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Aphid parasitoids respond to vegetation heterogeneity but not to fragmentation scale: An experimental field study

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Abstract

How animal populations respond to habitat manipulations is a central theme in ecology. In recent years, the role that vegetation heterogeneity plays in regulating arthropod populations has received particular attention in both conservation science and agricultural ecology. Numerous observational studies have demonstrated that herbivores and their natural enemies are sensitive to vegetation heterogeneity, but the individual effects of percentage land cover, degree of fragmentation and patch size remain little understood. We present here the results of a manipulative field experiment that explicitly incorporates both habitat heterogeneity and the degree to which that heterogeneity is fragmented in order to determine the effects of each factor on parasitism in an agroecosystem. We deployed combinations of broccoli (crop) and weedy vegetation (non-crop) in linear arrays that varied in their percentage devoted to crop and in the degree at which crop patches were fragmented with weeds, and recorded parasitism rates on two aphid species multiple times during two years. Parasitoids responded to the percentage of crop in plots, but not to the spatial scale at which they were fragmented. Our results suggest that vegetation heterogeneity may be more important than fragmentation scale in biological control by parasitoids.

Zusammenfassung

Wie Tiere auf Veränderungen ihres Lebensraumes reagieren ist ein zentrales Thema der Ökologie. In den letzten Jahren hat die Rolle, die die Heterogenität der Vegetation bei der Regulation von Arthropodenpopulationen spielt, in Naturschutzbiologie und Agrarökologie besondere Aufmerksamkeit erfahren. Zahlreiche beobachtende Studien haben gezeigt, dass Herbivoren und ihre natürlichen Gegenspieler empfindlich auf die Heterogenität der Vegetation reagieren, aber die einzelnen Effekte von prozentualen Landschaftsanteilen, Grad der Fragmentierung und Anbauflächengröße blieben weitgehend ungeklärt. Wir präsentieren hier Ergebnisse eines manipulativen Freilandexperiments, welches explizit sowohl Habitatheterogenität als auch den Grad der Fragmentierung dieser Heterogenität einschließt, um die Einflüsse der beiden Faktoren auf die Parasitierung in einem Agrarökosystem zu bestimmen. Wir richteten Kombinationen von Brokkoli und Unkrautvegetation in linearen Anordnungen ein, die in Hinblick auf den Flächenanteil des Brokkoli und das Ausmaß der Fragmentierung der Brokkoliflächen durch Unkrautflächen variierten. Wir erfassten die Parasitierungsraten bei zwei Blattlausarten mehrmals innerhalb von zwei Jahren.

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Die Parasitoide reagierten auf den Flächenanteil des Brokkoli aber nicht auf die räumliche Skala der Fragmentierung. Unsere Ergebnisse legen nahe, dass bei der biologischen Schädlingsbekämpfung durch Parasitoide die Heterogenität der Vegetation wichtiger als die Skala der Fragmentierung sein könnte.

Keywords: Percent crop cover; *Diaeretiella rapae*; *Brassica oleraceae*; *Brevicoryne brassicae*; *Myzus persicae*; Foraging, Weedy vegetation

Introduction

A central theme in applied ecology is the role that landscape heterogeneity and fragmentation at different scales plays in the regulation of animal populations. In both conservation science and agricultural ecology, understanding how habitat patchiness influences species interactions has been increasingly studied over the past two decades (Levin 1992; Haila 2002; Fahrig 2003; Hambäck & Englund 2005). In conservation science, zero-sum resource scenarios have inspired the "SLOSS" debate over whether a single large habitat patch is more effective at sustaining populations than several small patches comprising the same area (Gilpin & Diamond 1980; Wilcox & Murphy 1985; Simberloff 1988; Ovaskainen 2002). In agroecosystems, successful biological control relies heavily on understanding how both natural enemies and their prey respond to the spatial patterning of habitat patches within and around cultivated fields. Recent meta-analyses have demonstrated that the response of natural enemies to landscape complexity often differs greatly from that of prey (Chaplin-Kramer et al. 2011). Parasitoids, widely understood to be attuned to the spatial distribution of their hosts, offer an ideal opportunity to study the complex relationship of natural enemies to their prey and to vegetation patterning in agroecosystems.

Arthropod response to habitat heterogeneity has been intensively studied in agroecosystems over the past four decades; Root's (1973) work outlined two critical mechanisms aimed at explaining why more diversified landscapes may attract and sustain fewer herbivorous (pest) arthropods. His "resource concentration" hypothesis posits that herbivores may more easily find host plants embedded in monocultures than those in polycultures; furthermore, after colonizing host plants, herbivores are more likely to spend more time in monocultures than in polycultures. In his "natural enemies" hypothesis, Root posited that more diverse agroecosystems should harbor diverse prey and hence attract more natural enemies – thus exerting more predation pressure and subsequently more pest suppression in polycultures compared with monocultures (Root 1973). The importance of these two mechanisms, particularly with reference to the relationship of biodiversity and pest control, has been extensively debated and tested over the past several decades (Vandermeer 1989), with a recent renewed focus on "appropriate" vs. "inappropriate" landings (referring to host plant vs. non-host plant colonization) (Finch & Collier 2000, 2012). Several meta-analyses have documented an overall pattern of higher herbivore abundance in monocultures than in polyculture and higher natural enemy abundance in polyculture than in monoculture (Risch et al. 1983; Andow 1991; Altieri 1994; Tonhasca & Byrne 1994) – though the effects of vegetation diversity on both herbivorous insects and natural enemies are likely to be scale-dependent in many cases (Bommarco & Banks 2003). These studies provide valuable insights into overall patterns of arthropod response to vegetation heterogeneity, but they were all generated using meta-analyses of experiments designed to test differences between simple (monoculture) and complex (polyculture) habitats conducted at a variety of spatial scales. Here we describe a field experiment in which we explicitly address the relative importance of vegetation heterogeneity and the spatial scale at which that heterogeneity is deployed (fragmentation) on parasitism in a fully factorial design field experiment.

Over the past several decades, a spate of both theoretical and empirical studies have explored the relationship among parasitoids, their hosts, and vegetation heterogeneity at the landscape scale (hereafter "landscape complexity") in agroecosystems (Hassell & May 1973; Marino & Landis 1996; Menalled, Marino, Gage, & Landis 1999; Landis, Wratten, & Gurr 2000; Bianchi, Booij, & Tscharntke 2006; Marino, Landis & Hawkins 2006; Tscharntke et al. 2007; Letourneau, Bothwell Allen, & Stireman 2012). Many of these studies have focused on parasitoid foraging and oviposition behavior in response to agroecosystem vegetation diversity, with an emphasis on resource subsidies (Casas 1989; Heimpel & Jervis 2005; Lavandero et al. 2005; Lee, Andow, & Heimpel 2006; Lee & Heimpel 2008; Bianchi & Wäckers 2008). Spatial dissociation of resources important to parasitoid survival (e.g., floral resources, alternative hosts) may affect parasitism rates in diversified landscapes (Banks, Bommarco, & Ekbom 2008; Vollhardt, Bianchi, Wäckers, Thies, & Tscharntke 2010; Ramsden, Menéndez, Leather, & Wäckers 2015). To date, most studies where vegetation heterogeneity has been explicitly considered have been observational rather than manipulative (Vollhardt et al. 2010; Scheid, Thies, & Tscharntke 2011; Gagic et al. 2011, 2012). Furthermore, most of these studies assume that habitat fragmentation increases as the percentage of the landscape devoted to crop decreases – but these factors of scale and fragmentation have seldom been teased apart (but see Thies & Tscharntke 1999; Plećaš et al. 2014).

Because migration rates of both parasitoids and their hosts may depend on patch size (Sheehan & Shelton 1989), we