博士論文の要約

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論文題目 Evolution of symbiotic systems in extreme and heterogeneous environments

The evolution in a symbiotic system is tightly linked with the ecological and demographical background where the symbiotic system lies. At the same time, the evolutionary consequence of symbiotic traits could have a significant impact on the ecology or demography of the system. As previous theories suggest, the exploitation of a symbiotic partner species by another is a key factor that drives evolutions in a symbiotic system. However, despite many empirical and theoretical studies devoted to the evolution of the exploitation in mutualistic systems, few studies take into account the eco-evolutionary feedback. Similarly, even in the well-developed literature on the evolution of virulence in parasitic systems, little is known on the eco-evolutionary feedback in hosts and parasites living in heterogeneous habitats. Here I theoretically investigate the evolution of exploitations in symbiotic systems in extreme and heterogeneous environments to reveal the link between their evolution and ecology.

In chapter 2, I focus on a unique mutualistic system of tubeworm and sulfur-oxidizing bacteria in the deep-sea ecosystem. Symbiont bacteria produce organic products by chemosynthetic reaction and provide nutrients for their host tubeworms. In return, tubeworms provide a specific organ as the habitat of their symbiont bacteria. Although the mutualistic relationship is essential for both species to survive in an extreme deep-sea environment, this mutualism has several puzzling features in their symbiotic lifecycle. After acquiring sulfur-oxidizing bacteria from the environment, tubeworms become fully dependent on their symbiont bacteria for nutrient intake. Once ingested by the tubeworm larva, no additional symbionts join from the environment, and no symbionts are released until the host tubeworm dies. Despite this very narrow window to acquire symbionts, some tubeworm species can live for >200 years. Such a restricted release of symbionts could lead to a shortage of symbiont bacteria in the environment without which tubeworms could not survive. In my study, I examine the conditions under which this mutualism can persist, and whether the symbiont-controlled host mortality induced by the exploitation of symbiont bacteria evolves toward a low value, using a mathematical model for the tubeworm-symbiont bacteria system. My model reveals that mutualism can persist only when the host mortality rate is within an intermediate range. With co-habitation of multiple symbionts strains in the same host, symbiont-controlled host mortality rate evolves toward a low value without driving either host or symbiont to extinction when competition among symbionts is weak and their growth within a host is slow. We also find the parameter conditions that lead to an unlimited evolutionary escalation of host mortality rate toward coextinction of both tubeworms and symbionts populations (evolutionary double suicide). The generality of this evolutionary fragility in obligate mutualistic systems, as well as the contrasting evolutionary robustness in host-parasite systems, are discussed.

In chapter 3, I focus on a general host-pathogen system and examine the effect of metapopulation heterogeneity on the evolution of virulence, the degree of exploitation by a pathogen. The spatial structure of populations and communities has never been entirely ignored in ecology, but most general theories of ecology and population biology have been built on the assumption of panmixis. Here we develop a general theory on the evolution of a pathogen trait under metapopulation heterogeneity of their hosts, in which epidemiological and genetic dynamics in local populations in heterogeneous conditions are intermixed by migrations of individuals. Such heterogeneity would bring differential selection pressures to local populations, which are then mingled through migrations to form an evolutionary trend in the entire metapopulation. Here I study the effect of metapopulation heterogeneity on the evolution of virulence by analyzing the evolutionary and epidemiological dynamics in host metapopulation. The model reveals the following key findings on the evolution of virulence in a heterogeneous metapopulation. (1) Heterogeneity in net migration inflows to local populations always increases pathogen virulence, i.e., the evolutionarily stable virulence is always higher with heterogeneity in net migration inflows than without. The same is true for the heterogeneity in intrinsic growth, carrying capacity, immunity loss, or any parameter that affects the dynamics for pathogen mutant only through equilibrium susceptible densities (resident-mediated heterogeneity). (2) The increment of pathogen virulence due to such heterogeneity is approximately proportional to the variance of the heterogeneous parameter over metapopulation. (3) The increment of pathogen virulence by introducing resident-mediated heterogeneity is analytically expressed as the covariance of the local selection pressure and the local reproductive value. (4) The reason why such heterogeneity always increases the pathogen virulence is explained by the fourfold concordance between the variable parameter at the local population, the equilibrium local density of susceptible hosts, the local selection pressure, and the local reproductive value. (5) Although these analytical results are shown under the assumption that heterogeneity of a small degree is introduced into a homogeneous metapopulation, the robustness of the results is shown for a large degree of heterogeneity and the cases where further heterogeneity is introduced into an already heterogeneous metapopulation. (6) Unlike heterogeneity in migration, intrinsic growth, carrying capacity or immunity loss (resident-mediated heterogeneity), heterogeneity in host natural mortality, recovery rate, infectivity, or any parameter that directly affects the dynamics of a pathogen mutant has no such unequivocal effect on the evolution of virulence. However, whether the heterogeneities in the latter parameters increase or decrease pathogen virulence can be predicted by the sign of a quantity defined by model parameters. These results would cast new theoretical insights into the evolution of pathogen virulence in the heterogeneous world.

In chapter 4, I discuss future extensions of my results of the evolution of symbiotic systems. As a strength of the theoretical study, both of my models for mutualism between tubeworms and sulfur-oxidizing bacteria and for the host-pathogen system with metapopulation heterogeneity have a large potential for the extension to apply other types of symbiotic interactions. Although there is still uncertainty about how eco-evolutionary feedback acts in diverse symbiotic systems, I believe that my models can take a big step towards our understanding of the evolution in symbiotic systems that underlie complex and diverse natural ecosystems.