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Ideal Free Distribution of Multiple Species in a Time-Periodic and Patchy Habitat

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Abstract. Dispersal strategies that lead to the ideal free distribution (IFD) were shown to be evolutionarily stable in various ecological models. In this paper, we investigate this phenomenon in time-periodic environments where N species – identical except for dispersal strategies – compete. We extend the notions of IFD and joint IFD, previously established in spatially continuous models, to time-periodic and spatially discrete models and derive sufficient and necessary conditions for IFD to be feasible. Under these conditions, we demonstrate two competitive advantages of ideal free dispersal: if there exists a subset of species that can achieve a joint IFD, then the persisting collection of species must converge to a joint IFD for large time; if a unique subcollection of species achieves a joint IFD, then that group will dominate and competitively exclude all the other species. Furthermore, we show that ideal free dispersal strategies are the only evolutionarily stable strategies. Our results generalize previous work by construction of Lyapunov functions in multi-species, time-periodic setting.

AMS subject classifications: 34D23, 34C25, 92D15, 92D25

Key words: Ideal free distribution, evolutionarily stable, time-periodic patch model, multiple-species model.

1 Introduction

The ideal free distribution predicts how organisms distribute themselves in heterogeneous environments to optimize individual fitness [18]. It is based on two key assumptions: individuals possess complete knowledge of habitat quality, and they are free to

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move. The concept of IFD originated from observations of territorial patterns in birds [48] and has been central to understanding the evolution of dispersal [29].

An IFD is achieved when every individual has the same fitness across the habitat; otherwise, some individuals could improve their fitness by adopting a different dispersal strategy. In spatially heterogeneous but temporally constant environments, a species achieves IFD when its distribution of individuals perfectly matches resource availability, ensuring fitness to equilibrate throughout the habitat [5, 40]. In such a context, it is demonstrated across various modeling frameworks that dispersal strategies leading to IFD are evolutionarily stable strategies (ESS), see [7] for reaction-diffusion-advection models, [28] for patch models, [9, 14] for nonlocal diffusion models, and [10] for integrodifference models. These studies further demonstrated that dispersal strategies that can produce IFD qualify as ESS in temporally constant environments. The concept of ESS is central in evolutionary biology [16, 46], and has strong implications in the study of biological invasion, habitat selection and population distribution. However, ESS depends on the class of admissible strategies and does not always lead to IFD [11, 20, 30, 33, 37, 42].

Most natural environments exhibit diurnal or seasonal variations. Incorporating time-periodicity in the modeling, however, often leads to considerable mathematical difficulties. For instance, the characterization of IFD is no longer a static location selection as in temporally constant environments, since the locations that maximize individual fitness may change over time. Temporal periodicity significantly alters the evolutionary dynamics of dispersal. It is for instance a driver of the diel migration in copepods [47]. It is demonstrated in [2, 25] that for reaction-diffusion models of two competing species with strictly unconditional dispersal, if the environment is time-periodic, then either fast or slow diffusion rate can be selected, or they could coexist. This stands in contrast with the seminal work of [1, 17, 21] establishing the selection of only slow diffusion rate in static environments. It is natural to ask the following questions: (1) How do we define IFD in time-periodic environments? (2) Are ideal free dispersal strategies ESS in time-periodic environments? These questions were addressed by Cantrell *et al.* [3, 6] by introducing a notion of generalized IFD via pathwise fitness of a typical individual within a population in the context of time-periodic reaction-diffusion-advection models. But [3, 6], as with most previous work, apply only in the restrictive context of two competing species due to the reliance on monotone dynamical system theory [23, 24, 31]. For three or more competing species, most existing studies focus on the permanence or the existence of equilibrium solutions, and there is a gap in the understanding of long-term dynamical and evolutionary aspects [8, 15, 32, 39].

We will study the evolutionary stability of IFD for multiple competing species in the adaptive dynamics framework. The motivation lies in the fact that multiple species can achieve IFD even though each single species cannot do so, forming the so-called joint IFD [19]. The evolutionary stability of such situations is interesting and cannot be captured by models of two competing species. For competition systems of multiple species in temporally constant environments, the joint IFD was defined to describe a combination of distribution for multiple species that exactly matched the resource [5, 8, 39]. In that