

local environment: the plant line of development. They partitioned their structure into a root and a shoot, and eventually the use of products (wood) to adapt their shape during growth became feasible. They became masters of the art of torpor to escape bleak periods and evolved a much more open (but slow) mass communication between cells. The embryo/adult stages arose independently for this group.

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Allometry and Growth / Compartment Models / Ecotoxicology / Individual-Based Ecology / Integrated Whole Organism Physiology / Metabolic Theory of Ecology / Phenotypic Plasticity / Stress and Species Interactions / Stoichiometry, Ecological

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## ENVIRONMENTAL HETEROGENEITY AND PLANTS

### GORDON A. FOX

*University of South Florida, Tampa*

### BRUCE E. KENDALL

*University of California, Santa Barbara*

### SUSAN SCHWINNING

*Texas State University, San Marcos*

Environmental heterogeneity—variation in environmental conditions over space, time, or both—drives much of plant biology. There are a multitude of plant adaptations for tolerating or capitalizing on environmental heterogeneity, and these vary with the scale of the heterogeneity relative to the size and longevity of individuals. It has been difficult to scale up from physiological processes

at the level of organs and individuals to that of entire canopies or populations. In both of these problems, the difficulty arises mainly because leaves, roots, whole plants, and indeed entire biomes interact with one another by modulating patterns of heterogeneity, creating dynamic feedbacks so that one cannot simply apply nonlinear averaging. To date, the most successful approaches to heterogeneity at both the ecosystem level and the population level have treated the underlying feedback mechanisms selectively or else as unspecified or stochastic. However, there are important applications, including in the global change context, that require an improved understanding of how physiological processes at the organ level scale up to properties of populations, communities, and ecosystems, and this remains an important challenge.

#### RESPONSES OF ORGANS AND INDIVIDUALS TO ENVIRONMENTAL VARIATION

Environments vary on spatial scales from the molecular to the global. Most ecological study of temporal variation concerns scales from the diurnal to the generational. On any particular scale, environmental heterogeneity occurs in multiple quantities. Some of these are plant resources—CO<sub>2</sub>, water, light, and nutrients—and so by definition can be consumed and locally depleted by individual plants. In turn, resource heterogeneity directly affects rates of resource uptake, and thus growth, reproduction, and survivorship. Heterogeneity also occurs in many quantities that are not plant resources—like temperature, humidity, and wind speed—which cannot be consumed by plants but are also locally affected by the presence of plants. Heterogeneity in these physical parameters affects plant function by modifying metabolic rates, stomatal control, or morphology, and thus resource processing.

At scales smaller than individuals, environmental heterogeneity is typically met by adjusting organ function to local conditions. For example, a forest tree may have specialized “sun leaves” in the top of the canopy (thicker leaves with higher photosynthetic pigment content per area) and “shade leaves” below (thinner leaves with less pigment per area). Another example is that of nutrient “hotspots” in the root zone, leading to highly localized proliferation of fine roots and root hairs. Such local organ adaptations are suitably interpreted by economic analogy; minimizing the cost of resource capture to maximize carbon gain at the whole-plant level.

Heterogeneity at the scale of individuals and populations can produce individuals of very different overall function and morphology, a phenomenon referred to as

phenotypic plasticity. For example, root area–leaf area ratios can change dramatically in space or time, to balance the uptake of two or more essential resources (e.g., water and light). In extreme cases, leaves or fine roots may be shed entirely, when their carbon costs no longer justify their upkeep. Leaf phenology is an important factor in predicting the function of ecosystems, and one with worldwide implications for migratory species and climate–vegetation feedbacks. Environmental heterogeneity at the scale of individuals can also produce species or genotype sorting, matching species (or genotypes within species) with the specific environment in which they achieve higher function.

The functional integration of individuals, plasticity, leaf phenology, and species sorting leads to three major challenges for addressing the effects of heterogeneity on plants: understanding how environmental variation at scales smaller than individual plants scale up to whole-plant physiological processes, understanding how physiological processes at the organ and individual levels scale up to the function of ecosystems, and understanding how variation among individuals affects the growth and decline of populations. This entry addresses the latter two of these challenges; the first is considered elsewhere in this volume. As will be seen later, these problems are closely related, as the ecosystem level response to heterogeneity depends on the balance of species serving specific ecosystem functions.

## HETEROGENEITY: FROM LEAVES TO ECOSYSTEMS

Heterogeneity impacts at the ecosystem level is a central problem in ecology, as it is plant primary production that determines food availabilities to all heterotrophic organisms, and vegetation patterns that provide habitat, or at least contribute largely to habitat quality. On first consideration, the scaling from organ function to ecosystem function may seem simple enough, as the biochemical machinery of photosynthesis on land and in water is highly uniform across species and environmental conditions, barring the relatively small, and well-documented, variation between the  $C_3$  and  $C_4$  photosynthetic pathways and the more profound photosynthetic variants of a rare group of organisms: purple and green sulfur bacteria.

Almost all organic compounds in the world are produced through the interaction of two processes: the Light Reaction, wherein light is intercepted by pigments and radiation energy transformed to chemical energy producing dioxygen as an end product, and the Carbon (“Dark”) Reaction, wherein the carriers of chemical energy (ATP,

NADPH) are used to construct organic carbon molecules,  $(CH_2O)_n$ , from inorganic  $CO_2$ . Thus, light (specifically light in the visible wavelength range) and  $CO_2$  are the fundamental plant resources limiting the rate of primary production, but additional macro- and micronutrients are needed for building the machinery of photosynthesis: pigments, enzymes, and electrolytes. Additionally, photosynthesis on land is almost always water-limited, due to the inescapable constraint that uptake of  $CO_2$  from air leads to loss of water vapor. Thus, land plants need to constantly replenish water lost from leaves with water taken up from the ground, necessitating a large investment on nonphotosynthetic biomass: stems and roots.

A key strength of ecosystem ecology is the expression of ecological processes at any scale, from organelles to biomes, in units of common currency—e.g., carbon, water, and nitrogen. However, the challenge of ecosystem ecology lies in the scaling from fundamental processes well understood at one level of organization to another level of organization. The difficulties arising in this context are of two kinds: spatial and temporal averaging of functions that depend nonlinearly on environmental heterogeneity, and, more problematically, feedbacks between environmental heterogeneity and plant function.

These challenges may be exemplified by the relatively simple task of scaling  $CO_2$  exchanges from the leaf to the canopy level. The gas exchange of individual leaves can be described quite accurately by light,  $CO_2$ , humidity, temperature, and other types of response functions. However, every leaf in a canopy will also modify the local environment. For example, light interception raises leaf and air temperature and reduces light levels for leaves further below. Concurrently, water vapor evaporation will humidify the air and have a cooling effect on leaf temperature. Changes in light, humidity, and temperature not only change leaf gas exchange levels directly, but consistent exposure to modified environmental conditions will feed back on leaf construction, modifying the very functions that relate gas exchange rates to light, humidity, and temperature.

While one can construct and parameterize simulation models that scale from leaves to canopies, for example, this is much harder to do for natural canopies, which are typically constructed from individuals of mixed species of uneven height in possibly structured arrangements. For some problems, solutions can be found by using different conceptual frameworks for different levels of organization. For example, the water and energy exchanges of whole canopies are more easily described by coupled water and energy budget equations that treat the entire canopy

as a uniform surface, where the effects of species composition and canopy structure affect only a few parameters (e.g., albedo and surface roughness) and where empirical functions relate plant-available water in the root zone to evapotranspiration. What is lost by applying different models to different scales is the ability to dynamically link effects of small-scale heterogeneity to plant function at larger scales.

Another important but presently unresolved scaling problem leads from the physiology of individuals to the demographic processes that govern population growth and decline. At the simplest level, growth is constrained by the rate of carbon assimilation. But decomposition analysis of individual growth rates shows that the latter also depend on biomass allocation to leaves versus stems, roots, or reproductive structures, which are controlled by internal physiological and molecular processes interacting with environmental conditions and triggers. Among the most difficult problems is prediction of mortality rates. What level of plant water deficit is lethal? At what point are internal carbon reserves too low to revive a plant from herbivory or fire? When is the resource availability to seedlings too low to maintain positive carbon balance? Where mortality rates have proved to be predictable—in the important case of self-thinning in plant populations—we do not understand it at the physiological level.

Scaling up from the physiology of plant organs has proved to be difficult at both the population and the ecosystem level. But all is not lost: considerable success has been achieved by approaches that rely on a basic physiological understanding but deliberately do not specify many of the mechanistic details. In particular, such approaches have guided much of our understanding of the consequences of heterogeneity at both the biome and population levels.

The fundamental requirements of photosynthesis—chiefly light, water, and temperature above freezing—dominate broad-scale responses of vegetation to environmental heterogeneity, especially the spatial distribution of distinct biomes across the global terrestrial land area. The location and extent of major biomes, from desert scrubland to tropical rainforests depends, perhaps surprisingly, largely on only two major drivers: mean annual temperature and mean annual precipitation. The former is strongly correlated with the length of the growing season and with the necessity for low temperature tolerance in plants. Mean annual precipitation, in conjunction with temperature, determines the degree of drought tolerance required and correlates with fire frequency. This relatively simple state of affairs has made it possible to predict the

distribution of major biomes, each represented by one or more characteristic plant types, and to assign biome-specific biogeochemical response characteristics. Biogeochemical and biogeography models take center stage in addressing the timely problem of global vegetation–atmosphere interactions.

Due to fundamental tradeoffs in plant form and function, plant species tend to maximize fitness within a narrow range of environmental conditions. While these conditions can span a large geographic range, plant species inevitably will be replaced by other species at their range limits. Where suites of species are replaced by other suites of species, transition zones are recognized as ecotones. The dynamics of ecotones have recently attracted much research interest, as it is here where range expansion and contraction occurs and where signs of biome redistribution and reorganization may be first recognized.

Even though biome function at the global scale can often be approximated by just one vegetation type, any community contains multiple species with strikingly different forms of adaptation to the local climatic drivers. Ecosystem models operating at a finer grain of temporal and spatial resolution have addressed this complexity by dividing the many coexisting species into a small number of plant functional types. In the community context, plant functional types are recognized as players realizing contrasting adaptive strategies in a game of largely shared environmental constraints. For example, desert ecosystems typically contain evergreen perennials with high drought tolerance, drought-deciduous perennials with somewhat reduced drought tolerance, and wet season ephemerals with no tolerance for drought at all, at least in the vegetative state.

Another way of looking at plant functional types is therefore as a collection of broad ecological niches, and scaling issues emerge in the form of niche interactions. Overyielding—the increased productivity of species mixtures in relation to area-based average yield of monocultures—shows that the integrated function of a species mixture is not merely the sum of its parts. Novel properties at the community scale are the result of complementarity among species in response to environmental heterogeneity.

It is thus no surprise that shifts in functional type composition can have profound effects on ecosystem processes. For example, the global conversion of open grasslands into woodlands for the last 100–150 years is thought to have accelerated carbon sequestration, creating a global sink that may have ameliorated CO<sub>2</sub>

accumulation in the atmosphere. In a contrasting example, the “annualization” of sagebrush steppe in the western United States by the invasive species *Bromus tectorum* has introduced a frequent fire cycle that may lead to the irreversible loss of this biome.

There has been much debate as to whether diversity beyond the scale of plant functional types affects ecosystem function. Typically, virtually indistinguishable ecosystem functions are served by many species, suggesting that 1000 species can maintain ecosystem function just as well as 20 species. The counterargument is that uninterrupted ecosystem function requires a degree of functional redundancy, analogous to the fail-safe design of complex machines. It has been suggested that certain types of heterogeneities across space and time subtly favor different species of the same functional type or spread the risk of local extinction between species of similar function, thus stabilizing ecosystem function over space and time. However, this argument has to be weighed against expected increases in extinction risk in smaller populations, and so we now turn to considering the demographic consequences of environmental variation and their effects on population growth rate and extinction risk. The distribution of species and functional types responds to small-scale variation in microclimate or site conditions. For example, community composition often changes between the north- and the south-facing slope of a hill. Species sorting can, but does not always, involve direct positive or negative interactions between individuals. An example where direct interactions do occur is in the “nurse plant” effect, the improvement of seedling survivorship under the canopy of an established perennial. On the other hand, differential germination of seeds in different year types does not involve interactions between species.

A theoretical challenge of recent concern is to understand the roles of dispersal versus site selection. Compared to mobile animals, sessile individual plants have much less control over the site of their establishment or that of their offspring. In reality, it is often difficult to determine whether a spatial association of conspecifics is the result of favorable site conditions, limited dispersal range, or site selection by a dispersal vector like seed caching granivores.

## HETEROGENEITY: FROM INDIVIDUALS TO POPULATIONS

Environmental factors varying on the scale of individuals or stands lead to demographic heterogeneity among

individuals, and this affects population growth rates and extinction risks.

Interactions between populations, or between individuals within populations, can also cause environmental variation that leads to demographic heterogeneity. For example, the densities of neighboring plants, pathogens, herbivores, or mycorrhizae may vary for plants within a population. Processes like these may also be considered spatial heterogeneity, but it is often useful to consider them separately because their causes and dynamics are quite different from factors like differing parent materials in soils.

Temporal environmental variation can lead to demographic heterogeneity in two different ways. First, different cohorts experience different environmental conditions—for example, weather, fire, plant densities, and pathogens can all vary substantially from year to year. Because these differing conditions occur at different life stages for different cohorts, they often have strong effects on the average demographic performance of individuals. These cohort effects tend to either destabilize inherently stable population dynamics or stabilize inherently unstable dynamics.

There is also an indirect effect of temporal environmental variation. It is well established that in the long term, selection opposes among-year variance in the population growth rate. Much research on mechanisms like seed heteromorphisms has focused on the intriguing possibility that these are bet-hedging adaptations that trade off the mean and variance in population growth rate among years. But if they lead to heterogeneity in survival, mechanisms like these are selectively favorable even without a mean–variance tradeoff, because populations with among-individual heterogeneity in survival have larger long-term growth rates than monomorphic populations with the same mean survival. Thus, many mechanisms that can act as bet hedges are also favored even without a mean–variance tradeoff.

In sum, there are many environmental factors that vary in space or time (or both) and lead to demographic heterogeneity. There are, of course, two further sources of demographic heterogeneity: genetic variation and non-genetic parental effects. These are not caused directly by environmental heterogeneity, but they may be correlated with it. As is well known, genetic variation can be eroded by natural selection, while the other causes of demographic heterogeneity may persist.

The prevalence (and strength) of natural selection in plant populations provides strong evidence that demographic heterogeneity is, indeed, both ubiquitous and

important. Natural selection can occur only in populations with demographic heterogeneity. The reverse need not be true, as it is possible for demographic heterogeneity to be random with respect to phenotypes in a population. The evolutionary effects of demographic heterogeneity are well understood; this section considers its effects on population dynamics.

General theory suggests that heterogeneity in survival, especially if an individual retains its relative (dis)advantage throughout its life, can reduce demographic stochasticity, increase the low-density growth rate, and increase the equilibrium density. The latter two results are an effect of cohort selection: as a cohort ages, the individuals with higher mortality risk preferentially die off, leaving increasingly more robust individuals as the population ages. In a population context, this increases the average survival of individuals at the stable age structure, relative to a homogeneous population with the same average survival rate. These general models have not been applied to structured plant population models.

Environmental heterogeneity can cause individuals to grow at different rates, even in the absence of interspecific competition. Herbaceous plants, especially annuals, often grow nearly exponentially (at least while uncrowded) in their pre-reproductive phase. Heterogeneity in the growth constant (called the relative growth rate, RGR) can cause a cohort of initially identical individuals to develop a log-normal size distribution, with the skew increasing with the amount of variance in the RGR. A great deal of effort in the 1970s and 1980s went into trying to understand whether the shape of this distribution provides any information about the intensity or nature of interspecific competition. However, one consequence was largely overlooked: a population with a heterogeneous growth rate will have a larger mean final size than a population of identical individuals with the same mean growth rate. In 1985, Holsinger and Roughgarden incorporated this into a plant population model; if seed production was positively related to size (as it is in many plants), then increasing RGR heterogeneity increases both the low-density growth rate and the equilibrium population density. Such heterogeneity may also be important to include in perennial plant population models as well, but this has not been explored.

The demographic process of reproduction is much more idiosyncratic than survival—What is the distribution of seed size and number? What is the germination rate? How likely is it that a seedling will recruit to the reproductive population?—so there is not, as yet, a general theory about the demographic effects of reproductive

heterogeneity. In isolation, its effects are probably usually modest, as reproductive heterogeneity does not change the phenotype distribution in the way that survival heterogeneity does. Nor does it modify mean performance in the way that growth rate heterogeneity does. However, reproductive heterogeneity can exaggerate or mitigate the impacts of those other types of heterogeneity.

Demographic heterogeneity is also likely to have strong impacts on the genetic structure of populations. Natural selection has well-known effects on the genetic composition of populations, and heterogeneous populations will generally have smaller effective population sizes than homogeneous populations. Heterogeneity thus can be expected to contribute to genetic drift as well as to selection. Moreover, insofar as it is caused by spatial environmental heterogeneity, demographic heterogeneity may also have substantial effects on gene flow.

Finally, demographic heterogeneity may have large effects on the coexistence of competing species, through either of two mechanisms. In an influential model, Chesson in 1990 showed that coexistence (or exclusion) can result from the way in which populations' sensitivities to competition covary with their sensitivities to spatial or temporal environmental variation. Using a rather different argument, in 2010 Clark proposed that heterogeneity within populations of coexisting plants can make it possible for intraspecific competition to outweigh interspecific competition, although the particular empirical case for which he proposed this mechanism—trees in the southern Appalachians—has since been disputed.

## CONCLUSIONS AND CHALLENGES

Environmental heterogeneity drives plant ecology and diversity. We have a satisfactory understanding of its effects at the organ level for small time scales. However, its effects on larger/longer scales are not additive, because there are feedbacks and interactions of many kinds—back to the environment itself as well as among organs, individuals, and stands. Understanding ecosystem and population-level consequences of environmental heterogeneity has been accomplished by ignoring most of the possible feedbacks and concentrating on specific feedbacks deemed important or instructive. In the case of physiological scaling from leaves to ecosystems, the aim is to accurately track the exchange of elements and energy. In the case of populations, heterogeneity in the function of individuals is taken as given and then the larger-scale, longer-term consequences are explored.



However, there are important problems for which progress may require pursuing the coupling between the ecosystem and population perspectives. At a time of rapidly changing ecosystem function, accelerated species extinction rates, and the real threat of global climate regime change, a pressing issue is the extent to which species diversity and ecosystem productivity and stability are related. Models and experiments exploring this question in particular systems may require at least an approximation of the underlying physiological issues at the population scale, rather than the black box of hypothesized heterogeneity. Conversely, ecosystem science would likely benefit from improved representation of demographic processes, including recruitment, mortality, and dispersal, to predict ecosystem dynamics.

Ecologists recognize that areas like ecophysiology, evolutionary biology, community ecology, and ecosystem ecology are not really separate; in practice, they are, sub-disciplines that tend to develop independently of one another. The view outlined in this entry suggests that many large questions in ecology depend on tighter coupling among these lines of inquiry. Such coupling may allow us to make inroads in some of the fundamental problems in ecology.

#### SEE ALSO THE FOLLOWING ARTICLES

Integrated Whole Organism Physiology / Plant Competition and Canopy Interactions / Phenotypic Plasticity / Population Ecology / Stochasticity, Demographic / Stochasticity, Environmental / Stoichiometry, Ecological

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## ENVIRONMENTAL STOCHASTICITY

SEE STOCHASTICITY, ENVIRONMENTAL

## ENVIRONMENTAL TOXICOLOGY

SEE ECOTOXICOLOGY

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# EPIDEMIOLOGY AND EPIDEMIC MODELING

LISA SATTENSPIEL

University of Missouri, Columbia

Epidemiology is the study of how, when, where, and why diseases occur, with special emphasis on determining strategies for their control. Originally the term referred to the spread and control of the great historical infectious disease epidemics that swept through human populations in Western Europe on a regular basis. The term now relates to the study of the causes, distribution, and control of chronic as well as infectious diseases in humans and other living organisms. Because a full description of all types of epidemiology is beyond the scope of this article, the discussion that follows is limited to infectious disease epidemiology. Readers interested in a broader view of the discipline are encouraged to consult the general epidemiology references listed at the end of this article.

## SOME BASIC PRINCIPLES OF EPIDEMIOLOGY

Epidemiology is a population-centered discipline, and as such, it has strong ties to many areas within ecology. A core emphasis in epidemiology is the nature of interactions between the pathogen(s), one or more hosts, and the environment. Therefore, most epidemiological studies consider the biology and behavior of both the hosts experiencing disease and the pathogens that are responsible for the disease, as well as the environmental influences (e.g., climate, nutrition, stress, and the like) that may affect the development and manifestations of the disease.

A number of specialized terms have arisen during the development of epidemiology. The term epidemic is used