



# Climate change effects on behavioral and physiological ecology of predator–prey interactions: Implications for conservation biological control



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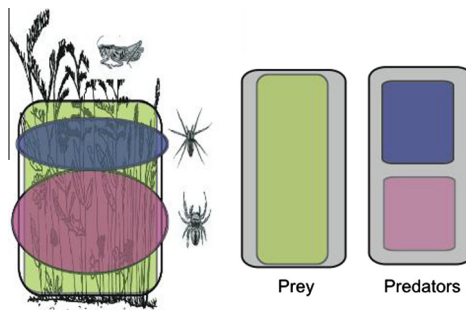
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## HIGHLIGHTS

- Habitat domain is a concept to understand predator and prey movement and interactions.
- Habitat domain can vary with other species present, thermal environment and plant structure.
- Global warming may alter species' thermal environment and species composition of communities.
- Habitat domain helps to forecast how climate change will alter predator and prey interactions.

## GRAPHICAL ABSTRACT

The habitat domain concept is a way of quantitatively representing predator or prey microhabitat choice and extent of spatial movement to predict contingent effects of environmental changes on predator–prey interactions.



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## ABSTRACT

Habitat management under the auspices of conservation biological control is a widely used approach to foster conditions that ensure a diversity of predator species can persist spatially and temporally within agricultural landscapes in order to control their prey (pest) species. However, an emerging new factor, global climate change, has the potential to disrupt existing conservation biological control programs. Climate change may alter abiotic conditions such as temperature, precipitation, humidity and wind that in turn could alter the life-cycle timing of predator and prey species and the behavioral nature and strength of their interactions. Anticipating how climate change will affect predator and prey communities represents an important research challenge. We present a conceptual framework—the habitat domain concept—that is useful for understanding contingencies in the nature of predator diversity effects on prey based on predator and prey spatial movement in their habitat. We illustrate how this framework can be used to forecast whether biological control by predators will become more effective or become disrupted due to changing climate. We discuss how changes in predator–prey interactions are contingent on the tolerances of predators and prey species to changing abiotic conditions as determined by the degree of local adaptation and phenotypic plasticity exhibited by species populations. We conclude by discussing research approaches that are needed to help adjust conservation biological control management to deal with a climate future.

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## 1. Introduction

The use of predatory species (defined as any natural enemy species including predators and parasitoids) is typically considered a

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laudable natural means to control damaging effects of herbivore prey that are pests on plants because it can reduce the widespread use of chemical pesticides (Landis et al., 2000; Letorneau et al., 2009). But, to be effective, biological control programs must ensure that there are suitable environmental conditions that will allow a diversity of predators to persist within agricultural landscapes (Landis et al., 2000; Crowder and Jabbour, 2014). To this end, conservation biological control is seen as an important ecologically based approach to support predatory species diversity through the creation and management of habitat conditions that provide alternative prey or hosts and suitable microclimates (Landis et al., 2000; Letorneau et al., 2009).

The idea of conservation biological control stems from the recognition that agricultural landscapes are difficult environments for predators in that they are under frequent and intense disturbance regimes that cause key resources to be unavailable at critical times in species' life cycles (Landis et al., 2000; Crowder and Jabbour, 2014). The ultimate goal of habitat management under the auspices of conservation biological control is to create conditions that ensure ecological interactions between predators and prey species can persist spatially and temporally within agricultural landscapes. The success of such habitat management is predicated on understanding the life-cycle timing between predatory species and their prey as well as how habitat structure and modifications influence predator–prey species interactions (Landis et al., 2000; Letorneau et al., 2009). And, indeed, considerable research effort has been dedicated to produce such understanding for extant agricultural environmental conditions (reviewed in Landis et al., 2000; Letorneau et al., 2009).

Nevertheless, such research has only recently begun to consider the potential effects of alterations in abiotic conditions (temperature, precipitation, humidity, wind, etc.) brought about by climate change. Changes in abiotic conditions have the potential to disrupt the life-cycle timing and the nature and strength of interactions among species of predators and prey (Schmitz et al., 2003; Tylianakis et al., 2008; Both et al., 2009; Thackeray et al., 2010; Traill et al., 2010; Tylianakis and Binzer, 2014; Welch and Harwood, 2014). Here we provide an overview of how climate change might influence the nature and strength of species interactions in communities to offer insight into how it could mitigate many current conservation biological control efforts. We identify the kind of mechanistic insight needed to begin developing a predictive framework for devising habitat conservation measures that will enable management to begin adapting to this emerging environmental stressor.

Offering a predictive mechanistic framework is challenging. It requires explaining the context dependency that arises from myriad potential idiosyncrasies in species interactions due to predator and prey identity and the nature of their habitat utilization (Straub et al., 2008; Schmitz, 2010; Tylianakis and Romo, 2010; Tylianakis and Binzer, 2014) as well as explaining how this context-dependency will change under climate warming. We propose that context-dependency can be addressed by first envisioning that predator and prey species are entangled in an adaptive game (Lima, 2002; Schmitz, 2010) in which predators commonly cause prey to undertake evasive strategies through behavioral means, to which predators respond with counteractions. The exact way predator and prey species interact depends on functional traits of predator species including body size, hunting modes, gape width, etc. (Schmitz, 2007, 2010; Straub et al., 2008; Northfield et al., 2012). It also depends on the mobility of prey, which is a function of their foraging traits (e.g., sedentary specialist sap-feeders, widely roaming generalist leaf chewers, etc.) and their vulnerability to predation by natural enemies (Schmitz, 2005, 2010; Tylianakis and Romo, 2010; Northfield et al., 2012; Klecka and Boukal, 2013). Thus, predator and prey species may interact with each

other in malleable ways in which predator and prey species make behavioral, physiological and morphological adjustments that change how they behave, where they live, and what they eat (Hawlena and Schmitz, 2010; Schmitz, 2010). Despite the seemingly dizzying complexity that such context-dependency introduces, we can begin to resolve it systematically using the concept of habitat domain (Schmitz, 2005, 2010; Northfield et al., 2012). This concept provides a basic framework for understanding how different predators and prey engage each other in interactions and how environmental change might alter the nature and strengths of those interactions.

## 2. Resolving complexity due to context-dependency: a framework

### 2.1. The concept of habitat domain

Habitat domain, which can be either narrow or broad (Fig. 1), differs from conventional ways of defining habitat use (e.g., microhabitat choice) in that it considers both microhabitat choice and the extent of spatial movement in space and time (Schmitz, 2005). The habitat domain concept helps to envision how a diversity of predator and prey species could overlap spatially, either along environmental habitat gradients or within the same habitat, or temporally within the same habitat due to synchrony (or asynchrony) in the timing of life-cycle development (Polis and Holt, 1992; Woodward and Hildrew, 2002; Welch and Harwood, 2014). Climate change could cause shifts in both spatial and temporal overlap as species seek out thermally more favorable spatial conditions or undergo shifts in their life-cycle development.

We illustrate how the habitat domain concept works by focusing here on predator species overlap within shared habitats, since there has been much empirical work exploring predator species interactions in such contexts (Schmitz, 2007). Predator habitat domain is determined to some extent by predator hunting mode because it determines the spatial extent of movement. Predators can be generalized into one of three main hunting modes (McLaughlin, 1989): (1) sit-and-wait or ambush, when a predator remains primarily motionless and attacks a prey only when it moves within immediate catching distance (e.g., praying mantids, web building spiders, nursery web spiders, damsel bugs); (2) sit-and-pursue, when a predator remains motionless until a prey moves within chasing distance (e.g., wolf spiders); and (3) active hunting, when a predator continuously moves through its environment to find, follow and chase down prey (e.g., jumping spiders, ground beetles, ladybeetles). Sit-and-wait predators have relatively narrow habitat domains. Sit-and-pursue and active hunting predators can have either narrow or broad habitat domains. Prey, especially insect herbivores, may have either broad or narrow habitat domains depending on their degree of movement (Schmitz, 2005, 2010) and the degree of specialization on plant species or plant parts (Straub and Snyder, 2006; Northfield et al., 2012). Habitat domain has much potential to be a useful way of conceptualizing and measuring how different predators and prey will interact with each other because it can address contingencies in outcomes (Schmitz, 2010; Northfield et al., 2012; Miller et al., 2013). Moreover, habitat domain size appears to be consistent among predators with similar hunting modes (Miller et al., 2013).

### 2.2. Quantifying a species' habitat domain

Habitat domain of predators and prey can be quantified by measuring vertical and horizontal spatial movements of individuals within the vegetation canopy during replicate daily activity cycles (Schmitz and Suttle, 2001; Schmitz, 2005, 2010). It requires

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