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Natural enemy diversity and biological control: Making sense of the context-dependency

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Abstract

Numerous studies have demonstrated that diverse predator assemblages can be more effective at controlling prey populations. Yet, other studies have shown no effect of predator diversity on prey mortality, or even negative effects (for example due to intraguild predation or interference). Much research emphasis has been placed on the traits of predators that maximise functional complementarity. However, comparatively less attention has been paid to the traits of the prey or habitat that may maximise predator diversity effects, even though there must be a variety of prey niches available to be partitioned in order for niche complementarity to occur. Following this logic, we review six hypotheses for when diverse enemy assemblages should be most effective: when 1) prey communities are diverse; 2) prey have complex life cycles; 3) prey are patchily distributed in space or time; 4) studies are conducted at larger spatial and temporal scales; 5) plant structures are complex; 6) prey are abundant. Many of these hypotheses lack direct tests, particularly in agricultural systems, but we find little or no direct or indirect support for hypotheses 1, 4, 5 and 6. However, previous work does provide some support for hypotheses 2 and 3. We discuss methods to test these hypotheses directly, and suggest that natural enemy diversity may only benefit the biological control of arthropods in heterogeneous systems.

Zusammenfassung

Zahlreiche Studien haben gezeigt, dass diverse Räubergemeinschaften Beutepopulationen effektiver kontrollieren können. Andere Studien haben dagegen keinen Effekt der Räuberdiversität auf die Beutemortalität nachweisen können oder sogar negative Effekte gefunden (z.B. durch Prädation innerhalb der Prädatorengilde oder Interferenz).

Besonderes Augenmerk hat die Forschung auf die Merkmale von Räubern gelegt, die die funktionale Komplementarität maximieren. Vergleichsweise geringe Aufmerksamkeit wurde indessen den Merkmalen der Beute und des Lebensraumes geschenkt, welche die Auswirkungen der Räuberdiversität maximieren, auch wenn eine Auswahl von zu verteilenden Beutenischen vorhanden sein muss, damit Nischen-Komplementarität auftreten kann.

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Dieser Logik folgend besprechen wir sechs Hypothesen dazu, wann diverse Räubergemeinschaften am effektivsten sein sollten, nämlich 1) wenn die Beutegemeinschaften divers sind, 2) wenn die Beuteorganismen komplexe Lebenszyklen aufweisen, 3) wenn die Beute ungleichmäßig in Raum und Zeit verteilt ist, 4) wenn die Untersuchungen auf größeren räumlichen oder zeitlichen Skalen durchgeführt werden, 5) wenn die Pflanzen strukturell komplex sind, 6) wenn die Siedlungsdichte der Beutetiere hoch ist.

Für viele dieser Hypothesen gibt es keine direkten Tests, insbesondere keine aus Agrarökosystemen, aber wir finden wenig oder keine direkte oder indirekte Unterstützung für die Hypothesen 1, 4, 5 und 6. Dagegen gibt es aus vorhandenen Arbeiten einen gewissen Rückhalt für die Hypothesen 2 und 3.

Wir diskutieren Methoden, diese Hypothesen direkt zu testen, und formulieren die These, dass die Diversität natürlicher Gegenspieler die biologische Kontrolle von Arthropoden nur in einer heterogenen Umgebung begünstigen sollte.

Keywords: Biodiversity; Ecosystem functioning; Niche partitioning; Pest; Agriculture; Insect; Parasitoid; Management; IPM; Intraguild predation; Habitat complexity; Heterogeneity

Introduction

Predation is an important structuring force in ecological communities (note, here we use the term "predator" analogously to "natural enemy", as the hypotheses we present apply equally to parasitoids). Each prey species often faces a number of different predator species, the impacts of which may be non-additive (Sih, Englund, & Wooster 1998; Casula, Wilby, & Thomas 2006; Letourneau, Jedlicka, Bothwell, & Moreno 2009). In addition to being interesting in their own right, these emergent multiple predator effects (MPEs) have received heightened interest with respect to the biological control of pests, as they may inform the introduction of multiple control agents (Hochberg 1996; Stiling & Cornelissen 2005), or determine whether conservation of natural enemy diversity is congruent with pest suppression (Straub, Finke, & Snyder 2008). More recently, expanding research on the biodiversity–ecosystem functioning relationship (Hooper et al. 2005) has provided a broader theoretical context for MPE research, identifying mechanisms whereby diverse enemy assemblages may be expected to better control their prey (Ives, Cardinale, & Snyder 2005; Duffy et al. 2007). For example, functionally diverse predator guilds may be able to partition the prey resource by attacking in different ways or at different points in space and/or time (i.e. niche complementarity; Loreau 1998), thereby allowing diverse predator assemblages to more effectively control prey. Indeed, numerous studies have observed a positive relationship between predator diversity and arthropod prey suppression (e.g., Aquilino, Cardinale, & Ives 2005; Wilby, Villareal, Lan, Heong, & Thomas 2005; Snyder, Snyder, Finke, & Straub 2006; Tylianakis, Tscharntke, & Klein 2006; Finke & Snyder 2008; Snyder, Finke, & Snyder 2008; Straub & Snyder 2008; Veddeler, Tylianakis, Tscharntke, & Klein 2010), and these predator diversity effects may even increase crop yield significantly (Cardinale, Harvey, Gross, & Ives 2003). Yet, despite this empirical support and theoretical underpinning, a number of studies have shown either no effect (e.g., Rodriguez & Hawkins 2000; Finke & Denno 2002; Sokol-Hessner & Schmitz 2002; Montoya, Rodriguez, & Hawkins 2003; Wilby et al. 2005; Straub & Snyder 2006), or even a negative effect (e.g., Finke & Denno 2004; Finke & Denno 2005) of predator diversity on arthropod prey suppression (see also Sih et al. 1998 for a review of earlier studies), and these effects can even reduce crop yield (Cardinale, Srivastava, et al. 2006). Understanding this context-dependency in the effects of natural enemy diversity (Schmitz 2007; Bruno & Cardinale 2008) will be crucial for predicting the success of multiple biological control agents, and understanding whether conservation of enemy diversity and biological control are compatible aims (Straub et al. 2008).

A considerable amount of research has examined the characteristics of natural enemy guilds that drive positive predator diversity effects. For example, niche complementarity could drive an increase in prey suppression when predator species differ in their density-dependence (Teder, Tanhuanpaa, Ruohomaki, Kaitaniemi, & Henriksson 2000), foraging location (Losey & Denno 1998; Schmitz 2007; Straub & Snyder 2008), hunting mode (Schmitz 2007) or prey life stage attacked (Wilby & Thomas 2002). There has been considerable interest in how these different mechanisms may operate in diverse enemy assemblages, and how positive or negative interactions among species may determine the range or direction of diversity effects (see e.g., reviews by Casula et al. 2006; Bruno & Cardinale 2008). A recent meta-analysis of biodiversity effects across trophic groups suggested that the identity of the most productive species can dominate the effects of biodiversity (Cardinale, Weis, Forbes, Tilmon, & Ives 2006). This finding, in accordance with the so-called 'sampling effect', mirrored that of Denoth, Frid, and Myers (2002), who found that a single species was responsible for more than half of the successful multi-enemy biological control efforts they reviewed. Similarly, a review by Straub et al. (2008) emphasised the importance of predator identity and traits that maximise complementarity. In contrast to these previous syntheses, less emphasis has been placed on the traits of the prey species or their habitat that make them more or less susceptible to the effects of multiple enemy species. Here we take a step away from the traits of predators that enhance diversity effects, and instead discuss the traits of pests or crop