学 位 論 文 内 容 の 要 旨/Dissertation Abstract

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Context dependence of species interaction and coexistence: the influence of multiple environmental variables across spatial scales on a rocky intertidal two species system
（種間相互作用と共存の状況依存性：
岩礁潮間帯の 2 種系における空間スケールにまたがる複数の環境変数の影響）

Species interactions and coexistence are fundamental for understanding biodiversity maintenance, with their environmental dependence reflecting complex ecological dynamics. The outcomes of species interactions are influenced by both population parameters—such as intrinsic growth rate (r_i), strength of intraspecific density dependence (a_{ii}), and strength of interspecific density dependence (a_{ij})—and environmental variability. Modern coexistence theory (MCT) integrates stabilizing mechanisms, equalizing mechanisms, and the mutual invasion criterion to explain coexistence, emphasizing the necessity for stronger intraspecific density dependence than interspecific density dependence. However, since the strengths of intra- and interspecific density dependence vary along environmental gradients, the species interactions of two species and their coexistence opportunities may be complexly altered by multiple environmental factors in natural systems, a phenomenon known as context dependence. While numerous previous studies about context dependence have explored the effects of single environmental factors on the species interaction, the causal processes among multiple factors, the causal processes among environmental factors and population parameters, as well as their influences on coexistence remain largely unexplored. Rocky intertidal habitats, characterized by intense competition for substratum space and drastic environmental gradients, along with two-species systems that represent the simplest population interaction models, provide an ideal setting for empirical studies on species interactions and the context dependence of coexistence.

In Chapter II, I first developed an assessment approach to evaluate the spatial variation of population parameters in response to changes in multiple environmental factors among two rocky intertidal sessile species, *Chthamalus dalli* and *Gloiopeltis furcata*. The approach incorporated causal relationships including direct and indirect effects among environmental factors and population parameters. Specifically, the intrinsic growth rates of each species were used as proxies for environmental suitability, representing a function of various environmental factors in the habitat. By using this approach with 18-yr abundance data in 33 quadrats in *C. dalli—G. furcata* system with 9 environmental factors in each quadrat, I aimed to evaluate the direct effects of environmental factors and the indirect effects of environmental factors through intrinsic growth rates of two species on strengths of intra- and interspecific density dependence, as well as the relative importance of these direct and indirect effects among different localities. Results showed that the indirect effects of environmental factors through intrinsic growth rates were the dominant contributors to spatial variation in the strengths of intra- and interspecific density dependence. While direct effects of environmental factors were detected in only a few pathways, the direct effects of intrinsic growth rate of each species

significantly influenced its own strengths of intra- and interspecific density dependence. These results highlight the importance of intrinsic growth rates in mediating the effects of environmental factors on species interactions and suggest that indirect pathways play a critical role in shaping species interactions in natural systems with complex causal processes.

Under the MCT framework, coexistence is driven by niche differences that outweigh fitness differences, which can be quantified by population parameters in Lotka-Volterra competitive model (r'_i, a'_{ii}, and a'_{ij}) directly. Additionally, positive invasion growth rates, where each species can grow when rare while its competitor is at equilibrium ($N_{eq,j}$), ensure successful coexistence. In natural systems, the invasion growth rates can be both expressed by (1) intrinsic growth rates (r_i) and the strength of interspecific density dependence at the competitor's population level ($a_{ij} \times N_{eq,j}$), or by (2) the difference in intrinsic growth rates between two species ($r_i - r_j$), combined with the product of difference between the focal species' intraspecific density dependence and the interspecific density dependence exerted by the competitor and the competitor's equilibrium density ($(a_{jj} - a_{ij}) \times N_{eq,j}$) in logarithmic Gompertz model. These two expressions demonstrate the same value but different ecological meanings. To quantify the coexistence opportunities in stable habitats (the same 33 quadrats in Chapter II) and transient habitats (12 quadrats that only one of two species were consistently present, meaning the stable coexistence is phenomenally absence), the relationship between invasion growth rates of two species, and the combination of fitness difference and niche difference were calculated and compared across habitat types. Furthermore, to further investigate how coexistence opportunities vary with population parameters in response to changes in multiple environmental factors, the relative importance of components of invasion growth rates, the direct effects of environmental factors on invasion growth rates and their components, and the indirect effects of environmental factors on invasion growth rates and their components mediated by environmental factors were assessed in stable habitats. The results showed the two species in all habitats can coexist, and there is no significant difference in invasion growth rates or the combination of fitness and niche differences across stable and transient habitats. Moreover, intrinsic growth rates of two species and their differences were the primary drivers of spatial variation in invasion growth rates, with bare space availability and effective shore level being critical environmental factors. The coexistence of these species appeared to be primarily driven by equalizing mechanisms rather than niche differentiation, indicating that similar competitive abilities were more important than stabilizing effects in maintaining coexistence. These findings also revealed the limitations of studying coexistence in two-species systems, as they may fail to capture the broader coexistence dynamics within multispecies communities.

This thesis emphasizes the complexity of causal relationships between environmental factors, species interactions, and coexistence, highlighting gaps between theoretical and empirical research. Hierarchical causal structures among environmental factors and population parameters were shown to be crucial for understanding context dependence of species interaction and coexistence mechanisms in natural systems. While the proposed approach effectively decomposes the effects of environmental factors into direct and indirect pathways, it does not account for temporal variations and cannot accurately predict coexistence in species-absent habitats. Despite these limitations, the study advances understanding of species interactions by providing a framework to evaluate the context dependence of species interaction and coexistence mechanisms in natural community-based empirical study. Future research should aim to investigate how coexistence mechanisms respond to multiple environmental factors across diverse ecosystems, bridging the gap between theory and practice to establish general patterns of coexistence in natural communities.