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〈Review Paper〉

Heterogeneous Habitat for Increasing Biological Diversity

Sang Don Lee

Department of Environmental Science and Engineering, College of Engineering, Ewha Womans University, Seoul 120-750, Korea

Abstract - Habitat heterogeneity can enhance biological diversity by providing variation in structural diversity. This paper reviewed heterogeneous habitat serves as a population stability and superior demographic performance (e.g., high density, survivorship, reproductive rate) can be observed compared with organisms with inferior demographic performance. The idea of habitat variation has been further developed in modelling. Furthermore the size and configuration (distribution) of a patch (of a particular habitat type) become effective for the stability of population through hiding places and food resources. Species diversity is related to habitat complexity that provides structural diversity to ground-dwelling organisms. Finally coarse woody debris can enhance habitat complexity thus stabilizing population fluctuation and increasing survivorship.

Key words : habitat, heterogeneity, species diversity, demography

INTRODUCTION

Organisms vary in the extent to which they need a diverse environment, and in patches of habitat due to soils, topography, and most importantly patterns of disturbance. Large scale disturbance (e.g., fires) constitute the an array of variety of habitat that animals and plants depend on. In spatial heterogeneity Forman (1995) described the patch-corridor-matrix model. In his model all land is composed only these three types of spatial element. In the patch woods, fields, and housing tracts are conspicuous whereas roads, hedgerows, rivers and powerlines are striking corridors. Grassland, forest, rice field often forms a background matrix. In the wide variety of land forms habitat heterogeneity functions as an important aspect of biological conservation. Diverse array of habitat can provide spatial diversity to organisms. Recent land development leads to fragmentation that often resulted in local extinction of specialists. A large scale of habitat helps to prevent local extinction by connecting surrounding habitat as an ecological corridor. In this scenario we should maintain quality habitat that organisms rely on. Heterogeneity thus includes spatial arrangement. In this paper I reviewed theoretical aspect of habitat heterogeneity and how habitat heterogeneity can enhance species diversity. In the last chapter I proposed coarse woody debris (CWD) to serve as variation in the forest ecosystem. Presumably small mammals can be benefited from increasing amounts of CWD on the forest floor to have better opportunity for cover and food resources (Lee 1995).

* Corresponding author: Sang Don Lee, Tel. 02-3277-3545, Fax. 02-3277-3545, E-mail. lsd@ewha.ac.kr

THEORETICAL REVIEWS OF HABITAT HETEROGENEITY

The importance of habitat heterogeneity is widely

Table 1. Comparison of different notations of habitat classification by Anderson (1980) and Hansson (1977)

Anderson (1980)		Hansson (1977)
Survival	Most favorable, High and constant density, High reproductive success, Not much extinction, Well-dispersed patches	Donor Habitat
Colonization	Low densities, Low emigration, Vary reproductive success, Frequent extinction, High immigration rates, High density fluctuation	Reception Habitat
Traversable	Not permanent	Transition Habitat

acknowledged for birds (MacArthur *et al.* 1962; Ulfstrand 1975; Roth 1976), lizards (Pianka 1967; Schoener and Schoener 1971), and small mammals. However, habitat heterogeneity can have various meanings to ecologists. It is difficult to measure the suitability of different habitat types. What factors make a habitat optimal and what criteria should be used to determine optimality are not agreed upon (Hansson 1977; Alibhai and Gipps 1985). Nonetheless, several theories suggest that habitat heterogeneity leads to population stability. Population stability will be achieved if population density is stable (i.e., non-cyclic), and when habitat that supports superior demographic performance (e.g., high density, survivorship, reproductive rate) is adjacent to habitat supporting inferior demographic performance (Stenseth 1980).

The idea of habitat variation has been further developed in modelling (Anderson 1980; Hansson 1977). Anderson (1980) speculated on the effects of habitat quality on vole populations by describing different habitat types: survival, colonization and traversable. He described survival habitats as persistently favorable and occurring in well-dispersed patches. He predicted that populations inhabiting them have high reproductive success, and infrequent extinctions. Colonization habitats are more extensive, generally occur near survival habitats, and their conditions can vary over time. Anderson (1980) predicted that vole populations within colonization habitats will have widely varying reproductive success, life expectancy, and density and are subject to frequent extinctions. However, recolonization usually occurs within a short time period by excess individuals from survival habitats. Traversable habitats are crossed by voles but are not used as permanent territories or home ranges. A similar idea of habitat variation has different notations (Hansson 1977).

Population stability can be achieved in a population with unique resource partitioning among individuals, as shown in a mathematical model (Lomnicki 1980).

A further consequence of unequal resource partitioning and a heterogeneous environment is the regulation of population density by emigration, which brings about lower population density, higher food density and even higher stability than without emigration (Lomnicki 1980). Roff (1974, 1975) suggested that the variance in environmental fluctuations leads to stability in a heterogeneous environment. In his model, stability can be achieved through dispersal. Habitat heterogeneity is likely to play a critical role in system performance, such as species abundance and stability. Hestbeck (1982) suggested that population stability can be achieved if there is a gradient of habitat qualities from and into which animals could disperse. All the vacant spaces in the optimal habitat would be filled first, the population being regulated by spacing behavior at this stage. Surplus individuals would then disperse into a suboptimal habitat until all vacant spaces were filled in the suboptimal habitat. Once this had been achieved, neighboring groups would 'fence' the central population and inhibit further emigration. This would cause an increase in population density which would be regulated by resource exhaustion. His model considers the role of habitat heterogeneity explicitly.

There is some evidence that the homogeneous nature of the habitat contributes to the ten-year cycles in the snowshoe hare (*Lepus americanus*), where populations in more discontinuous habitats fail to exhibit cycles (Hestbeck 1982). Stenseth (1980) demonstrated that increased (interpreted as different degrees of structural complexity of the habitat) leads to increased population stability. His theory is based on a predator-prey relationship in a generalized Lotka-Volterra system. Prey can escape more easily in a heterogeneous habitat with more hiding places, theoretically causing less population fluctuations. Three outcomes would result. First, enrichment of a habitat patch will stabilize the predation-prey interaction and result in greater density variation of the prey. Secondly, predator efficiency will destabilize the interaction and result in greater density variation of the prey. This suggests that predator efficiency will be reduced due to the increased ability of prey to escape from predators in heterogeneous habitats. This reduction of efficiency would result in greater stability. Lastly, the stability can be achieved by providing more refuges, thus reducing fluctuations in spatially heterogeneous habitats. However, Rosenzweig and Abramsky (1980) predicted that if greater cover corresponds to higher primary productivity, populations are predicted to be less stable in these sites in the plant-grazer model. If greater cover corresponds to increased prey refuges, then populations are predicted to be more stable.

The size and configuration (distribution) of a patch (of a particular habitat type) becomes important as these may affect the performance of small mammal populations (Hansson 1977; Anderson 1980; Bondrup-Nielsen 1985). The division of space into various local habitats and hostile areas was termed "macroheterogeneity" by Lomnicki (1988). For a population to respond to heterogeneity at this level, patch size must be smaller than the mean dispersal distance of the population (Bondrup-Nielsen 1987), otherwise the patch will be effectively homogeneous for most individuals. Habitat distribution refers to the proximity of habitat patches-either contiguous or separated by unsuitable areas. The success of individuals in colonizing patches might depend on proximity of the patches. Local habitats are those areas an individual is likely to visit in its daily wanderings. These habitats are also expected to be heterogeneous and this is called "microheterogeneity" by Lomnicki (1988). This idea later was developed as 'metapopulation'. Metapopulation is a series of small, separate populations that mutaully affect one another. In this scenario even if one individual population goes extinct, other populations survive and they supply individuals where the population became extinct (Hjermana and Ims 1996). In this matrix of habitat it is important to maintain source population to supply individuals of locally extinct.

HABITAT HETEROGENEITY LEADS TO SPECIES DIVERSITY

Many have found that species diversity is related to habitat complexity (MacArthur and Pianka 1966; MacArthur and MacArthur 1961; Cody 1975; Terbough 1977). The term 'complexity' and 'heterogeneity' has been used interchangeably since the demonstration of a positive association between bird species diversity and foliage height diversity: species diversity increased with increasing habitat complexity (MacArthur and MacArthur 1961). It is reasoned that highly complex habitats offer more potential niches than structurally simpler habitats (Klopfer and MacArthur 1960). Both increasing complexity and increasing heterogeneity can be demonstrated to increase species diversity by providing more niches in a unit of space (Levins 1976). Potential niches are distributed vertically in complex habitats and both horizontally and vertically in patch habitats. In small mammals, Bondrup-Nielsen (1985) showed that structural heterogeneity of the environment led to increased species diversity in a desert small mammal community. August (1983), however, separated the meaning of complexity and heterogeneity. He defined complexity as vertical variation in habitat physiognomy and heterogeneity as horizontal variation in habitat form. He suggested the total number of mammal species was positively correlated with habitat complexity but not correlated with habitat heterogeneity. He argued that abiotic factors such as the degree of flooding plays an important role in patterns of small mammal distribution and abundance.

COARSE WOODY DEBRIS AS HABITAT HETEROGENEITY

Most studies on habitat heterogeneity have compared sites with distinct vegetation (e.g., deciduous versus coniferous forest) or several habitat variables as opposed to site comparison characterized by variation in one critical habitat feature. Recently effects of ground structural diversity were measured using amounts of coarse woody debris (CWD) on small mammal community.

Small mammals performed better around the sites with CWD showing higher densities (Greenberg 2002). CWD function as a carbon and nutrient sources that function as an important role to mature forests from young growing stands to old and mature forests (Carmona *et al.* 2002). CWD in Candadian boreal forests also makes a substantial contribution to maintaining biodiversity leaving residual trees in clearcuts to benefit wildlife (Pedlar *et al.* 2002). Red-backed voles (*Clethrionomys gapperi*) were significantly related to the abundance of the most decayed logs of CWD (Bowman *et al.* 2000). CWD is a good indicator for the mature and old-growth forests constituting over 50% in volume (Siitonen *et al.* 2000). Recent fragmentation of forests and quality habitat leads to species extinction locally. In this case quality habitat with an accumulation of CWD may serve as a survival habitat to provide population into colonization habitat as indicated by Anderson (1980). In Korea as fragmentation and loss of habitat are accelerated due to development it is time to consider how to improve quality habitat for plants and animals.

The predictions of different habitat use can be tested by comparing spatial patterns and population demography of animal species and examining microhabitat use. Fallen logs function to increase habitat heterogeneity and add structural diversity. Logs serve as habitat for vertebrates that live in the decaying wood and also perform other ecological functions (Carey and Harrington, 2001; Franklin *et al.* 1981). At the same time, heterogeneity of habitat increases the spatial complexity of a habitat, and this may reduce social interactions (Krebs 1986). Few attempts have been made to discover the primary role of CWD, yet it has been shown to be an important factor in small mammal populations. Biocomplexity resulting from interactions of decay, understory development, and overstory composition provides pre-interactive niche diversification with predictable, diverse, small mammal communities

CONCLUSIONS

Heterogeneous habitat can enhance biological diversity by providing variation in structural diversity. Organisms in heterogeneous habitat resulted in population stability and superior demographic performance (e.g., high density, survivorship, reproductive rate) can be observed compared with adjacent habitat with less diverse structural habitat. The idea of habitat variation also proves that temporal and spatial diversity is important for demography of organisms in mathematical modelling. Furthermore the size and configuration (distribution) of a patch (of a particular habitat type) become effective for the stability of population via hiding places and food resources. Species diversity is related to habitat complexity that provides structural diversity to ground-dwelling organisms. In this regard coarse woody debris can enhance habitat quality by enhancing habitat heterogeneity.

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