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Habitat linkages in conservation biological control: Lessons from the land–water interface

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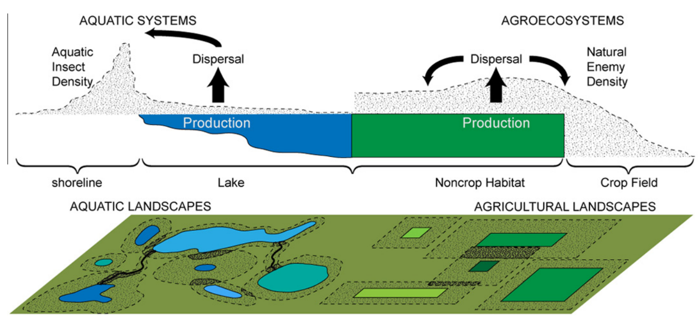
HIGHLIGHTS

- Aquatic–terrestrial and crop–noncrop linkages are conceptually similar.
- Exchanges in agroecosystems are governed by natural enemy production and dispersal.
- Donor habitats on the landscape determine the coverage of dispersal.
- Land-cover/use and climate change will impact habitats, natural enemy exchange.

GRAPHICAL ABSTRACT



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ABSTRACT

Terrestrial landscapes, including those with embedded agroecosystems, are a mosaic of cover types varying in size. Creating or maintaining habitats that support natural enemy populations to combat agricultural pests is the primary method of conservation biological control. Non-crop habitats can be managed in an attempt to maximize the exchange of natural enemies with adjacent agroecosystems with the expectation that they will suppress damaging pest outbreaks. Despite this goal, current habitat management relying on natural enemy spillover into crops has been unreliably effective at reducing pest abundance or increasing crop yield. Furthermore, the expansion and intensification of agriculture and changes in global climate patterns threaten the foundations of conservation biological control in future agroecosystems. However, the aquatic–terrestrial interface offers a natural boundary similar to the one between agroecosystems and their neighboring non-crop habitats that can provide useful insights to the challenges facing growers. Research of the exchanges between water and land suggests general biological and physical processes that govern the movement of organisms between disparate habitats. We propose that like aquatic insects moving from water to land, natural enemy dispersal from non-crop donor habitats into recipient crop patches on the landscape is a function of (1) the production of natural enemies in the source habitat which establishes the abundance of organisms that can disperse, (2) how and why mobile natural enemies disperse themselves into neighboring recipient habitats, and (3) the configuration of donor and recipient habitats on the landscape. We suggest that conservation biological control practitioners can focus on these main components of natural enemy production and dispersal to predict the effectiveness of conservation biological control measures and guide their adaptation to future global change.

1. Introduction

Agricultural landscapes are mosaics of crop fields, natural habitats, and urban areas (Tscharntke et al., 2002; Vasseur et al., 2013; Burkman and Gardiner, 2014; Chisholm et al., 2014). The

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juxtaposition of crop and non-crop habitats in agroecosystems creates the possibility for exchanges between them. From the perspective of growers, non-crop habitats may be the source of insect pests that infest crops (Carrière et al., 2004; Rusch et al., 2013). On the other hand, non-crop areas in landscapes can also be sources of beneficial species such as insect natural enemies that can help suppress damaging pest outbreaks (Jonsson et al., 2008; Landis et al., 2000).

Conservation biological control in agroecosystems largely depends on the natural occurrence of insect predators and parasitoids that act to depress pest populations. In their toolkit of approaches, biological control practitioners have relied on strategies aimed at increasing natural enemy abundance within crops (Kleijn et al., 2006; Landis et al., 2000), with the anticipation that this will prevent pests from reaching densities that lead to significant yield loss. Central among these strategies is capitalizing on non-crop habitats in the agricultural landscape, either those naturally-occurring or intentionally-created at both field and landscapes scales, as sources of natural enemies that can move into crop fields and in turn suppress pest populations (Landis et al., 2000).

Although general theory supports the notion of conservation biological control (Landis et al., 2000), in practice few studies have demonstrated that the availability of non-crop habitats in the agricultural landscape can decrease pest pressure and increase crop yields (Bianchi et al., 2006; Griffiths et al., 2008; Veres et al., 2013). Potential explanations for the mismatch between the demonstrated benefits of habitat conservation on natural enemy abundance and diversity (Letourneau and Bothwell, 2007; Samu et al., 1999) and crop protection may lie in other factors that limit or enhance the connectivity of crop and non-crop habitats through space and time (Schellhorn et al., 2008; Woltz et al., 2012). Understanding the key drivers of population abundance in source habitats, the degree of dispersal from these habitats, and the interactions between crop and non-crop patches on the landscape can help us determine under what specific conditions we may expect effective biological control to occur via conservation approaches (Tscharntke et al., 2012).

Conservation biological control fundamentally relies on the goal of linking habitats on a landscape through the movement of organisms. Understanding the attributes and features of habitat and ecosystem linkages is not new in ecology, especially at the interface of land and water (Ballinger and Lake, 2006). Research at the land–water interface has shown that transport of material and organisms across this boundary can be important to species interactions and ecosystem processes (Polis et al., 2004). For example, seaweed wrack deposited on marine island beaches by tropical storms increases the density of predators and herbivores (Piovia-Scott et al., 2011). Many studies at the freshwater–land interface show that aquatic insects are key resources for terrestrial predators such as spiders and lizards (Kato et al., 2004; Sabo and Power, 2002a), often boosting their abundances (Jonsson and Wardle, 2009; Sabo and Power, 2002a). Thus, through their effects on shared predators, the movement of insects from water to land or vice versa can indirectly affect predation on organisms in the recipient habitat (Baxter et al., 2005). These impacts are most prevalent close to donor habitats. Studies of insect emergence from lakes and streams suggest that aquatic insect density is almost always greatest directly adjacent to the water's edge, tapering off to background levels within tens of meters and following generalizable decay functions (Gratton and Vander Zanden, 2009) apparently governed by physical and biological characteristics of the water body and mobile organism.

But what does this have to do with conservation biological control? We argue that studies of linkages across the land–water interface provide a useful conceptual framework for understanding cross-habitat linkages. From studies of aquatic systems, we suggest that the flux of organisms from bodies of water (donor habitats) to land (recipient) is a function of (1) the production of mobile organisms in the source habitat through space and time, establishing the abundance of organisms that can potentially disperse, (2) the dispersal of these organisms into neighboring recipient habitat, and (3) the juxtaposition of donor and recipient habitats in a landscape. We contend that these factors occurring at the water-land interface are analogous to those operating among different terrestrial habitats within agroecosystems. Even though few emergent aquatic insects are predaceous as adults, the general tenets are applicable to mobile organisms at any trophic level. By drawing on these conceptual connections we can build on a rich body of ecological theory and empirical research to better inform our understanding of interactions in agroecosystems. In addition, this conceptual framework allows us to predict how conservation biological control may be affected by global environmental changes such as land-cover and land-use patterns or global climate change.

1.1. Environmental change and biological control

Well into the second decade of this century, humans are confronted with the prospect of environmental change outside of historical experience. To meet demand for food, we have expanded and intensified agriculture, now utilizing between one-quarter and one-third of the earth's net primary production and set to expand by a billion hectares by the middle of the century (Foley et al., 2005; Tilman et al., 2001). Land use development and fossil fuel combustion have increased the concentration of atmospheric greenhouse gases, raising global mean temperature and disrupting established climate patterns. Maintaining a system of agriculture that can feed billions without significantly degrading the biosphere is a major crisis facing agriculture in the 21st Century; difficult even without the destabilizing effects of environmental change.

The challenge of conservation biological control is to maintain or improve natural pest suppression as our landscapes and climate enter uncharted territory. Because conservation biological control relies strongly on the kind, amount, and placement of non-crop habitats in agroecosystems it is directly and indirectly threatened by the novel environmental context brought about by global environmental change. While there is considerable complexity and uncertainty inherent in how such changes will manifest themselves in space and time, by describing the major components of agroecosystems that support the production and dispersal of natural enemies, we hope to provide focus to individual or collective efforts to further pest suppression and ultimately create resistant and sustainable agriculture in an uncertain future.

2. Cross-habitat exchanges

2.1. Aquatic example from Lake Mývatn, Iceland

Our research at Lake Mývatn, Iceland provides an example of a strong connection between two neighboring ecosystems; in this case a highly productive lake and the adjacent shoreline (Dreyer et al., 2012; Gratton et al., 2008). Lake Mývatn is a large, shallow depression astride a geologically active region in northeastern Iceland (Thorarinsson, 1979). Warm (25 °C) subsurface springs rich in nutrients create an ideal mix that together with the shallow water (mean depth 3 m) and long day lengths promotes vigorous algal productivity (Einarsson et al., 2004; Thorbergsdottir and Gislason, 2004). This primary production feeds large numbers of insect secondary consumers in the lake, especially those consuming lake bottom algae. During years of peak production, the midge (Diptera: Chironomidae) density can reach 60,000 midges m^{-2}, or approximately 30 g dry weight m^{-2} yr^{-1} of secondary production