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PhD Preliminary Examination

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

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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, heterogeneity and organismal interaction, 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**

***Land Cover EH***

Two major components of landscape is composition and spatial configuration. Composition refers to what and how much is present of each habitat or cover type whilst configuration refers to a specific arrangement of spatial elements (Turner and Gardner 2015). Sometimes spatial structure or patch structure is used in lieu of configuration (Forman 1995). A patch can be defined as a surface area that differs from its surroundings in nature or appearance (Forman 1995). Compsition can be defined using the number of land cover type continuity across the landscape (Turner and Gardner 2015), such as forest or grass, and configuration and configuration can be defined using edge density or fractal dimension (Stein and Kreft 2015). Edge density is a measure calculated by dividing the length of particular edge class type by the estimated class area (Ramezani et al. 2010). Fractal dimension is another measure calculated using the patch area to perimeter ratio with an incorporation of patch length/diameter (Imre and Bogaert 2004). Landform can be identified on the basis of three characteristics: 1) relative amount of gentle sloping (<8%) land, 2) where and how much of the gentle slope lands (upper or lower portion of the slope), and 3) local topographic relief (Bailey 2009). Number three is more related to topographic EH and will be further discussed in that section. Land cover or landform can affect the ecosystem patterns and processes in different ways (Swanson, Wondzell, and Grant 1992). For example, the elevation, aspect, parent material, and slope of landform affects ground temperature, moisture, nutrients, and other materials available within the site, which inherently affects the type of vegetation that grows there and its distribution across the landscape. Landforms can affects wind patterns and thus the dispersal of seeds (Dixon, Turner, and Jin 2002), dictating what type of vegetation grows where. Furthermore, they can affect the frequency and spatial pattern of natural disturbances such as fire, wind or grazing (Turner and Gardner 2015), as well as influencing the transport of organic and inorganic materials around the landscape (Reiners and Driese 2003). Thus, land cover EH is the result of landforms and cover types, both which have various effects on vegetation and biochemical processes of the given area.

***Vegetation EH***

Vegetation is a widely-studied aspect of heterogeneity because the type of vegetation can directly affect the local species composition and abundance. Vegetation heterogeneity is associated with diversity in resources, shelter and roosting, and breeding and oviposition sites (Tews et al. 2004; Kissling, Rahbek, and Böhning-Gaese 2007). However, vegetation EH may also negatively impact animal diversity, such as insects, when the vegetation is dense; hence, increasing the required energy expenditure needed to move across the habitat, or the when taxa is more adapted to the open (Humphrey et al. 1999; Lassau and Hochuli 2004). Vegetation EH encompasses two main areas: the taxonomic profile of plants (i.e diversity), and measures of the physical structure such as foliage height diversity and trunk diameter (Stein and Kreft 2015). The most common measure of diversity is the Shannon index that takes into the account the number of individual of a particular species in a given area relative to their abundance to estimate species richness (Peet 1975). Leaf Area Index (LAI) and foliage height diversity are indicators of structural diversity and can be calculated using canopy to light ratio and light attenuation (Breda 2003; Sonnentag et al. 2007; Brantley and Young 2007). Now a days however, these measures can be taken using remote sensing techniques with high-resolution Light Detection and Ranging instruments (LIDAR) (Chen, Xu, and Gao 2015). The concept of ecological succession is particularly important when discussing vegetation EH. Succession is the sequential replacement of species after disturbance or abrupt loss of structure or biomass (Prach and Walker 2011). Succession affects heterogeneity vertically via canopy structure and horizontally by colonization of pioneer species and natural gaps (Dronova 2017). The diversity in the 3-D structure of plants is important because they control the transfer and interception of solar radiation, productivity, nutrient cycling, and sequestering of atmospheric carbon dioxide (Dronova 2017). Vegetation EH is important given the current climate crisis as vegetation can regulate greenhouses gases and aid in the management of the increased thermal phenomena.

***Climatic EH***

Earth’s climate is dynamic and has varied tremendously during the recent years. Broadly-speaking, climate varies by latitude, which influences temperature and moisture (Turner and Gardner 2015). Though, latitude and continental position are important, finer-scale heterogeneity can be dictated locally by topography (Bailey 2009), which introduces the notion of micro and macroclimate. Climate or macroclimate is measured as the long-term averages of the suit of meteorological variables such as temperature, precipitation, humidity and wind (Turner and Gardner 2015). Microclimate on the other hand are local variabilities in climate due to landscape heterogeneity, such as temperature under a tree canopy versus in the open. This is different from *weather*, which is daily averages of the above parameters (Barry and Chorley 2009). Changes in climate are expected to modify the type and distribution of ecosystems around the globe (Moritz and Agudo 2013). Climatic heterogeneity can alter disturbance regimes such as wildfires (Turco et al. 2014). Furthermore, climate can impact plant community assembly by dictating range shift and composition (Feeley et al. 2020), as well phonological activities such as fruiting and flowering (Panchen 2016). Many species are shifting their ranges northward or upward in elevation (Parmesan and Yohe 2003), but it will not be long before species can no longer mitigate for such extreme climatic changes. Thus, Climate EH can affect which species localize which areas and affect the distribution of plants and animals. It can also introduce heterogeneity horizontally through dictating the type of vegetation that grows in an area, but also vertically because physically plant structures can impact canopy microclimate (Ghazian, Zuliani, and Lortie 2020; Jennings, Brown, and Sheil 1998).

***Soil EH***

Soil is distinguishing characteristic of the landscape as it provides nutrients and minerals, water, and support to vegetation, as well as impacting drainage regimes. Soil generally forms through the process of weathering, either through chemical processes or physical abrasion (Schaetzl and Thompson 2015). Soils are an important indicator of landscape patterns because they differ in various chemical and physical properties, including texture, depth, pH, and mineral composition (Turner and Gardner 2015). Soils impact heterogeneity because their mineral availability, for instance nitrogen concentration, can influence the species of plants that can be supported in a particular area (Oelmann et al. 2007). The variability in water-holding capacities, nutrient concentrations, and organic content lead to dominance by plant species (Turner and Gardner 2015). Soils also impact disturbance dynamics. For example, the water retention availability of the soil provides a good estimate of response to drought (Hanson and Weltzin 2000). Additionally, soils can also affect microbial composition, abundance, and function (Buckley and Schmidt 2003; Waldrop and Firestone 2006). Hence, soil composition has a strong influence on the landscape, vegetation, and thus species dynamics.

***Topographic EH***

Topography is a key 3-D component of the landscape and therefore vertical heterogeneity. Topography is concerned with the landform and land features of the surface but it is more than the mere measure of elevation and can include measures like slope and aspect (Stein and Kreft 2015). Slope is defined as