



Influence of relative abundance and taxonomic identity on the effectiveness of generalist predators as biological control agents

Carlo R. Moreno^{*}, Scott A. Lewins¹, Pedro Barbosa

Department of Entomology, University of Maryland, College Park, MD 20742, USA

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ABSTRACT

A central yet relatively untested assumption of conservation biological control is that an assemblage of naturally occurring natural enemies is more effective at controlling pests than any individual species within the assemblage. However, often ignored in this assumption is that natural enemies typically vary in relative abundance, such that one or a few species are highly abundant while most are relatively scarce. Little is known of the combined roles of relative abundance and taxonomic identity in the mortality imposed by assemblages of natural enemies on pest species. We investigated the influence of relative abundance and taxonomic identity among three generalist arthropod predators found in collards (*Brassica oleracea* var. *acephala*) on the mortality of the imported cabbageworm, *Pieris rapae*. We altered the relative abundance of the generalist predators in experimental mesocosms and determined the mortality of 1st instar cabbageworms. The impact of relative abundance on cabbageworm mortality was mediated by the taxonomic identity of the highly abundant predator. Further, the level of mortality imposed by highly abundant predators was in some cases influenced by the occurrence of intraguild predation involving less abundant predators. Our results suggest that the success of management strategies involving the preservation of highly abundant predators in managed systems via conservation biological control tactics may be dependent on the identity of both the highly abundant and scarce natural enemies.

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1. Introduction

With several studies reaffirming the effectiveness of generalist arthropod predators as biological control agents (Settle et al., 1996; Holland et al., 1996; Chang and Kareiva, 1999; Symondson et al., 2002), the role of naturally occurring assemblages of generalist predators in suppressing pest populations has recently gained more attention. The putative importance of predator assemblages is particularly prominent in conservation biological control, where the central objective is to enhance pest mortality by preserving natural enemy communities present in managed habitats, primarily through cultural, agronomic, and ecological practices and manipulations (see Barbosa, 1998). While it has been shown that multiple predators can reduce pest populations more effectively than single species (Cardinale et al., 2003, 2006; Straub and Snyder, 2006; Snyder et al., 2006, 2008), there also is growing evidence that negative interactions such as intraguild predation and mutual interference can significantly dampen multi-enemy impacts rela-

tive to single, effective predator species (Rosenheim et al., 1993; Finke and Denno, 2004, 2005). Currently, there is increasing interest in identifying the “right” kind of natural enemy diversity needed to promote positive, pest suppressing interactions. However, despite numerous advances in identifying mechanisms by which natural enemy diversity enhances herbivore suppression as well as predator traits that directly or indirectly influence multitrophic interactions (Schmitz, 2007; Straub et al., 2008; Straub and Snyder, 2008; Letourneau et al., 2009), little has been done to clarify the role of relative abundance among multiple predators in regards to the mortality they collectively impose on pests.

Communities or assemblages of both plants and animals are generally characterized as having only one or a few species that are relatively abundant (i.e., numerically dominant), whereas the majority of the members of the assemblage are relatively scarce (i.e., numerically subdominant) with many of them occurring as singletons (Sugihara, 1980; Paarmann et al., 2001; Barbosa et al., 2005; McGill et al., 2007). The significance of sampling intensity as well as both stochastic (e.g., dispersal, local extinction) and deterministic (e.g., interspecific competition and other biotic interactions) factors in structuring communities and species abundance patterns has been the subject of many papers (Novotny and Basset, 2000; Ulrich, 2005; de Bello et al., 2007; Coddington et al., 2009). Nevertheless, many of the studies that have evaluated the impacts

^{*} Corresponding author. Present address: Department of Environmental Studies, University of California, Santa Cruz, CA 95064, USA. Fax: +1 831 4594015.

E-mail address: crmoreno@ucsc.edu (C.R. Moreno).

¹ Present address: Department of Plant and Soil Sciences, University of Vermont, Burlington, VT 05405, USA.

of natural enemy diversity on pest suppression have focused or utilized assemblages comprised of species of equal abundance (Cardinale et al., 2003; Finke and Snyder, 2008; Straub and Snyder, 2008). Furthermore, while the importance of relative abundance in assemblages and communities has been theoretically and empirically explored in many unmanaged habitats (see McGill et al., 2007 and references therein), the consequences of the pattern of relative abundance to the nature and outcome of interactions among predators in assemblages in managed habitats (and thus to the mortality imposed on pests) are still unclear.

Given that the interplay of positive and negative interactions in generalist predator assemblages can be a significant determinant of predator assemblage effectiveness (Snyder and Ives, 2001; Prasad and Snyder, 2004; Finke and Denno, 2004), it is important to determine how numerically dominant and subdominant predator species interact and collectively impact prey populations. Interactions among predators may be additive, whereby the total impact of an assemblage would be equal to the summed impacts of each species in the assemblage (Snyder and Ives, 2003). Alternatively, the impact of an assemblage may be positively non-additive; i.e., the combined mortality imposed on prey by all predator species is greater than the summed impact of each individual species. The enhanced impact is generally attributed to complementary resource use among predators (Soluk and Collins, 1988; Wilby et al., 2005; Casula et al., 2006) or functional synergism (Losey and Denno, 1998; Straub and Snyder, 2008). Obviously, the latter two types of interactions enhance the potential impact of predators. However, non-additive interactions also may be antagonistic and may lead to lower levels of pest suppression. This type of interaction includes intraguild predation and mutual interference (Rosenheim et al., 1995; Lang, 2003; Prasad and Snyder, 2004). Despite the potentially negative effects of intraguild predation, predator assemblages can still effectively reduce pest numbers when negative interactions occur (Snyder and Ives, 2003).

In addition to relative abundance, the taxonomic identity of predators in an assemblage also may be important because each species can vary in their effectiveness in finding, capturing and killing prey (Lundgren et al., 2006; Bologna, 2007). Depending on the differences in effectiveness among predator species in imposing mortality on prey, three intuitive yet contrasting assumptions can be made. The first is that the numerically dominant predator, regardless of taxonomic identity, imposes more prey mortality than an assemblage and is thus the key regulator of pest populations. This assumption relies on the expectation that predator abundance is tightly linked to its level of resource (prey) capture and consumption. The second assumption is that the taxonomic identity of the numerically dominant predator is important in determining whether it imposes more mortality than an assemblage. The third is that the numerically dominant predator imposes equal or less pest mortality than an assemblage. These last two assumptions suggest that (1) the numerically dominant species may be a significantly inferior predator on a given prey species (i.e., imposes less prey mortality) relative to the numerically subdominant species, (2) predator abundance is not necessarily linked to resource consumption, and (3) the foraging modes of the numerically dominant and subdominant predators may be complementary or otherwise synergistic thereby leading to positive, non-additive emergent impacts. Therefore, relative abundance and/or identity may be central factors determining the nature of interactions among multiple predator species, which in turn can enhance or diminish the ability of predator assemblages to suppress pest populations.

In this study, we investigated the importance of relative abundance and taxonomic identity of generalist species in a predator assemblage in collards (*Brassica oleracea* (Linnaeus)) on the mortality imposed on the imported cabbageworm, *Pieris rapae* (Linnaeus),

a major pest of cole crops. We tested two hypotheses, (1) regardless of identity, the numerically dominant species alone will impose greater *P. rapae* larval mortality than that imposed by an assemblage of generalist predators, and (2) the identity of the numerically dominant species determines whether it will impose greater *P. rapae* larval mortality alone than when part of an assemblage of generalist predators. Our study differs from recent works investigating the relationship between predator diversity and prey mortality in that we focus on two components of biodiversity, taxonomic identity and relative abundance. The results presented will expand our understanding of predator assemblages and their potential usefulness in management strategies such as conservation biological control.

2. Materials and methods

2.1. Sampling of foliar arthropod predators in collards

In Maryland collard fields, we found a species-rich assemblage of foliar arthropod predators that followed the pattern of relative abundance distribution described above, in that a few predator species were numerically dominant while most others were subdominant (Fig. 1, Table 1). Predators were sampled at collard (var. Vates, Meyers Seed International Inc, Baltimore, MD) plots established at the Wye Research and Education Center (Queens-

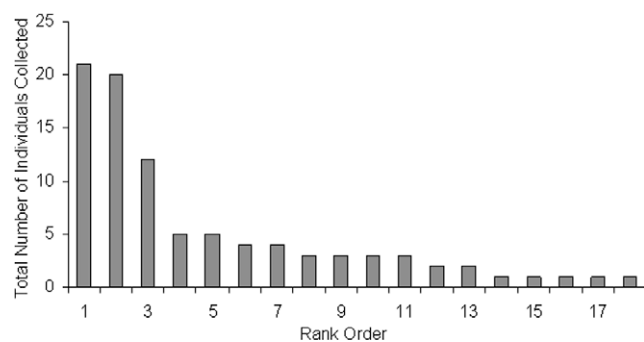


Fig. 1. Total number of foliar individuals of each species/morphospecies collected in Maryland collard fields from June–August 2004. Numbers on the x-axis represent the rank order of the species/morphospecies from most to least abundant. The names of all species/morphospecies are listed by rank order in Table 1.

Table 1

Taxonomic authorities and rank order of foliar arthropod predators collected in Maryland collard fields during June–August 2004. Underlined species refer to the predators used in this study.

Taxa	Rank order
<i>Nabis roseipennis</i>	1
<u><i>Coleomegilla maculata</i></u>	2
Tetragnathidae morphospecies 1	3
Lycosidae morphospecies 3	4
<i>Lygus lineolaris</i>	5
Araneidae morphospecies 3	6
<u><i>Coccinella septempunctata</i></u>	7
Lycosidae morphospecies 1	8
Araneidae morphospecies 2	9
Salticidae morphospecies 1	10
<u><i>Podisus maculiventris</i></u>	11
Salticidae morphospecies 2	12
<i>Chailognathus marginatus</i>	13
Lycosidae morphospecies 2	14
Thomisidae morphospecies 1	15
Lampyridae morphospecies 1	16
<i>Tetramorium</i> sp.	17
Syrphidae morphospecies 1	18

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