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Adaptive evolution of body size subject to indirect effect in trophic cascade system☆

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A B S T R A C T

Trophic cascades represent a classic example of indirect effect and are wide-spread in nature. Their ecological impact are well established, but the evolutionary consequences have received even less theoretical attention. We theoretically and numerically investigate the trait (i.e., body size of consumer) evolution in response to indirect effect in a trophic cascade system. By applying the quantitative trait evolutionary theory and the adaptive dynamic theory, we formulate and explore two different types of eco-evolutionary resource-consumer-predator trophic cascade model. First, an eco-evolutionary model incorporating the rapid evolution is formulated to investigate the effect of rapid evolution of the consumer's body size, and to explore the impact of density-mediate indirect effect on the population dynamics and trait dynamics. Next, by employing the adaptive dynamic theory, a long-term evolutionary model of consumer body size is formulated to evaluate the effect of long-term evolution on the population dynamics and the effect of trait-mediate indirect effect. Those models admit rich dynamics that has not been observed yet in empirical studies. It is found that, both in the trait-mediated and density-mediated system, the body size of consumer in predator-consumer-resource interaction (indirect effect) evolves smaller than that in consumer-resource and predator-consumer interaction (direct effect). Moreover, in the density-mediated system, we found that the evolution of consumer body size contributes to avoiding consumer extinction (i.e., evolutionary rescue). The trait-mediate and density-mediate effects may produce opposite evolutionary response. This study suggests that the trophic cascade indirect effect affects consumer evolution, highlights a more comprehensive mechanistic understanding of the intricate interplay between ecological and evolutionary force. The modeling approaches provide avenue for study on indirect effects from an evolutionary perspective.

1. Introduction

Ecological communities are influenced by numerous direct and indirect effects among species, which collectively determine community composition, structure and functions (Strauss, 1991; Wootton, 1994; Miller and Travis, 1996). Indirect effects occur when the impact of one species on another is mediated by a third species or through other links (Wootton, 1994). Indirect effects are ubiquitous in nature (Pace et al., 1999; Knight et al., 2005), and can be stronger in magnitude than direct interaction among organisms (Miller and Travis, 1996; Preisser et al., 2005). Indirect effects can influence population dynamics, community composition (Wood et al., 2007; Gribben et al., 2009), and nutrient cycling (Stief and Hölker, 2006). Indirect effects represent a major focus of ecological research and involve in many longstanding research areas (Walsh, 2013).

The ecological consequences of indirect effects of predation are well characterized in a diversity of ecosystems (Wootton, 1994). The indirect effects are also of essential evolutionary significance and there are several empirical examples of indirect effects driving trait evolution (Miller and Travis, 1996; Walsh, 2013). The evolutionary importance of indirect effects have garnered attention only recently. There are ample empirical evidence to suggest that indirect effects may mechanically drive and facilitate evolutionary changes via a variety of pathways (Walsh, 2013). Recent

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researches, spanning field and laboratory studies as well as terrestrial and aquatic ecosystems, have explored genetic variation (Astles et al., 2005), natural selection (Irwin, 2006), and evolution (TerHorst, 2010; Walsh and Reznick, 2010; Walsh, 2013) in response to indirect effects. The recent empirical examinations document the evolutionary response and consequences of indirect effects, and furthers the understanding of the link between the community and evolution. There are two main classes of indirect effects: density- and trait-mediated indirect interactions (Werner and Peacor, 2003). Despite the evolutionary consequence of indirect effect have been empirically tested, the mechanistic details or consequences of indirect effects affecting evolution behind an observed pattern, or whether or not the density-mediated and trait-mediated indirect effects produce different evolutionary outcomes are still unclear and are not well characterized.

Trophic cascade, an indirect effect that occurs when a top predator alters the density or traits of their prey, which, in turn, weakens predation pressure on the next lower trophic level, represent a classic example of indirect interaction ranging from the insides of insects to the open ocean (Wootton, 1994; Pace et al., 1999). Trophic cascades not only impact the ecology dynamics but also induce significant evolutionary consequence, which has been documented by empirical studies and experimental evidences (Walsh and Reznick, 2008, 2010, 2011; Abrams and Vos, 2003; Pace et al., 1999; Schmitz et al., 2004). The evolutionary consequences of indirect effects in especial trophic cascades have received even less theoretical attention (Fussmann et al., 2007), although this type of evolution may be common and important to the outcome of species interaction and evolutionary change. More importantly, when indirect effects such as trophic cascades are incorporated into evolutionary theory, they can provide new approaches to understand the structure and functioning of ecosystems. Although more about ecological consequences caused by trophic cascades have been well acknowledged (Pace et al., 1999; Knight et al., 2005), the evolutionary consequences have developed very slowly and less is known about the difference of between the evolutionary outcomes induced density-mediated and trait-mediated effects.

Body size, one of the most obvious features and fundamental characteristics of any organism (Loeuille and Loreau, 2006), captures many aspects of the ecology of a species and is related to physical activities, biological rates, evolutionary patters, and population characteristics (Cohen et al., 2003; Woodward et al., 2005; Brose et al., 2006). Moreover, many life-history traits are correlated with body size. The evolution of body size has potentially profound effects across multiple scales of biological organization from individual to ecosystem and has important implications for interaction strengths, population dynamics, and eventually the structure and functioning of food-webs and other ecological networks (Brose et al., 2006; Loeuille and Loreau, 2006; Woodward et al., 2005). There have been a growing body of empirical researches focusing on the evolution of body size (Doebeli and Dieckmann, 2000; Zu et al., 2010; Loeuille and Loreau, 2006; Walsh and Reznick, 2008, 2010). However, fewer theoretical studies demonstrate the potential for evolution of body size in response to indirect effect in trophic cascade system.

Existing evolutionary dynamic models are usually classified into two categories. One is quantitative trait (QT) model originally proposed by Lande (Lande, 1976). This approach assumes the ecology and evolution occur at the same time scale, and the dynamic equation of trait can often be incorporated into the ecological models (Fussmann et al., 2007). The other is the so-called adaptive dynamics (AD) model (Geritz et al., 1998), which assumes that evolutionary and ecological dynamics occur on different time scales and evolutionary processes are slower than the ecological processes. This theoretical approach has been proved to be a useful framework to model the evolution of quantitative traits and to study the long-term evolutionary outcomes of a small mutation in the traits expressing the phenotypes (Dieckmann and Law, 1996; Doebeli and Dieckmann, 2000; Diekmann, 2000; Zu et al., 2010, 2011). Recently, some advances have been made by incorporating body size into theoretical models (Doebeli and Dieckmann, 2000; Zu et al., 2010; Brännström et al., 2011). Further studies need to explicitly consider community interactions to more accurately quantify the evolutionary dynamics, particularly associated with indirect effects.

Motivated by the above considerations, the principal aim of this study is to theoretically investigate the trait evolution in response to indirect effects in a trophic cascade system and to expound the evolutionary consequences of density-mediate and trait-mediate indirect effects. We consider a three-species food chain (predator-consumer-resource), where predators eat their prey, reduce the abundance of consumers, which indirectly increase the abundance of the resource species at the lowest trophic level or the bottom of the food chain (i.e., trophic cascades). An ecological model is constructed with the help of Lotka-Volterra theory and then its dynamics are well explored. The trophic cascade model is based on a hierarchy among species and body size is a good candidate to explain this hierarchy. So, the body size is selected as the single key biological trait subject to evolution. Based on the quantitative trait approach, we formulate a rapid evolutionary model to investigate the influence of the rapid evolution and density-mediate indirect effect on the trait evolution and population dynamics. Then, with the help of the adaptive dynamics approach, we develop a long-term evolutionary model to elucidate the effect of the long term evolution and trait-mediate indirect effect on the trait evolution of consumer. In order to clarify the influence of indirect and direct effect, we further investigate the evolutionary dynamics of consumer-resource model (predator is assumed to be absent), predator-consumer model (resource is set to be constant), and predator-consumer-resource model.

2. Model formulation

In this section, we develop two modeling approaches to investigate the evolution of the consumer trait (i.e., body size) in response to the indirect cascade effects of predation on resource availability, and how the density-mediated vs trait-mediated effects works on the tri-trophic cascades dynamics. The first approach employs a quantitative genetic framework (Lande, 1976; Fussmann et al., 2007) to consider the rapid evolution of consumer body size in response to the indirect effect in the trophic cascade system. This approach allows us to examine both the effect of rapid evolution on population dynamic and explore the evolutionary outcomes in response to density mediated indirect effect. The second approach uses the adaptive dynamics framework (Dieckmann and Law, 1996) to expound the evolutionary dynamics of the consumer trait. In this approach, we assume that the evolution is slow process and investigate the long term evolution of the consumer trait (i.e., body size) in response to the indirect effect of predation on resource availability. This approach allows us to examine the evolutionary outcomes due to trait-mediated indirect effect.

2.1. The ecological model

Consider a simple ecological community or food chain with three trophic levels, a resource species, a predator species, and an intermediate consumer species. Let R, C, P be the densities of the resource species, the intermediate consumer species, and the top