



Natural enemies on the landscape – Integrating life-history theory and landscapes



Bernard D. Roitberg^a, David R. Gillespie^{b,*}

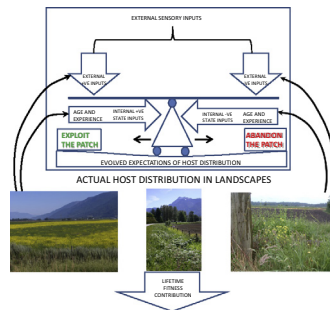
^a Evolutionary and Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada

^b Agriculture and Agri-Food Canada Research Centre, PO Box 1000, Agassiz, BC V0M 1A0, Canada

HIGHLIGHTS

- We propose a theory that connects patch-level foraging with landscape structure.
- This connection is often missing in biocontrol theory and practice.
- We embed conditional landscape descriptors into life-history theory.
- This allows prediction of optimal patch exploitation decisions.
- These can predict performance of biocontrol agents across variable landscapes.

GRAPHICAL ABSTRACT



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ABSTRACT

The relationship between patch exploitation by individual parasitoids and landscape levels of control by such parasitoids is complex and not well understood. Here we build on a classic concept of the structure function as a way of describing the landscape of a biological control agent from the agent's perspective. We include such structure functions into patch exploitation theory as way of connecting the two aforementioned levels. An important feature is that for any given focal individual, its resource-specific structure functions can differ dramatically in the environment; we explain how one might employ multivariate functions into our theory. Further, rather than employ these functions in a strictly descriptive manner we embed them in state-dependent life history. Parasitoid states include, eggload, energy state, mass and their impacts on the Darwinian fitness from patch exploitation. When taken together, our approach allows us to determine optimal exploitation decisions for agents across various landscapes and more importantly, to predict response of biocontrol agents to changes in landscape as a function of changes in agricultural practices. Finally, we show how these optimal decisions can be used to calculate pest-killing rates for biological control agents, and ultimately to facilitate the selection and management of agents.

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1. Introduction

The relationship between patch exploitation by individual parasitoids and landscape levels of regulation of host numbers by such

parasitoids, is complex and not well understood. Natural enemies interact with, and kill their target hosts at a patch level. In augmentative and classical biological control programmes, traits such as efficacy, host discrimination, intra-guild interactions, life history, and non-target interactions, are usually investigated at an individual or patch scale (e.g. Wajnberg et al., 2008 and chapters therein). Natural enemies evolve to optimize their individual, lifetime fitness within the context of patch variables (distribution and

* Corresponding author. Fax: +1 604 796 0359.

E-mail addresses: roitberg@sfu.ca (B.D. Roitberg), Dave.Gillespie@agr.gc.ca (D.R. Gillespie).

abundance of suitable hosts), and their distribution in the natal landscape. Important landscape variables include landforms, complex plant and animal communities, and spatial and temporal variation in abiotic factors such as temperature and rainfall (Welch and Harwood, 2014). Understanding how the individual and patch-level traits of natural enemies, which generally optimize fitness at the patch level, interact with landscape-level structure and processes, is essential to predicting and managing the impacts of biological control programmes on target and non-target organisms. This will become even more important as agricultural landscapes evolve due to changes in land use and agricultural practices, for example, the unprecedented move from small-scale family farms to large-scale industrial farms (Crowder and Jabbour, 2014). As these changes evolve, it is important to anticipate their impacts on natural enemies in the agricultural landscape. The typical approach is to seek correlations between performance and landscape parameters, but this can only be done on current landscapes (Burkman and Gardiner, 2014; Chisholm et al., 2014). Below, we develop a theory that connects the patch and the landscape within which it sits, which then allows us to move beyond existing data and ask “what if” questions. Note that our purpose is to develop a way of thinking about this scaling problem, and not to provide detailed analysis of a mathematical model.

1.1. Landscapes and individuals

Landscapes vary across space and time, at different scales. As natural enemies move through landscapes, they encounter positive (resources) and negative (risks) factors affecting individual fitness, in different proportions. Distributions of hosts or prey can change across time and space. Flowering of different plants can create variation in nectar availability in both time and space (Vollhardt et al., 2010; Welch and Harwood, 2014). Agricultural practices can disrupt the availability of hosts (Legrand et al., 2011). Crop rotations across seasons can change the proximity of crops containing key target pests, to critical overwintering habitat for natural enemies (Arrignon et al., 2007). Seasonal changes in weather can generate temperatures that impair interactions between natural enemies and their hosts within growing seasons and during overwintering periods (Bannerman et al., 2011; Gillespie et al., 2012; Hance et al., 2007). Thus, natural enemies must cope not just with landscapes, but with variable landscapes. Furthermore, organisms that feed on more than one resource must make complex resource-use decisions that balance fitness consequences of each (Rosenheim et al., 2010). Should individual natural enemies then exhibit adaptive behaviors that enhance lifetime fitness in the context of landscape-level variability, and more importantly, does this matter to the outcomes of biological control programmes?

Landscape studies are generally conducted on human scales, because that is what we see and measure. The abundance of weeds on farms, the proportion of natural habitat near to farms, or farming intensity, for example, are patterns that are easy to measure, and which are clearly correlated with natural enemy abundance and pest suppression (Chisholm et al., 2014). However, understanding the proximate mechanisms that cause these correlations requires understanding how individuals use landscape resources to maximize lifetime fitness. And this requires that we describe landscapes from the perspective of the natural enemy and its quest for resources.

The perceptual range of an animal (Olden et al., 2004) is the “spatial extent of the landscape for which information is available to make movement decisions”. Moreover, the perceptual range may be anisotropic – i.e. the attention of the individual may focus preferentially in one direction (Olden et al., 2004), as in upwind anemotaxis. For example, Roitberg and Prokopy (1982) showed that patch (tree) leaving decisions by frugivorous flies depended

upon distance to other patches. This view of the landscape is not necessarily one that is measured in landscape studies. Evidence and theory also suggest that the perceptual range will vary with natural enemy identity. Predators respond to different spatial scales than prey (Veres et al., 2013) and specialist natural enemies are influenced by landscape at a smaller scale than generalists (Chaplin-Kramer et al., 2011). Moreover, when balancing multiple resource needs (e.g. nectar vs prey), theory suggests that animals should forage preferentially on the resource that is most likely to limit fitness (Rosenheim et al., 2010) and this is likely to vary with state of the animal and time (Jervis and Ferns, 2004). Finally, like most animals, natural enemies likely use multiple modalities of perception (Hölldobler, 1999; Kulahci et al., 2008; Sabelis, 1994), vision, hearing, semiochemical senses, vibration, and each of these describes the landscape and the resources it contains, on different scales. Imagine a GIS map with different layers one for each modality but cross-referenced across mode and space. These different layers most likely integrate, providing the natural enemy with a Gestalt of the environment and the availability of resources (Hilker and McNeil, 2008; Schröder and Hilker, 2008).

It is well known that the host seeking and attack behavior of parasitoids and predators is determined in part by dynamic state variables such as egg load, age, and experience including perception of environmental signals (Wajnberg et al., 2008). These conditional, or dynamic behaviors allow natural enemies to optimize their lifetime fitness in response to the varying conditions they encounter in the landscape. Because we should be interested in the underlying mechanisms that generate observed responses to landscape complexity, it is important to consider the experience and perception of natural enemies as they move through the landscape.

1.2. Describing landscape structure

Semivariograms have been used to describe the distribution of resources on a landscape scale. Roitberg and Mangel (1997) used conditional semivariograms or structure functions (Mangel and Adler, 1994) to describe the likelihood of ‘prey’ encounter (rose hips) by the rosehip fly *Rhagoletis basiola* (Tephritidae), when moving through different landscapes. Semivariograms are a way of plotting autocorrelated data across distance. The slope of the semivariogram increases, or decreases, as points being compared become increasingly unrelated to the origin, and eventually converge on the environmental average for the measure being considered (Gustafson, 1998). Semivariograms describe, from a forager’s perspective, how resource availability changes as the forager moves from its current location, as described below.

Consider a predator that has just encountered prey that normally has a contagious distribution, such as aphids. The probability of encountering another aphid nearby is very high, and then declines to the average of the environment as distance increases (Fig. 1A). This describes the local prey landscape for that predator. If the predator were sitting at a location that did not have a prey, then the likelihood of finding a prey via movement would increase to the landscape average as the predator moved from its current point as in the dotted line in Fig 1A. In homogenous or fine-grained heterogeneous landscapes, all points beyond a certain distance from the current location would be equally likely to contain prey. In landscapes with large-scale structure, such as agricultural landscapes and disturbed habitats, there will be distances at which the likelihood of encountering a host is zero (Fig. 1B). At larger spatial scales this might occur at field margins. It is conceivable that for pests/hosts which accumulate on field margins, e.g. *Ceutorhynchus obstrictus* (Marsham) (Coleoptera: Curculionidae) in canola (Murchie et al., 1999), there would be an increased likelihood of encountering hosts at intermediate distances. At smaller spatial

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