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The distribution and abundance of organisms as a consequence of energy balances along multiple environmental gradients

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We argue that observed patterns of distribution and abundance of plant and animal species within space and time are related directly to species-specific energy costs and gains (energy balance) in response to the many (Hutchinsonian N-dimensional) environmental or resource gradients. Competition, predation and other biotic interactions operate principally by increasing energy costs to the species, and can be included in our energy balance methodology as additional environmental gradients of energy costs. Persistence of a population and, ultimately, the species in a given locality, will occur only where energy return on investment allows a significant energy profit in the form of propagules. At any given time, energy investment in physiological, behavioral or morphological adaptations that optimize abundance at one point within the N-dimensional hyperspace of environmental gradients precludes the investment of the same energy elsewhere. Within the spatial and temporal range where the species can reproduce, abundance is related to the stochastic nature of important environmental interactions, because energy balance is ultimately controlled by the sum of organismal responses to all environmental influences. Populations tend to be most abundant where their genome allows the optimization of energy profits. Therefore, population dynamics reflect the cumulative effect of environmentally-induced shifts in organismal energy balance. If this energy balance approach is robust, it has the potential of synthesizing ecology at many levels.

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The distribution and abundance of species and populations is a central issue in ecology (Andrewartha and Birch 1954, Andrewartha 1961, Krebs 1985). Population ecology is concerned with the distribution of individuals of a particular species over space and time, community ecology examines the distribution of species congregations over space and time, and ecosystem science considers materials transfer and other processes as they may influence the collective distribution and abundance of organisms within defined environments over time. These issues are equally important to plant and animal ecologists, as well as to those who study behavior and other interactions.

Observed patterns in the distribution and abundance of biota

How are species distributed over space and time? We note several important generalities. Usually individuals of a species are more abundant near the middle of their geographic range and become progressively rarer toward the edges, a pattern that approaches a normal curve, or sometimes a skewed normal curve (Whittaker 1975, Brown 1984, Brussard 1984, Austin 1987, Bock 1987, Root 1988). This generality relates to the assumption that distribution and abundance of a species reflects the probability density distribution (stochastic and/or

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deterministic) of the species' required environmental resources and biotic interactions (Brown 1984). A corollary is that populations of species are often found in a greater variety of habitat types near the middle of their geographic range compared to the edges (Brown 1984, Brussard 1984, Bock 1987).

In any given environment some species are relatively abundant, but most are relatively rare (Preston 1948). Furthermore, species that are abundant in the center of their range tend to have widespread distributions, and the rarer species may be rare everywhere (Bock 1987). Relative abundance is also undoubtedly influenced by differential survival and reproduction (Hughes 1986, among many others), although factors that cause those differences are often not readily apparent and are rarely quantified.

Another important generality is that species or population abundances usually do not follow repeatable patterns over long time periods in a given environment, even though the number of species may persist. While examples of relatively constant populations certainly exist, such as *Spartina* grass in many coastal environments (C.A.S. Hall pers. obs.) and brown trout in small streams (Newman and Waters 1989), most populations that have been studied over long time periods seem to fluctuate widely in abundance, even when plotted on a log scale (Shelford 1951, Watt 1969, Illies 1971, Varley et al. 1973). As pointed out by Soberon (1986), Hall (1988), Fogarty et al. (1991) and others, population dynamics are often stochastic and should not be described or modeled by a deterministic or logistic equation. We agree with Huston (1979) that in most environments populations are almost continually minimized by random environmental disturbances and equilibrium conditions simply cannot manifest. Unfortunately, this generality has too often been overlooked when attempting to predict population dynamics.

Many abiotic (e.g., temperature, moisture, light, nutrients) and biotic (e.g., predation, competition, parasitism, dispersal) factors have been shown to influence the various patterns of distribution and abundance represented by the preceding generalizations. However, ecologists have tended to focus their research around one or another of these causative agents, so that many papers concentrate on the effect of factor "a" on the distribution and/or abundance of species "b", where "a" is a single variable, either abiotic or biotic. Perhaps this is because, historically, ecology has been influenced more by Liebig's "law of the minimum", which emphasizes the influence of single factors, than by synthetic approaches. Even though Hutchinson (1958) provided a rationale for integrating various physical impacts on a species, his widely-quoted idea has rarely been examined empirically.

The need for an integrative approach

Other authors have remarked on the general lack of an integrative approach to assessing potentially important factors affecting distribution and abundance and the need for more comprehensive approaches: "Most research to date has focused on plant responses and adaptations to single features of the environment..." (Chapin et al. 1987); "Comparatively few studies of lotic macroinvertebrates provide data on patterns of resource utilization along more than one resource dimension" (Rader and Ward 1987); "...there is as yet no general theory that links vegetation patterns to basic plant processes" (Smith and Huston 1989 and references therein); "there are no field studies in which all components of the (energy cost-benefit) budget have been measured for any fish species" (Kitchell 1983); "Although earlier research usually concentrated on single factors, field studies made it clear that plants are often subjected to multiple limitations and stresses..." (Mooney et al. 1987).

The effects of two or three factors operating simultaneously have been demonstrated in some empirical studies and clearly establish the inference from the above statements that more integrative approaches are needed. For example, Andrewartha and Birch (1954: 282) showed isopleths of egg production for an insect species as a function of temperature and moisture. Wali and Krajina (1973) showed the response of boreal tree species to three environmental variables: water, light and nitrogen. In both of these examples, the analyses showed that all factors examined were clearly important in determining the distribution and abundance of the populations in question. A single factor approach would have been misleading. It is also possible that even determining the effects of several factors could lead to incorrect inferences if some other unmeasured factor was also critically important.

Admittedly, the difficulties and costs associated with measurement of multiple factors in ecological studies are great, especially over time periods required to demonstrate interannual variation which may be essential to inferences (Magnuson 1990). But, we believe that the lack of multi-factor empiricism in ecology is also rooted in the lack of a general, unifying theory that 1) integrates the myriad of biotic and abiotic factors that influence species distributions and abundances and 2) provides a mechanism for explaining how organisms or species identify resources and evaluate (or "tradeoff") the costs associated with either obtaining them or adapting to alternatives.

Other synthetic approaches

Based on Fig. 18 of Shelford (1951), Maguire (1976) examined the growth response of a phytoplankter as a function of two (or, in theory, more) environmental gradients (e.g., temperature and a nutrient). He then examined how these resources changed over time as the season progressed and temperatures warmed while nutrients were reduced. By integrating the environmental changes in relation to concomitant changes in growth of that species over the year, or between years, he was able to show how abundances and distributions changed as environmental conditions waxed and waned. This seems substantially superior to assuming a constant rate of growth and a fixed carrying capacity, as is the case in logistic models.

Many studies have identified the "tradeoffs" associated with different resources or adaptations in relation to biotic distributions and abundances. Some very good examples pertain to plant life history strategies, where investments in chemical defense vs regrowth (van der Meijden et al. 1988, Feeney 1990), fixation of carbon vs nitrogen (Chapin et al. 1987), efficiency of water use vs carbon uptake (Orians and Solbrig 1977), or growth rate vs structural integrity (Chazdon 1986) have been quantified. A particularly interesting example is one pertaining to nitrogen concentration of leaves. There is a remarkably linear relation between leaf nitrogen concentration and growth rates of plants (Field and Mooney 1986). Aspen *(Populus tremuloides)* and other plants with high nitrogen concentrations have high growth rates, probably due to the presence of high levels of carbon fixation enzymes. Moreover, leaves high in nitrogen are also more desirable food for many heterotrophs, from microbes to moose (Pastor et al. 1988). This means that high growth rates may also be associated with high loss rates through herbivory, and high rates of herbivory can induce plants to produce chemical defenses (e.g., Schultz and Baldwin 1982). Our point is that approaches emphasizing tradeoffs are important when trying to understand biotic distributions and population dynamics because essentially every resource can be obtained only at the expense of other resources.

Smith and Huston (1989) proposed a general theory linking vegetation patterns to species-specific physiological and life history traits in relation to energetic constraints on the capture and use of resources. Their approach emphasized fundamental tradeoffs facing plants, such as: CO_2 uptake vs water retention (at the level of stomates as well as the whole plant); root vs shoot allocations in relation to the costs of acquiring water and/or nutrients vs sunlight; and, allocation of photosynthate to leaves vs the whole plant. They developed the case that plants are very plastic with respect to these tradeoffs, both among and within species, by virtue of adaptations (see also Mooney 1972, Morris 1982, Bazzaz et al. 1987).

Tilman (1988) developed explicit models for such tradeoffs, in particular, between light and nitrogen availability, which predict the competitive advantage, or more explicitly growth, of various plants as resources change with successional development. Similarly, Orians and Solbrig (1977) discussed the tradeoffs for plants living in mesic vs xeric regions, especially with respect to leaf shape and physiology. They stated that such tradeoffs "prevent any one plant from being the best adapted to more than a fraction of the earth's complex patterns of temperature and moisture availability".

Most ecologists are probably aware of these elegantly developed studies, and clearly more work of this type is needed to foster a more synthetic understanding of biotic responses to changing resources. But, even these approaches do not fully permit the assessment that we think is needed to truly understand and, hopefully predict, the distribution and abundance of plants and animals. We offer three arguments.

First, current approaches to the problem do not normally analyze, or give procedures for assessing, the tradeoffs that exist among more than two or three factors. Second, although they may provide empirical assessments of the tradeoffs among different adaptation suites, they normally do not give explicit explanation as to why these tradeoffs should exist or the mechanisms by which they operate relative to the observed distribution and abundance of a population or species (cf. Smith and Huston 1989). Third, they do not start from first principles, an approach that tends to work very well in other disciplines. In particular, the above partial syntheses (except for Orians and Solbrig) are not based on, or explicitly constrained by, species-specific bioenergetics.

Energy is the "common currency" of ecology and is necessary for any biophysical process to occur. Thus, it seems to us that energy is fundamental in the development of an ecological theory that attempts to explain the distribution and abundance of animals and plants in relation to the myriad of ecological factors that impinge on all populations.

An integrative approach based on bioenergetics

The essence of the approach developed here is to integrate energy costs and gains along all appropriate environmental gradients to yield net energy gain in the form of biomass elaboration and reproduction. In this way the observed distribution and abundance relationship may be explained in terms of the net energy balance or budget of the organism, population or species. Our central tenet is that a sufficient, positive energy balance must be sustained through time and space such that a significant number of individuals effectively reproduce. If this does not occur, then eventually the population and ultimately the species will decline toward extinction or, through the process of natural selection, adapt some other energy strategy that will permit survival.

Although it would be preferable to present herein a comprehensive, species-specific analysis of energy balance in relation to distribution and abundance and operational environmental gradients, data do not apparently exist for any particular plant or animal. Consequently, we develop only the conceptual basis while giving examples from studies where parts of the required analyses have been done. We emphasize terrestrial macrophytes and fish because those are the organisms for which the most appropriate studies are available. However, the approach we present should be applicable to nearly any species.

The first step is to establish the energy basis for our approach.

Five important principles about energy and ecology

First, energy contributes to survival and reproduction of organisms in accordance with contemporary evolutionary mechanisms (Orians and Solbrig 1977, McNabb 1980, Ware 1982, Bazzaz et al. 1987). We believe that the most appropriate way to express this relationship is energy per time, or power (Odum and Pinkerton 1955). In the words of Ware (1982): "Optimal life history is concerned with power allocation". Energy is vital to organisms in that, other things being equal, the more energy an organism can sequester per unit time, the larger its energy reserves will be to help meet stress and contingencies. Therefore, if an organism can maximize energy intake, it is more likely to reach age of reproduction rapidly and maximize the number of propagules it can propel into the future to perpetuate its genome (e.g., Hankin and Healy 1986). Orians and Solbrig (1977) summarize this view: "a plant capable of increasing photosynthesis within the constraints of its available resources and the physical environment should gain advantages in competition with other plants, defenses against herbivores, and should have more energy to devote to reproduction".

Second, an examination of an organism's ongoing energy balance allows a less circular definition of fitness than is possible through the more commonly used criteria of reproduction itself. Although at various times in an organism's life its ability to accumulate energy can be satiated, in nature this is very rare (Kirkwood 1983, Kitchell 1983, Pagel et al. 1991). This is especially true with respect to high quality food items, which usually are of limited availability (Boyd and Goodyear 1971, Benke and Wallace 1980).

Third, energy balance is important from the perspective of how much energy an organism must divert from growth and reproduction to overcoming contingencies such as adverse environmental conditions. In general organisms reproduce only from the energy surplus after meeting other contingencies in their life, including growth to a reproductive size (e.g., Vannote and Sweeney 1980, Ware 1982, Kitchell 1983). However, when conditions become so extreme that the organism itself has a high probability of death, all available resources often are put into reproduction (Tilman 1988).

Fourth, energy as it affects organisms encompasses far more than just environmentally available and/or stored (i.e., trophic or elaborated) energy. It includes, among other things, metabolic energy drains imposed on organisms by non-optimal environmental conditions or added stresses (e.g., Odum 1967, Lugo 1978, Lugo and McCormick 1981), thermal energy gained or lost by behavioral modifications (cf. Porter and Gates 1969) and biotic interactions as discussed below. Most important, however, it includes the energy costs of respirational inefficiencies as well as energy required for an organism to live in and to exploit particular environments, especially suboptimal environments. For example, a rainbow trout is isotonic to water of about one quarter the salt content of sea water. In fresh or salt water that fish must use at least 30% more energy for basal metabolism simply for osmotic adjustments (Fry 1971). This is probably one reason that estuaries are such important fish nurseries (Day et al. 1989). Fish can grow better in environments where their basal metabolism is lower.

Fifth, in order to grow and ultimately reproduce, organisms require resources and must invest stored energy reserves to get them. Moreover, all resources vary in quantity and quality. The most important point about energy and its relation to other resources is not that everything can be reduced to energy (which is false) but rather that every material (and most non-material) resource has an associated acquisition energy cost. Most resources become limiting in part because their acquisition may require too great an energy investment on the part of the organism. Thus, high quality resources are often those that require less energy expenditure per unit of resource obtained (Hall et al. 1986). However, with sufficient energy reserves and as constrained by its genome, an organism can divert energy to the acquisition or mobilization of essentially whatever other resources are in short supply, even when their quality is low.

There is the possibility of confusion here because "high quality" is a term that already has use in feeding and optimal foraging ecology, where it refers to the nutritional value of the food. Likewise, quality also reflects the value of the energy per kcal of heat content so that, for example, a kcal of food has more utility to an animal than a kcal of incident solar energy (Odum 1988). We define high quality resources as those that are available to the organism with relatively low energy investment.

We conclude that bioenergetics can provide a comprehensive and explicitly testable set of mechanisms for predicting where species will be found and for determining why they are not found in other locations, although it cannot account for conveyance of propagules to new sites. While it is true that organisms need resources other than energy, for example various nutrients, these

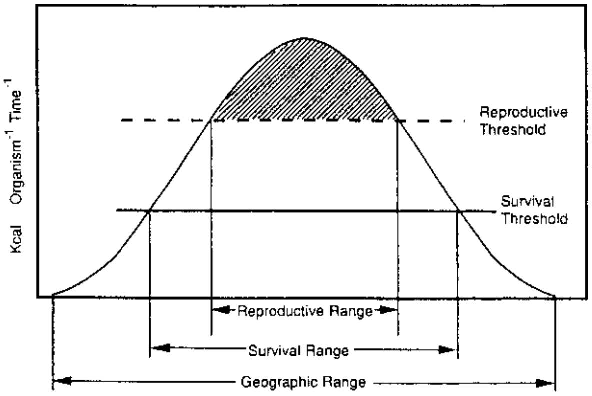

Fig. 1. Net energy balance of a species over its geographic range. The horizontal solid line represents zero net energy gain for the species (survival threshold); that is, conditions where energy gain is just sufficient to compensate for basal metabolic energy, plus the energy required to capture food and overcome stress. Below that line, organisms can exist only by consuming energy reserves. The broken line indicates the larger amount of energy intake needed to generate sufficient energy surplus for reproduction (reproductive threshold). The hatched area of the curve is the only part of the range in which the species can exist in the long term.

other resources can be examined from the perspective of their acquisition energy cost.

Net energy balance: the elusive integrator

Each factor that impinges upon an organism has energy costs, and in many cases, potential energy gains. The life history strategy (phenology) of an organism is the outward expression of the genetic codification of past successful trials of an organism's energy return on investment. At each point in an organism's life it must invest energy for obtaining more energy, while decreasing energy drains and assessing tradeoffs about which contingency is most deserving of whatever energy reserves might be available. Tradeoffs occur because most energy gains are obtained only by increasing energy costs, that is, by increasing energy investments. Energy investments by plants to grow leaves vs roots is one obvious example. Another is energy investment by animals in motility for the purpose of optimizing energy intake from food resources.

Life is a continuous balance of energy investments, each with potential gains but also real and potential costs. As one simple example, plants have energetic tradeoffs whereby the advantage gained by early reproduction tends to be at the cost of future reproduction (Law 1979). For another example, longer-lived but slower growing trees often put large energy investments into energy-intensive structural fibers that generally allow them to survive storms and other contingencies, but at the cost of reduced growth and reproduction (Smith and Huston 1989). Similarly large, long-lived trees that are easy for insects to find tend to be more heavily defended with secondary compounds that operate to discourage insect feeding (Feeny 1990). Generally plants that are exposed to high levels of infestations increase their investments in secondary compounds in subsequent years (Schultz and Baldwin 1982).

In summary, our energy balance perspective derives from fundamental energetics ideas of Shelford (1951) and Maguire (1976) and involves examination and integration of all pertinent energy costs and gains throughout the life history of the organism. Populations (or species) may be examined in the same context, if one accepts that the net energy balance of the population results from the cumulative energy balance of individuals within the population (or species). This gives a less circular and more mechanistic set of tools to assess tradeoffs facing an organism or population, and ultimately the relative success of its genome, than by using fitness (potential reproductive output) as a direct function of multiple environmental gradients. Ideally both approaches would give similar answers to the same question.

Energy costs and gains in relation to environmental gradients

As noted above, population densities tend to be higher in the middle of the species' geographic range because physical, chemical and biotic resource gradients are optimal there and allow maximal energy profits. Gradient analysis demonstrated this fundamental ecological pattern (Ramensky 1924, Whittaker 1956, 1967, Fry 1971, Wikum and Wali 1974, Kessell 1977, Bunce et al. 1979, Iverson and Wali 1982, James and McCulloch 1985, Wilson and Keddy 1986, and many others). In terms of our energy balance approach, we infer that individuals of a species will be distributed over space and time in a way that may be idealized as a more or less normal curve representing energy return on investment along a gradient (Fig. 1).

Two important points derive from Fig. 1. First, individuals near the center of the collective distribution enjoy a high energy profit, which allows a large net gain of energy, growth and either numerous offspring per effort or frequent reproduction. Individuals on the margins of their physiological, territorial, or nutritional range with respect to the gradient are unable to generate a sufficient energy profit to produce population growth. Competition may also be more important at the margins of the range because it raises the cost of resource acquisition and creates more of an impact on individual energy gain in locations on the gradient where the net gain is small. Hence, if the gradient is favorable and temporally stable, the species will be abundant and widespread, which is consistent with the first generality of observed patterns of distribution discussed above. The second point is that rare species are those whose particular physiologies morphologies and behaviors do not allow them to be abundant anywhere because they never make a sufficient energy profit. This is consistent with the second generality of observed patterns of distribution discussed above.

Temperature, moisture, nutrients, and many other physical and chemical variables interact to create the physical template (sensu Southwood 1977, see also Dunson and Travis 1991) upon which organisms are arrayed. Much of ecology is devoted to demonstrating how plants and animals are distributed along abiotic resource gradients. For plants, light, water and nutrients are clearly important in this context, and for animals food derived from photosynthate and (generally) oxygen are essential.

Our approach emphasizes that all abiotic variables that may be influential to bioproduction of any species may be examined in the context of the energy costs and gains to that species. This is regardless of whether resource limitation is examined in the context of availability of the resource or the ability of the species to obtain the resource. For example, at very low nutrient concentrations, such as the 1 $\mu g\ l^{-1}$ of bioavailable phosphorus that commonly occurs in oligotrophic lakes (where phytoplankton production is often phosphorus limited), a 10 μm plankton cell is surrounded by roughly 100 atoms of phosphorus in the 10 μl of water adjacent to the cell. Even though it may seem that phosphorus atoms are relatively abundant, bioavailability of phosphorus atoms is more influenced by the very large concentration gradient that exists between the inside and the outside of the cell membrane. Uptake of phosphorus by the cell to mediate growth requires energy expenditure (active transport). Therefore, nutrient uptake at low concentrations is critically influenced by light (e.g., Dodds and Priscu 1989). The critical inference is that a low concentration of bioavailable nutrients acts as an energy drain to the phytoplankter, increasing the energy cost of obtaining nutrients required for growth, and this energy balance is influenced directly by position of the phytoplankter in the water column owing to the influence of depth on quality and quantity of light penetration.

We note that temperature, which we and others (cf., Krebs 1985) consider the "master regulator", is vitally important to any energy-based construct. Moreover, temperature gradients are very often clearly correlated with species abundances and geographical distribution (cf., Whittaker 1956, Neave and Hanavan 1960, Billings 1970, Makarewicz and Likens 1975, Vannote and Sweeney 1980, Ward and Stanford 1982, Root 1988, Stanford et al. 1988).

Finally, various biotic interactions may also be considered as gradients in our energy balance context. For example, natural selection operates to optimize the risks of predation versus the benefits of exposure to predators in such a way that net energy gains are optimized. Thus, it is possible to view predation energetically from a "Lloyds of London view". In the old days of sailing ships, Lloyd's knew that a certain proportion of the ships they insured would founder in any given year; but, they also knew that if no ships left port, no profits would be forthcoming to the shipping industry (or to Lloyd's). On the other hand, captains who loaded too much sail trying to maximize profits usually foundered (or otherwise lost more than they gained) and were selected against. As an analogous example, Gilliam and Fraser (1987) found that the risk taken by minnows could be manipulated by changing the energetic return of a foray into predator-infested waters, and that the behavior of minnows in accepting risk was predictable from an energetic model of energy gains and costs (see also Holbrook and Schmitt 1988). Likewise, it costs energy to avoid predation, including both the direct costs of avoiding food rich areas that contain predators (Magnhagen 1988) or of manufacturing defenses; there are also the indirect costs of decreased motive efficiency (cf., Kerfoot and Sih 1987). Using similar reasoning, competition (both inter- and intra-specific) usually reduces the availability of a resource for one or both of the competitors, and hence may reduce the range or move the optimum location of an organism along the resource gradient. Hence, competition for resources may reduce the net energy profits, unless the organism is a very good competitor, in which case net gains may indeed be enhanced.

Some examples of energy tradeoffs in response to resource gradients

An important aspect of any analysis of energy balance in relation to resource gradients is that there are "opportunity costs" to being a particular species or genome (Hall et al. 1986). This simply refers to the fact that energy investment in life history strategies that produce prosperity at one place along an environmental gradient (opportunity costs) precludes adaptation to other conditions. Thus, inherent in the concept of phenological energy balance in response to an environmental gradient is the concept of tradeoffs. At any given time, the energy available to adjust to contingencies or to reproduce effectively usually is limited and must be invested "wisely".

Often the relations defining costs and gains (tradeoffs) along a gradient are non-linear. Such non-linearities, at least in principle, can produce many of the classic hump-shaped growth curves along a gradient found in the literature (e.g. Kendeigh 1969, Brittain 1983, Hokanson and Koenst 1986, Hauer and Benke 1991). In the case of the growth of a particular aquatic insect or fish as a function of temperature, foraging rates increase, often linearly at least up to a point. But

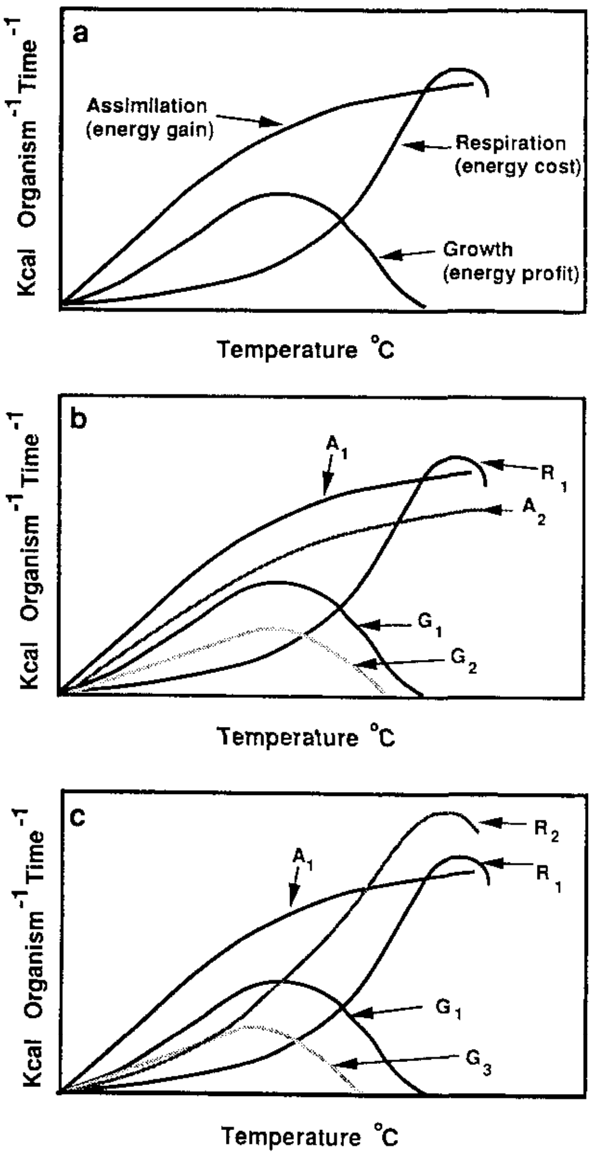

Fig. 2. a) Growth of a poikilotherm in response to an environmental gradient (in this case temperature). We hypothesize that net energy profit, which equals growth plus reproduction, is the result of changing energy costs and gains along the gradient. The commonly observed bell-shaped growth curve is the net difference between metabolic energy expenditures (respiration) and gains (assimilation), realized as individual growth (energy profit). b) Factors that reduce energy assimilation (curve A_1 changes to curve A_2) will result in a decrease in individual growth rate (G_1 to G_2). Decreased quantity or quality of food assimilated may be the result of abiotic factors (e.g., nutrient availability, disturbance) or biotic factors (e.g., competition or predation pressure). c) Factors that result in increased respiration (R_1 increases to R_2) will also decrease individual growth rate (G_1 to G_3). Increased respiration may be the result of changing abiotic conditions (e.g., caused by disturbance) or manifestation of biotic interactions (e.g., increased search time for food due to competition; increased activity caused by predation pressure).

respiration increases more rapidly as temperature rises, because of its Q10-type response (Fig. 2a). More complicated relations can exist, especially at the extremes of the gradient, but even so the maximum net gain is normally near the middle of the gradient, even for homeotherms (Kendeigh 1969), including humans (Sundberg and Silverman 1988). The net energy return to an organism is the difference between energy gains and energy costs. Thus the observed growth curve vs temperature relation can be explained as the difference between energy gains and costs along a temperature gradient (Fig. 2). A clear tradeoff exists between temperature and growth for many organisms. Vannote and Sweeney (1980) elegantly showed how this idea applied to distribution and fecundity of different species of mayflies.

Bunce et al. (1979) measured photosynthesis and respiration of eight plant species that had different distributions over the elevational gradient of moisture on a mountain in Arizona, and calculated the carbon balance of each species as a function of moisture and hence elevation. They found that the lower limit of each of the species was approximately 200 m above the zero carbon balance elevation predicted from their field measurements. In other words each species would not be able to make a significant carbon, and hence energy, profit very much beyond the measured limits of their range. The actual mechanisms for drought tolerance or avoidance were complex, but the net effect was well predicted by their model. Thus, tradeoffs along the moisture gradient were apparent between species. Some had mechanisms, such as a relatively large area of open stomates, favoring high carbon gain mediated by high rates of photosynthesis, but they were also prone to high water losses. Other species were more conserving of water, but had lower carbon gains.

Trout in a river are principally drift feeders (Bannon and Ringler 1986). If they are able to maintain position in rapidly flowing water, the current brings more food to them, but the energy costs of swimming rapidly to maintain position may be too great to maintain a positive energy balance in the long term (Smith and Li 1983). Bachman (1983, 1984) developed a general theory of the energy costs and gains of trout feeding in waters of different velocities. Dominant and/or fastest-growing fish were found approximately where the difference between the costs and gains were greatest (Li and Brocksen 1977, Bachman 1983, 1984). Thus, dominant trout grew faster where the current was optimal relative to food delivery (energy gains), swimming speed and duration (energy costs). Young steelhead trout were also distributed along the velocity gradient of a stream approximately as predicted from this model (Smith and Li 1983). The same kind of result held for pelagic fish and their swimming speeds (Ware 1975). Ware found that young bleak voluntarily swam at velocities (107 mm s^{-1}) similar to velocities that theoretically optimized their net energy gains (111 m s^{-1}).

In a more general sense, Dill (1978) and MacLean and Seastedt (1979) developed an energy gain-cost relation where gains are asymptotic as the organism reaches the limits of its ability to use resources, but the costs, in terms of energy that can be devoted to raising young, increase (linearly in their example) as a function of territory size, resulting in a bell-shaped net return curve. McNicol and Noakes (1984) found that brook trout changed the area they defended, and their antagonistic displays, as a function of changes in water velocity in a way that maximized the energy efficiency with which they defended their territories. Covich (1976) likewise gave a figure similar to Fig. 2a where energy return on investment was related to the distance traveled by a forager. Both food yield and predation pressure increased non-linearly as distance traveled to forage increased. Finally, size of an organism can affect the tradeoff between feeding efficiency and energy loss to respiration (e.g., Stemberger and Gilbert 1987).

Molecular and cellular tradeoffs

While it is not difficult to find organisms responding to gradients, there is not a well developed or recognized procedure for why organisms should do well at certain parts of gradients and not well at others, or for why this should affect energy gains and costs. There are probably many reasons, depending upon the gradient considered, but a very important point is that many enzymes controlling growth, maturation and reproduction tend to have great specificity. Moreover, this specificity is greatly influenced by the environment, especially temperature (Precht 1958, Prosser 1964, 1986). Enzymes exhibit thermal optima that correspond closely to body temperatures in the case of homeotherms, or to the preferred habitat temperatures in poikilotherms. Organisms tend to seek temperatures where their particular enzyme variants are most effective; therefore, the distributions of closely related species may be explained by variable enzymatic responses within an environmental gradient (Zimmerman 1979, Powers 1983). At temperatures below the thermal optima, enzymes function slowly. This is due partially to low levels of kinetic energy and partially to the constraints on flexibility because of the specificity of temperature-mediated activities, such as folding, at the active site. Above the thermal optima the weak chemical bonds that are responsible for formation of transition state structures, and ultimately catalysis, are weakened and break (Somero 1978, Hochachka and Somero 1984).

Various physiological mechanisms have evolved to broaden the functional range of temperatures and lower Q10 values. Clearly, however, there are limits to the functional range of a given protein molecule (McGlade and Allen 1986). In addition, the number of isozymes with different thermal optima available to an organism necessarily is limited to the number of alleles for that enzyme, a maximum of two in the case of diploids (assuming no genetic duplication). There are exceptions. Rainbow trout *(Oncorhynchus mykiss)* a fish with a relatively broad thermal tolerance among salmonids, are tetraploid (Ohn et al. 1968). As a consequence they have twice as many alleles to generate enzymes as other trouts. Presumably this allows various races of the rainbow to be adapted more specifically to warm or cool water.

It is probably efficient for organisms to have enzymes with a relatively narrow temperature range for metabolic activity, because enzymes that operate well at a given temperature appear to operate less well at other temperatures. This has been demonstrated empirically for different subpopulations of the killifish *(Fundulus heteroclitus)* by Powers (1983). Each subpopulation of the fish had an optimal operating temperature where metabolic efficiency was maximized. Moreover, an associated optimal temperature for maximum kinetic performance of lactate dehydrogenase B was observed, which related to swimming efficiency and hatching success. Such tradeoffs along gradients are also important for the structural components of cells. Membrane lipids, for example, are subject to functional alteration at different temperatures. Cellular membranes act as barriers to the free diffusion of atoms and molecules, thus maintaining the integrity of the intracellular environment. They regulate the active transport of substances, and act as micromilieu to the numerous membrane-bound enzymes, receptor molecules, and ion pumps that coordinate cellular function. All of these important roles are dependent upon the maintenance of the liquid-crystalline membrane, which is a highly temperature-sensitive structure. Thus, thermal gradients influence structural aspects of physiology as well as functional ones. As in the case of enzymes, the capacity for physiological adaptation is well documented. For example, rainbow trout alter the proportion of unsaturated fatty acids in membrane lipids at different temperatures in a manner that conserves membrane "fluidity" (Hazel 1984). But, there are tradeoffs as organisms optimize membrane structures at different temperatures that affect the energetic efficiency of their operation as well. Such physiological tradeoffs along various axes together can explain the coexistence of sympatric species in nature (Pruitt 1988).

Extension to N gradients

Not all the gradients affect an organism's welfare equally, because some, such as temperature and food quantity and quality, have a very large effect on metabolism whereas others, such trace metals, often have minimal effect. But the cumulative effects will be reflected in the organism's integrated net energy balance

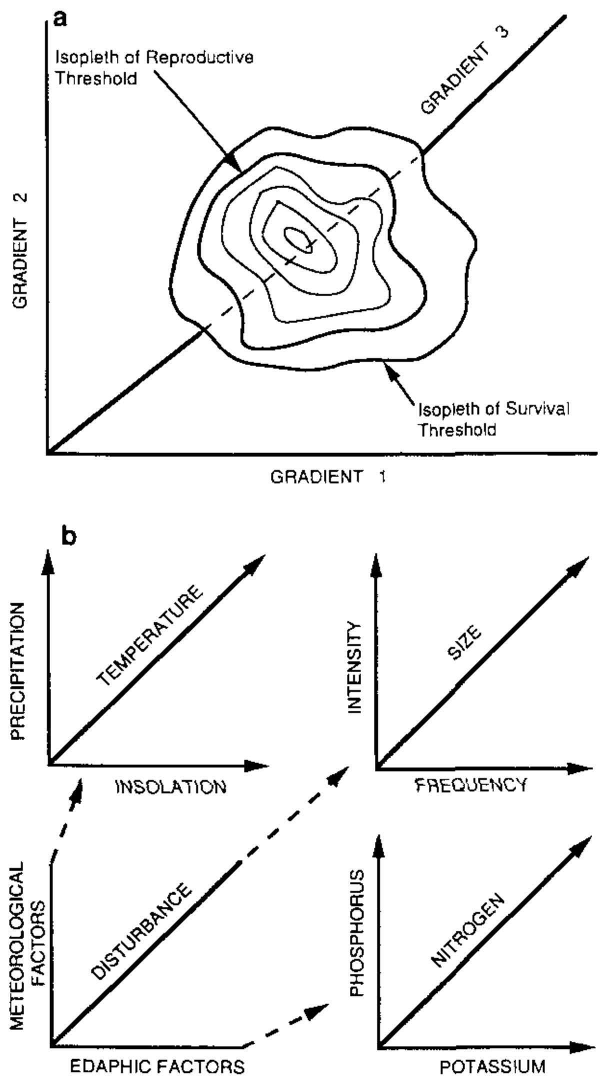

Fig. 3. a) Isopleths of net energy profits, defined as energy gains minus costs, of a species as a function of 3 environmental gradients. Net energy profits and, hence, species distribution and abundance respond to the influence of each environmental gradient involved in the energy balance of the species. Smaller energy profits therefore are shown as isopleths occurring successively outward from the point of optimum profit in relation to these three gradients. Although drawn hypothetically here in just three dimensions, in reality energy profits are influenced by many (N) environmental gradients and should be visualized in the context of an N-dimensional hyperspace (see text). b) One way to display the effects of more than 3 gradients simultaneously. In this case the figure is showing 9 gradients (three each: edaphic, disturbance, and meteorological) thought to influence the distribution and growth of plants and animals in the Luquillo Mountains of Puerto Rico. Edaphic gradients include soil nutrient (e.g., N, P, K) concentrations; disturbance gradients include intensity, size and duration of hurricanes, landslides, and tree-falls; and meteorological gradients include the relation between precipitation, temperature and solar insolation at different altitudes in the mountains.

in relation to each relevant gradient. For example, a tree species may grow progressively well or poorly from the bottom of a mountain to the top, due to differences in temperature. Likewise, it may do well or poorly as a function of sunlight or moisture gradients from one side of the mountain to the other.

Shelford (1951) introduced, and Hutchinson (1965) developed the idea that the "realized niche" of an organism could be determined empirically by plotting the boundaries of that organism's existence as a function of the "N" factors that influenced the distribution of the organism. The resulting "N-dimensional hyperspace" is the definition of the range (and sometimes niche) of that organism.

A species is the aggregate genetic code, and its phenotype is the organism that can generate a sufficient energy profit to reproduce at some place along each possible environmental gradient. Since it apparently does not "pay" to exist along the entirety of each environmental gradient, natural selection of each species is "focused" on the part of each gradient that allows a sufficient profit for the species to survive and reproduce. This may be a strong factor favoring speciation. Widespread species are those which have evolved mechanisms for making significant energy profits within a large portion of the hyperspace created by all gradients that impinge on the phenology of the species. Species are often composed of subpopulations or ecotypes with a wide variety of particular genotypes, but nonetheless each is "fine tuned" to the environments where they are found. For example, Vannote and Sweeny (1980) and Matthews (1985, 1986) found that various individuals of particular species of mayflies and minnows over a wide geographic range had very similar temperature tolerances, indicating conservative physiologies, especially as compared to other species.

Hutchinson's concept of "N-dimensional hyperspace" can be extended such that all relevant resource gradients, and the energy costs and gains for an organism to live along each of those gradients, are integrated graphically and mathematically (Fig. 3). The well being, growth and eventual reproductive success of the organism is defined by the interpretation of energy costs and gains on all gradients that influence the organism's phenology.

For purposes of illustration, these energy profit gradients can be envisioned as a "Chinese egg" set of N-dimensions, with the exterior egg representing the limits of the organism's range. Where individuals of a species range beyond where they can survive for long periods, the next interior egg represents the survival range, and so on. Reproduction takes place within some interior egg, which represents an even greater optimization within the hyperspace. Maximum reproduction takes place at a "center of gravity" representing simultaneously the mid-range of all impinging gradients. Thus, many gradients can be represented and analyzed as in Fig. 3.

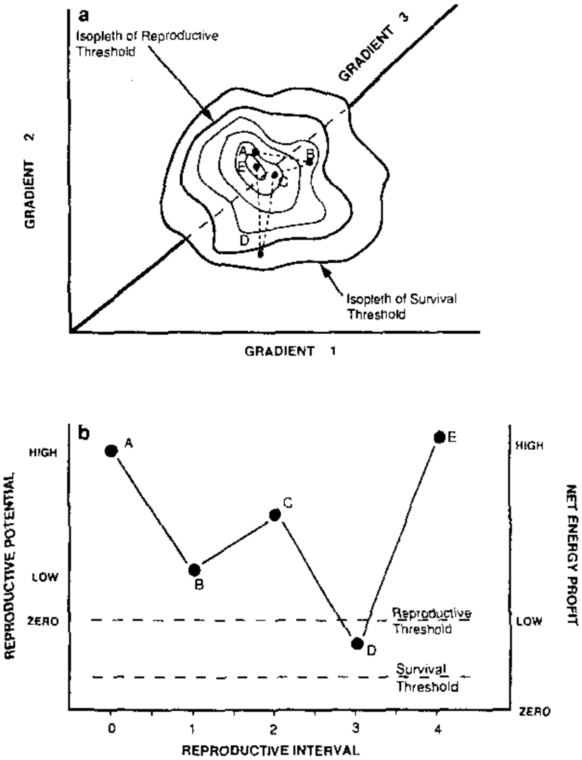

Fig. 4. a) Net energy balance (isopleths) of a population existing at A–E different positions within the N- (in this case 3) dimensional hyperspace determined by important ecological gradients that influence growth throughout the life history. b) Temporal reproductive potential of the population represented in a). In this example the cumulative energy gains of individuals exceed losses and the population survives, although investments in reproduction are variable over time. For genomes that die after a single reproductive effort and do not have multiple cohorts (e.g., many insects), population extinction would occur at D. For organisms that live many years (e.g., most commercially important fishes) such year to year fluctuations in reproduction and similar changes in death rates leads to the population dynamics that we observe.

Niches, succession and competition

In the context of our energy balance perspective, a Gaussian niche is the volume of all possible energy profits for a species within the hyperspace of all gradients to which the organism might be exposed. A Hutchinsonian niche is the volume of all realized energy profits for a species, and is at least partly dependent upon the geographical history of the species.

Succession, then, may be caused in large part by the changing energy profit regimes of the environment, in response to the presence or absence of various species and the changes produced on that site by various species over time. It is not clear whether species generally affect other species by any other mechanism than by changing the quality, and hence energy cost, of resources. For example, trees influence understory plants by shading or lowering available nutrients. The conditions favoring a positive energy balance for particular species change over successional time.

Competition often has been invoked as the principal mechanism that causes the distribution patterns of organisms (e.g., Connell 1961, Hutchinson 1965, MacArthur and Levins 1967, Cody and Diamond 1976, Roughgarden 1983, Schoener 1983), but that view seems to be increasingly called into question (e.g., Simberloff 1982, Strong et al. 1983, Hairston 1986, Mitchley 1987, Hall 1988, 1991). The data of Whittaker, for example, show plant species distributed along elevational gradients in more or less random patterns, rather than in "avoidance" patterns that would be more consistent with competition. This indicates that the species are not causing each other to move "away" from one another on the gradient. Although few ecologists would argue with the existence of competition in nature, there is a very large difference between establishing its presence and attributing to this one factor the fundamental role in structuring communities. Where competition is demonstrated to be operational, it can be factored easily into the energy balance analysis promoted herein. As noted above, exploitive or interference competition can alter the availability of a resource and impact the energy balance of the competitors. For example, light intolerant shrubs are aided by the shading of other plants (exploitation) or one species may produce a substance that is toxic or stressful to another (interference). Such influences can be treated as additional gradients (axes) that impinge on the organism's energy balance. If enough axes are examined, the concept of competition may not be as relevant in explaining the displacement of different species along resource gradients. Each species simply does not have the morphological, behavioral or, especially, physiological (biochemical) wherewithal to provide an energy balance that allows it to exist along the full length of all important gradients.

Methodology for measuring energy balance within N gradients

Species-specific responses of individuals at locations within many environmental gradients result in a complex pattern of energy costs and gains. This seemingly intractable pattern can be analyzed and predicted by using simulation modeling, if the basic input data for each gradient exist. First, an appropriate time loop is generated. Then the environmental gradients are established mathematically according to historical or simulated patterns (e.g., Fry 1971, Nelson et al. 1977, Chabot and Bunce 1979, Gilliam and Fraser 1987. Geographical specificity can be included. For example, procedures have been developed for projecting meteorological information from a single station to a montane landscape (e.g., Wooster 1989). Next, the individuals are located mathematically along each relevant environmental gradient for each time unit (month or day or hour) as a function of the species' known preferences or behavior in response to each gradient. Data on the energy costs and gains are needed for each gradient as per Fig. 2. Then all costs and gains are summed across gradients for the time period of interest and/or as the various state variables (gradients) are changed.

Of course, these model runs are nothing more than ways to better understand the empirical information upon which they are based. To verify model output, variables and organisms must be manipulated to allow quantification of energy balance within multivariate experiments derived from field-based inferences. For example, many aquatic insects can be reared in flow-through microcosms to produce growth responses (e.g., as in Fig. 2) to controlled conditions (e.g. temperature, food quantity and quality, substratum, current velocity) that relate experimentally to natural environmental gradients (e.g., along an altitudinal stream profile).

Energy balance and population dynamics

A final point is that the multifactorial energy balance approach given here should be useful in attempting to understand population dynamics. Very simply, the net energy balance of a species changes as environmental conditions change. Temporal variations are inherent in resource gradients, and phenological energy balances will likewise vary (cf., Resh et al. 1988, Pagel et al. 1991). Therefore, populations will be dynamic in relation to net energy profits invested in offspring, and the energy balance of those offspring as environmental conditions become more or less favorable over space and time (Fig. 4). This replaces the dogma that r and K are the principal determinants of future population levels (Kingsland 1984, Hall and DeAngeles 1985, Hall 1988) and leads to mechanistic, explicitly-testable hypotheses that can be applied to any individual or population. One very good example of where the energy balance approach might be useful in producing a more realistic explanation of year to year variation in abundance of a species is in regard to recruitment variability and the dynamics of commercial marine fisheries. For years fisheries managers have focused harvest goals on density-dependent (logistic) responses in considering controls on stock-recruitment dynamics (e.g., Ricker 1954). However, in the multi-species, environmentally-complex world of most exploited marine fisheries the implications of the analysis in Fig. 4 seem to us to be much more appropriate based on the rationale of this paper (see also Caddy and Sharp 1986, Hall 1988).

Conclusions

We began with a discussion of generally observed patterns of biotic distributions. We conclude that these patterns may be explained as a consequence of energy balance along multiple environmental gradients. Some species are relatively abundant but most are relatively rare in any given environment because energy balance is optimal for only a few species in any given time or space. Barring major climatic shifts or other large scale natural or anthropogenic disturbances, species richness is surprisingly invariable from year to year in a given environment because energy balance usually is positive, in spite of substantial environmental variation; thus, extirpation or extinction are rather rarely-occurring natural events when considered on a scale of years. However, species or populations usually do not follow repeatable abundance patterns from year to year because energy balance is directly responsive to the stochasticity of multiple environmental conditions.

Although there has not been any explicit testing of such predictions, assessing energy costs and gains along environmental gradients is not difficult. The most direct approach is to measure growth and reproduction at various points along the gradient (e.g., Fitzpatrick 1973, Brown and Fitzpatrick 1978) and reinforce those interpretations with controlled experiments (e.g., Lonsdale and Levinton 1985). Of course, when multiple gradients are involved, interaction effects can complicate interpretations. However, analyses of the response of a species to several gradients demonstrate that it is possible to construct models that can reasonably reflect actual growth (e.g., Kitchell and Stewart 1977, Martin et al. 1991), which strongly suggests our approach will work. While some investigators will argue that too much data are required, such criticism can be resolved by initially choosing organisms that are clearly responding to only a few gradients.

Holistic energy perspectives in the past have been complicated and controversial (Odum and Pinkerton 1955, Johnson 1981, Jørgensen and Mejer 1981). This is not meant as a prejudicial statement on these analyses, because our approach probably can be enhanced when considered in light of these more elegant syntheses. Rather, our goal is to offer an approach that is straightforward enough to require very little in the way of going beyond most traditional views in ecology. If the energy balance theory is robust, it has the potential of synthesizing ecology at many levels.

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