



Tools and techniques for investigating impacts of habitat complexity on biological control



Paul J. Chisholm^{a,*}, Mary M. Gardiner^b, Elliott G. Moon^a, David W. Crowder^a

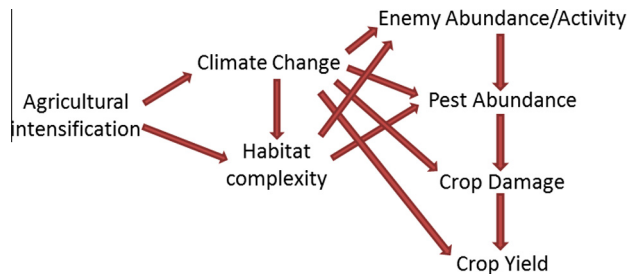
^a Department of Entomology, Washington State University, PO Box 646382, Pullman, WA, USA

^b Department of Entomology, Ohio State University, Columbus, OH, USA

HIGHLIGHTS

- Habitat diversity often increases the effectiveness of biological control.
- Many methods exist to measure biological control in response to habitat complexity.
- Researchers often define habitat diversity in different terms.
- New statistical, molecular, and digital technologies can aid research in this area.
- More standardized methodologies are needed for cross-study comparisons.

GRAPHICAL ABSTRACT



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ABSTRACT

Across the globe, landscapes are becoming altered as natural habitats are converted to agriculture or development. Consequently, a critical question is how changes in habitat complexity and composition might influence ecosystem services such as biological control. Although the development of new statistical, molecular, and digital technologies offers exciting opportunities to explore this issue, the appropriate usage of these tools is crucial to any successful study. This review examines the tools and techniques employed to investigate relationships between habitat complexity and biological control, and their appropriateness in different contexts. We examine various definitions of the explanatory variable, habitat complexity, and methods to experimentally measure the response variable, biological control. We conclude with a summary of the different statistical techniques available to assess linkages between habitat complexity and biological control. This review will facilitate future research on habitat complexity and biological control and will thus aid in the conservation of this valuable ecosystem service.

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1. Introduction

Current projections indicate that the global human population will exceed 9 billion people by 2050 (UN, 2009), and worldwide agricultural output will have to rapidly increase to avoid large-scale famine (Alexandratos, 1999). To meet rising demand for agricultural commodities, ever-increasing amounts of land are being cultivated. Between 1961 and 2009, global agricultural acreage

increased by 12% to 1.53 billion hectares (Fuglie and Nin-Pratt, 2012). Although conversion of land to agriculture has stagnated in the developed world, the Food and Agriculture Organization (FAO) projects that agricultural acreage will increase by another 12% in developing countries within the next 40 years (Bruinsma, 2009).

One consequence of agricultural intensification is a decline in habitat and faunal diversity (Vitousek et al., 1997; Siemann et al., 1998). This is concerning because many ecosystem services such as biological control lose functionality when biodiversity is degraded (Hooper et al., 2005; Crowder et al., 2010; Crowder and

* Corresponding author.

E-mail address: paul.chisholm@email.wsu.edu (P.J. Chisholm).

Jabbour, 2014). Consequently, many nations have enacted policies to promote natural habitat conservation in agroecosystems. In Europe, for example, many nations have devised “agri-environment schemes” to compensate farmers for productivity lost due to biodiversity preservation. However, habitat diversification under agri-environment schemes does not always lead to greater biodiversity (Kleijn et al., 2001, 2006). Moreover, recent meta-analyses suggest that although florally-diverse landscapes promote higher densities of invertebrate predators, pest abundances and crop yields do not always respond favorably to habitat diversification (Letourneau et al., 2011; Chaplin-Kramer et al., 2011).

These results indicate that there is much to learn about how habitat complexity influences biological control (see also Burkman and Gardiner, 2014; Dreyer and Gratton, 2014). Fortunately, recent advances in experimental and statistical techniques provide exciting new tools to investigate this topic. Molecular and digital technologies have expanded opportunities for characterizing and quantifying biological control, and recently developed statistical packages offer new tools for examining and defining habitat complexity across landscapes. Consequently, with so many new and emerging options available, choosing an approach can prove daunting. Here, we provide a comprehensive review of the experimental and analytical methodologies employed to investigate the relationships between habitat complexity and biological control. These techniques are critical to deconstruct the mechanisms by which climate change and agricultural intensification interact with biological control, both now and in the future.

2. What constitutes habitat complexity? Defining the explanatory variable

Before embarking on a study exploring effects of habitat complexity on biological control, investigators must first address the question: what does it mean for a habitat to be “complex?” There are many methods used to quantify habitat complexity, and it is important to account for these differences when making cross-study comparisons. First, complexity occurs at both local and landscape scales. Methods to augment local complexity include the preservation of field margins, intercropping, and trap-cropping, and effects of these schemes on biological control have been reviewed (Landis et al., 2000). However, comparatively few studies have examined the merits of various methods used to define habitat complexity across landscapes (often referred to as landscape complexity). Here, we outline and discuss several competing definitions of habitat complexity at a landscape scale. Moreover, we discuss the context(s) where they are appropriate, depending on the data available *a priori* to researchers (Fig. 1).

2.1. Structural habitat complexity

The majority of researchers define landscapes in terms of “structural habitat complexity”, which measures the different habitat types present in an ecosystem. One of the most common ways to characterize structural habitat complexity is to determine the percentage of semi-natural habitat in a landscape. For example, if one were interested in the diversity of natural enemies on a farm, one might calculate the proportion of natural habitat within a certain distance of the farm. The proportion of semi-natural habitat in a landscape is arguably the simplest metric of habitat complexity, and it is widely used in part because it is often correlated with Shannon's diversity index (Thies and Tschardtke, 1999; Steffan-Dewenter et al., 2002). Studies have found this metric is positively related to the abundance of natural enemy guilds including arachnids and predatory beetles (Purtauf et al., 2005; Drapela et al., 2008; Gardiner et al., 2009b, 2010). Moreover, semi-natural

habitat has been shown to be positively associated with natural enemy diversity, predation, and parasitism (Chaplin-Kramer et al., 2011).

However, the tendency to divide land cover types into discrete natural and agricultural categories, known as the habitat-matrix paradigm (Fischer and Lindenmayer, 2006), may be an oversimplification that fails to acknowledge variation among natural and agricultural habitats (Fabrigh et al., 2011). For example, Woltz et al. (2012) found low correlation between semi-natural habitat and Simpson's diversity index in landscapes in the north central United States. They hypothesized that the landscapes examined were functionally different than European landscapes, where many studies using proportion of semi-natural habitat as a measure of habitat complexity have been conducted. Fig. 2 illustrates why this metric may fail as an appropriate index of habitat complexity in some cases. Throughout Washington state, potatoes are generally grown in landscapes with 20% or less “natural” habitat. However, although the percentage of surrounding *natural* habitat is universally low, the complexity of *agricultural* habitats ranges from low to very high. In southern Washington, potatoes are often cultivated in a diverse mosaic of cropping systems, where up to 20 crops such as corn, alfalfa, apples, peas, and wheat are grown (Fig. 2a and b). In contrast, potatoes in north-central Washington are commonly grown in landscapes consisting of primarily wheat/fallow rotations (Fig. 2c and d). In this case, lumping all cultivated acreage into a “percentage agriculture” metric would ignore distinct differences between agricultural fields such as cropping type, management (organic vs. conventional), and permanence (perennial vs. annual). Consequently, a simple metric of non-agricultural habitat would not distinguish between the two landscapes illustrated in Fig. 2, despite the fact that these habitats may have dramatically different functional effects on pests and natural enemies.

Habitat complexity can be measured more directly using Simpson's or Shannon's diversity indices, patch richness (numbers of unique habitats), or patch evenness (the relative abundance distributions of habitats). Simpson's diversity index is calculated as $D = 1/\sum(p_i)^2$ where p_i is the proportion of habitat in the i th habitat category (Gardiner et al., 2009a). Shannon diversity index is computed as $-\sum p_i \times \ln(p_i)$. Both metrics increase with greater richness and evenness. Using these metrics, rather than proportion of non-crop area, provides a metric that in some cases may be more comparable across studies from different regions. For example, the potato field in Fig. 2 located in the wheat landscape has low diversity indices compared with the field in the complex landscape, despite them both having similar proportion of natural habitat. Each of these metrics can be calculated using computer packages such as Fragstats (McGarigal et al., 2012) or patch analyst (Rempel et al., 2012), which run on geographical information systems (GIS) platforms.

Finally, other authors have defined landscape categorizations more precisely, breaking down natural areas (Kruess and Tschardtke, 1994; Gardiner et al., 2009a; Werling et al., 2011) and croplands (Carriere et al., 2004, 2006) into more specific categories (e.g., forest, meadow, potatoes, wheat). This approach may be beneficial if certain crop types impact the community or process of interest, rather than broad-scale definitions of complexity. For example, Carriere et al. (2006) found that alfalfa, but not other crops, acted as sources for *Lygus hesperus* (Hemiptera: Miridae) pests into cotton fields. Had the authors simply looked at proportion of non-natural habitat, they may have missed this important source-sink effect. The biodiversity literature suggests that the presence of particular species is often more predictive of ecological processes than a broad measure of diversity (Cardinale et al., 2006), indicating that identifying effects of unique habitat types may be appropriate in many assessments of habitat complexity.

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