Chapter 2
Space and Time in Ecology: Noise or Fundamental Driver?

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In this chapter I frame the central issue of the book, namely is spatial and temporal complexity in ecological systems merely noise around the predictions of non-spatial, equilibrium processes? Or, alternatively, do spatial and temporal variability in the environment and autogenic space–time processes in populations fundamentally alter system behavior such that ideal models of nonspatial and equilibrium processes do not represent the fundamental dynamics of ecological systems?

If the former is correct, then the task for ecologists is seems relatively simple, if practically daunting. If variation across space and through time are noisy but not transformational, then the task of ecologists is simply one of increasing the scope of inference to maximize precision. That is, with the additional noise inhering to ecological processes due to spatial and temporal variability, larger and more extensive empirical samples will be needed to obtain precise estimates of underlying parameters through either inferential or Bayesian approaches. This would emphasize the critical need for broad scale, consistent, large sample data collection efforts. It would also put a fundamental limit on the precision of predictions that would be possible for a specific fine-scale location at a specific time. Similarly, such a relationship between spatial and temporal variability and system behavior would require only modest changes to nonspatial and equilibrium theoretical and predictive models. Under such a scenario, the expected value of ideal, nonspatial and equilibrium models would be unbiased, assuming correct identification of important driving variables and proper parameterization. However, the precision of the estimates of such models would be questionable, as the amount of variability in observed phenomena due to spatial variability and temporal fluctuations would likely often be substantial.

Scale would play a particularly critical role in determining precision of estimates from both empirical inferences and predictions of ideal nonspatial, equilibrium models. Specifically, if spatial and temporal variability are simply noise, then there will be a consistent relationship between scale and the precision of estimates

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from empirical data and of predictions of theoretical models. Simply put, if spatial and temporal variability are noise clouding ideal processes, then precision will increase monotonically with the extent of measurement across space and time. At fine spatial scales and over short time periods variability will be high and reliability of empirical data to infer underlying process, or of process models to predict empirical patterns, will both be low. However, given an unbiased expected value, this variability will average out and precision will greatly increase as extent increases in both temporal and spatial dimensions, and as sample sizes increase in density within space and time.

However, there is a catch to this solution to variability through expansion of the scope of analysis. In a word it is nonstationarity. In the previous paragraph we argued that increasing extent of analysis in space and time will average out variability due to spatial and temporal complexity. This is true, so long as one remains within a stable "scale domain" in which relationships between pattern and process are constant. However, one of the most basic concepts in ecology is that ecological patterns vary across space and time along complex gradients of spatially structured environmental drivers. Pattern and process relationships are likely, more often than not, to be spatially nonstationary. And this tendency to nonstationarity is directly and monotonically related to scale as well, and unfortunately in the inverse way as precision. The larger the spatial and temporal scope of analysis, the higher the chance of severe nonstationarity in the major pattern–process relationships governing the system. Therefore, we face a dilemma, with large scope of analysis needed to deal with spatial and temporal variability, but small scope of analysis needed to ensure a sufficiently coherent and stable set of pattern–process relationships. This is a major practical challenge to ecologists hoping to obtain high precision predictions across space and through time. Fortunately, there are approaches to incorporating space, time and scale into analysis to address this challenge, which is the topic of the next chapter.

If, on the other hand, spatial and temporal variability fundamentally alter pattern–process relationships, then the challenge is even more severe. Instead of being noise around an unbiased expected value predicted by nonspatial and equilibrium processes, spatial and temporal variability in this case would fundamentally alter pattern process relationships. It is important to clearly articulate what this means. In the previous paragraph we discussed nonsationarity of pattern process relationships, but implicitly assumed that there could in principle be a scale domain at which one could assume a stable and stationary relationship between pattern and process. If on the other hand, pattern and processes relationships are sensitive to spatial and temporal complexity across the full range of spatial and temporal scale then this collapses all the way down. In such a case one cannot assume nonspatial and equilibrium processes will be sufficient at any combination of scales. In such a case it will therefore be necessary to incorporate spatial and temporal factors directly into the theory proposed, the method used, and to ensure that the data collected are measured at scales at which pattern–process relationships are strongest.

In the introductory chapter we argued that ecology is at a major transition, marked by rapid advances in methodology which enable much broader scale collection

of detailed spatial data, much more vast data storage and more sophisticated data organization, and vastly more powerful data handling, manipulation and modeling. These changes in method and data are now feeding back to theory, and providing some traction on the very difficult challenges posed by spatial and temporal variability in ecological systems. The remainder of this chapter is a kind of historical retrospective on the emergence of awareness of the critical role spatial and temporal variability play in ecological systems and how ecology has struggled to begin incorporating them

2.1 Space, Time and Ecological Communities

Ecological communities are not crisply defined, discrete and stable entities. Indeed, the concept of community is an abstraction made to facilitate investigation. It is useful; its definitions provide the scale and boundaries within which hypotheses can be developed and tested. However, it should always be kept in mind that the "community" is an aggregation in flux, varying through space and over time (Levin 1989). The spatial and temporal dynamics of ecological systems affect the interactions of organisms with each other and their environments in complex and synergistic ways.

The functions of temporal and spatial processes within communities are poorly understood. One key question is, how precisely does variability in space and time affect species interactions? Particularly, in what ways are competitive and predator–prey dynamics influenced by habitat geometry, stochastic events, and temporal trends or cycles? Are community structures largely a result of history, chance and the influences of spatial and temporal heterogeneity, or do they reflect underlying nonspatial processes and tend to an ultimate equilibrium? Resolving these questions is among the most challenging and important problems in modern ecology (Huston 1979; Kareiva 1989; Roughgarden and May 1989). In the remainder of this chapter we review the discoveries and theoretical advances that lead to the formation of these questions and consider current theory regarding the effects of heterogeneity in space and time on species interactions and community structure.

2.1.1 Lotka–Volterra, Gause, Hutchinson and Whittaker

Lotka (1932) and Volterra (1926) demonstrated mathematically that two species which are limited by a common resource cannot coexist in a finite system. The simplicity and elegance of their formulation was seized upon by ecologists who hoped that, as in physics, universal laws of ecology could be expressed in simple formulas. The Lotka–Volterra model gained support from the experimental work of Gause (1934, 1935). Gause's experiments indicated that when two species with common resource requirements are forced to coexist in an undiversified

environment one will inevitably become extinct. This "law" became known as the "competitive exclusion" or competition principle. The competition principle provided a theoretical explanation for the observation by community ecologists that the species which coexist in any system are a small subset of what might co-occur (Roughgarden and Diamond 1986). This "limited membership" (Elton 1927) was believed to result primarily from exclusion of potential members by established species.

Competitive exclusion, coupled with the idea of limited membership gave studies in community ecology a focus, but it was not until the ecological niche concept was formalized by Hutchinson (1957) that a truly powerful theory of community organization emerged. Hutchinson defined a species' fundamental niche as an n-dimensional hypervolume, in which each dimension represents the range a necessary condition or resource could have and meet the requirements of the species for survival and reproduction (Fig. 2.1). The fundamental niche, then, describes the "space" in which an organism's requirements are met, and thus "where" the organism can potentially survive. Importantly, space in this conception is "ecological space" defined in terms of environmental variables and not in the familiar three dimensions of geographical space. The influences that merging these two models of "space" would have on ecological theory are critical, and will be elaborated upon later in this discussion.

To achieve or hold membership in an ecological community a species must have and maintain "niche space" in geographic space and through time (Fig. 2.2). To have niche space first requires that the resources and conditions needed by the species are available, and secondly that these resources are not co-opted and the conditions are not changed by the actions of other species. If interactions with one species reduce the resources available or change conditions needed by a second species then the two species compete. If this interaction reduces the niche space of one or both of the species then competition is a structuring factor in the community. If the realized niche of a species is sufficiently reduced then one or more of the resource dimensions will be insufficient and the species will be excluded. Thus the composition of any community is determined both by the availability of required resources through space and time (Gleason 1926; Whittaker 1956) and the ability of each species to maintain access to those resources and conditions in the face of interspecific competition (Gause 1935).

This is the central logic of the classical competition theory of community structure. The classical theory predicts that, given an initial set of potential members, the composition and structure of the community will trend toward equilibrium. Species that have similar resource needs compete and the inferior competitors are excluded from some or all of their fundamental niche space. A species excluded from all of its fundamental niche space will be excluded from the community. Over time the community is expected to stabilize at a sort of competitive climax which is conceptually similar to the "climatic climax" of Clements (1936).

The theory, in strict form, is an idealization. It is logically consistent, and therefore correct, within its assumptions. It is a useful mental model, but its assumptions are usually met only briefly and at fine spatial scales in the real world. Also, interspecific

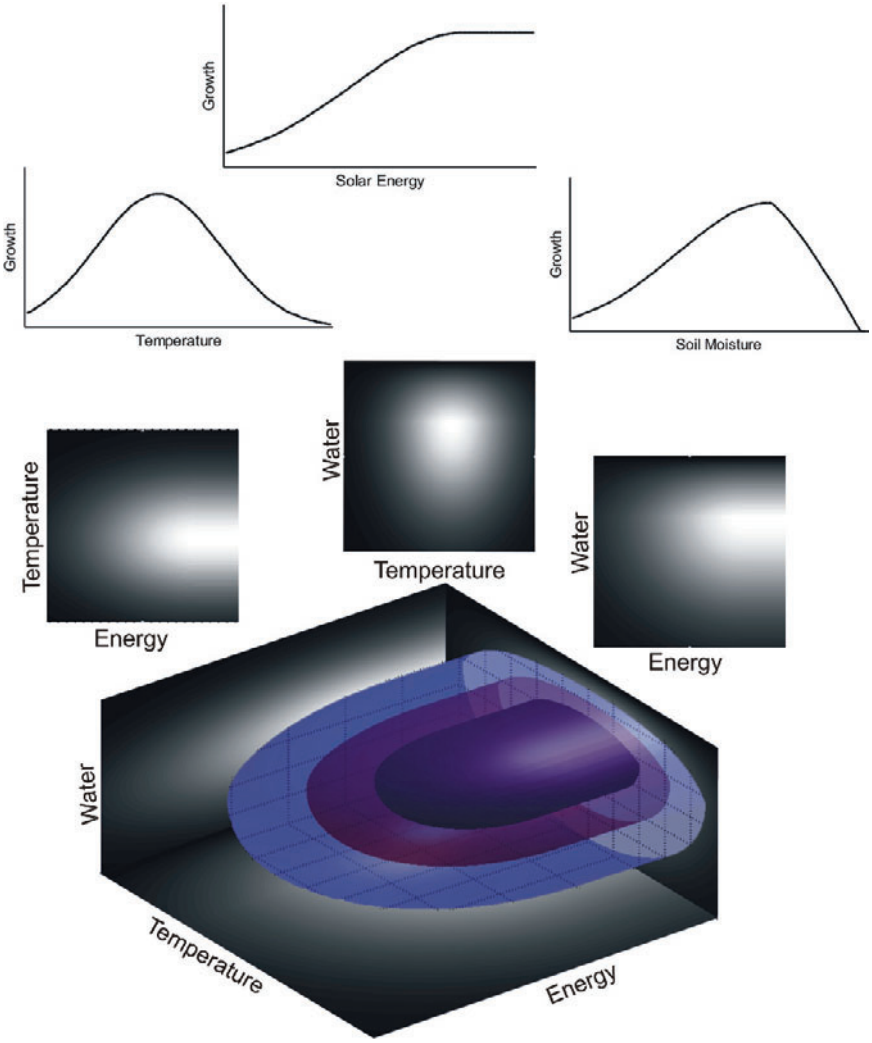

Fig. 2.1 Idealized fundamental niche as zone of tolerance and optimal fitness along three environmental dimensions

interactions are more complex than simple models of competition would suggest. Interactions between herbivory, predation, parasitism, direct, indirect and apparent competition are complex and have influences on determining niche space and ability to maintain membership in communities across space and time that are difficult to predict. This does not invalidate the logic of the model, nor does it necessarily indicate that new mechanisms beyond the niche concept and limited membership need be sought. It does suggest, however, that temporal and spatial dynamics of the environment, autogenic population processes driven by predators and parasites,

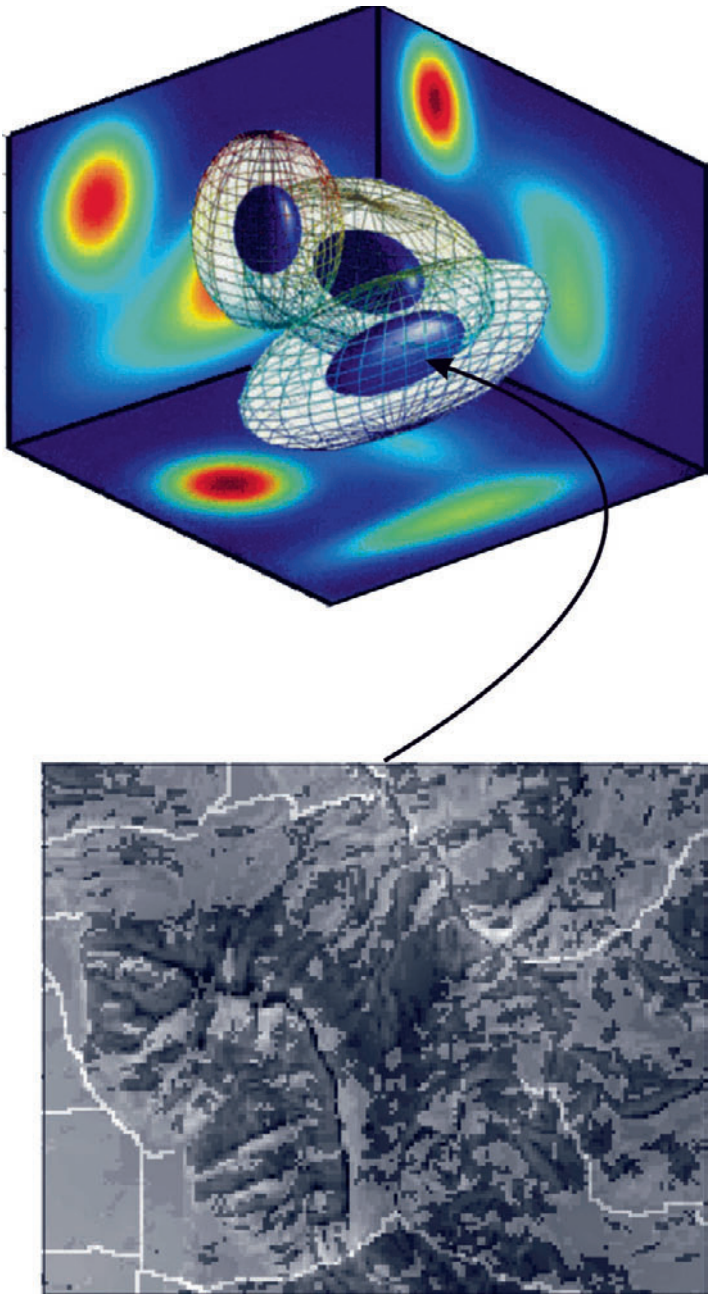

Fig. 2.2 Projection of a fundamental niche from n-dimensional ecological space to geographical space. The projection is most easily thought of in terms of applying a habitat suitability model to each location in a landscape in which each niche axis is a predictor variable. The outcome is a map of niche-suitability for the species of interest across geographical space

and their interactions, may create a spatially dynamic, non-equilibrium reality where the predictions of classical models are seldom if ever achieved.

2.1.2 Assumptions of the Competition–Equilibrium Theory

Hutchinson (1959) identified competition as the predominant process limiting species diversity and distribution, and hypothesized that it is what creates and maintains community structure. In the 1960s and 1970s many ecologists sought to apply this competition–equilibrium theory to explain community structure (e.g. Schoener 1974; Slatkin 1974; Armstrong and McGehee 1976). The theory predicted that if sympatric species were too similar then the less competitive species will go extinct according to the Lotka–Volterra model, and over time a stable equilibrium is achieved where the remaining species in the community each limit their own expansion through intraspecific competition more than they limit the population growth rates of other species (Hubbell and Foster 1986). It is hypothesized that coevolution of the member species over long periods leads to finer niche partitioning which allows for increased community diversity. Diversity is explained as the result of resource partitioning among species whose needs do not overlap completely. The concept of limiting similarity is evoked whenever two similar species coexist. As a net result, it was believed, coevolution, in conjunction with repeated invasions of "exotic" species that remixed the community yielded communities in which the theoretical limits of similarity were approximately achieved. This would give communities very predictable properties (Slatkin 1974; Paine 1984; Chesson and Case 1986).

The theory was formalized into a number of mathematical models which predicted the outcome of species interactions in model communities (MacArthur and Levins 1967; Cody 1974; Schoener 1974; Slatkin 1974). These models of community structure were tremendously influential in ecological theory in the 1970s; however, they make a number of limiting assumptions about species interactions which raise questions about their power to predict real world processes. As mentioned above (1) populations and communities are assumed to be at equilibrium set by resource scarcity; (2) competition for resources and selective pressure on resource-exploiting attributes is continuous and intense; (3) this competition is the major selective force determining the distribution of species (Wiens 1977).

2.2 Objections to the Strict Theory of Competition–Equilibrium

The validity of the theory's assumptions depends on several key conditions, including that physical and biotic interactions are of even frequency and intensity throughout the community and that historical effects, temporal trends, stochastic

factors, spatial complexity and heterogeneity, migration and occasional perturbations are insignificant (Chesson and Case 1986). Space is assumed to be homogeneous and the system is assumed to be well mixed so that dispersal can be ignored (Wiens et al. 1986). However, in any real biological community the environment is a temporally varying patchwork or system of complex spatial gradients (Chap. 5, McGarigal and Cushman 2005), resulting from the space–time intersection of underlying environmental gradients with biotic and disturbance processes. In addition, organisms may often generate spatial pattern in community structure and composition autogenically through predator–prey and other interactions even in continuous and homogeneous environments (Roughgarden 1978; Kareiva 1987). Furthermore, the strength of interspecific competition is likely to vary among taxa (Schoener 1974). It is expected to be high in sessile organisms in crowded conditions, and low in phytophagous insects, for example. And for any taxonomic group the constancy of competition as a limiting factor over space and time is likely to vary markedly.

Not surprisingly, given these observations, a controversy ensued over whether violations of assumptions were "noise" obscuring the underlying competition–equilibrium processes, or whether the model itself failed generally to account for real-world community structure. A number of key papers investigated the effects on community processes when one or more of the assumptions are violated.

2.3 Key Papers: Challenges to Equilibrium Theory

Hutchinson (1957), in a paper which united the Lotka–Volterra competition model with the n-dimensional niche concept, wrote that the only conclusion that could be drawn was that although communities appear qualitatively to be constructed as if competition were regulating their structure, there are always difficulties in proving causality even in the most well studied systems. In the following 30 years a tremendous literature accumulated in clarifying this questions, with the same points being echoed and expanded prominently by Connell (1983) and Hairston (1985)

2.3.1 Fugitive Species and the Paradox of Plankton

Skellam (1951) coined the term "fugitive species" to describe situations where a poor competitor with a high reproductive rate coexists with a good competitor which reproduces slowly. Hutchinson (1951) identified stochastic disturbances as the key to the persistence of fugitive species. Persistence, in the fugitive species model, results from an equilibrium between the rate of exclusion and the rate of recolonization of newly created disturbance patches by the poorer competitor.

An important expansion of this idea is that disturbance and other changes in circumstances may interrupt or even reverse the direction of competition before

it has run its course to an equilibrium state. Proctor (1957) in a study of two species of green algae found that in permanent pools one species inevitably excluded the other. In intermitted ponds, however, the other, more drought resistant species could persist because during dry periods it had the competitive advantage. This led Hutchinson (1957) to speculate that there could be many instances where the direction of competition is never constant enough to allow the elimination of competitors. He used this logic to resolve the so called "paradox of plankton" (Hutchinson 1941, 1944, 1961).

It had long been noted that many more species of plankton coexist than can plausibly be explained by the classic competition–equilibrium theory (Chesson and Case 1986). Hutchinson speculated that the lack of equilibrium could be an explanation. Physical conditions, such as temperature, light and nutrients, are highly variably temporally and spatially in the marine environment. This variability could promote species richness of phytoplankton by repeatedly changing the direction of competitive advantage of the component species across space and through time (Hutchinson 1961).

The resolution of the paradox of plankton was that space–time variability leads to interruptions or reversals of competitive interactions, and this slows or prevents competitive exclusion. Hutchinson (1961) argued that if environmental fluctuations occur with a period roughly equal to the time for competitive exclusion then the species would coexist and a community more diverse than expected would be maintained. But if the period between environmental changes is markedly different from the time for competitive exclusion then exclusion would sill occur (Horn and MacArthur 1972).

2.3.2 Intermediate Disturbance and Predator Mediated Coexistence

A number of researchers in the 1970s used simple mathematical models to explore the potential effects of temporal nonequilibrium in the environment on competitive interactions. For example, Chesson and Warner (1981) used simple mathematical models to show that environmental variability promoted coexistence in lottery competitive systems. Similarly, Koch (1974), Leigh (1975), Schoener (1976) and Levins (1979) showed that fluctuations in the environment could lead to coexistence by interrupting or reversing competition periodically.

Caswell (1978) modeled the influence of one species of predator on competition between two prey species in a "community" of 50 cells, each of which is equally accessible to individuals of each species. Without predation, one species inevitably became extinct. However, with predation the two competitors coexisted for over 1,000 generations. Caswell called this "exploiter mediated coexistence." Exploiter mediated coexistence was also observed earlier empirically in Paine's (1966) classic experiments. Paine (1966) demonstrated the importance of a keystone predator in maintaining the diversity of an intertidal community. When the sea-star predator

was removed, a process of community succession occurred in which barnacles settled and excluded other species, and in turn were themselves excluded as mussels came to dominate the site. The community was reduced from 15 to 8 species following the removal of the sea-star. This classic work provided a dramatic illustration of the interaction between quasi-deterministic processes of competition for space and the effect of predation as a disturbance event (Paine 1984). Paine and Levin (1981) noted that stochastic physical disturbances had comparable effects to intermediate levels of predation in maintaining species within the community.

These results are explained by the "intermediate disturbance hypothesis" (Connell 1978). The highest levels of diversity are expected at intermediate levels of disturbance. Predation and stochastic physical disturbances can both lead to the coexistence of competitors. If the disturbance is too rare or not intense enough local competition tends toward equilibrium and the fugitive species are eliminated. If, on the other hand, disturbance is too frequent or too intense most species are eliminated. At intermediate frequencies competition is interrupted or reversed periodically and high diversity can be maintained (Kolasa and Pickett 1991). The important factors are the rate of disruption relative to the rate of exclusion (Connell 1978).

Cushman and McGarigal (2003) evaluated the effects of landscape-scale disturbances on avian diversity in the Oregon Coast Range. Their analysis found that the highest diversity of bird species were found in landscapes with a mixture of seral stages resulting from an intermediate level of disturbance. Interestingly, they found that in landscapes with low levels of disturbance the community structure changed in a highly predictable way, characterized by the selective loss of species associated with early seral habitats. Cushman et al. (2008) found that the early seral species in this system were much more highly related to fine-scale, plot-level habitat features, and less responsive to landscape-level patterns of heterogeneity and fragmentation. This perhaps suggests that they act as fugitive species in this system, such that they have lower competitive ability in mid and late seral forests that dominate the system, but that they may be superior colonizers given that their occurrence is not constrained by landscape composition or structure, but only by occurrence of required resources at the home-range scale.

2.3.3 Lottery Model

Sale (1977) studied the causes of community structure in coral reef fish communities. He emphasized that the reef community is both space and food limited. Nonetheless, the community is very diverse, with more species than predicted by the equilibrium hypothesis. This explanation follows from the fact that fish eggs and larva are pelagic. Coexistence results from the random process of larval settlement into the vacant space left when a predator or disturbance removes an established adult competitor (Roughgarden 1986). Thus population dynamics are governed by chance colonization which is similar to a lottery.

Hubbel and Foster (1986) note that in tropical forests the diversity of tree species is extremely high, and that many of the species seem to occupy similar niches. The stochastic process of gap formation by wind throw is thought to give all sub-canopy species, so long as they are evenly distributed, an equal probability of establishment in the canopy. Thus there is a lottery process, analogous to that on the coral reef, in which all species are given approximately equal chance of success and tend to coexist for long periods even though they may occupy similar niches.

Finding examples in communities as different as coral reefs and tropical forests suggests that such a lottery process may be in action in many communities in which there are limited and stochastically developing opportunities for establishment, and equally prolific and evenly distributed propagules or juveniles of the constituent species. A number of researchers have argued that in spatially extensive systems with many species chance events of mortality and colonization may result in systems in which exclusion of inferior competitors may take extremely long periods to achieve (e.g. Diamond 1979; Case and Sidell 1983)

2.3.4 Huffaker and Others

Huffaker (1958) performed a classic study on population dynamics of a predator–prey system in a heterogeneous environment. Working with a predatory mite and a prey mite that feeds on oranges, he manipulated spatial heterogeneity by varying the number of oranges, rubber balls, Vaseline barriers and wooden poles in a laboratory microcosm. When the system was homogeneous the predator invariably consumed all the herbivores and both species became extinct. However, when spatial complexity was added, sustained predator–prey oscillations resulted. Including sufficient spatial heterogeneity resulted in waves of predation which were out of phase with prey abundance (Huffaker 1958). This allowed the predatory–prey interaction to stabilize and the two species coexisted.

Huffaker's results inspired a number of studies on how spatial heterogeneity affects predator–prey and competitive interactions (e.g. Hassell and May 1974; Hilborn 1975; Caswell 1978; Hassell 1978; Hastings 1978; Levin 1978; McMurtie 1978; Crowley 1979; Atkinson and Shorrocks 1981; Ives and May 1985; Kareiva 1987). Patchiness was investigated with mathematical models which showed that fundamental properties of multi-species communities can be changed whenever spatial heterogeneity is important in interspecific interactions (Kareiva 1987). Levin (1974) demonstrated that subdivision of habitat into patches and interpatch dispersal may permit coexistence of species which would otherwise exclude one another. Other models repeatedly predicted that predator–prey or host–parasite interactions are stabilized if patterns of attack are sufficiently aggregated allowing some prey patches to escape predation (Kareiva 1986; Hassell and May 1974).

One example of Huffaker's work moved to the field is Kareiva's (1986, 1987) study of the effects of spatial heterogeneity on the interactions between predatory coccinellid beetles and herbivorous aphids. Patchiness resulted in aphid densities

ten times those observed in a homogeneous control plot. Patchiness reduced ladybug predator dispersal rates by 50%. This led to more aphid colonies escaping predation for long periods. The net result was that with increasing patchiness of vegetation the ladybug–aphid interaction changed so that aphid populations increased, occasionally to autocatalytic outbreak densities.

Kareiva noted that while Huffaker's theory predicts that patchiness stabilizes predatory–prey interaction, in this case it led to destabilization, as the prey species oscillated in and out of large population explosions. This suggests that the actual effects of spatial heterogeneity depend on the details of demography and foraging behavior of the species involved in interaction with the scale and pattern of heterogeneity (Kareiva 1986). Kareiva also notes that insect populations rarely reach levels at which competition plays a major role. The effects of unpredictable fluctuations of environmental conditions predominate and there is little evidence of density dependent mortality (Kareiva 1986; Kolasa and Pickett 1991). Thus, this taxonomic group does not follow Lotka–Volterra community theory (Kareiva 1986).

2.4 A Non-equilibrium, Spatially Dependent World

It is clear that most of the assumptions of the "equilibrium–competition" theory do not hold in real biological communities. It is also clear that violations of the assumptions are not noise obscuring "true" underlying equilibrium processes. Spatial and temporal heterogeneity, historical effects and stochastic factors are key causal agents creating and maintaining community structure (Huston 1979; Kareiva 1986). Disturbance is so universal in natural communities that it is likely that truly equilibrium situations almost ever occur in nature (Begon et al. 1990). Even in the absence of clear disturbances and perturbations, spatial complexity in the environment and fluctuations in conditions overtime both alter population processes fundamentally in ways inconsistent with equilibrium–competition theory. Two questions thus arise: (1) does variability in space and time make the properties of communities unpredictable? (2) If no equilibrium point is achieved, will community structure be dominated by chance and historical effects? (Chesson and Case 1986). The answer is yes, on both points, and no.

2.4.1 Structure of Non-equilibrium Communities

Communities are not quasi-organisms. They are the collection of organisms of all species coexisting within some set of spatial bounds defined by the observer. Each one of these organisms has met the requirements for its survival. These are the dimensions of its fundamental niche. Assuming that an organism has geographic access to the region, its persistence at that location first depends on whether its fundamental requirements are available, and second whether other species control

them or change them such that they no longer meet the needs of the organism. We believe the niche concept and interspecific competition are the foundation of any explanation of community structure, even though in the real world equilibrium are seldom if ever achieved.

It is futile to try to develop a general theory of communities, as communities are simply the collection of organisms living in one place at one time. To understand the "structure" of a "community" requires that you understand (1) the fundamental requirements of each species, (2) how these required conditions vary spatially, (3) how they vary temporally with directional environmental change, (4) how stochastic events are likely to affect them, (5) how their availability is influenced by the actions of other species and (6) how these influences vary spatially and temporally.

The individualistic concept of the community notwithstanding, we can make generalizations about some responses of species to common processes. When environmental conditions vary in space and time, many species may coexist on a single resource (Chesson 1985). This requires that fluctuations also occur in the competitive ranking of the species. Populations at one location may experience fluctuations which are out of phase with other adjacent locations (Chesson 1983, 1985; Comins and Noble 1987; Atkinson and Shorrocks 1981). Fluctuations in competitive ranking can occur in two ways. The first is differential variation of migration rates among species into particular patches, leading to flip-flops in numerical advantage within patches over time. The other is that changes in local environments may reverse the competitive advantage within a given patch (Chesson and Case 1986).

Coexistence in such a patchy environment depends on the geometry of he landscape and the relative dispersal abilities and habitat specific mortality rates of the interacting species. If there is too much movement among patches then the system behaves like one patch. If there is insufficient dispersal, populations will disappear from patches more rapidly than recolonization can occur (Kareiva 1987; Pulliam et al. 1992). Dispersal is always a key parameter, as it determines the coupling between patches, the degree of mixing in the environment and the ability of predators to follow prey populations (Kareiva 1989; Cushman 2006).

Nearly identical species will not coexist in an unvarying environment. In a spatially homogeneous or temporally unvarying environment, two species whose niches overlap will compete and the superior competitor will exclude the inferior one from the portion of its fundamental niche which overlaps. In a varying environment, the same process will always be in operation. However, the heterogeneity and temporal variability of the real world will often prevent equilibrium from occurring. At any moment, at any location, one species will have the advantage over the other in competition for their common resource. But, conditions may well change and shift the competitive balance before exclusion occurs. Alternatively, spatial heterogeneity in the pattern of competitive ability will enhance persistence. The combination of spatial heterogeneity of competitive advantage coupled with temporal fluctuations in this advantage across space are probably the major underlying factors maintaining biological diversity greater than predicted by classic equilibrium theory.

Also, abiotic or biotic factors, such as disturbance or predation, may reduce the numbers of the superior competitor, or of both species, below the point where interspecific competition is limiting. After that, both species will grow for a time without competing with each other (Hanski 1981). The metapopulation process of local "patch" extinction due to environmental factors, predation or chance may permit competing species to colonize and grow for a time without interspecific competition. So long as the spatial pattern and temporal frequency of these "extinctions" match the demographic and dispersal abilities of the fugitive species it will persist indefinitely even though it is always a poorer competitor.

Whereas it was once thought that environmental variability acted primarily to eliminate species, we now know that variability in may instances may act to promote diversity. Stochastic environments can convert competitive exclusion into competitive coexistence (Kareiva 1989). The key is the combination of a fluctuating, spatially variable environment and the possession of certain life-history traits (Chesson and Case 1986). This is an explanation of the coexistence of strongly competing species from different taxonomic groups (i.e. harvester ants, finches and rodents). Differences in life history, physiology and behavior in these groups lead to different responses to environmental pattern and change. Thus, a fluctuating spatially complex environment can promote coexistence.

A biological community is defined as a collection of organisms which all maintain niche space within a given area. Their effectiveness at holding this "space" at a given time is a measure of the Darwinian fitness of individuals of the species. Individuals which hold space less effectively relative to their con-specific conspecific competitors will produce fewer offspring, and a species which in general fails to hold space will be excluded by other species, and will become locally extinct. If conditions fluctuate around a stable mean value, then niche space of a species will expand and contract in phase with the fluctuation. While the space for one species expands due to a given fluctuation, that of a competitor may be contracting. Meanwhile, in an adjacent patch environmental conditions may be fluctuating in a different manner, leading to expansions and contractions that are spatially out of phase. This combination of spatial and temporal environmental variability promote coexistence by interrupting or redirecting the direction of competition.

However, when the mean value of conditions change over time and space the situation is different. Real world environments don't often fluctuate around a stable environmental mean. Slow, directional changes are constantly occurring in physical conditions due to climate change and geomorphic processes (Hubbel and Foster 1986). If the changes are sufficiently slow, then most organisms in the community can track them equally well through evolutionary change. However, if some organisms track better than others, community structure will change. Species which track poorly will experience reduced access to their fundamental niche, or their competitive ability to hold it relative to other community members will decrease. Since the relative abundances of the species present in a community are constantly adjusting to new conditions, but never complete the adjustment before conditions change, past abundances of species remain relevant. History plays an important role in the present abundances and composition of organisms in real communities (Chesson and Case 1986).

As conditions change continually, organisms are constantly decaying with respect to current conditions. The fitness of all organisms is expected to decrease with changes. But some species may be impacted more than others. Some species are more tolerant of change than others due to physiological or other ecological characteristics. For example some species plastic than others, and can behaviorally differentiate their niche space in response to changes. Other species can track environmental change more effectively through evolutionary change. The real world is a Red Queen world. Species in a community always "run" to keep up with environmental and competitive change. Species are affected individualistically, but not independently. Community structure reflects the moment to moment fluctuation of the niche space of individual species about a drifting mean value that is punctuated by stochastic disturbances.

Community structure at any moment is a snap-shot of this process. Organisms do not anticipate the future, and prepare for coming changes. Nor are they the best they can be given current conditions. They never have time to fully adjust. They were simply good enough individually in the past to survive, reproduce and maintain membership in the pool of species persisting at this place at this time. At present, under current conditions, a species may be at equilibrium, expanding relative to competitors, or declining toward extinction. We can say little about their fitness, or the composition of the community, in the future unless we know how conditions will change over time and space and how each organism will respond.

2.5 Irony of the Red Queen

We can now justify the answers to the two questions posed above. The questions were: (1) does variability in space and time make the properties of communties unpredictable, and (2) if no equilibrium point exists, will community structure be dominated by chance and historical effects? We are clearly dealing with a vastly more complicated world than classical ecological theory assumes or is equipped to deal with. The answers are clearly yes. Community structures will always be unpredictable to a degree because individual species responses will be determined in part by unpredictable, chance events such as disturbance, colonization and predation. These chance events undoubtedly play a much larger role in community structure than has been previously believed (Kareiva 1989). The answer is also yes because of spatial complexity. Even holding the environment constant, spatial complexity of the environment can lead to apparently chaotic and unpredictable population dynamics of multi-species communities (e.g. Huffaker 1958; Kareiva 1987). Real environments vary dramatically at multiple spatial scales, and the challenge of sufficiently representing the spatial pattern of key limiting resources for multiple interaction species across spatial extents relevant for population processes is enormously daunting. Even should we be able to measure and quantify such patterns, linking them through mechanisms and responses to population dynamics is exceptionally difficult. The challenge is even greater when one considers the

interaction of variability in space with variability in time. We have argued that variability in either of these fundamentally alters outcomes in biological communities from the predictions of classical theory, and in many cases may make changes exceptionally difficult to predict and thus make current patterns exceptionally difficult to explain based on observed processes. In real biological communities, however, these two act in concert. Spatial patterns vary continuously at multiple scales, and temporal fluctuations occur across these complex landscapes continuously and at multiple scales. We believe the fundamental four-dimensional complexity of nature makes the future at any given location in space in large part unpredictable.

But in another sense the answer is no. Given any event, be it physical disturbance, directional environmental change, predation or colonization, the response of the community is the sum of the responses of the individuals of the individual species within it. These responses will be determined by the ways the events affect the resources and conditions within each species' fundamental niche, and how they affect their ability to maintain access to that niche space in the face of interactions with other species. Thus, if an event is known and its effects on each species across space are known, hen the response of the "community" can be determined. But, as conditions are changing continually through space and time, each moment and each location will yield different predictions about the future. With infinite knowledge of each location at all moments, and infinite knowledge about how these conditions will affect the interactions of individual organisms, it is in principle possible to predict future outcomes. This "in principle" possibility has been hopefully termed "Consilience" by Wilson (1998).

This digression has had a purpose. It takes us back to the thesis we laid out at the beginning of the chapter. The classical theories of ecology are based on equilibrium and non-spatial idealizations of systems and processes. The classical theory of community structure predicts that, given an initial set of potential members, the composition and structure of the community will tend toward equilibrium. A species excluded from all of its fundamental niche will be excluded from the community. Overtime, the community is expected to stabilize at a sort of "competitive climax". This is precisely what may be occurring everywhere, at every moment.

At any moment, within any unit of space, community structure will tend toward and equilibrium. But, it will rarely if ever get there. Chance disruptions of that trend will set it off on another course. Intermittent reversals of competitive advantage and transient most limiting factors will prevent progress toward equilibrium. Spatial variability in the environment will interact with these temporal fluctuations in complex ways. At any moment in any unit of space the observed trajectory of change is completely predictable, in principle. The classical theory is correct entirely in an ideal world, but almost always fails in real life. We believe we know the dominant mechanisms and processes. No new theory of cause and effect need be invoked. But we will always fail to understand the causes of current community structure and fail to predict future conditions because we can never know enough about how relationships in complex systems change over time. The mystery is dead; long live the mystery.

Is this a message of despair, or a message of inspiration? The reality of nature is marvelous and mysterious. We believe this abiding mystery is a source of inspiration.

Not in a mystical sense of worshiping an unknowable mystery, but in the sense of the challenge to understand, the mystery to be explored. There are several main messages that this chapter has been intended to evoke. First, idealized models often effectively describe the nature of important processes, but fail basically to predict how these processes act the context of a spatially and temporally complex world. Second, given the failure of such models, future progress in ecology we believe will focus on particulate and contextual analysis. As we discussed at the beginning of the chapter, we believe analysis will have to "step-into" spatial and temporal complexity, by applying process models to particulate reality, rather than globally. By particulate, we mean the interactions of particular individual organisms with the details of their particular environment. The second part of this "stepping-into spatial and temporal complexity is by conducting analysis contextually, by studying the interactions of particular organisms, in particular locations, at particular times. Third, in order for particulate and contextual analysis to be informative it must also be integrative, in a sense similar to the calculus. In calculus integration is the process of predicting the integrated response of continuous differential functions. In a similar way, in this view of ecology, integration will be a "stitching together" of a vast number of particulate and contextual pattern–process relationships across space and time. Many of these particulate relationships will act at multiple spatial scales, some of which will be continuous at fine spatial scales. Thus, conceptually this integration is much like calculus. The difference is that in calculus one is integrating an equation and seeking a closed form solution.

In ecology this will rarely be possible. In ecology, we will be integrating space–time processes continuously across space and time, where response and dependent variables both change both in value and in kind over space and time, and pattern–process relationships may change fundamentally as response and dependent variables change. One of the primary reasons for the popularity and influence of many classical non-dynamic theories in ecology is that they do provide tidy mathematical solutions. These tidy solutions may apply at fine spatial scales over short time periods in a spatially and temporally complex world. The challenge is integrating these across fundamentally nonstationary spatial and temporal domains. Thus, the fourth message we wish to evoke is the difficulty of achieving global prediction from closed-form equations. If ecological reality is particulate and contextual, and therefore nonstationary, it will generally be impossible to derive closed-form theory to make predictions across complex systems.

This therefore raises two critical themes which are twin backbones of this book. The first is the central and critical need for high quality *data* over *space* and through *time* on *environmental* conditions and *species* distribution, abundance, fitness, and behavior. If ideal theory will not provide reliable predictions, then we will have to rely on data to a much larger degree. In classical ecology, theory was supreme and data was secondary, in a sense, called upon mainly to parameterize and validate theory. Now, if integrating theory across particulate and contextual non-stationary space–time domains is found to be intractable, then data will be primary, with theory being applied locally and temporally, but relying explicitly on particulate and contextual data to be useful.

The second backbone is the ascending role of computational simulation. In the absence of closed-form solutions to theoretical models across particulate and contextual environments, simulation will be the primary tool to investigate complex ecological systems. Simulation does not require closed-form, global solutions or stationarity of space–time processes. The rise of powerful computing environments enables researchers to directly investigate the interaction of spatial complexity, temporal variability and population processes in particulate and in context. By coupling extensive spatial and temporal data collection to powerful spatial modeling environments it will be possible to integrate local and ephemeral dynamics across space and time (Cushman 2006).

Detailed, quality data gathered continuously through space and time and powerful, spatio-temporal simulation modeling are not alternative solutions to the problem of complexity in ecology. Rather they are complementary and mutually interdependent (Fig. 2.1). At the beginning of the chapter we asserted models without data are not compelling, while data without models are not informative. We can now further explain our meaning. Detailed, quality data on environmental conditions, and species distribution, abundance, and fitness can be used in statistical modeling to infer process from patterns. This is the meaning of the top left–right arrow in Fig. 2.1, namely that detailed spatial and temporal data on ecological systems is necessary to provide material to infer processes inductively from the data. The data alone, however, are not informative regarding process. Data alone is mere pattern. Statistical modeling seeks to link these patterns to potential explanatory processes (through the bottom left-right arrow). However, regardless of whether a refutationist, inferential analytical approach or a confirmationist, likelihood/Bayesian approach is used to infer this pattern–process linkage, there is an inevitable logical inconclusiveness. It is known as affirming the consequent through induction. The analysis evaluates the consistency of the data with one or many alternative explanations, or the likelihood of several explanations given the data. In either case, observing consistency of the pattern with an inferred process does not in any sense prove that causation. In the inferential case, the best we can do is fail to reject the hypothesis, which logically is entirely different than proving it. In the confirmationist case, the best we can do is rank the relative support of the alternative explanations, which inevitably are a vanishingly small fraction of possible alternatives. In either case asserting a proof of causality from an empirical correlation is an example of affirming the consequent through induction, in that any number of untested alternatives may exist, leading to a large probability of failing to evaluate the correct alternative in the confirmationist approach and the impossibility of rejecting all reasonable alternative hypotheses in the refutationist approach.

Conversely, through deduction we can go the other way, from process to pattern, from mechanism to response. This is the bottom right–left arrow in Fig. 2.1. In the context of this discussion, this is done through space–time simulation of ecological processes, given our expectation that ideal closed-form mathematical models will not apply to non-equilibrium and nonstationary ecological systems. In this effort, we design a space–time system consisting of entities located

in space, space characterized by one or several driving variables, and time. The simulation proposes a space–time process, a set of rules which govern the interaction of entities with each other as functions of distribution and density of entities of different kinds, their behavior, the structure of the environment and how these change over time. The simulation then allows the "actualization" of the proposed process through the execution of the process in particulate and contextually within the "world" represented by the simulation. We asserted that models without data are not compelling. Without realistic data on patterns and processes to develop a simulation model, it is extremely unlikely that it its results will have much kinship with reality. Further, without reliable data of the appropriate variables at appropriate scales in space and time it is not possible to evaluate the degree to which model results conform to actual patterns in the real world. For a model to be compelling it must simulate a reasonably meaningful system and produce results reasonably consistent with observations in the real world. However, as in the case of inferring process from pattern, there is an unavoidable logical inconclusiveness in using process to recreate observed patterns. It is called affirming the consequent through deduction. Proposing a process governing a system, simulating that process, and observing the results are consistent with the observed pattern does not prove that causation. The model evaluated a single or perhaps several alternative processes. Observing that one of these recreated a response pattern that is consistent with an empirical observation does not materially lessen the likelihood that there could be any number of other processes that could also recreate the pattern, leading to a large probability of failing to model the correct process.

We have argued that the particulate, contextual and nonstationary nature of ecological systems strongly invokes the need for quality spatial and temporal ecological data collection, and sophisticated space–time simulation approaches. However, it would appear that in the previous two paragraphs we have torn down inference from data and deduction from process as viable routes to reliable knowledge. Theories are always underdetermined by facts; facts never fully confirm a theory. Here is our main point regarding the interdependent role of inference from data and deduction from process. While it is never possible to avoid the logical risk of affirming the consequent in science, the combination of inference from data directly with deduction from process is a potentially powerful framework to greatly lessen the risk. Through the collection of large spatial and temporal samples of appropriate ecological data it is possible through both refutationist and confirmationist methods to identify plausible explanatory processes. In and of themselves, these are relatively weak logically due to affirming the consequent through induction, as discussed above. However, this hypothesized explanatory process then can be used as a starting point for simulation, in which the process is assumed and the model then recreates the pattern the data would have if the process were correct. As discussed above, this in and of itself is logically weak due to affirming the consequent through deduction. However, if the simulation based on an inferred process is able to recreate the pattern seen in the original data, there is much less likelihood that the explanation is an error of affirming the consequent.

Specifically, affirming the consequent through induction and affirming the consequent through deduction are independent errors, and therefore the chance of both errors occurring together, simultaneously with regard to a single pattern–process hypothesis is geometrically less than either alone. Thus, regarding induction from data and deduction from theory, both are necessary for reliable knowledge.

Thus, to summarize, we believe that spatial and temporal variability in ecological systems are not noise clouding ideal pattern–process relationships, but rather that they are fundamentally important to the processes themselves. Therefore, understanding ecological systems will require a reconceptualization of pattern–process relationships to focus on particulate interactions of organisms with their environments in the context of spatial location and temporal moment. This simultaneously will require a paradigm shift in the three areas of method, data and theory. First, we believe ideal theories will seldom be able to provide reliable predictions for large systems, and that pattern–process relationships will collapse down to local and ephemeral dynamics in space and time. Second, to address this will require development of new methodology. The recent explosion of computational technology, remote sensing, GIS, spatial statistics and space–time modeling have enabled rapid development of key components of this new methodology. Third, these advances have enabled vast improvements in our ability to collect, store, integrate and analyze large, fine-scaled spatial and temporal data on environmental patterns and organisms distribution, abundance and performance (Fig. 2.3). Finally, this feedback between method, data, and theory enables us to be hopeful that this a message of inspiration rather than despair; that this positive feedback between explosive progress in computing, computational simulation, remote sensing and other methodological advances, the extent, frequency and quality of data being collected and our ability to represent explanatory processes will enable rapid progress. We believe this progress will be built on a conception of logical linkage between inferring process from data, and then recreating data patterns from process, and involve the application of ecological theory in particulate and contextual context, at the level of the interactions of individual organisms with each other and their physical environment, integrated across heterogeneous space and over temporally dynamic time.

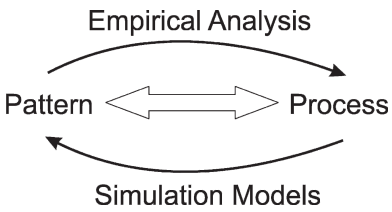

Fig. 2.3 Feedback between theoretical models and empirical data collection and analysis. Empirical analysis is used to infer process from patterns observed in data. Theoretical and process models are used to evaluate the ability of the inferred process to create the observed pattern. The feedback between these two enables much stronger inferences about pattern–process relationships than either alone and markedly reduces the severity of risk of affirming the consequent

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