

Applications of the Hertzsprung–Russell star chart to ecology: reflections on the 21st birthday of *Geographical Ecology*

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Robert MacArthur's *Geographical Ecology* turned 21 last year. As it enters adulthood, we may ask whether or not it is still influencing contemporary approaches to ecology. The opening sentence, 'To do science is to search for repeated patterns, not simply to accumulate facts...', is a theme of the entire book. As ecologists, we are faced with the problem of finding patterns when there is a large number of species, an even larger number of possible pairwise interactions, and when these are dispersed across a bewildering array of habitat types. How do we look for general patterns in nature? The Hertzsprung–Russell star diagram provides an inspiring example for meeting MacArthur's challenge.

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The night sky presents us with a perplexing array of celestial objects. We might begin our investigation of this sky by classifying the objects there (e.g. stars, planets, constellations), assigning individual names to the members of each class (Procyon, Betelgeuse, Sirius...) and recording information about each of these named objects (e.g. size, colour, distance from Earth). This exercise is basically one of collecting and cataloguing. Eventually, however, the mere collection of star data becomes routine and boring. Questions we need to answer are:

- What are the meaningful patterns or relationships among these objects?
- What do we need to measure to compare them?
- What processes underlie these relationships?
- What further measurements can we make that are insightful as opposed to routine?

The Hertzsprung–Russell star diagram (Fig. 1) (also called the temperature–luminosity diagram) was developed independently by two early 20th century astronomers, Ejnar Hertzsprung and Henry Norris Russell¹. It ordinales stars along two axes: luminosity (in magnitudes

relative to our sun) and surface temperature. This one relational diagram tells us a great deal about stars.

- The axes tell us which specific properties need to be measured to compare stars in this manner.
- Stars with similar characteristics (e.g. Red giants or White dwarfs) fall out close to one another in this phase space.
- Trends emerge which reflect a process – the origin, 'evolution' and eventual 'death' of individual stars.
- Prediction becomes possible. The size of a star appears to determine whether it will collapse into a black hole or a White dwarf.
- Deviations stand out. We know which stars fall along the typical axis (main sequence), and which are unusual.

The very complexity of living systems presents us with three obstacles: (1) an overwhelming number of species; (2) a mind-numbing set of possible pairwise interactions; and (3) a bewildering array of habitat types. However, by looking for patterns along measurable axes, we can, like a skilled practitioner of a martial art, transform an apparent enemy into an ally. Let us look at these obstacles in turn, and some prospects for overcoming them.

Large numbers of species

MacArthur² suggested that the complexity caused by large numbers of species might be reduced by creating a periodic table of life history types. Two recent approaches instead accept continuous variation in life history types, and use a Hertzsprung–Russell style of analysis by looking for simple axes on which all species can be ordinated. Southwood^{3,4} (Fig. 2a) has proposed that life history strategies of organisms can be plotted and compared along two habitat axes: (1) durational stability/disturbance; and (2) favourableness/adversity/stress. Three regions of this diagram correspond to three main life history strategies (*r*, *K*, *A*). Grime^{5,6} similarly suggests that two such axes have given rise to three primary plant strategies (*C*, *S* and *R* plants). This Southwood–Grime diagram has a great deal of intuitive appeal. It may also be possible to plot other factors in this space: there are reasons for expecting

competition to increase from the lower right to the upper left, for example. However, like so many other appealing theoretical models, it has one significant drawback: the axes have no units on them! We cannot measure the position of species along these two axes. We therefore cannot put this diagram into the same scientific category as the Hertzsprung–Russell diagram.

We could try to make position along these axes measurable. Grime⁵ proposed that the position of species (and habitats) along these two axes can be inferred from traits (Fig. 2b)⁷. He presented a triangular ordination of plant species which compares large numbers of species based on two traits: a 'morphological index' (based on height and lateral spread) and relative growth rate (Fig. 2b). This provides a quantitative way of spatially comparing different plant species or habitats. This approach has been criticized for several reasons^{8–10}, but nonetheless, Grime's diagram, with its measurable axes, brings us a step closer to MacArthur's goals (perhaps another writer would follow the periodic table analogy into the recent literature on functional groups). In general, exploring quantitative relationships of species along trait axes may be a useful strategy in ecological research¹¹, but, if so, the challenge is to find measurable traits that are directly related to important general axes such as those in Fig. 2a.

Pairwise interactions

There are three principal pairwise interactions in ecology: predation, mutualism and competition. In much of the existing literature, there is a tendency to study them using pairs of species picked

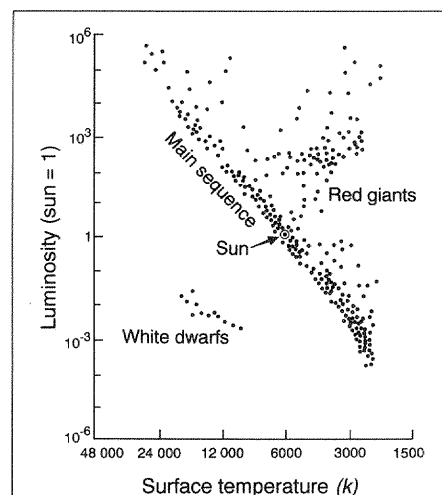
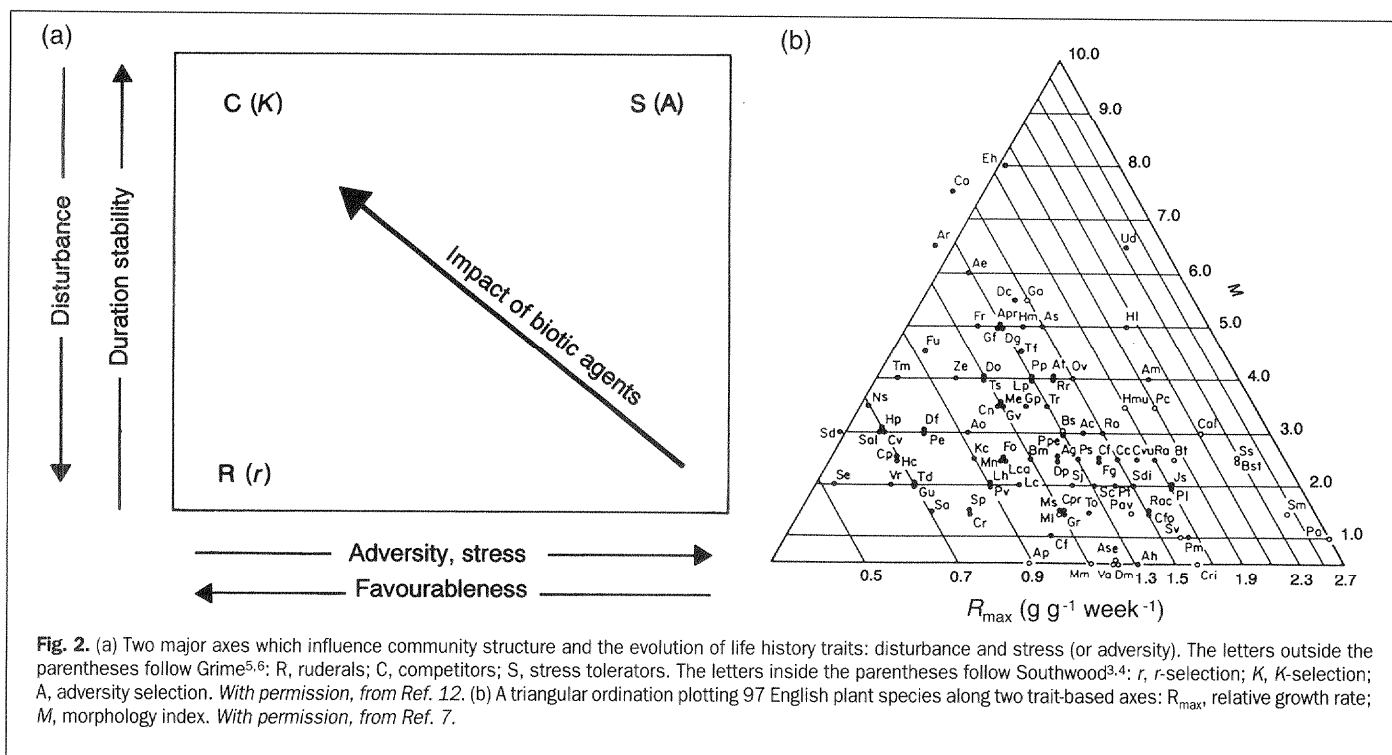


Fig. 1. The Hertzsprung–Russell star chart relates stars to one another based upon their luminosity and surface temperature. The main sequence goes from upper left to lower right. Redrawn, with permission, from Ref. 2.



haphazardly, or, perhaps even worse, for their natural historical appeal¹². When we try to look for patterns in these papers, not only do we have a non-representative subset of the world's biota, but because each study is carried out differently, they are exceedingly difficult to compare.

Let us explore competition as a representative pairwise interaction. Extensive reviews of competition^{13–15} reveal the difficulty in drawing conclusions from literature surveys. Doubling the number of papers by collecting more-whimsical pairwise interactions is unlikely to improve the situation. All it may accomplish is to make the task of future compilers more egregious. We could, instead, begin designing experiments to detect pattern. Consider the three possible approaches (many more are conceivable) outlined below.

Intensity and asymmetry

Two of the defining characteristics of any pairwise competitive interaction are its intensity and its asymmetry¹². We could design a series of studies which systematically and quantitatively explore patterns in their relationships. Questions might include: (1) What is the relationship between intensity and asymmetry? (2) What kinds of environmental factors determine the degree of asymmetry in pairwise interactions? (3) Do more-similar organisms have more-intense and more-symmetric interactions? (4) Are there some regions of enquiry with high or low densities of observations? If so, why? (5) Do certain kinds of organisms, such

as birds or echinoderms, have certain kinds of interactions – perhaps plant/plant interactions are generally intense and asymmetric, whereas bird/bird interactions are weak and symmetric? Figure 3a (Ref. 16) examines intensity and asymmetry in a pairwise fashion. Although large, it includes only a small group of wetland plants. One principal conclusion was that intraspecific competition (circles; lower right) has greater intensity but less asymmetry than interspecific competition (diamonds) or inter-guild competition (squares). Therefore, it appears that as species increase in similarity, competition intensity increases and competition asymmetry decreases. We need to know what other organisms might reveal if examined in a similar way.

Intensity of competition and environment

Asymmetry and intensity are both characteristics of any pairwise interaction between species. In intact communities, we can also measure and explore relationships among other aspects of competition, such as competition intensity and diffuse competition. Debates about competition intensity have raged over several decades, but I still do not know of a diagram plotting the intensity of competition against resource levels across a series of experiments! No wonder there is disagreement if we cannot even plot the few existing studies that exist along the same axes! If we cannot plot studies along the same axes, we simply cannot compare them, forcing us to substitute acrimonious debate for calm data analysis. Wilson and Keddy¹⁷

proposed a method for measuring competition intensity (at the time we called it 'diffuse competition') and found that it increased with soil resource availability (measured as soil organic content) (Fig. 3b). Five years later, I still know of no other published examples of such diagrams. Without standard procedures comparing different habitats and gradients, we cannot move forward.

One way to get around the problem of comparing studies with different species, habitats and experimental designs is to coordinate large cooperative ventures. Richard Reader (University of Guelph, Canada) and Scott Wilson (University of Regina, Canada) have done just this with an international study using 12 different study sites on three continents with more than 20 collaborators. The objective was to test for trends in competition intensity along biomass gradients – a multisite extension of Fig. 3b. In spite of great emphasis upon using a common experimental design and test species, they still had difficulty enforcing standard techniques and in reaching agreement in data analysis and interpretation²⁴. If there is difficulty in the analysis and interpretation of carefully designed, cooperative data-sets, what hope is there of usefully comparing studies haphazardly plucked from the literature?

Traits and competitive ability

Some organisms may be better competitors than others. If so, they presumably possess traits which confer competitive ability. A way to test this is to develop standardized measures of competitive

performance and explore their relationships with plant traits. The largest published exercise of this sort used 44 wetland species (Fig. 3c)¹⁸. More than two-thirds of the variation in relative competitive ability was accounted for by one trait – above-ground biomass. Other questions arise: (1) Are there better ways to measure these axes, such as more-accurate estimates of relative competitive performance? (2) Which other traits should be measured? (3) Do existing patterns hold for other habitats and other herbaceous plants? (4) What patterns exist for mammals, benthic invertebrates and other organisms? (5) Can the axes be modified so that, for example, trees and vertebrates can be plotted on the same diagram?

Large numbers of habitats

The apparent problem posed by large numbers of habitats can be turned to our advantage by finding or constructing environmental gradients to provide quantitative axes for comparative work. I have recently provided an operator's manual listing eight techniques for taking advantage of this approach¹⁹. However, one of my favourite examples was published by Lieth nearly 40 years ago in German, and adapted in English nearly 20 years ago in Whittaker's *Communities and Ecosystems*²⁰.

Lieth and Whittaker described the distribution of world vegetation types along two axes: (1) average annual precipitation; and (2) average annual temperature (Fig. 4a). The 'main sequence' on this chart goes in the sequence tundra, taiga, temperate forest, tropical rain forest. Shrublands, thorn forests and deserts fall off this main axis. This diagram could form the foundation for an entire series of studies which look at other functional properties of these ecosystems, such as rates of nutrient cycling, biological diversity, food web structure and so on. Entire chapters of astronomy textbooks are structured around the Hertzsprung–Russell diagram (e.g. Goldsmith¹). Entire chapters of an ecology text could be built around quantitative generalizations from the Leith–Whittaker diagram.

On a smaller scale, Grime²¹ proposes that species-richness patterns can be explained, in part, by comparing habitats along a gradient of standing crop and litter (Fig. 4b). Because these axes are measurable, they have generated a great deal of explicit testing in herbaceous vegetation types around the world. This figure is also noteworthy because it does not provide a simple regression line along which points must fall. Rather, it presents upper limits to diversity and there-

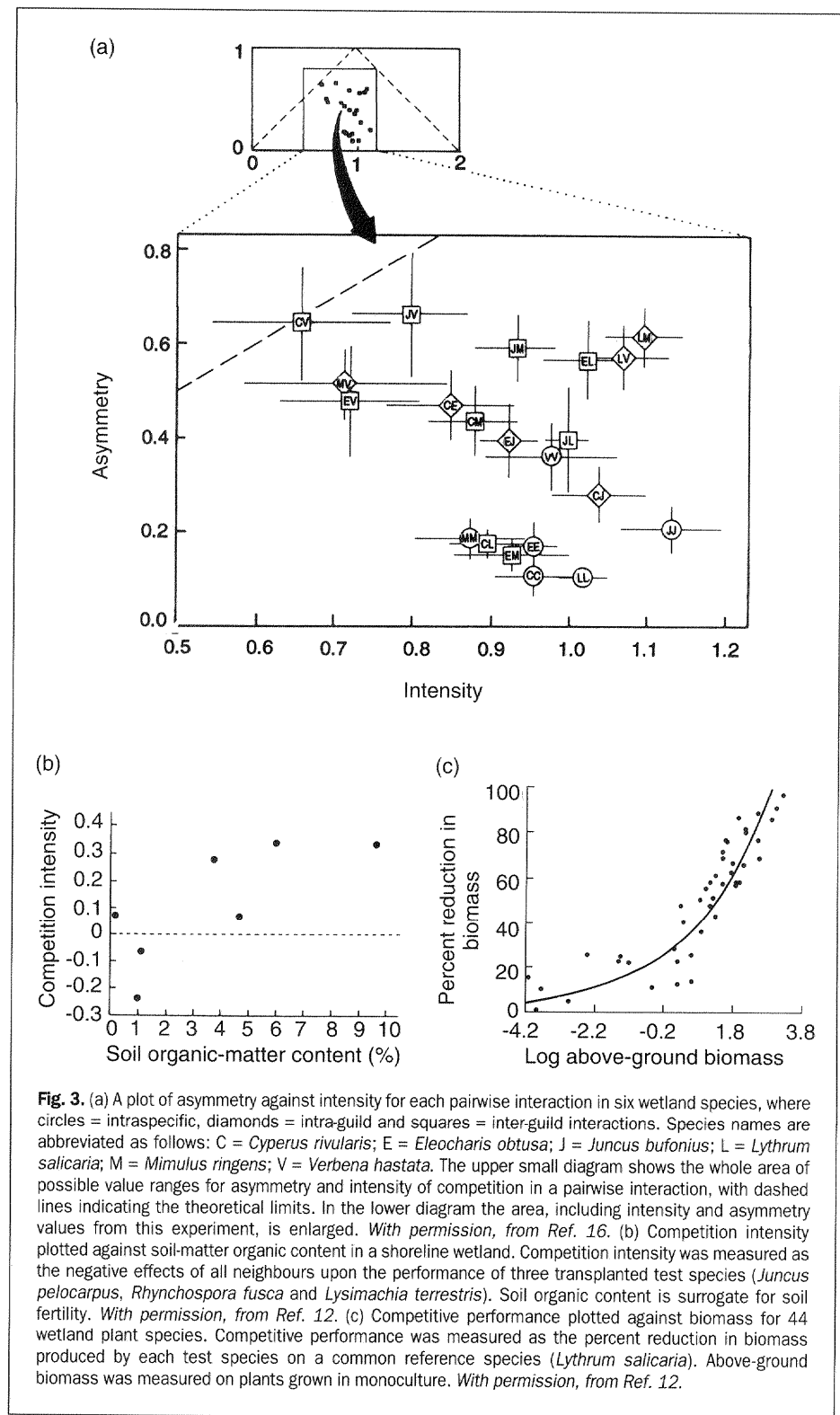


Fig. 3. (a) A plot of asymmetry against intensity for each pairwise interaction in six wetland species, where circles = intraspecific, diamonds = intra-guild and squares = inter-guild interactions. Species names are abbreviated as follows: C = *Cyperus rivularis*; E = *Eleocharis obtusa*; J = *Juncus bufonius*; L = *Lythrum salicaria*; M = *Mimulus ringens*; V = *Verbena hastata*. The upper small diagram shows the whole area of possible value ranges for asymmetry and intensity of competition in a pairwise interaction, with dashed lines indicating the theoretical limits. In the lower diagram the area, including intensity and asymmetry values from this experiment, is enlarged. With permission, from Ref. 16. (b) Competition intensity plotted against soil-matter organic content in a shoreline wetland. Competition intensity was measured as the negative effects of all neighbours upon the performance of three transplanted test species (*Juncus pelocarpus*, *Rhynchospora fusca* and *Lysimachia terrestris*). Soil organic content is surrogate for soil fertility. With permission, from Ref. 12. (c) Competitive performance plotted against biomass for 44 wetland plant species. Competitive performance was measured as the percent reduction in biomass produced by each test species on a common reference species (*Lythrum salicaria*). Above-ground biomass was measured on plants grown in monoculture. With permission, from Ref. 12.

fore specifies a region into which field data must fall. Looking for simple correlations or regressions between two variables may be overly simplistic in many cases in ecology.

General principles guide new experiments

Much might be gained if we deliberately set out to make future ecological studies more relational, more empirical²² and more pragmatic¹¹. Patterns not only

provide *post hoc* interpretations of the literature, but, perhaps even more importantly, guide us in deciding which new experiments are important and which are trivial. Consider another astronomical analogy – the study of faint and distant radio sources at the edges of the known universe. In a recent overview of the study of these distant radio galaxies, Miley and Chambers²³ state: 'It is impractical to carry out time-consuming, high sensitivity optical observations of

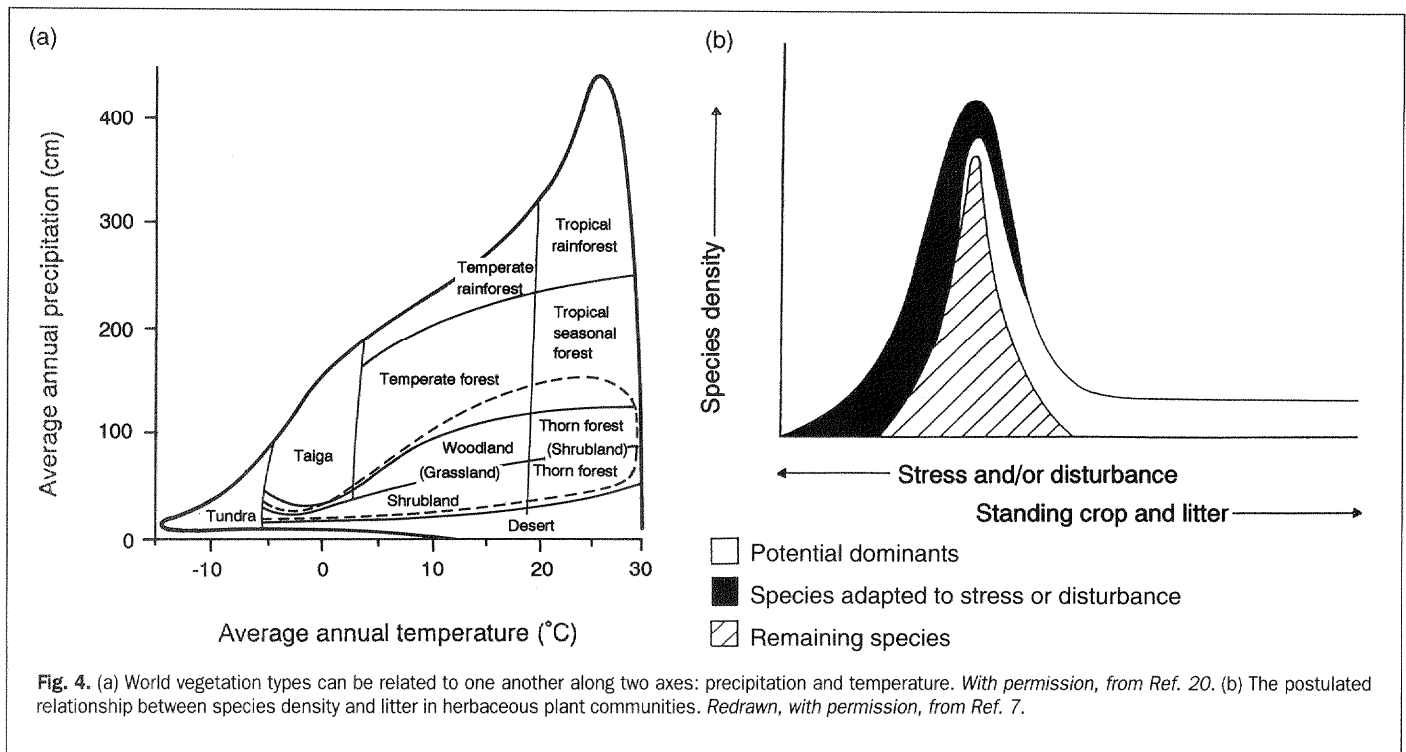


Fig. 4. (a) World vegetation types can be related to one another along two axes: precipitation and temperature. With permission, from Ref. 20. (b) The postulated relationship between species density and litter in herbaceous plant communities. Redrawn, with permission, from Ref. 7.

the tens of thousands of fainter radio sources that are now known' and that methods have been devised to 'select the best, most distant, candidates' for further study. Much of our current work in ecology may be trivial precisely because we lack criteria for defining worthwhile candidates for further study.

In the broadest sense, the Hertzsprung-Russell diagram illustrates an approach to science that depends upon pattern recognition. Loehle (pers. commun.) suggests that pattern recognition has a central role in the discovery process, in part because our brains are wired for pattern recognition. Placing species, ecological interactions and habitats along measurable axes, such as I have done here, is an essential part of the pattern-recognition process. Such ideas also draw upon the American philosopher Henry James, whose work is also rooted in the study of human psychology, and whose ideas on the pragmatic method have much to say about the design of ecological work to permit us to find useful patterns. The Hertzsprung-Russell diagram is a success largely because it presents a verifiable pattern. We can design our work so that we enhance, rather than impede, pattern recognition. An essential part of this process is seeking unified patterns in living organisms and avoiding scientific balkanization.

It appears that *Geographical Ecology's* challenge to find general patterns has been an elusive goal. Perhaps ecologists are too easily distracted by the natural historic detail in their system, too divided into taxonomic castes. Early this century,

J.B.S. Haldane²⁵ wrote: 'In ecology...we are at present often lost in detail' but, he added that we are constantly finding general factors, such as soil acidity, that predict the occurrence of entire communities. More recently, R.H. Peters²² has discussed the uneasy alliance of natural history with general empirical models. *Geographical Ecology* has therefore been but one of many voices addressing pattern and generality. Although MacArthur is often praised, and held up as an example for us, perhaps we have been too hasty in passing over MacArthur's opening sentence and therefore in failing to consider his goals. And so we might re-read this first page of *Geographical Ecology*. We might place greater emphasis upon deliberately looking for measurable axes so that we know what we are trying to measure and why. We might explicitly look for general patterns. We might even keep a copy of the Hertzsprung-Russell star diagram on our office walls for inspiration.

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