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PhD Preliminary Examination

PhD Cognate Area 2

**A review of environmental heterogeneity in ecology.**

Nargol Ghazian

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Dr. Suzanne MacDonald (Supervisor)

Dr. Christopher J. Lortie (Co-Supervisor)

Dr. Laura McKinnon (Advisor)

Dr. Bridget Stutchbury (Graduate Program Director)

1. **Introduction**

***Historical background***

One of the main goals of ecology is understanding the effects of environmental heterogeneity on diversity, disturbance, ecosystem services, and ecosystem resilience. Ecosystems are evidently heterogeneous; however, throughout much of history, heterogeneity was looked upon as an unnecessary complication, and homogeneity was assumed for the sake of convenience and simplicity (Cadenasso and Pickett 1995). Even when considered, the term ‘heterogeneity’ is rarely defined leading to confusion and ambiguity (Tamme et al. 2010). Environmental heterogeneity (EH) is broadly defined as, “non-uniformities in physical and ecological landscape characteristics” (Dronova 2017). Environmental heterogeneity can influence biodiversity (Stein et al. 2015; Mace, Norris, and Fitter 2012), agricultural productivity (Kremen and Miles 2012), and resilience of natural and human ecosystem stressors (Levine et al. 2016; Oliver et al. 2015). Spatial variation and patterns in nature were a concern of early ecologists but they lacked the long history of empirical studies and the conceptual and mathematical models used in today’s studies (Lovett 2005). Early notions of environmental heterogeneity were discussed embedded in the discourse concerning ecological succession such as when Cowles (1899) attempted to explain spatial patterns and temporal change in vegetation as the result of interactions between plants, soil, and the physical environment (Cowles 1899). The greatest debate was about the factors that cause spatial patterns in vegetation that took place between Gleason and Clement. Gleason (1926) argued that Clement’s model (Clements 1936) of describing vegetation patterns as set associations (predictable species composition in a community), for example, oak-maple association, assumed too much homogeneity and instead offered the ‘individualistic concept of ecology’ where the real diversity of vegetation depends completely on “the phenomena of the individual” meaning each individual present in the ecosystem. Additionally, Gleason argued that associations of species with the surrounding species and environment are random (McIntosh 1975). Another area where EH was historically implicitly discussed was the concept of niche differentiation focusing on the spatial differences in species distributions such as in Grinnel’s (1917) study of bird distributions in California. Swanson and Sparked (Magnuson 1990) argued that “significance of research results is difficult to interpret if site’s context in space is not understood.” They termed this the ‘invisible place’ where misleading conclusions of short-term studies can be made. Today, EH is a term that encompasses spatial environmental heterogeneity such as non-uniform land cover, vegetation, climate, soil and topography and temporal variability such as short-term seasonality and long-term transitions of successional vegetation and land cover (Dronova 2017). Environmental heterogeneity can be divided into biotic EH and abiotic EH (Stein, Gerstner, and Kreft 2014). Much of the present efforts focus on developing methods and conceptual models that make it easier to incorporate the concept of heterogeneity into the ecological research. (Lovett 2005). Ecologist have begun to appreciate the importance of patch dynamics and disturbances and it is thus clear that assumption of homogeneity in spatial and temporal is simply unrealistic. The concern for ecological sustainability is one the greatest challenges today. Incorporating a heterogeneous paradigm to sustainable environmental goods and services will likely be key in the future.

***A closer look at key definitions of environmental heterogeneity***

Environmental heterogeneity has been discussed under a wide umbrella of terms and ecological interpretations of heterogeneity are extremely broad. In recent reviews, it was shown that are numerous terms used to denote heterogeneity, which are undefined or have conflicting underlying concepts (Stein and Kreft 2015). Some distinguish heterogeneity as the horizontal habitat variation as opposed to the complexity in the vertical component (Grelle 2003); though, others argue that spatial and temporal heterogeneity can have more than two dimensions (Kolasa and Rollo 1991). Others simply defined variability and complexity as constituents of heterogeneity (Li and Reynolds 1995). Other terms used in the literature include: altitudinal variation, elevational or environmental variability, habitat, landscape, or vegetation complexity/diversity/heterogeneity/structure, spatial heterogeneity/variability, and structural complexity (Stein, Gerstner, and Kreft 2014). Variability in definitions may obscure the importance of EH in ecology. Thus in this review, I simply define environmental heterogeneity as the variation/complexity in spatial and temporal components, and/or structure in the environment, regardless of the three dimension direction. EH can be divided into two broad categories: temporal heterogeneity and spatial heterogeneity. Temporal heterogeneity refers to variability in environmental conditions including stressors and climatic fluctuations through different scales of time (Menge and Sutherland 1976). Spatial heterogeneity on the other hand has to do with heterogeneity in the physical structure of the ecosystem and spatial dynamics, including fluxes of organisms, materials, and energy within the landscape (Cadenasso and Pickett 1995). For the purposes of this review, I will mainly consider the concept of spatial heterogeneity. EH can be divided into five main subject areas including two biotic components land cover, vegetation, and three abiotic components climate, soil, and topography (Stein and Kreft 2015; Stein, Gerstner, and Kreft 2014) (Table 1). Given the variability of terms in the published literature and the used of synonymous terminology, it is important the studies define terms well to better aid the readers in understanding the concept of heterogeneity, both in empirical studies and future syntheses. In the following sections we will describe each EH subject area in detail, as well discussing the role of disturbance on heterogeneity, heterogeneity on disturbance, and the future of the field given the immense anthropogenic pressures of today’s ever-changing world.

**Table 1.** Definitions table for keywords related to environmental heterogeneity.

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| Keyword | Definition |
| *Environmental Heterogeneity (EH)* | Term that encompasses spatial environmental heterogeneity such as non-uniform land cover, vegetation, climate, soil and topography and temporal variability such as short-term seasonality and long-term transitions of successional vegetation and land cover . |
| *Temporal heterogeneity* | Variability in environmental conditions including stressors and climatic fluctuations through different scales of time. |
| *Spatial heterogeneity* | Variation in the physical structure of the ecosystem and spatial dynamics, including fluxes of organisms, materials, and energy within the landscape. |
| *Land cover EH* | Heterogeneity between two habitats in terms of complexity and configuration between patches. Focuses on habitat and vegetation types. |
| *Vegetation EH* | Heterogeneity in plant diversity and vegetation structure such as canopy and foliage height. |
| *Climatic EH* | Heterogeneity in micro or macroclimatic conditions. |
| *Soil EH* | Heterogeneity in soil nutrients, acidity, or type. |
| *Topographic EH* | Most often discussed in terms of elevation range, this is the heterogeneity that incorporates micro topographic structure and large-scale relief. |

1. **Drivers of Environmental Heterogeneity**