groups of species might, in the wild, be functionally equivalent to each other. Such thinking seems to have begun with Robert MacArthur, who compared island faunas and asked how many species one should expect to find on different islands purely on account of the size of the island and its isolation from the nearest mainland. In an important way this was a continuation of Darwin's and Wallace's studies of the flora and fauna of archipelagos, yet the notion that different species might be treated as functionally equivalent was, in another sense, profoundly un-Darwinian. The unification of spatial ecology attained the status of a theory with Stephen Hubbell, whose unified neutral theory of biodiversity and biogeography[6] laid the foundations for a geometrical kind of ecology that has been remarkably successful in proposing ecological laws. The characteristic of these laws is that they describe numbers of species and other taxonomic categories to be found in areas of different sizes and distances from each other. They depend on evolution as a process of speciation, and in turn provide important underpinning for evolutionary work about diversification and adaptation.

Only a few attributes of species are treated by laws of spatial ecology, typically those relating to dispersal abilities and speciation propensities. The next area of ecological laws that we consider concerns species' attributes in all their complicated diversity. Functional trait ecology goes back to the roots of biological observations, as naturalists have speculated about the functional significance of species' traits. Since the late 20th century, however, advancing statistical capabilities and the accumulation of global data sets have facilitated an enormous growth in theorising about correlations among traits across different species. Why are most needle-leaved trees evergreen and lacking adaptations to spread their seeds far afield? Why do species of smaller birds tend to be shorter-lived and lay more eggs? Combining insights from evolutionary thinking with those from physiology — another of ecology's neighbouring disciplines — has allowed the emergence of relationships that should be considered as laws. The plant economics spectrum is a recent set of ideas that deserves to be popularised and may even constitute a theory. Laws have been discovered describing how adaptations that help plants conserve resources, like having needle leaves and being evergreen, tend to be associated with other adaptations that help them cope with more stressful environments, such as a tendency to grow in clumps of the same species.[7] The much older *r*-versus-*K* selection theory also provides a measure of law-like explanation — suggesting, for example, that species that produce offspring more prolifically tend to be shorter-lived — and so do the relatively new universal scaling laws,[8] which are part of a theory relating organisms' lifespans, body sizes and fluid transport networks. All these relationships are important for understanding both evolutionary and general biology: in fact they tend to provide a bridge between the two. General biology can often explain how traits come to be expressed in an organism and some of the physiological links between them; evolutionary biology explores how particular associations between traits are part of an organism's adaptation to a certain environment.

The final area of ecological laws we will look at is those pertaining to ecosystems. Given the prominence of the ecosystem concept in our culture, it is surprising to find that only a minority of scientific papers in ecology mention ecosystems. It also seems as though there has been less progress in discovering general laws that pertain to ecosystems, although plenty of measurements have been made of ecosystem properties. Quantities like biomass at different levels in a food web, energy fluxes between these levels, concentrations of different nutrients in the water, air and soil and in the bodies of organisms: all of these have been measured in different places and over timeframes ranging from minutes to decades — and indeed relationships have been detected. Some of the most general relationships may be the so-called resource-response models, with equations relating overall chlorophyll concentration, plankton biomass or primary productivity to the total phosphorus concentration of a lake, for example.[9] A further oddity about ecosystem ecology is how little it connects with the rest of biology — a point that we will reflect on later. Nevertheless, the ecosystem is the highest level of biotic phenomena we can recognise: a level that integrates all biotic functions and processes and connects them with non-living phenomena.

The four areas we have looked at are very different in terms of what kinds of phenomena they concern. From numbers of individuals to quantities of matter and energy, and from spatial patterns of organisms to their actual characteristics, very different kinds of prediction are possible, with applications in diverse areas from pest control to international policy, and from conservation planning to crop breeding. These four aspects of ecology still have much in common, however. All of them typically raise questions about spatial scale, and the patterns they seek are only detected with sufficiently large amounts of data gathered by zooming out to appropriate areas of observation — not too small, but not too broad either. All four aspects can also be related easily to considerations of natural selection and evolutionary change. We have hinted at some of the dependencies; we might now expect that, on closer investigation, different aspects of evolutionary theory are most relevant to these different aspects of ecology. It is, therefore, to evolutionary thinking that we now turn.

How Evolution Depends on Ecology

The scientific study of evolution is peculiar in several related ways. For one, it is difficult to make and test predictions. This is not a unique feature of evolutionary science: geology and sociology, for example, also weigh light on predictions, as do many other sciences. This is related to a crucial feature, that evolutionary science takes a special interest in the past. This historical focus is an important characteristic that will help us build an integrated view of the biological sciences.

There are other sciences that focus on the past, of course. Cosmology concerns, among other things, the development of the observed universe from a simple initial state — as in the Big Bang model. Geology explains the formation of the physical features of the Earth. Archaeology concerns the development of human civilisations. And evolutionary science concerns the history of life on Earth. Archaeological reconstructions, geological models and cosmological narratives are hypotheses, and one of the aims of evolutionary science is the construction of family trees. Perhaps the ultimate aim is a giant tree showing the relationships of all living organisms to each other — and to create this would of course require knowledge of deceased relatives. This cannot be done by direct observation or record-checking, as it often can with human family trees: it requires scientific analyses of markers of relationship, such as genetic sequences. And, by our definition of science given above, it must be the scientific nature of these analyses that give evolutionary trees their scientific interest. Merely positing an order among a given set of species is not a scientific achievement, but evolutionary scientists can do this on the basis of scientific reasoning.

Next, we should note that the processes studied within each of these historically-oriented disciplines have their origins in other, related scientific fields. Cosmology depends on the physics of fluids, energetic reactions and gravity; geology depends on various aspects of materials science; archaeology depends on diverse scientific theories in chemistry, biology, ecology, sociology and so on. So, what does the study of evolution depend on? Where do the various strands of evolutionary science find their home? We suggest that the scientific habitat for the web of evolutionary studies is the field of ecology.

Neo-Darwinian evolution is a very simple theory in essence, but an ecological context is needed to bring to life the beautiful tautology at its heart. The core principle of evolution by natural selection is essentially a logical one: among a set of things that can replicate themselves after their own kind, those kinds that replicate faster and survive longer will subsequently be proportionally more abundant. But to move from the resulting notion of 'survival of the fittest' to a theory of biological evolution calls for a biological model. First, we need a model describing inheritance with variation, that is, descent with modification. This much was provided in the neo-Darwinian synthesis of Dobzhansky with Ronald Fisher, J. B. S. Haldane and Sewall Wright, which drew upon the earlier work of Gregor Mendel. Inheritance was explained by the transmission of genetic material: DNA sequences being physically copied and passed into cells that give rise to offspring, while variation was mostly the result of random errors — mutations — in the copying process. Secondly, we need a model of natural selection. Using these two components it is easy to simulate evolution in a computer program — as has been done many times (e.g. 10). But such 'artificial life' simulations have rather contrived algorithms for selection. The choice over which entities to cull may be based on a range of criteria, but it is difficult to find many that relate to the world of living organisms. In some cases the filter even uses a human criterion of 'greater complexity' — introducing a teleological component that most biologists would strenuously resist. No: to understand evolution as a biological phenomenon, we need theories of ecology.

Ecology is a science whose roots are closely intertwined with those of evolutionary theory and the scientific community's gradual adoption of the ideas of Charles Darwin and Alfred Russel Wallace. Independently, and inspired by observations in different parts of the world, these two Victorian naturalists imagined how an enhanced survival rate for individuals with favoured characteristics could lead to gradual and potentially unlimited changes in the characteristics of a lineage. And this principle of evolution by natural selection helped turn scientific attention to the homes (habitats) of plants and animals, because if Nature were selecting favoured individuals and races, it must be doing so through the environments in which they eked out their living. It is, after all, with utter dependence on particular places and conditions that organisms live their lives, reproduce and die. So whether natural selection acts via direct competition, like two vultures fighting over a carcass, indirect competition, as when plants send roots into the same zone of soil, each extracting nutrients and water at the expense of others, or even apparent competition, as when an increase in numbers of one species bolsters the population of a predator and all the predator's other prey species then suffer as a consequence — in all cases the consideration of the environment is crucial for any understanding of the outcome. The environment is the *context* within which natural selection takes place, giving direction to the selective forces. Which animals happen to meet each other, which seeds land in proximity, which hapless individuals are washed or blown away — such random happenstances as these play a part in the overall course of evolutionary change. And ecology, as we have seen, is the science that seeks order in the juxtapositions and encounters, the accidents and serendipity, as they occur to living organisms. This science took root in the much older science-crafts of natural resource management: forestry, agriculture and fisheries,[11] and indeed Darwin himself contributed significant ecological studies of orchids[12] and of the earthworm.[13]

We may summarise by saying that evolutionary processes occur in an ecological context. But can ecological science complement evolutionary explanations?

Evolutionary Ecology

We noted in the previous section that merely putting a set of items in an order barely qualifies as a scientific activity unless it is done on the basis of some kind of scientific analysis. Evolutionary order, as in the family trees known as phylogenies, is scientific insofar as it is hypothesised on the basis of evidence of a scientific nature — using tools from fields such as genetics and geology — and explained in terms of regular patterns in birth, reproduction and death — which means ecology. Ecology is the crucial context for thinking about evolution because the characteristics of living organisms can only be interpreted in the context of their lives in some environment or other. Traits such as the beak of a bird and its length, or the fruit of a tree and its sugar content, are not absolute goods for organisms to have, or to have in greater measure: they can only benefit the organism in question by improving its survival and reproduction rates in the circumstances that it faces from moment to moment and from day to day. A trait that is advantageous in one year can easily be disadvantageous in another. To understand evolutionary patterns in traits, we therefore need to understand how those traits function in the struggle for existence — those interactions where individual organisms risk their lives or win reproductive success. Such interactions are the subject of ecology.

The importance of ecology for understanding evolution was for a long time obscured by fascination with the notion of inner forces of evolutionary progress. Indeed, the very term 'evolution', according to its etymology, means a rolling out, as if there might be a great predetermined chain of life-forms waiting to be revealed, like patterns on a rolled-up carpet. This pre-deterministic, law-like sense of 'evolution' is reflected in its use by chemists to mean the release of a gas in a chemical reaction: dropping sodium into a beaker of water causes the evolution of hydrogen, for example (and an explosion!). The neo-Darwinian paradigm, and evolutionary thinking in general, does of course take for granted an increase in complexity in the bodies and behaviours of many lineages of living organisms simply because of the assumption that the first living organism of all must have been very simple, and now we have myriads of species that are more complex. But this has never, to our knowledge, been successfully formulated as a testable law, or as the development of any kind of prescribed complexity — notwithstanding some fascinating debates about how far physical necessity may constrain the forms of complexity that we see.[14] The evolution of species is not a predictable kind of progress since it is difficult to find a sense in which it can be called 'progress' at all. Species that exist today are not 'better', 'higher' or 'more adapted' than those that have existed in the past. They are simply adapted to the context in which they find themselves today — a context that includes all the other living things they interact with in their communities. Communities of the past were very different from those of today, and hence the context of each species is also very different.

Small degrees of evolution are sometimes predictable, at least in laboratory conditions, where, for example, antibiotic resistance tends to arise in bacterial strains exposed to a particular antibiotic. Such resistance tends to be metabolically costly to produce, and hence tends to be lost when the stress is removed, and cannot be seen as part of a progressive evolutionary journey. More importantly, we must recognise that a phrase like 'selection will favour antibiotic resistance', while it may be a scientific prediction, cries out for an ecological context (the presence of an antibiotic) lest it should be taken as positing a teleological or animistic 'guiding hand'. Natural selection is a scientific metaphor for the outcome of diverse kinds of interactions between heritable traits and the environments in which organisms present them. It therefore needs an ecological explanation.

Ecologists love to find order in the contingent and the unpredictable: what happens when plants, animals and microbes are free in the wild to flee from or feed on each other, to escape fires or be struck by landslides, and so on. So, the importance of ecology in evolutionary studies has grown as the notion of evolutionary progress has receded. A tenet of scientific investigation is the continuity of underlying processes through time: scientists seek to discover processes and laws that are universally applicable at all times and places where relevant conditions and entities occur. This is where evolutionary ecology comes in. Evolutionary ecology is the study of how natural selection actually happens. It examines patterns in birth, reproduction and death rates: how it is that organisms do better or worse in the struggle for existence in terms of their heritable traits. Competition among individuals of the same animal species may occur in sexual (territorial behaviours, mating rituals, etc.) and non-sexual contexts (e.g. for food). Competition among plants of the same species occurs through competition below ground as root systems forage for nutrients and absorb water; it also occurs through competition for pollinating insects to produce the most abundant and fertile seeds. The results of such competitive interactions have been the subjects of ecological study for a long time, and now we have a pretty good idea of when they cause competitive exclusion, and when they have other effects, both direct and indirect.

We have said that ecologists study the haphazard and unpredictable encounters and fates of living organisms, which echoes the unpredictability of most evolutionary change. But earlier on we outlined a wide range of kinds of ecological laws that have been, and are being, discovered, and now we have suggested that this lawfulness of ecology actually makes an important contribution to the scientific status of evolution. This raises the thought that there might yet be more predictability in evolutionary change itself than is yet appreciated. With this in mind, we now turn at last to focus on the question of the reintegration of biology.

Making Sense of Biology: A Reintegration

In view of its prominence, we might suspect that evolution is seen as something more than a theory, even in scientific circles. Thomas Kuhn's celebrated book *The Structure of Scientific Revolutions*[15] provides an important concept that can help us make sense of the structure of biology and its major themes.

A paradigm, according to Kuhn and his interpreters, is a framework of accepted scientific problems and typical solutions, of textbook examples and approved methods, that characterises a particular field of research in a particular period, being recognised by the relevant scientific community as framing legitimate research in that field. It is, we might say, a framework of meaning for a programme of research. Kuhn's own examples of paradigms are drawn from the physical sciences — the paradigms of Newton's dynamic physics and of Einstein's General Relativity being two of the most comprehensive. But the application to biology is what concerns us here. The phrase of Dobzhansky with which we began this chapter suggests that he saw evolution as the reigning paradigm of the biological sciences: a framework in which everything in biology can make sense. In his address to the Zoological Society of America, Dobzhansky spoke of the twin themes of unity and diversity which the idea of evolution brings to the study of biology, and indeed the prominent place of evolutionary theory in biology textbooks and courses endorses the importance of this. But is there more to be said about how biology holds together? Let's notice that Dobzhansky's oft-repeated claim doesn't actually seem to depend upon the mechanism by which evolution occurs. The unity-in-diversity of living organisms is an insight arising from the principle that all living things ultimately arose from a single common ancestor (or it needn't be much weakened if we posited a few original life-forms instead of just one). But what about the principle of natural selection? Does that shed light on the whole of biology too?

At this point we could return to our earlier remark about 'evolution' referring to a materialist worldview, where indeed the principle of natural selection is heralded as a logical law with a creative force, which holds out the possibility of reducing biology to a kind of physics (see the chapter by Gatherer). But at this stage in the development of biology, and as evidenced by other chapters in this book, that reductionistic approach is not at all promising. Instead, we should look the other way. The principle of natural selection, we are suggesting, shows how evolution depends upon ecology. And there may be an ecological paradigm that sheds light on evolution itself.

To say that there are other paradigms besides evolution in the biological sciences is trivial. There are paradigms in developmental biology, in genetics, in plant and animal physiology and so on, each of which gathers communities of researchers, typical research goals and kinds of methodologies and data with which to achieve them, and specialised journals in which discoveries and ideas are published. And in ecology, the four areas of ecological laws mentioned above may be recognised as emerging from paradigms. We have a population paradigm, a spatial paradigm, a trait paradigm and an ecosystem paradigm. It is striking how much overlap and even cross-fertilisation among these paradigms there is: for example, there have been proposals of grand unifying theories of biodiversity that might sound like an endpoint for ecological research, but that turn out upon closer inspection to be laws concerning patterns in numbers of species as ranked from most to least abundant, or in numbers of species to be found in areas of different sizes and separation distances.[16]

But what kind of paradigm might give meaning to natural selection? We have noted the fallacy of taking natural selection as a 'guiding hand' — on the model of human agents engaged in the artificial selection of animals and plants to breed from in seeking to improve varieties for agriculture, for example. And we have mentioned that it is by means of ecological interactions that natural selection actually happens. Perhaps the most important way to understand natural selection is by considering the ultimate significance of the traits of organisms. Ultimately, our interest in evolution is in how species and other groupings come to differ from each other and to do different things — and this means understanding their traits. Traits, moreover, are in general the features of organisms that must be referred to in any account of ecological interactions concerning individuals. Functional trait ecology, then, is the paradigm that focuses on finding order among disparate individuals by measuring features that they have in common and seeking to understand the adaptive significance of these. There are questions of how different traits in a species relate to each other physiologically — what Darwin referred to as laws of growth, which he recognised would mould the effects of natural selection up to the point where such laws might change under selective pressure. There are the all-important questions of how particular traits affect the survival of individuals in conditions and circumstances that threaten them — from before birth through infant and juvenile stages to the period of reproductive activity, and including dispersal phases. There are also important questions concerning traits involved in sexual selection and other behavioural traits or tendencies that mediate survival and reproductive success. All of these are the subject of functional trait ecology.

To Dobzhansky's famous adage, therefore, we should add that nothing in evolution makes sense except in the light of ecology, and in particular the ecology of species' traits. Ecology, in turn, makes no sense apart from an understanding of the organismal and cellular fields of biology that account for the structures and functions of organisms which are manifested as traits. There is no foundational discipline among the biological sciences (Fig. 9.1).

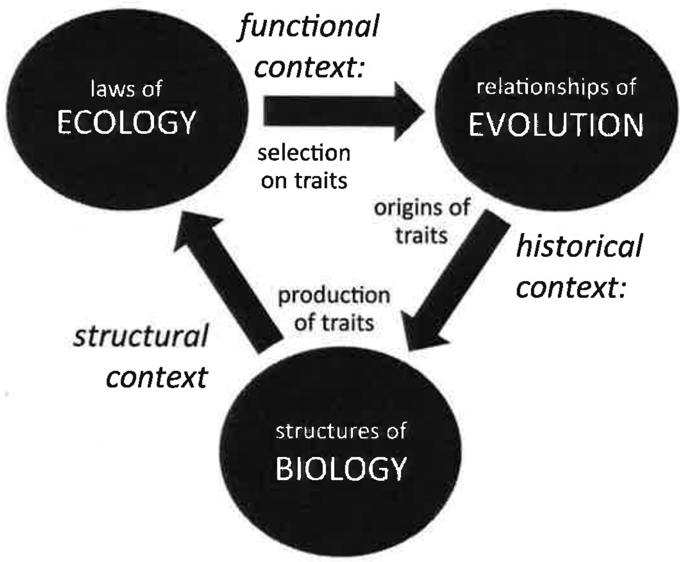

Figure 9.1. A model for the interdependence among the biological sciences. Ecology, evolution and general biology depend on each other, representing complementary facets of scientific thinking, and each providing an indispensable context for the others.

Outlook

How might people's understanding of biology be enhanced if ecology were properly understood as an indispensable link in the circle of life sciences? A reintegrated view of biology could bring benefits as far-reaching as improvements to our health, our family and social life and the impacts of our lifestyles on the environment. A less reductionistic and more ecological view of biology should, for example, affect our approach to diet, mental health, medicine, aging and long-term healthcare — some of which are explored in other chapters of this book. It could also directly affect our attitudes to nature conservation, land management and animal husbandry, as we appreciate more deeply the inter-relationships among living organisms.

We should also consider a reintegrated biology curriculum in education. A more ecological approach to evolution and a more evolutionary approach to ecology could enliven the teaching of both subjects. Evolution arguably needs to be better grounded in a geographical approach, which would encourage students to ask where natural selection may actually be happening — which calls for ecological insights into the various processes of competition. Ecology in turn needs to be better grounded in an understanding of how biology shapes and constrains the production of actual traits in plants, animals and other organisms. This should encourage students to ask how ecosystems might be different, and how emergent ecosystem processes like food webs and nutrient cycles reflect selective pressures on individual organisms — also helping locate ecosystem ecology with respect to other paradigms. Ultimately, we might see biology textbooks with a more integrated structure. They might be shorter rather than longer, and students might engage with biology less as a subject about complicated facts, and more as a discipline of ecological thinking.

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