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SIMILARITY PRINCIPLES IN ECOSYSTEM DYNAMICS

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INTRODUCTION

Although the use of similarity principles has a long and fascinating history going back at least as far as Galileo, this lecture is intended mainly to describe the current state of the art and to make some guesses as to what will happen in the future.

The organization of the lecture is as follows:

1) What are we talking about?
2) Why -- of what value is it?
3) What has been done so far?
4) What comes next?

WHAT ARE SIMILARITY PRINCIPLES?

A similarity principle is any kind of general rule about the relationship between different objects. This means that we can use one object as a model for another and use a similarity principle to scale the results. A simple example is the relationship between mass and weight in physics; if we know that the gravitational force on a 1 kg mass is about 10 Newtons, then we can predict that the weight of a 100 kg mass should be about 1000 N. However, we have to be sure that we specify the class of objects to which the similarity principle applies. So long as we deal with objects near the surface of the earth, the above calculation is valid, but if we are dealing with a 100 kg mass near the surface of the moon it is very misleading -- the correct weight is actually only 140 N.

Most similarity principles in biology are expressed as allometric laws of the form

$$y=ax^b$$

where x is some measure of size (weight, length, etc.) and y is some physiological variable such as growth or respiration. The constants a and b depend on the class of organisms to which the principle applies, which has been a constant source of confusion and frustration to biologists. Whereas physicists can usually agree on the class of objects they are describing (e.g., Newton's law of gravitation applies to "all material bodies"), biologists get results which tend to reflect individual research interests. For example, a similarity principle connecting two variables like body size and respiration will usually have different constants depending on whether it is fitted to data on humans, mammals, vertebrates, all animals, or living organisms in general. In light of this problem, it is fair to ask:

OF WHAT USE ARE SIMILARITY PRINCIPLES IN ECOLOGY?

The use of similarity in physics and geometry is well established and goes back to the dawn of scientific work in both

Eastern and Western civilizations (Gamow 1961, Mason 1962). Perhaps the first scientist to use it for quantitative physiological calculations was Galileo (1638), who showed that bone size had to increase faster than body size in large terrestrial animals. The dominant figure in modern times is unquestionably D'Arcy Thompson (1942), who clearly showed that allometric relations are widely found among living organisms. Thompson concerned himself chiefly with morphological characteristics, but in more recent times there has been a growth of interest in the relationships between dynamic processes in different organisms, and most recent work has focussed on physiological rates. The existence of allometric relationships governing such rates has been shown time and again, but because different researchers tend to consider different groups of animals, there is no agreement on the precise form of these relationships. Furthermore, these laws are only approximate, and the large degree of scatter that is usually encountered has made many scientists sceptical of their value, or even of their underlying validity.

From the viewpoint of the ecologist the imprecision of most similarity principles is more than compensated by their generality. There may be thousands of different species present in a single ecosystem, and it is not possible to obtain detailed physiological data on all of them. There is however a need to estimate such variables as community respiration and productivity, and similarity principles often provide a way to obtain such estimates from the kind of data which are available. Thus they can play an important utilitarian role in ecology. However, there is considerably greater value than this in the study of similarity. It seems to many of us that these principles reflect fundamental properties of living organisms. If this is true, then understanding of mechanisms which can explain similarity principles as well as deviations from them may play an important role in helping us learn how ecosystems evolve.

OUR PRESENT UNDERSTANDING OF SIMILARITY PRINCIPLES

The basic method used in the physical sciences for deriving similarity principles is dimensional analysis, and the same approach has been tried in biology (Stahl 1961, Schmidt-Nielsen 1970, Gunther 1975, Platt and Silvert 1981). Analysis of the simple pendulum provides a familiar example of the method. This consists of a point mass m at the end of a weightless string of length l. The period of the pendulum, t, can depend only on m, l, the gravitational field g, and dimensionless numerical constants. It follows that this dependence must be of the form

$$t=am^{b}l^{c}g^{d}$$

where a, b, c and d are pure dimensionless numbers (Bridgeman 1931). Since the dimensions of the two sides of the equations must balance, it turns out that the only possible values for the latter three constants are b=0, c=1/2, and d=-1/2. Thus the three exponents are uniquely determined by dimensional considerations, while the coefficient a cannot be derived without using further theoretical or experimental information.

Attempts to apply the same type of reasoning to biological systems are complicated by the fact that these systems are so complex that it is difficult to identify a small set of dimensional variables which play the fundamental role of m, l, and g in the above example. However, if living organisms really are as complex as they seem, then it is difficult to understand why they exhibit the high degree of regularity indicated by the existence of simple allometric laws governing physiological rates (Fenchel 1974, Humphreys 1979, Banse and Mosher 1980, Banse 1982). This regularity seems to indicate that these rates may in fact depend on just a few dimensional quantities, only one of which is a variable (Platt and Silvert 1982). The constant quantities appear to be the caloric content of living tissue and the density of tissue, while the variable is some measure of size; most authors have reported data based on some measurement of mass, such as wet or dry weight, but it may be that surface area is a more fundamental variable (Harding 1977, Brodie 1982).

Clearly this type of analysis, even if valid, can only be approximately true. Neither of the two "constants" described above are true constants, and practically any quantity one might choose to define as a constant for biological systems is likely to vary by perhaps a factor of two. Furthermore it would be foolish to pretend that taxonomic differences are totally insignificant. In fact the same is true in physics, and the period of a "simple" pendulum really does depend on the mass when realistic factors (the weight and elasticity of the string, air resistance, etc.) are taken into account.

A further complication is that the allometric exponent of mass appears to be somewhat greater for terrestrial organisms than for aquatic ones. Platt and Silvert (1981) have suggested that

since terrestrial organisms have to cope with gravity whereas aquatic animals are instead required to displace water in order to move, the density should be expressed in terms of weight on land and of mass in water. The dimensional difference between the two quantities leads to different exponents; for example, for specific rates with dimensions of $(\text{time})^{-1}$ the exponents of mass are -1/4 for terrestrial organisms and -1/3 for aquatic ones. These values are fully consistent with observation. However, despite the satisfactory agreement we may question whether caloric content and density really are the most important quantities affecting the physiological dynamics of living creatures. In particular, although the effort of displacing a mass of water must be a major metabolic cost for large marine vertebrates, it is probably less important than viscosity for small animals (S. Pearre, personal communication). If we replace density by viscosity in the dimensional formula (Platt and Silvert 1981) we obtain an exponent of -1/2. Data on small invertebrates are inconclusive on this point (Banse 1982), but it would not be surprising to see a change in the allometric exponent with Reynold's number.

At present it seems that the existence of similarity principles governing not only shape but also dynamical rates such as production, respiration, growth and related physiological quantities, are well-established in biology, even though there are certainly many other sources of variation in these quantities. The allometric exponents corresponding to these similarity principles can be derived from first principles using assumptions which are plausible if not totally convincing, and the results agree satisfactorily with experiment. If these assumptions prove valid they provide a valuable insight into the forces facing the evolution of living forms. Even if the assumptions underlying the derivation of the allometric exponents prove false, however, we may still treat the allometric laws as phenomenological models which let us estimate such quantities as total production for ecological communities when we lack enough detailed physiological data to estimate production directly.

WHERE DO WE GO FROM HERE?

As was pointed out previously, one of the difficulties in studying similarity principles in biology is that the forms of allometric laws depend on the groups of organisms to which they are applied. If we look at a plot of a specific rate, r, as a function of body size, m, for many different types of animals, then we find that we can either fit a single allometric law

$$r=am^{b}$$

to all the data, or we can fit a set of different laws individually to distinct groups such as unicellular organisms, invertebrates, and mammals. However, if we fit these major taxa separately we find that the values of b are roughly the same for all of them, even though the values of a are different; in other words, the different allometric lines are parallel on a log-log plot (Fenchel 1974, Banse and Mosher 1980). As we proceed from the smallest unicellular organisms to the the largest mammals in size, the value of any specific rate follows a zig-zag trajectory as shown in Fig. 1. As we go from an invertebrate to a fish or from a fish to a mammal of the same size we find that the physiological rates (e.g., growth, respiration, etc.) increase to reflect the

greater metabolic cost of a higher degree of complexity and organization. If on the other hand we simply look at all organisms together then we identify a single line with a somewhat larger (more positive) slope, and the taxonomic differences mentioned earlier appear simply as scatter about the dashed line in Fig. 1. If we went to a more detailed and less aggregated description then we might identify more lines scattered about the solid lines shown; if we compare Fig. 2 of the Fenchel (1974) paper with Fig. 6 of Banse and Mosher (1980) we see just this, as the latter authors use several categories which are much more detailed than Fenchel's.

If we think of different groups of organisms as representing different design strategies, then we can view the existence of similarity principles in nature as in a sense an engineering problem. When an engineer designs a bridge he needs to find the type of bridge which will suffice at reasonable cost. For the largest distances he has to build a suspension bridge, but these are too expensive to use for small distances, and in this part of the size range they cannot compete with cantilever or other designs. Similarly, it appears that mammals represent the only physiological strategy that is sufficient for the largest animals, but the costs of the mammalian design are great; the smaller mammals, the smaller shrews for example, are extremely inefficient and can survive only where conditions are ideal and food is abundant. At the other extreme of size, the smallest organisms are of course unicellular, but there is a limit to how large a single cell can be and still be viable. Thus each broad taxonomic grouping represents a design strategy which is potentially optimal over a certain size range, and there is some degree of overlap between these size ranges. This is similar to the bridge analogy mentioned above, since bridges of a certain design tend to lie within a restricted range of lengths, but for a given length there may be several possible designs, depending on secondary factors. However, the fact that all of these separate curves seem to cluster about a universal one, the dashed line in Fig. 1, suggests that there are some globally valid considerations which can be used to deduce the kinds of "design" which are likely to be optimal within a given size range. This idea of a global set of constraints on organisms which may be completely different in terms of structure and function is supported by the similarity of the slopes of the solid lines in Fig. 1, which represent the allometric exponents for these different groups.

The type of design limitations which can give rise to these types of regularities is a matter of conjecture, but there are some considerations which are obviously likely to be important. These include the problem of extracting nutrients from the surroundings and distributing them throughout the organism. Since the surface/volume ratio and the physical size of organisms increase with increasing mass, we find that larger organisms have developed complex methods for increasing their effective surface area (e.g., lungs and guts), as well as sophisticated transport systems for distributing nutrients throughout the body. These in turn call for more and more elaborate control systems, such as the central nervous system. These control systems in turn impose an additional metabolic cost, and that is why we see the

physiological rates shown in Fig. 1 jump as we move from a solid line representing one level of complexity to another.

Underlying the above discussion is the idea that similarity principles and the allometric laws which express them are not merely convenient patterns which can be used by ecologists in lieu of satisfactory experimental data, but that they reflect fundamental aspects about the organization of living organisms. If this is true, then we should try to identify what the basis of these principles is and to understand the nature of deviations from the patterns they represent. It was after all through the study of analogous patterns in planetary motion that Newton was able to identify the fundamental principle of universal gravitation and deduce his laws of motion (Gamow 1961); if there are any fundamental laws underlying the science of biology then the study of similarity principles is likely to prove an effective way to discover them.

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FIGURE CAPTION

Figure 1. Typical log-log plot of a physiological rate having dimension $(\text{time})^{-1}$ vs. body size. After Fenchel (1974) and Banse and Mosher (1980).

September 1980 BODY MASS AND ANNUAL *P/B* RELATIONSHIPS

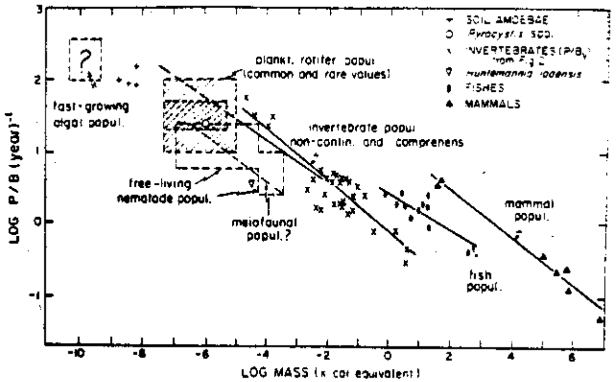

FIG. 6. **Annual *P/B* as a function of adult mass (mammals) or mass at maturity (fishes, invertebrates). Fish and mammal data (Table 4) with regression lines (Table 2, eqs. 13, 14). Invertebrate data from Fig. 2, regression lines from Fig. 2 and Fig. 4 ("Noncontinuous"). For algae, amoebae, rotifers, and nematodes, see text.**

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Body Size and Intrinsic Rate of Increase 321

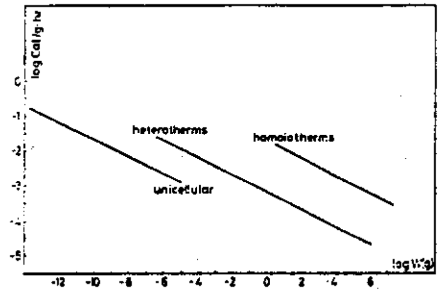

Fig. 2. **The relationship between body weight and metabolic rate per unit weight for the animal kingdom. Data from Hemmingsen (1960)**

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