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978-0-521-54935-6 - The Ecological Consequences of Environmental Heterogeneity

Edited by Michael J. Hutchings, Elizabeth A. John and Alan J. A. Stewart

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Chapter 1

The world is heterogeneous: ecological consequences of living in a patchy environment

A.J.A. Stewart, E.A. John and M.J. Hutchings

Recent years have witnessed considerable progress in addressing the question of how environmental heterogeneity impacts upon organisms and ecological processes. The principal aim of this Symposium was to gather insights from as wide a range of approaches as possible, focusing specifically on the ecological consequences of heterogeneity. Other aspects, such as the measurement and quantification of heterogeneity, were outside the scope of the meeting. This volume starts with chapters that explore how heterogeneity can be defined and categorized, together with consideration of the agents and processes that create, maintain and influence it (Wiens, Pickett *et al.*; Wilson). A series of chapters deals with impacts of heterogeneity on individual plants (Wilson, Fitter *et al.*; Hutchings *et al.*; Casper *et al.*; Watling and Press) and animals (Hunter *et al.*; Brown, Godfray *et al.*). The focus then moves to the effects of heterogeneity on population processes (Rees *et al.*), genetic structures (Boshier and Billingham) and community-level interactions (Power and Rainey). Four chapters deal with the potential impact of anthropogenically induced heterogeneity on the persistence of populations and species: from a theoretical standpoint (Dytham), with reference to tropical forests (Corlett) and temperate agricultural landscapes (Macdonald *et al.*) and with respect to the restoration of fragmented landscapes in general (Bakker). Finally, a series of common threads are drawn together, with some signposts towards future research opportunities (Lawton).

Organisms live in habitats that are highly heterogeneous, both in space and in time. Field research has often focused on the effect of heterogeneity in habitat quality on the distribution and abundance of plants and animals, whereas experimental designs have tended to emphasize the importance of minimizing variability within treatments rather than addressing its consequences directly. Modellers have tended to exclude heterogeneity in an attempt to avoid complicating the picture (Pickett *et al.*). As Wiens points out, this old paradigm of ecology made environmental homogeneity the starting assumption and ‘emphasized simplicity at the expense of reality’. However, there is now a growing recognition that, far from

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being an irritating complication, heterogeneity is the norm in the natural environment and that its effects on individuals, populations and communities are therefore worthy of direct and serious study in their own right.

In the ecological context, heterogeneity is not an easy concept to define and, as Sparrow (1999) has pointed out, researchers differ in their approach to this problem of definition. The concept makes an explicit connection between spatial and temporal variation in environmental constraints on the one hand (whether these are provided by differences in soils, microclimates, organisms, etc.) and the responses by organisms to variability in these constraints. One practical approach defines heterogeneity as any factor that induces variation in individual demographic rates (Rees *et al.*); this approach has the advantage that the effects of heterogeneity are both specific and measurable. Within this definition there are nested spatial scales at which heterogeneity can operate (e.g. site, habitat, landscape) and to which ecological responses may differ. Rees *et al.* provide a means of partitioning heterogeneity hierarchically, and apply mathematical models to field data to demonstrate the implications of each category of heterogeneity for the evolution of the age at which flowering takes place in monocarpic perennial plants. In an elegant demonstration of the potential impacts of heterogeneity on the evolution of plant life histories, they show that it is only by including heterogeneity that realistic models can be derived. As a further consideration, Wiens draws attention to important distinctions between the quantitative and qualitative components of spatial variance and to whether or not the variance is spatially explicit (i.e. whether the measure of heterogeneity incorporates the spatial relationships between constituent patches, or is simply an aggregate property of the area as a whole).

While environmental heterogeneity often results from variation in abiotic factors, such as the physical and chemical properties of soils, microtopography and microclimate, organisms themselves may create or influence abiotic heterogeneity in a variety of ways (Pickett *et al.*; Wilson). In fact, organisms can create heterogeneity in otherwise relatively uniform environments. For example, plants may affect heterogeneity of abiotic factors through their production of leaf litter or exudates, or through interception of light and rainfall. Similarly, there are many examples of animals both generating and maintaining environmental heterogeneity through activities such as grazing, trampling or burrowing. Some organisms, so-called 'ecosystem engineers', can exert far-reaching influences on whole communities and the ecological processes acting within them by altering the state, availability, and perhaps degree of heterogeneity, of biotic or abiotic materials that are available to other organisms (Pickett *et al.*; Lawton). A further layer of heterogeneity may be provided by stochastic or deterministic patterns of disturbance, whether natural or anthropogenic in origin, which impact upon both the physical environment and the organisms within it. These different sources of heterogeneity interact in ways that are a challenge to disentangle.

Wilson explores the relationship between species diversity and heterogeneity. While it is clear that habitat heterogeneity can enhance diversity, as exemplified by

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MacArthur's familiar positive correlation between structural heterogeneity of trees and bird diversity (Lawton), the converse is less clear. Species richness in itself increases biotic heterogeneity; for instance, a species-rich plant community provides a heterogeneous habitat for phytophagous insects. However, there is a growing body of evidence that suggests that diverse communities are likely to be associated with smaller spatial and temporal fluctuations in abiotic parameters than less diverse communities[†]. A diverse community is likely to exploit resources in space more completely and show smaller temporal fluctuations in ecosystem processes. For instance, a diverse plant community will contain species with a range of rooting depths and phenological patterns of physiological activity, which together are likely to absorb more completely nutrients that are spatially and temporally heterogeneous. Wilson also explores the interesting and important idea that organisms control not only the degree but also the scale of heterogeneity, and that scale is an important determinant of the effects of heterogeneity on individual organisms. Thus, for example, trees may create large-scale spatial heterogeneity in water availability via hydraulic lift, making the soil environment less suitable for species that operate at a smaller scale.

Indeed, environmental heterogeneity is important for individual organisms only when it occurs at a scale to which the organism itself can respond. If the scale is greater than this, the result is merely a difference in performance between spatially separated locations. However, an important recent development has been the recognition of the importance of the opposite situation: i.e. conditions in which environmental heterogeneity occurs at a scale that is within the organism's normal ambit and to which it can respond in alternative ways. The critical question then becomes whether the ecological response (measured as change in fitness, growth, or whatever) differs as a consequence of whether the mean condition or total resource is presented homogeneously or heterogeneously.

Similar logic can be applied to considerations of temporal heterogeneity; life spans must be great enough to experience and respond to the time scale over which the heterogeneity operates. Similarly, individuals may experience changing modes of heterogeneity during their lifetime as a consequence of their own growth and development. Thus, the scale and category of heterogeneity experienced by an oak seedling will be very different to that experienced by the tree when it reaches maturity. This also applies to more mobile organisms and ones that undergo phase shifts during their lifecycle: the fine-scale heterogeneity between leaves experienced by a caterpillar will be radically different from that experienced by the nectar-feeding adult butterfly.

Our understanding of the ecological consequences of heterogeneity for individual plants, populations of plants and plant communities is developing rapidly, and a number of chapters reflect this current interest (Fitter *et al.*; Hutchings *et al.*; Casper *et al.*; Watling and Press). At first sight, plants, as relatively sessile organisms,

[†] See references in Chapter 19.

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are less able to engage in habitat selection and foraging than the more mobile animals. However, effective habitat selection in plants is now being studied from two angles:

1 by investigating ramet position and its consequences in clonal plants (multiply rooted clonal plants can occupy more than one location, and their rhizomes and stolons effectively allow them some mobility); and

2 by investigating the ability of plants that root at a single site to respond to spatial heterogeneity (the proliferation of sections of the root system in resource-rich patches is a feature of many plants so far investigated; Fitter *et al.*; Hutchings *et al.*).

Studies to date have shown a great deal of variation in the precision with which plants are able to match the placement of resource-acquiring organs to the available resources, although in some cases the precision is quite remarkable (Hutchings *et al.*). Understanding the ecological implications of this variation is a goal of a number of current research programmes. The responses of plants to temporal heterogeneity have been studied less, but it is clear that over short time periods, such as brief sun-flecks experienced by tropical forest floor plants, there may be species-specific physiological constraints which limit the abilities of plants to respond rapidly to a short pulse of extra resource (Watling and Press).

When the performance of plants is compared in environments in which the same quantity of resources is supplied homogeneously or in various heterogeneous arrangements, it is found that some species are more productive in heterogeneous environments than in the equivalent homogeneous environment (Hutchings *et al.*). As species differ in their responses to heterogeneity of resource supply, it has been predicted that population and community structure should both respond to heterogeneity, although studies to date have not confirmed this (Casper *et al.*). So far, most studies of the effects of heterogeneity on plant performance have examined the effects of heterogeneity on biomass accumulation rather than plant fitness. A more detailed examination of the effects of heterogeneity on the latter will be an important challenge for researchers in future.

As roots of several plants tend to access the same nutrient patch in heterogeneous environments, and may travel quite some distance to do so, it might be expected that heterogeneity would lead to more intense underground competition. However, there is no evidence as yet that this is so. Casper *et al.* explore the inadequacy of most attempts to model competition among plants for dealing with heterogeneous environments, particularly underground, given that we still know very little about how most competing plants' roots are distributed within the soil with respect to each other.

One of the most stimulating aspects of the symposium was the degree to which animal and plant ecologists were able to integrate and exchange ideas, especially on issues to do with foraging and habitat selection. These areas have traditionally been regarded as the preserve of animal ecologists. The examination of plant responses to local resource heterogeneity has given plant ecologists a new insight into the dynamic nature of plant foraging and habitat choice, and an incentive to review the

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ways in which theories that were developed for animals could also be applied to plants.

Plants, as resources for herbivores, are intrinsically highly heterogeneous, both spatially and temporally. However, there are still many unanswered questions surrounding exactly what impact this heterogeneity has on higher trophic levels. What effect does variation in plant quality have on herbivore population densities and on the mechanisms that control them? How important is heterogeneity in resource quality as compared with the actual quantity and availability of the resource? To what extent can plants capitalize on their spatial heterogeneity and temporal unpredictability to defend themselves from attack by herbivores? Hunter *et al.* provide evidence that variation in plant quality affects two components of insect herbivore life histories: voltinism and the impact of natural enemies. It is, of course, a moot question as to whether such impacts affect the actual regulation of herbivore populations, rather than simply adjusting the equilibrium population size. However, against a historical background preoccupied with the importance of density dependent factors in population regulation, the potential for variation in plant quality to act in a density-independent (or perhaps even inversely density-dependent) manner, poses some interesting challenges for the development of population models.

At the individual level, models involving habitat selection and patch use behaviour (e.g. Charnov's marginal value theorem and the ideal free distribution) have been applied to many animals operating in heterogeneous environments. Drawing upon detailed and long-term studies on squirrels, Brown shows how the behaviour of related species responds differently to the trade-off between food consumption and predation risk. This in turn dictates spatio-temporal patterns of species in a number of ways: from how animals forage in patchy environments to the coexistence and geographical distribution of closely related and potentially competing species.

Insect parasitoids are also faced with a highly heterogeneous environment (Godfray *et al.*); their hosts are very patchily distributed in space and host densities may vary considerably between patches and over time. In response to this uncertainty, parasitoids have evolved a complex suite of behavioural traits that enable them to locate suitable patches, exploit their hosts and then depart in search of new patches in an efficient manner. At the population level, the non-random search of parasitoids between patches that are distributed across a heterogeneous landscape has long been recognized as the key to stabilizing models of host-parasitoid interactions, although whether or not density-dependent aggregation by the parasitoids is essential for stability remains controversial. In such circumstances, the spatial arrangement of parasitoids may conform to a metapopulation model, where extinction and re-colonization of local populations are dependent upon moderate, but not excessive, rates of dispersal between host patches. In this context, habitat heterogeneity is important for creating the asynchrony in dynamics between spatially separated local populations that is essential for metapopulation persistence.

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Power and Rainey provide a new framework for examining the spatial sources of trophic resources, introducing the term 'resource shed' (analogous to watershed) to describe the geographical area from which an organism's resources are derived. Our ability to delimit resource sheds has far-reaching consequences for many aspects of pure and applied ecology (for instance food-web analysis and conservation biology), and is advancing rapidly with the range of stable-isotope techniques that are now available. Examination of an organism's resource shed can produce surprisingly counter-intuitive results and shows that resources can often move over large distances. For instance, riparian plants growing at high altitudes in Alaskan coastal watersheds may receive a significant input of oceanic nitrogen via a predator cache of salmon carcasses, derived from fish that had returned to the upper reaches of the stream to spawn.

Given the alarming rate of habitat destruction at a global scale, there is an urgent need for conservation biologists to provide predictions of how such large-scale anthropogenically imposed heterogeneity will affect constituent populations. The spatial pattern of modern development at a landscape level usually involves progressive habitat fragmentation, where remnant fragments of original habitat become smaller in area and increasingly isolated from each other. It is not yet clear how best to model the effects on populations of the large scale habitat heterogeneity that this creates; species-area models have now given way to models based on metapopulation structures (Dytham; Lawton). In any case, it is clear that specific predictions of the effects of habitat fragmentation across species, locations and habitat types will not be easy. As might be expected, empirical data suggest that generalist species will fare better than habitat specialists; unfortunately, the rarest species are likely to be in the latter category. Similarly, a consideration of how fragmentation affects the genetic composition of remnant populations and gene flow between them will be essential (Boshier and Billingham). More importantly however, data from highly modified tropical forests suggest that the persistence of a species in remnant fragments does not guarantee its long-term survival (Corlett); continuing loss of species even from protected habitat fragments suggests that extinction will continue long after the fragmentation has ceased. This is likely to be especially true for long-lived organisms such as trees, in which effects will take a long time to manifest themselves and population recovery rates will be slow. For this reason, Dytham warns against simplistic predictions of species loss based on area of habitat destroyed; the 'extinction debt' (Tilman *et al.* 1994), where currently surviving species are already locked into a downward spiral towards extinction, may take a long time to be paid off.

At a more local scale, the arable farmland landscape, with intensively managed fields separated by seminatural field margins, comprises a heterogeneous mosaic of habitat types. Conventional agricultural management practices impose periodic and dramatic perturbations upon this spatial structure, in the form of tilling, sowing, and harvesting operations and the application of nutrients, herbicides and pesticides. This landscape therefore provides a suitable arena in which the differential effects of environmental heterogeneity in space and time can be examined

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experimentally. Macdonald *et al.* demonstrate that the ecological effects of such heterogeneity (on individual species, communities and overall ‘biodiversity’) are both case-specific and highly scale-dependent. Thus, at one extreme, landscape-level studies show that the greater temporal stability and increased spatial heterogeneity of organic farming systems have a positive effect on population size and species richness of small mammals and selected invertebrate groups in comparison to conventional farms. At a fine scale, heterogeneity imposed by small-scale mowing experiments on field margins produces effects that interact closely with the detailed autecology of individual species.

This type of detailed knowledge will be essential for the successful restoration of semi-natural communities that have been degraded or destroyed as a result of modern agricultural practices. Bakker emphasizes that successful restoration of plant communities involves more than just the cessation of damaging practices and that it is necessary to understand the heterogeneous nature of both propagule availability and soil nutrient availability in order to predict whether restoration will succeed. He also points out the important role that vertebrate grazers can have in creating a heterogeneity of micro-sites, and patchiness in vegetation structure, which allow a diverse range of plant species to coexist in a community.

Several common threads emerge from the collection of contributions to this Symposium. Firstly, results from recent research re-emphasize what ecologists have known for many years: that heterogeneity, at a variety of spatial scales, is all-pervasive in natural environments. Ecologists can not afford to ignore such heterogeneity, even though it greatly complicates the task of untangling the various environmental influences on organisms. In order to respond, individual organisms must be able to perceive the heterogeneity; whether they are good or bad at dealing with heterogeneity will depend substantially on whether they have the phenotypic plasticity to respond to it. In fact, there are good reasons for suggesting that many species will have evolved strategies for coping with, and capitalizing upon, environmental heterogeneity as the norm in natural systems. The other side of this coin is that therefore one would expect to see, at least in some species, a reduction in performance when faced with homogeneity compared with their performance in certain types of heterogeneous environments; some single-species studies are now beginning to provide exactly this sort of evidence (Hutchings *et al.*). In fact, different species are likely to show a range of responses to heterogeneity; some will be able to respond positively to a particular form or scale of heterogeneity, whilst others will not. In this context, ability to respond to heterogeneity becomes an important species attribute that ecologists will need to consider alongside the other conventional attributes that are used to characterize species.

Secondly, while evidence is accumulating that natural heterogeneity has important effects on the performance and fitness of individual organisms, the implications of heterogeneity for populations and communities have been, as yet, less well explored. This presents an exciting challenge for the future. Amongst other factors, the amount of genetic variation will influence the degree to which organisms can respond to heterogeneity at the population level (Boshier and Billingham).

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Finally, while we might expect many organisms to have evolved mechanisms for dealing with natural heterogeneity, anthropogenically imposed heterogeneity at the landscape level will have severe consequences for the long-term persistence of many species, particularly those that have high habitat specificity and limited powers of dispersal. Problems will arise for such species if the scale of habitat fragmentation is larger than the scale of heterogeneity to which the organisms are adapted. Unfortunately, these species are likely to be both rare and vulnerable and therefore the ones of greatest conservation concern.

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Chapter 2

Ecological heterogeneity: an ontogeny of concepts and approaches

J.A. Wiens

Introduction

Heterogeneity is scarcely a new or novel concept in ecology. After all, the work of von Humboldt and other plant and animal geographers in the 19th century, which established the foundations of modern biogeography, was based on recognizing distinct patterns in the distributions of species or community types (McIntosh 1991). At finer scales, ecologists were analysing the dispersion patterns of plants well before many of today's ecologists were born, frequently documenting that the distributions of individuals departed significantly from random—there was spatial heterogeneity or pattern (Greig-Smith 1979, 1983; Dale 1999). By the middle of the century, laboratory experiments (e.g. Gause 1935; Huffaker 1958) had demonstrated that environmental heterogeneity could alter the dynamics of populations or communities. Alex Watt's Presidential Address to the British Ecological Society (1947) and, later, Elton's (1966) detailed treatment of habitat patterns in Wytham Woods showed clearly the reticulate spatial structure of natural environments and the interplay of spatial patterns with spatial processes.

An awareness of environmental heterogeneity and its consequences, then, appeared early in the history of ecology. Our current interest in heterogeneity, however, is a consequence of a relatively recent paradigm shift. Beginning in the 1950s, a view that ecological dynamics are played out in local habitats that are spatially homogeneous and temporally equilibrated rapidly gained force, and it came to dominate ecological theory and a good deal of ecological practice during the 1960s and 1970s. There were both philosophical and practical reasons for the widespread acceptance of this view. Philosophically, the notion that ecological systems could be thought of as closed and internally homogeneous fitted closely with the typological view of nature that was the foundation of community classification as well as of taxonomy (Mayr 1976; Pickett *et al.* 1994). Equilibrium thinking also accorded well with a Western world view of the balance of nature (Wiens 1984; McIntosh 1985; Pimm 1991; Wu and Loucks 1995). Practically, the assumptions of homogeneity and equilibrium provided the simplification of a more complex reality that was

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necessary for theory (especially mathematical theory) to develop. Because theory provided the framework for posing questions and testing hypotheses, however, empirical studies increasingly were designed with equilibrium and homogeneity in mind. Thus, short-term studies became the norm, and ecologists were admonished to seek homogeneous study areas to discern clear community patterns (MacArthur 1972). Ecosystem ecologists came to consider entire watersheds as internally homogeneous areas with regard to biogeochemical inputs and outputs (Bormann and Likens 1979). Ecologists conducting laboratory experiments justified their neglect of spatial and temporal variations by emphasizing that laboratory studies should address recurrent ecological processes of general significance, rather than the idiosyncratic and unique situations studied by field ecologists (Mertz and McCauley 1980; see also Lawton 1999). The new paradigm offered the prospect of far-reaching and unifying generalizations. As Cody and Diamond (1975) observed, the new paradigm ‘transformed large areas of ecology into a structured, predictive science that combined powerful quantitative theories with the recognition of widespread patterns in nature.’ Over time, the simplifying assumptions of homogeneity and equilibrium became widely accepted.

Just as it was theory and theoreticians who led ecology down the pathway to homogeneity and equilibrium, however, it was to a large degree theoreticians who provided the catalyst for a paradigm shift. By the mid-1960s and early 1970s, theoreticians were beginning to introduce temporal and spatial variation into their models (e.g. MacArthur and Levins 1964, 1967; Levins 1968, 1970; Horn and MacArthur 1972; Levin and Paine 1974), often with interesting results. The potential for a population to persist, for example, or the continued coexistence of competitors or of predators and prey, or the augmentation of local biodiversity, were all enhanced by the addition of spatial heterogeneity to models. By generating new predictions for field and laboratory ecologists to test, the theories focused attention once again on heterogeneity. Moreover, the incorporation of heterogeneity into theory made it an acceptable topic for ecological investigation, and challenges to the waning paradigm could now be published without the authors being labelled heretics (e.g. Van Valen and Pitelka 1974; Levin 1976; Wiens 1977, 1983; Simberloff 1980). The focus on spatial and temporal variation that had attracted the attention of an earlier generation of ecologists was renewed, setting the stage for an explosion of interest in heterogeneity and its consequences (e.g. Shorrocks and Swingland 1990; Kolasa and Pickett 1991; Levin *et al.* 1993; Rhodes *et al.* 1996; Tilman and Kareiva 1997). The recent development of perspectives on self-organizing properties of complex systems (Kauffman 1993), chaos theory (Gleick 1987) and fractals (Milne 1997) has provided fresh ways of thinking about heterogeneity in ecology. Complexity, however, is not quite the same as heterogeneity. In principle, a system could be complex but not vary in time or space—homogeneous complexity. Whether such complexity is seen as homogeneity or heterogeneity, however, depends on the scale on which it is viewed, a point to which I will return later in this chapter. In any case, we now recognize that models built on assumptions of homogeneity in space and equilibrium in time may be valuable in generating null