



UMEÅ UNIVERSITET

# Evolution of Ecological Communities in Spatially Heterogeneous Environments

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**Abstract**

Evolutionarily stable communities are the endpoints of evolution, and ecological communities whose traits are under selection will eventually settle into them. Hence, the properties of such communities are of particular interest, as they can persist over long evolutionary time scales. The notion of an evolutionarily stable strategy—an evolved strategy that cannot be beat by any other once established—has now been part of theoretical ecology for almost 50 years, and the theory for evolutionarily stable strategies and communities, and how they are reached has become increasingly versatile. However, for environments where conditions vary in space, so-called heterogeneous environments, efficient analytical and numerical tools for studying evolutionarily stable communities and how they come about have been lacking. Hence, many questions regarding how evolutionarily stable diversity is generated and maintained when ecological and evolutionary forces vary in space remain unexplored. In particular, how spatially averaged selection and selective forces derived from spatial variability can act together to either promote or inhibit evolutionarily stable diversity is not well understood.

In this thesis, I use a two-pronged approach towards answering such questions by developing the necessary analytical and numerical tools for assembling and analyzing evolutionarily stable communities in heterogeneous environments, and by then employing these tools to study communities of resource competitors and food webs. Specifically, I derive expressions for directional and stabilizing/disruptive selection when the spatially heterogeneous ecological dynamics of a community are described by reaction-diffusion equations. These expressions allow us to understand selection across an environment in terms of local selection pressures, and also enable efficient numerical implementations of evolutionary community assembly procedures that lead to evolutionarily stable communities.

Applied to the communities of resource competitors and food webs I find that the selective forces derived from spatially averaged selection and those derived from spatial variability can act both in concert or in opposition. If these forces act in opposition and if the spatial variability of local selection is high, a high diversity of organisms can form even when spatially averaged selection is stabilizing. In contrast, if spatially averaged selection is disruptive, it can prevent more diverse communities from forming by creating few globally unbeatable strategies. However, these forces can also act disruptively in concert to create more diverse communities. Together, these results demonstrate a surprising variety of qualitatively different outcomes when evolutionarily stable communities are assembled in heterogeneous environments.

**Keywords**

Spatial models, reaction-diffusion equations, eco-evolutionary models, adaptive dynamics, evolutionarily stable communities

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