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Jianguo Wu*

Department of Ecology & Evolutionary Biology
Princeton University
Princeton, NJ 08544
and
Center for Theory and Simulation
Cornell University
Ithaca, NY 14853

EMAIL: WU@ENO.PRINCETON.EDU
OR: JWU@MAXEY.UNR.EDU

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* Current address: Biological Sciences Center, Desert Research Institute, University of Nevada System, Reno, NV 89506-0220. (702) 673-7419 (o) (702) 673-7397 (fax) jwu@maxey.unr.edu

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Jianguo Wu[†]

Department of Ecology & Evolutionary Biology, Princeton University, Princeton, NJ 08544
and
Center for Theory and Simulation, Cornell University, Ithaca, NY 14853

ABSTRACT

The only thing about Nature that is certain and absolute is patchiness in space and time. All landscapes are patchy over a range of scales as consequences of natural and anthropogenic processes. To understand the dynamics of hierarchically structured, heterogeneous systems, models are important in several ways. Models can be used to generate new hypotheses, to clarify and test existing hypotheses, to identify key components in complex systems, to suggest critical experiments, to synthesize knowledge, and to make assessments or predictions for the purpose of decision making.

Most traditional paradigms in ecology deemphasize or completely ignore spatial patchiness in ecological systems. As an emerging integrative paradigm, patch dynamics emphasizes spatial heterogeneity and multiplicity of scales and provides a conceptual framework for linking metapopulation theory, landscape ecology and conservation biology. Metapopulation dynamics lays a cornerstone for landscape ecology which in turn offers knowledge about the context in which the behavior of metapopulations must be understood. Conservation biology may guide the development of metapopulation theory and landscape ecology by posing real-world problems concerning the sustainability of ecological systems and the human society. On the other hand, metapopulation theory and landscape ecology will continue to provide fundamental theoretical elements and applicable approaches for conservation biology.

Key words: pattern and process, patchiness, patch dynamics paradigm, landscape ecology, metapopulation theory, conservation biology

[†]Dr. Jianguo Wu is Oversea Guest Associate Professor at the Department of Systems Ecology, Chinese Academy of Sciences, Beijing, and is currently Assistant Research Professor at Biological Sciences Center, Desert Research Institute, University of Nevada System, Reno, NV 89506-0220.

INTRODUCTION

The interrelationship between spatial pattern and ecological process is a central issue in ecology in general and in landscape ecology in particular. Studying ecological process in its context and searching for pattern based on understanding of ecological process has gained an unprecedented momentum in recent years. The word "pattern" here means the spatial arrangement or configuration of landscape elements, whereas "process" refers to a series of actions or operations towards a specific result. Ecological processes include population growth, foraging patterns, dispersal, competition, predator-prey interactions, plant succession, spread of disturbance, nutrient dynamics, etc. Process modifies existing pattern and creates new pattern; pattern enhances or constrains ecological processes. Because of the dual relationship, ecologists must link pattern and process in their theoretical and applied endeavors in order to adequately understand and properly manage ecological systems.

The most salient spatial feature of ecological systems is patchiness. Landscapes are mosaics of patches that differ in size, boundary condition, content, and successional age. Biotic and abiotic processes in landscapes take place across a range of spatial, temporal and organizational scales. Therefore, a scaling and hierarchical perspective must be emphasized in studying dynamics and persistence of biological diversity. This also entails the integration of metapopulation theory, landscape ecology and conservation biology. Indeed, these three emerging fields are forming an exciting and fruitful trio in ecology. This integration requires development of new theories and new methodologies and approaches. While field observation and experimental studies are always crucial, modeling is an indispensable tool to integrate ecological processes across spatiotemporal domains and to bridge different disciplines.

There are three types of landscape models: whole landscape models, distributional models and spatially explicit models based on the levels of aggregation (Baker, 1989; Wu, 1993). Whole landscape models use highly aggregated variables to model landscape phenomena as a whole, concentrating on the value of each variable (e.g., the total number of structural or functional elements or the total species richness of a particular landscape). These models are of limited use due to their inability to provide information specific enough for much landscape research. Most landscape models are of the distributional type, which have many varieties in terms of modeling philosophies, mathematical approaches and degrees of detail. These models focus on the distribution of values of each variable among different categories of landscape components (e.g., the distribution of land area or species richness among landscape elements). The least aggregated and most detailed landscape models are spatial models, which explicitly incorporate information on location and configuration of landscape elements and, therefore, are in principle able to answer specific questions about a particular landscape. However, spatial models are still in their early stage of development and have been delayed by lack of data and understanding of landscape processes and computational limitations (Baker, 1989; Wu, 1993).

In this paper, I shall briefly discuss some aspects in which theory and models can play an important role, then elaborate on the ubiquitousness of patchiness in ecological systems and, afterwards, introduce the emerging patch dynamics paradigm in modeling fragmented landscapes. Finally, I shall explore the necessity and possibility of integrating metapopulation theory, landscape ecology and conservation biology, and try to shed some light on the conceptual and modeling linkages among these three fields.

MODELING AS AN INDISPENSABLE TOOL IN ECOLOGY

A model may be simply defined as an abstraction and, therefore, necessarily a simplification of reality. Models are the basic units of theoretical investigation (Levins,

1968). They are as necessary "to theoretical problems as experiments are to empirical problems" (Caswell, 1988). They are indispensable to our understanding of ecological systems and, in fact, our conception of nature is virtually a model of it. The pathway to understanding complex systems is simplification, i.e., separation of signal from noise. Models can be qualitative (expressed in words or diagrams) or quantitative (expressed in mathematical equations or computer languages). The latter are called formal models, and this discussion is restricted to such models. Although it may take many forms other than the mathematical, much of ecological theory today is expressed in largely mathematical terms because mathematics provides ecologists the most precise language to describe complex phenomena and is also an ideal tool for prediction (Roughgarden et al., 1989). Indeed, mathematical formulations usually force us to make the assumptions and conclusions clear and unambiguous.

There are two major types of quantitative ecological models: analytical models and simulation models, each of which uses quite different mathematical methods. The analytical modeling approach is characterized by finding exact solutions to a set of mathematical equations with relatively complex mathematics. It is usually feasible only for systems that can be described in a few variables with mostly linear relationships. This approach has been heavily employed in population ecology and population genetics for decades. The simulation modeling approach, on the other hand, is characterized by dependence on computers and providing numerical rather than analytical solutions to a large system of equations. Simulation models are able to deal with complex ecological systems that may contain many variables and highly nonlinear relationships with the aid of high speed computers. Because ecological systems are, in general, inherently more complex than physical systems, the simulation modeling approach is frequently found more suitable for many practical and theoretical studies in ecology (Hall and DeAngelis, 1985; Loucks, 1985, 1986).

The roles of mathematical models in ecology include generating and testing hypotheses, predicting the dynamics of complex systems, synthesizing knowledge and ideas, and serving as a powerful tool for assessment and optimization (Levin, 1981; Caswell, 1988; Fahrig, 1988; Hall, 1988a,b; Onstad, 1988; Roughgarden et al., 1989). Generating hypotheses is one of the most important uses of ecological models (Hall and Day, 1977). The well-known experiment by the Russian ecologist Georgii F. Gause (1934), which led to the principle of competitive exclusion, was inspired by the Lotka-Volterra model (Levin, 1981). There have been many instances in ecology where models suggest protocols for observations and experiments in both the field and the laboratory. As an example, MacArthur and Wilson's dynamic equilibrium model of island biogeography has inspired numerous field observations and manipulative experiments in the studies of biogeography and ecology (Wu, 1989, 1990; Wu and Vankat, 1991a, 1994). Also, Lindeman's (1942) trophic-dynamic model has had profound influence on the development of ecosystem ecology and systems ecology. Models become inevitable when we deal with both spatial and temporal dynamics of systems simultaneously and when the scale (spatial and/or temporal) of the phenomenon is very large. The rapid development of computer simulation modeling has greatly enhanced our understanding of nature and effects of human interventions and holds the promise to unify ecological theory (e.g., Meadow et al., 1972; Huston et al., 1988). Current understanding of global environmental issues such as acid precipitation and the greenhouse effect depends largely on modeling efforts (e.g., Armentano et al., 1984; NAPAP, 1990).

The development of ecological theory and modeling may be greatly promoted by intercommunication between the theorist and the empiricist, although too often has this been an overlooked in ecology. Levin (1981) asserted that theoretical ecology and empirical ecology draw strength and inspiration from each other, but develop with some degree of independence. Theoretical investigation and observation should be considered

equally important as intellectual exercises (Levin, 1981; Caswell, 1988), but the bridges between them are imperative for either of them to be fruitful.

Modeling philosophy often plays an important role in the modeler's system conceptualization and thus model construction. While the reductionistic approach seems to be dominant in recent ecological studies, the holistic approach also has wide acceptance, especially in the context of systems ecology. In many cases it is almost impossible, and not necessary, to make a clear-cut distinction between reductionism and holism. Researchers are more holist when emphasizing the integrity or emergent properties of a system, but more reductionist while trying to give mechanistic explanations for the consequence of interactions among system components (O'Neill et al., 1986). Attempts to explain community or ecosystem phenomena in terms of populations without consideration of system integrity at higher levels represent inappropriate reductionism. On the other hand, studies focusing only on emergent properties without mechanistic interactions at lower levels can have only limited insights. It should be desirable to integrate Gleasonian individualistic-reductionistic views and Margalef-Odum functional-holistic views by adopting hierarchy theory (Allen and Starr, 1982; O'Neill et al., 1986; Wu, 1991a).

The two approaches are not contrary, but complementary. The reductionistic approach favors case-specific mechanistic studies and inductive reasoning while the holistic one tends to lend itself to developing comprehensive views and generalizations of systems using a deductive methodology. On one hand, an inductive method usually formulates generalities based heavily on observations and empirical data; on the other hand, the deductive approach typically involves testing of hypotheses under an array of specific conditions. To a great extent, bottom-up approaches are inspired by reductionism, whereas top-down approaches are more consistent with the holistic philosophy. Generalization is important in both inductive and deductive methods. It is generalizations that bring order of some sort to an otherwise seemingly disorderly world, though they can never account for all the details in Nature. A good modeling philosophy should take into account the significant contributions of both reductionistic and holistic perspectives to understanding the overall functioning and dynamic behavior of systems.

A PATCH DYNAMICS MODELING PARADIGM

Patchiness and Patch Dynamics

Fragmentation of vegetation brought about by increased human activities has become an omnipresent phenomenon. Most conspicuously, contiguously forested landscapes have been broken up into isolated forest patches or habitat islands (e.g., Curtis, 1956; Burgess and Sharpe, 1981; Harris, 1984; Wilcove et al., 1986). Many species, especially rare and habitat-sensitive species, are jeopardized by the increasing insularization of natural landscapes. For example, Diamond (1984) estimated that there was a yearly loss of 1-30% of the bird species in oceanic islands and tropical forest fragments. To quote Wilcox and Murphy (1985), "habitat fragmentation is the most serious threat to biological diversity and is the primary cause of the present extinction crisis".

Actually, patchiness is ubiquitous in nature due to both natural and anthropogenic forces, occurring in both terrestrial and aquatic ecological systems across all spatio-temporal scales. Patchiness refers to the spatial pattern of patches and/or the variability in such spatial pattern in terms of patch content, size, size distribution, density, diversity, juxtaposition, and structural and boundary characteristics. Physical and biological patchiness are most likely to be interactive and interwoven across scales.

Patch dynamics refers to (1) the temporal change in spatial pattern and variability resulting from within-patch turnover and interpatch interactions, i.e., change in patchiness in time; (2) The field of study of the spatial pattern, formation, evolution, and decay of patches, as well as mechanisms and consequences of patchiness; and (3) An emerging ecological paradigm that emphasizes spatio-temporal heterogeneity, non-equilibrium properties, and hierarchical nature of ecological systems (see Wu et al., 1992; Levin et al., 1993). The patch dynamics paradigm focuses on the coupling of pattern and process at different scales, offering a promising approach to the bridging of the conceptual and methodological gaps between terrestrial and marine ecology and between micro- and macro-ecology.

The Theory of Island Biogeography -- The Beginning of a Patch Dynamics Paradigm

MacArthur and Wilson (1967) theorized that the number of species on an island is primarily determined by two processes: immigration and extinction. If there are a limited number of empty niches or habitats available on an island, the more species already there, the less likely a successful immigration of a new species and the more likely an extinction of a species already present. For a given area and degree of isolation, immigration and extinction rates are expected to monotonically decrease and increase, respectively, as the number of established species increases. For a given number of species, the immigration rate decreases with distance from the source of colonizing species because species have different dispersal abilities -- this is called the "distance effect." On the other hand, the extinction rate will decrease with island area because the larger the area, the larger the species' populations and thus the smaller the probability of extinction -- this is referred to as the "area effect." When the rates of immigration and extinction are equal, the island's biota is at a state of dynamic equilibrium, i.e., the number of species remains relatively constant while a compositional change of species continues. These changes in species composition result from concurrent extinction of existing species and replacement by immigration of new species and are termed "species turnover." The rate of change in species composition is termed turnover rate. The mathematical description of the MacArthur-Wilson model takes the following general form:

$$\frac{dS(t)}{dt} = I - E \quad (1)$$

where S is the species diversity (richness in particular), I is the immigration rate, and E is the extinction rate.

The theory of island biogeography (MacArthur and Wilson, 1967; Wu, 1989; Wu and Vankat, 1991b, 1994) has been a conceptual framework for much of the study concerning impacts of fragmentation on biological diversity in particular and conservation biology in general (e.g., Diamond, 1975; Wilson and Willis, 1975; Diamond and May, 1976; Simberloff and Abele, 1976a,b, 1982; Pickett and Thompson, 1978; Burgess and Sharpe, 1981; Gilpin and Diamond, 1981; Harris, 1984; Lovejoy, 1984; McLellan et al., 1986; Wu and Vankat, 1991a). The theory has been applied to the issue of optimizing the size of habitat islands to maximize species diversity. A key aspect of heated debate was whether a single large or several small reserves (SLOSS) would better protect species diversity (Diamond, 1976; Simberloff and Abele, 1976a,b, 1982; Terborgh, 1976; Whitcomb et al., 1976; Gilpin and Diamond, 1980; Higgs and Usher, 1980; Cole, 1981; Simberloff, 1983; Soule and Simberloff, 1986; Wu, 1989, 1990). While the question is significant, the debate oversimplified the problem and deemphasized such crucial aspects as minimum critical area and dynamics of species

extinctions (Cole, 1981; Wilcox and Murphy, 1985; Soule and Simberloff, 1986; Burgman et al., 1988).

Upon reviewing existing models in island biogeography, population dynamics, and population genetics, Burgman et al. (1988) asserted that because the MacArthur-Wilson model centers on species richness only and overaggregates many causal factors into the two variables of area and degree of isolation, it provides little insight on the mechanism of population dynamics and extinctions in fragmented habitats over a landscape. Pickett and Thompson (1978) emphasized that species extinction is more important than species immigration as a population process in such habitat islands as nature reserves. They thus proposed the concept "minimum dynamic area" (the minimum area which insures internal recolonization sources despite the effect of natural disturbance) as a strategy for conservation practice. Although the MacArthur and Wilson's dynamic equilibrium theory has been one of the most influential concepts in biogeography, ecology, and evolutionary biology, several aspects of the equilibrium theory remain unsubstantiated, and, while it appears to hold in some specific cases, it does not in many others. Uncritical application of the theory to nature conservation is unwarranted and may lead to misleading conclusions.

Nevertheless, the criticism does not negate the value of the theory of island biogeography. Qualitative use of the theory can result in valuable contributions to studies even when its quantitative application may be invalid. More specifically, the theory was and still is important in guiding scientists in constructing conceptual frameworks for addressing relevant questions in which patchiness and isolation otherwise may not have been sufficiently emphasized or even identified. In fact, as indicated in the preface of their book, even MacArthur and Wilson did not believe that the equilibrium model would exactly fit all field observations; instead, they hoped that the theory would provide stimulus and impetus for advancing "new forms of theoretical and empirical studies." In this regard, the equilibrium theory of island biogeography is one of the most successful theoretical developments in the history of biogeography and ecological science.

Population Viability Analysis and Metapopulation Modeling

Shaffer (1981) proposed a comprehensive review on species persistence and extinction in terms of "minimum viable populations" (MVP), a concept which had been used previously (Allee et al., 1949) but had not attracted much attention. His quantitative definition of MVP was "the smallest isolated population having a 99% chance of remaining extant for 1000 years despite the foreseeable effects of demographic, environmental, and genetic stochasticity, and natural catastrophes." The MVP concept connecting a population's size with its probability of extinction has become popular in the studies of persistence of isolated populations (e.g., Leigh, 1981; Shaffer, 1981, 1983; Schonewald-Cox et al., 1983; Shaffer and Samson, 1985; Gilpin and Soule, 1986; Soule, 1987; Simberloff, 1988; Thomas, 1990).

The MVP concept implies that there exists "some threshold size for a given population or some multivariate set of thresholds", above which the population will persist within an acceptable risk level for a given time period (Gilpin and Soule, 1986; see also Shaffer, 1981 and Burgman et al., 1988). The process of estimating minimum viable populations has been termed as "population vulnerability analysis" or "population viability analysis" (PVA) and a comprehensive conceptual framework has also been proposed (Gilpin and Soule, 1986; Gilpin, 1987; Shaffer, 1990). Although the term itself is somewhat controversial (Soule, 1987), the MVP idea has permeated much of the work in conservation biology and provided significant insights into the dynamics of isolated populations.

All species live in patchy environments. A metapopulation is a system of local populations in spatially discrete habitat patches separated by unsuitable environment and functionally connected by dispersal fluxes. The term metapopulation, describing “a population of populations,” was first coined by Levins (1970) in a now-classical paper on group selection and extinction, although the idea that spatially heterogeneous populations experience local extinctions and recolonizations had been expressed in the context of population genetics (Wright, 1940), population dynamics (Andrewartha and Birch, 1954), and species diversity in isolated habitat patches (MacArthur and Wilson, 1963, 1967).

Three spatial scales may be involved in metapopulation dynamics: local, landscape (metapopulation), and geographical scales (Hanski and Gilpin, 1991). The interactions among individuals are high at the local scale (within a habitat patch), are relatively frequent among subpopulations of the same metapopulation at the landscape scale, and are typically negligible among different metapopulations at the biogeographical scale. Because spatial patchiness is also manifested at smaller scales than the local population, Hanski and Gilpin (1991) usefully distinguished between the dynamics of aggregated populations and metapopulations, although parallels may exist for many processes. As they pointed out, there exists a common dispersal pool in each generation for an aggregated population, but not for a metapopulation with a hierarchical population structure.

Two prominent driving-force processes of metapopulation dynamics are local population turnover and interpatch colonization. The dynamics of individual subpopulations and the interactions among them necessarily result in a shifting distribution pattern of populations over a landscape. Hanski (1991) identified the three elements required for metapopulation persistence: asynchronous dynamics of subpopulations, interpatch dispersal, and density-dependent regulation of subpopulation dynamics. These mechanisms may differ greatly in their degree of importance in maintaining system stability of different metapopulations.

Much of the current understanding of metapopulation dynamics is based on mathematical modeling work, though an increasing number of field observational (e.g. Dickman, 1987; Quinn and Harrison, 1987; Harrison et al., 1988) and experimental studies (e.g., Lovejoy et al., 1984; Kareiva, 1987; Robinson and Quinn, 1988; Holt and Gaines, 1993) have been conducted. Levins (1969, 1970) initiated the patch-occupancy modeling approach, which has served as a fundamentally important conceptual framework for metapopulation studies. Mathematically sophisticated, structured metapopulation dynamics models, which explicitly describe changes in within-patch population sizes, have recently been developed (Hastings and Wolin, 1989; Hastings, 1991). A rapidly increasing number of metapopulation studies involves not only single-species metapopulations, but also multi-species metapopulations such as predator-prey, host-parasitoid, and interspecific competition patchy systems (e.g., Hanski, 1983; Murdoch et al., 1985; Gilpin and Hanski, 1991; Wu and Levin, 1993). The term metacommunity has been introduced to describe a community of metapopulations, i.e., an assembly of habitat patches shared by two or more species (Hanski and Gilpin, 1991).

“Modeling populations of plants and animals presents a greater challenge than finding good representations of molecular behavior” (Roberts, 1978). Models of population dynamics in heterogeneous environments have been developed during the past two decades. Most of them fall into two distinctive categories: patch-occupancy and diffusion-reaction models (Levin, 1976, 1978; DeAngelis et al., 1986). Patch-occupancy models deal with a large number of patches and involve both single-species dynamics and multi-species coexistence (e.g., interspecific competition and predator-prey interactions). The state variables are usually the proportions of patches occupied and unoccupied by one or more species. A simple and widely used patch-occupancy model is Levins’ (1969, 1970) original model which describes the dynamics of a single

species metapopulation in a heterogeneous environment composed of homogeneous (identical) patches:

$$\begin{aligned}\frac{dp}{dt} &= mp(1-p) - ep \\ &= (m-e)p\left(1 - \frac{mp}{m-e}\right)\end{aligned}\quad (2)$$

where p is the proportion of patches occupied by the species and m and e are constants that are related to the colonizing ability and extinction rate of the species, respectively. Patch-occupancy models have been widely used in studies on the dynamics of patchy populations (e.g., Levins, 1970; Levins and Culver, 1971; Hanski, 1983, 1991).

The framework of the diffusion-reaction models takes the following general form:

$$\begin{aligned}\frac{dY_i^u}{dt} &= f_i^u(Y^u, X^u) + (\text{net exchange with other patches}) \\ &\quad + (\text{net exchange with matrix})\end{aligned}\quad (3)$$

in which Y^u is the vector $(Y_1^u, Y_2^u, \dots, Y_n^u)$ of state variables for a given patch u , X^u the vector $(X_1^u, X_2^u, \dots, X_n^u)$ of parameters accounting for the same patch, and f^u the specific functional relationship (Levin, 1976; Okubo, 1980). These models take into account both temporal and spatial heterogeneity for given state variables, such as population densities, with the aid of the analytical power of mathematical diffusion theory. These models can further be divided into continuous and discrete types according to their different conceptualization and mathematical details. A simple, yet representative, example of the continuous diffusion-reaction model may be in the partial differential equation form of

$$\frac{N(x,t)}{t} = Nf(N) + \frac{[D \ N(x,t)]}{x^2}\quad (4)$$

where $N(x,t)$ is the population density relative to the spatial position x , D is the diffusion rate of individuals of the population, and $f(N)$ is the population growth rate (Hastings, 1990). The corresponding discrete model may be written as

$$\frac{dN_i}{dt} = N_i f(N_i) + \sum_j d_{ij} (N_j - N_i)\quad (5)$$

where d_{ij} is the exchange rate of individuals between patch i and patch j , and N_i and N_j are population sizes in the two patches, respectively (cf. Levin, 1974). Patch-occupancy and diffusion-reaction models have made significant contributions to our current understanding of patch dynamics from a population perspective.

Population models incorporating spatial extent and heterogeneity seem to show that populations that are transient in a small patch might persist over a landscape with interacting patches through dispersal and risk-spreading (see DeAngelis and Waterhouse, 1987 and Wu and Loucks, 1992 for reviews). These models have been developed mainly for theoretical considerations of species competition or prey-predator coexistence. The traditional equilibrium view of ecological systems, based on the premise that a balance of nature exists, has been challenged and de-emphasized since the

1970s, and this transition from equilibrium to non-equilibrium perspective has been reflected in modeling efforts in ecology.

Most of the models concerning population dynamics in heterogeneous environments are of the analytical type. However, because of overwhelming mathematical details, it is often extremely difficult to build comprehensive realistic models with the analytical approach without making too many oversimplifying assumptions. In this regard, their applications are substantially limited. The simulation approach, on the other hand, can more easily handle a large number of variables and their interactions by taking advantage of computers; therefore, it is usually more suitable for modeling complex systems. Simulation models of ecological systems have a voluminous literature covering great variations in details of modeling methodology and philosophy (Wu, 1991b). Nevertheless, realistic comprehensive population models are urgently needed in order to achieve a complete and insightful understanding of population persistence and species extinctions over fragmented landscapes. Although some work has been done (e.g., see DeAngelis et al., 1986), it is still a great challenge to develop a comprehensive population dynamics model which integrates knowledge from island biogeographic theory, population vulnerability analysis, and landscape ecology.

A Patch Dynamics Approach to Spatial Modeling

A landscape may be viewed as a hierarchical mosaic system of patches that are different in their age, size, shape, content and other aspects. The spatial variability of the patch mosaic results in the landscape pattern, whereas the phase change of individual patches at the local scale and temporal change in patch mosaics at larger scales give rise to the landscape dynamics. This view holds for many, if not most, terrestrial ecosystems simply because disturbances at different spatial and temporal scales are general phenomena which significantly structure a variety of biological communities. With enormously increasing awareness of and research emphasis on spatial heterogeneity, the study of patchiness and patch dynamics is becoming a major theme in both marine and terrestrial ecology (e.g., Pickett and White, 1985; Wu et al., 1992; Levin et al., 1993; Wu and Levin, 1993).

The conceptualization of ecological systems as mosaics of patches is evident in several theoretical and empirical works. A classic masterpiece of this sort is the "pattern-process hypothesis" by A. S. Watt (1947), which emerged from his study on plant community structure and dynamics. Levin and Paine (1974, 1975, Paine and Levin 1981) developed a mathematical description of the pattern and dynamics of an intertidal landscape, consisting of a system of partial differential equations. Other outstanding examples include the patch mosaic dynamics perspective by Whittaker and Levin (1977), the "shifting mosaic steady state" hypothesis by Bormann and Likens (1979), and also the patch dynamics perspective in community ecology exemplified by the work of Pickett and others (e.g., Pickett and Thompson 1978, Loucks et al. 1985, Pickett and White 1985, White 1987). Patch dynamics is also conceptually linked with metapopulation theory (Levins 1970, Gilpin and Hanski 1991, Wu et al. 1990, 1993). The wave-form dynamic hypothesis put forward by Loucks' (1970) is an excellent parallel patch dynamic example from a temporal perspective. While the physical or biological meaning of a patch may vary substantially across biological systems, the effect of spatial patchiness on pattern and process in marine ecosystems has long been recognized (see Hutchinson 1953, Steele 1978). In addition, patch dynamics as a conceptual framework has been central to landscape ecology in theory and practice since the emergence of landscape ecology in North America (Forman 1981, Forman and Godron 1986, Vankat et al. 1991).

While the patch dynamics perspective has provided insights into ecological studies at population, community and landscape levels, a great challenge is to apply it to develop quantitative and predictive models. In fact, the patch dynamics conceptualization has been inspirational to the development of models that are different from traditional population or ecosystem counterparts. Levin and Paine (1974) first constructed a quasi-spatial patch demographic model to characterize and predict the dynamics of distribution pattern of an age- and size-structured patch population on an intertidal landscape. Clark (1991a,b) and Kohyama (1993) developed quasi-spatial patch models to couple the disturbance patch demography with tree species population dynamics on a shifting mosaic landscape. These above-mentioned models all ignore the spatial locations and overlaps of patches. The quasi-spatial patch models also include a group of computer models of forest dynamics, which have been called gap simulation models (see Shugart 1984). Recently, spatially explicit gap models have also been developed based on gap modeling principles (e.g., Smith and Urban 1988, Coffin and Lauenroth 1989). These models take a grid-based approach in which patches are considered as single grid cells or aggregates of multiple cells within a regularly divided grid. Therefore, the boundaries of grid cells in these models are, to large extent, arbitrary and carry no biological meaning. Also, these models may become inadequate and impractical when overlapping among patches is common and complex, which is often the case in many ecological systems.

Inspired by the earlier work on patch dynamics, Wu and Levin (1993) have developed a spatially explicit patch dynamics modeling approach, based on a serpentine grassland in the Jasper Ridge Biological Preserve of Stanford University. The spatial patch dynamics approach has several unique features. In contrast with raster- or grid-based approaches, the boundaries of patches using this approach are ecologically definable. The approach naturally fits the patch dynamics conceptualization of ecological systems, and transforms it from a qualitative description into a quantitative and predictive model. Unlike in the grid-based modeling approaches where patches are single or multiple non-overlapping cells, this patch-based modeling approach treats patches as individual objects changing continuously in size and spatial location. The approach more realistically deals with complex overlaps in a mosaic of patches of different age and size.

Wu and Levin's (1993) model consists primarily of two modules: a spatially explicit disturbance patch demographic model and a spatially explicit, multispecific, patch-based population dynamic model. The parallel formulation of the patch population model and species population model facilitates the study of the dynamics and spatial pattern of both the gopher mound and plant populations. This also makes the modeling framework suitable for studying a range of problems, ranging from population dynamics in a fragmented environment where patches are habitats, to plant-parasite and plant-insect interactions where patches are individual plants. In general, the spatial patch dynamics modeling approach can be used as a general modeling platform for studying pattern and process dynamics at local and landscape scales, to examine the spatio-temporal patterns of the age- and size-structured patch populations, and to examine how local processes affect landscape pattern.

INTEGRATING METAPOPOPULATION THEORY, LANDSCAPE ECOLOGY, AND CONSERVATION BIOLOGY

There has been increasing awareness of the importance of integrating the emerging fields of metapopulation dynamics, landscape ecology, and conservation biology. Although the idea of spatially structured populations dates back to Wright's seminal work on population genetics in the early 1940s, it was not until the late 1980s that the concept of metapopulation was rediscovered and spurred greatly by interests in

population dynamics in heterogeneous environments, conservation biology, and landscape ecology (e.g., Quinn and Hastings, 1987; Opdam, 1988, 1991; Harrison et al., 1988; Merriam, 1988; Hanski, 1989; Harrison and Quinn, 1989; Hastings and Wolin, 1989; Gilpin, 1990; Wu et al., 1990, 1993; Gilpin and Hanski, 1991; Merriam et al., 1991). On the other hand, landscape ecology and conservation biology have been greatly enriched in both theory and practice by the rapid development in metapopulation theory.

The interactions between patches in a fragmented landscape may play an important role in the dynamics and persistence of metapopulations. The persistence of species may be related to matrix characteristics and the number, area, spatial arrangement, and disturbance regime of patches. These subject matters are also central concerns of the emerging field of landscape ecology (Forman, 1981, Forman and Godron, 1981, 1984, 1986; Urban et al., 1987; Vankat et al., 1991) and conservation biology (Soule, 1986, 1987; Wu, 1992). A landscape approach is needed to understand population persistence over a landscape and to protect both species and landscape diversity (e.g., Romme and Knight, 1982; Noss, 1983, 1987; White, 1987; Vankat et al., 1991). On the other hand, metapopulation dynamics may, to large extent, affect or determine the spatial-temporal heterogeneity and pattern-process relationships of landscapes.

The metapopulation dynamics paradigm resembles the MacArthur-Wilson model of island biogeography in that extinction and colonization are the key processes in both of them (Hanski and Gilpin, 1991). However, there is a permanent mainland source of colonists in the MacArthur-Wilson model, whereas colonization in metapopulation dynamics usually takes place among subpopulations, all of which may be subject to local extinction. Also, the state variable in the MacArthur-Wilson model is species diversity, but population size or the fraction of patches occupied by the species of interest is used in metapopulation models. Nevertheless, Hanski and Gilpin (1991) showed that the Levins' model and the MacArthur-Wilson model represent the two extremes of a continuum of metapopulation structures, i.e., a system composed of same-sized small patches vs. a patch system with at least one large patch functioning as a mainland. They believed that most metapopulations would exhibit behavior intermediate between what these two models predict.

Landscape ecology emphasizes the development and dynamics of spatial-temporal heterogeneity and their influences on biotic and abiotic processes of landscapes (Risser et al., 1984; Forman and Godron, 1986; Turner and Gardner, 1991). Recent theoretical studies in landscape ecology have a focus on the relationships between spatial and temporal patterns and underlying processes (Turner and Gardner, 1991). The metapopulation dynamics paradigm relates population processes to spatial landscape characteristics and is becoming an integral part of landscape ecology (see Merriam et al., 1991 and Opdam, 1991). While holistic and hierarchical perspectives are dominant in landscape ecology, metapopulation studies have primarily taken a deductive approach with heavy use of mathematical models. The integration of landscape ecology with the metapopulation dynamics approach should produce a fruitful and exciting scientific synthesis (Hanski and Gilpin, 1991).

Conservation biology is the core discipline of the science of nature conservation (Wu, 1992). It is a highly synthetic, transdisciplinary subject that is concerned with both present crisis and long-term viability of species, communities, and ecosystems (Soule, 1985). The theory of island biogeography was a main focus in the early development of nature conservation science and has made significant contributions to the formation of conservation biology (Simberloff, 1988; Brussard, 1991; Wu, 1990, 1992). Recent conservation biology studies have focused intensively on population viability analysis, advocating the idea of minimum viable population size. Also, the metapopulation perspective has been well received, as habitat fragmentation and reserve design are of primary concerns in conservation biology (Simberloff, 1988; Soule, 1987; Wu, 1992). The integration of PVA with metapopulation dynamics is desirable

and necessary in both theory and practice. While many recent metapopulation studies have been motivated and inspired by conservation biology, their results have in turn enriched conservation biology. Certainly, this will continue to be the case in future.

Metapopulation theory, landscape ecology and conservation biology are forming a new trio in ecology. Their developments are interactive, interdependent and complementary. While metapopulation dynamics are crucial to landscape pattern and process, a genuine understanding of the dynamics and persistence of fragmented populations in the patchy world must go beyond what a population-centered approach can possibly offer. Landscape ecology represents not only an emerging field, but also a new perspective that emphasizes patchiness and multiplicity of scales. This perspective can shed much light on issues in metapopulation dynamics and conservation biology. Knowledge from metapopulation theory and landscape ecology provides an important theoretical basis and practical guidelines for nature conservation and environmental protection, whereas conservation biology can certainly help stimulate and promote a healthy development in the other two areas. The patch dynamics modeling paradigm provides a promising framework to link the three emerging fields, and will hopefully make the emerging trio sound more accordant and robust at an even higher tempo.

CONCLUDING REMARKS

Like many other species, we human beings are living in a dangerously fragmented, patchy environment. To understand how ecological systems really work and to develop sustainable landscapes, we must take into account the spatial and temporal patchiness and the multiplicity of scales in ecological systems. In response to this need, a patch dynamics paradigm has been emerging. We need to move beyond the traditional dogmas and metaphors like "superorganisms," "balance of nature," and "Nature knows best." New concepts, theories and paradigms are needed to enrich the state-of-the-science of ecology. To protect our biological diversity and environment, we need to integrate knowledge across different disciplines as well as across a range of spatiotemporal scales. Among others, metapopulation theory, landscape ecology and conservation biology provide a fundamental basis for building a sustainable society. Interaction and integration among these disciplines are crucial and, indeed, such integrations among different fields have just begun, with marked efforts in dealing with regional and global environmental issues such as deforestation, nature conservation, and climate change and its biological consequences. While field observation and experimental approaches are always critically important, modeling has been and will continue to be an essential tool, especially for understanding and predicting large-scale, spatiotemporal dynamics of ecological systems.

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