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

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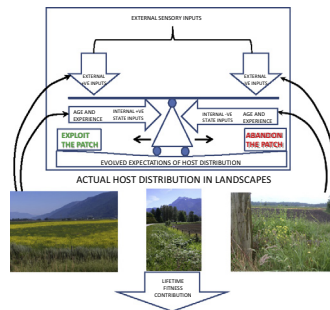
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HIGHLIGHTS

- 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

ARTICLE INFO

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

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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. Semiovariograms are a way of plotting autocorrelated data across distance. The slope of the semiovariogram 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). Semiovariograms 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
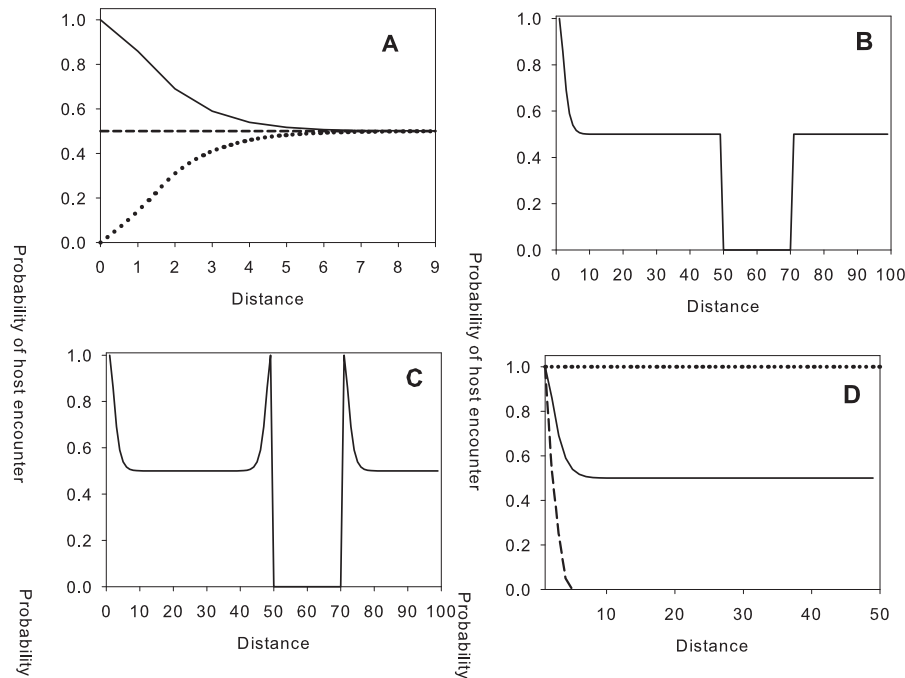
Fig. 1. Structure functions describing the probability of encountering a resource, for example, prey patches, at different landscape scales (*x* axis) assuming a natural enemy is in a patch of prey that show a contagious distribution at landscape scales. In (A), because prey patches are aggregated, over short distances the probability of encountering another prey patch declines to the local average, or in the case of an individual at a location without prey, increases to the local average as in the dotted line. In (B), assuming a disrupted distribution of prey resources, as might be found where there separate fields containing prey, the likelihood of prey encounter declines to zero. In (C), assuming aggregation of prey at field edges as occurs with many herbivores invading agricultural fields, the likelihood of prey encounter increases as the field edge is approached, declines to zero and then increases sharply at the next edge. In (D), resources such as nectar sources might be distributed at random as in the solid line, or, if present in structures such as insectary strips, might be anisotropic, with the likelihood of encounter declining quickly to zero perpendicular to the strip as in the dashed line, and remaining consistently high along the axis of the strip, as in the dotted line.

scales within row crops, important anisotropic effects might arise where probability of prey encounters would decline to a landscape average along rows as in the solid line in Fig. 1A, but across rows, present a step function appearance as in Fig. 1B. If pests accumulate at edges of crops as is the case in many crops then the probability of encountering a host may increase dramatically as the edge of a field is approached, as in Fig. 1C. Hosts are not the only resource that can be described by semiovariograms. If plants that have a contagious distribution provide the usual nectar source for a parasitoid adult then the solid line in Fig 1D would describe the probability of encountering another nectar resource for a parasitoid that is currently located on such a resource. If nectar resources are provided in flower strips as in some conservation biological control programs then the likelihood of encountering another nectar resource may be strongly anisotropic, with a constant likelihood on the long axis of the strip as in the dotted line in Fig. 1D and falling quickly to zero perpendicular to the long axis as in the dashed line in Fig. 1D.

Hosts or prey are only one dimension of landscapes that can be described by structure functions like the above. Elevation, plant diversity, distribution of essential non-host resources such as flower-derived nectar, and landscape permeability could all be described to some degree by semiovariograms (Gustafson, 1998). These describe the landscape in a general way in relation to a reference point. This reflects both the perceptual range of an organism, and the shape of the landscape that the animal expects to see. This makes semiovariograms particularly useful for thinking about landscape-level problems from the perspective of individual natural enemies. Recall, however, that much of the pest attack dynamics occur at the patch level. We briefly discuss patch level dynamics and then connect them to the landscape.

A fundamental feature of research into the behavior of parasitoids has been to understand the rules by which parasitoids exploit patches of hosts (Alphen et al., 2003). Patch-leaving decisions are particularly important in biological control because the efficiency with which parasitoids use patches of hosts translates directly to their impacts on pests. Patch leaving decisions are well-studied, but most, if not all, assume a flat "landscape" beyond the edge of the patch, as in Charnov (1976). By this, we mean that hosts and units containing hosts are assumed to be randomly distributed, and a movement by the parasitoid of any magnitude in any direction is assumed to yield an equivalent likelihood of host encounter. However, at the landscape scale, likelihood of host encounter changes with distance moved, and anisotropic effects come into play, i.e. the direction in which a natural enemy moves may yield very different outcomes. Hosts and plants containing hosts are not randomly distributed. Pests tend to be aggregated and the distributions of patches may have other structure imposed by the distribution of plants, as in orchards or row crops. Thus, semiovariograms can describe the landscape on leaving a patch from the perspective of a natural enemy, and offer a way to link landscape-level patterns and processes with the foraging behavior of individuals.

Parasitoids may use incremental or a decremental rules for deciding when to leave the patch (van Alphen et al., 2003), whereby encounters with healthy hosts either increase or decrease the likelihood that the parasitoid will leave the patch. The thresholds at which the patch is abandoned can be either fixed or modified by experience (Alphen et al., 2003; Jenner and Roitberg, 2009; Roitberg et al., 2010; Wajnberg, 2006). The mechanisms and their plasticity are in fact, a reflection of the expected distribution and occurrence of hosts (Iwasa et al., 1984; Jenner and Roitberg, 2009), other resources and constraints, and have been determined by natural selection (van Alphen et al., 2003). Where the rules for patch leaving are fixed, the parasitoid necessarily has an innate estimate of host density. More commonly the rules for patch

exploitation and leaving are plastic, and are modified, for example, by age, experience, extrinsic signals and intrinsic energy states (Boivin et al., 2004; Dauphin et al., 2009; Gardner et al., 2007; Goubault et al., 2005; Liu et al., 2009; Lucchetta et al., 2007).

2. Linking patches and landscapes

Given the current deep understanding of within-patch foraging decisions and their fitness consequences, we clearly need a way to link those decisions to the landscape. We borrow from the, largely causal, Dethier/Miller and Strickler (Miller and Strickler, 1984) rolling fulcrum model, which provides a very clever method for visualizing insect feeding decisions. The original model considered how external positive (e.g. plant nutrients) and negative (e.g. plant secondary compounds) stimuli determine expression of caterpillar behavior, i.e. accept or reject hosts, which is also based upon the position of a rolling fulcrum, which is further based on internal insect states. Patch-leaving decisions can be considered by using a similar kind of model (Fig. 2) however, note that we have added two important features to the model. First, unlike the original theory, we provide the common currency of fitness for the various stimuli, which is determined by life history theory. This allows one to directly compare disparate cues (e.g. host density vs risk from predation). Second, we provide another factor that determines the position of the rolling fulcrum, knowledge of the landscape (inherited or ascertained). Below we describe a functional approach that can be used to calculate landscape movement payoffs, again using the currency of fitness. For example, based upon evolutionary history, a low payoff for moving in particular landscapes would push the fulcrum to the left and reduce patch-leaving tendency.

A point that needs to be reemphasized is that predators or parasitoids that have evolved with particular kinds of prey, will evolve an expectation of the landscape for such prey and could readily evolve rules to exploit such distributions. By that we mean that natural enemies need not be omniscient to efficiently exploit prey. All such organisms would need is to evolve movement rules for exploiting patches and moving between patches (Ma et al., 2009). Thus predators that exploit prey that are highly contagious in distribution should evolve different exploitation rules than those that attack uniformly distributed prey, all else being equal. This obviates the need for instantaneous omniscience though it does suggest a kind of inherited knowledge. Of course, inherited estimates of landscape structure can be further modified by experience. For example, parasitoids might use host-patch odors or other signals to update their innate estimates regarding host patch densities (Louâpre et al., 2011; Roitberg et al., 2010) (see the recent literature on Bayesian updating (e.g. Thiel, 2011).

The discussion above shows how patch exploitation can be tied to the landscape; we also argued that patch exploitation rules will evolve based upon Darwinian fitness associated with such rules. We further suggested that natural enemies may vary their exploitation rules depending upon their expected landscape and their internal states (e.g. energy stores). The role of the scientist then is to uncover such rules and translate them into patch and landscape levels attack rates (see below). However, this demands that we understand how patch exploitation translates into fitness that then drives the evolution of exploitation rules.
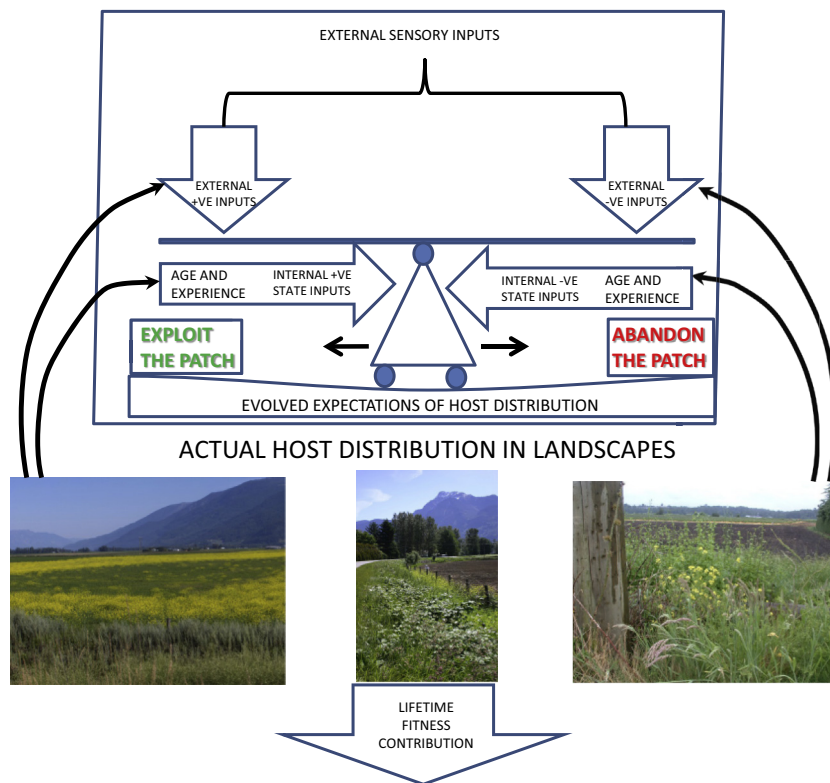

Fig. 2. Exploitation and abandonment decisions at the patch level have been previously conceptualized by Detier's rolling fulcrum model (Miller and Strickler, 1984). Here we extend the model to include the effects of landscape on conditional decisions and their outcomes. The resting position of the fulcrum is determined by the organism's evolved expectation of host distribution on landscapes, represented by a curved surface. The position of the fulcrum determines the relative influence of positive and negative influences on decision making, but this will tend to centralize because of the evolved expectations of host distribution. The positive and negative influences, i.e. the determinants of the conditional decision, are modified by external sensory inputs from the patch and the landscape, and by internal states from experience on the patch and the landscape. We illustrate three possible distributions of host plants, *Brassica* spp. possibly containing a hypothetical insect host.

Calculating lifetime fitness of a natural enemy is no easy task; however we can rely on the field of life history theory to help us in that regard (Roff, 1992; Stearns, 1992). Life history theory explains the schedule of key events in an organism's life (e.g. development, fecundity schedules, senescence, etc.) in terms of contribution to the population gene pool (fitness). Life history theory also considers tradeoffs. For example, time spent exploiting the current patch and eggs deposited therein will not be available for exploiting future patches of resources. Life history based evaluations are rarely made with explicit consideration to landscapes. That is a goal of the work described below. We provide novel theory to link life history to landscape for different resource spatial profiles. We will largely concentrate on host or prey resource profiles since we are interested in biological pest control but we will show how other resources (e.g. food) might play important roles in natural enemy efficacy.

3. A model linking life-history and landscapes

First, let us develop a general life history based foraging theory and then modify it according to landscape structure i.e. we develop a formal rolling fulcrum model as described above. We start with several assumptions that can be easily modified if necessary:

(1) Our focal biocontrol agent is an egg-limited, solitary, pro-ovigenic parasitoid.
(2) There is a large population of pests thus oviposition activities by an individual, focal parasitoid has no impact on subsequent encounter rates with those prey.
(3) The parasitoid can accurately estimate host density.
(4) The parasitoid can accurately estimate the structure function for the relevant resource (or has inherited such information).
(5) Different parasitoid activities (e.g. searching (m_S), ovipositing (m_O), moving (m)) have different survival values associated with them.
(6) Some time is required to move across the landscape. We describe this by a distance over velocity metric i.e. k_i/v where k_i is the distance moved under condition i.

We can build a model that incorporates landscape and life history following the lead of Roitberg and Mangel (1997) who developed theory for fruit flies searching on a landscape of rosebushes. Their model falls within the general classification of dynamic state variable models that have been championed by Mangel, Clark, McNamara and others for studying condition-dependent phenotypic plasticity (Houston et al., 1988; Mangel and Clark, 1988). These models can be used to calculate condition or state-dependent fitness in stochastic environments. Here, we consider the fitness accrued from expressing patch-exploitation behavior in different landscapes. Recall that there are two structure functions to consider, each representing a different condition, one where the wasp finds itself at a site devoid of hosts and a second where hosts are present. For the former, the following equation holds:

$$F_0(t, T; k_0, k_1, r) = (1-m)^{k_0/v}$$
$$\begin{bmatrix} p(k_0|0)F_1(t+k_0/v, T; k_0, k_1 r) \\ +(1-p(k_0|0))F_0(t+k_0/v, T; k_0, k_1, r) \end{bmatrix} \quad (1)$$

Our interpretation of Eq. (1) is as follows: on the left hand side, for a wasp at time t with some maximum length of life, T, that employs a strategy $[k_0, k_1, r]$ (i.e. move k_0 distance units from a site with no resources, k_1 distance units from a site with resources and apply r units of resource exploitation before moving – in this case, no hosts are present at the current site and no fitness can be accrued from exploiting the empty patch), the expected

reproductive success is detailed on the right hand side. Here there are three lines. The first line discounts future fitness by per-unit-time survival raised to the exponent time (distance over velocity) while traveling k_0 units. This is the chance of being alive in the future after having moved through the landscape matrix. The second line shows expected future fitness weighted by the probability of arriving at a host-occupied cell after having moved k_0 units. The third line shows expected future fitness weighted by the probability of arriving at an empty cell after having moved k_0 units from an empty cell. Notice that the future begins after time has been invested moving (k_0/v). Also, recall that the conditional probabilities are drawn from the structure functions.

Compare the expected fitness above with that of a parasitoid that finds itself at a site with resources.

$$F_1(t, T; k_0, k_1, r) = f(r) + (1-m_{O.r})(1-m)^{k_0/v}$$
$$\begin{bmatrix} p(k_1|1)F_1(t+m_O+k_0/v, T; k_0, k_1, r) \\ +(1-p(k_1|1))F_0(t+k_0/v, T; k_0, k_1, r) \end{bmatrix} \quad (2)$$

The major difference between Eqs. (2) and (1) is that in the latter there is the opportunity to derive fitness from exploiting resources at the current site according to resource exploitation function $f(r)$. In addition to the current fitness that will be accrued from attacking r hosts at the current patch, the agent can expect to accrue fitness in the future after moving k_1 units however that future fitness will be discounted by the probability of living into the future. Again, it is important to recall that the future fitness will also be determined by the distribution of resources across the landscape, which is defined by the structure functions k_0 and k_1, which are integral parts of the state variable models. This is our connection between patch and landscape, in a life history context.

Taken together, there is an optimal strategy set $[t; k_0, k_1, r]^*$ for how parasitoids at time t, should respond to the distribution of resources across the landscape that is conditional on the resource state at the current site. This set includes, optimal distance to move from an empty cell, optimal distance to move from a host-occupied cell and the optimal exploitation of the current cell. There are many such strategy sets and Roitberg and Mangel (1997) describe how the optimal strategy sets are determined. What should be clear is that the payoff from such strategy sets will be strongly affected by landscape structure and the species-specific (and state-specific) states of the natural enemies. Second, as noted earlier, there are tradeoffs. Here, investment in current resources can impact ability to exploit future resources when considerable time is required to exploit current resources.

3.1. Incorporating eggloads

In order to tie this notion of landscaped-based life histories to biological control, we add an additional state variable, eggload. Those very eggs that are employed to control insect pests are key elements in our life history theory and in particular, tradeoffs: any eggs that are placed into or onto hosts at the current site will not be available in the future. Similarly, time expended exploiting hosts at the current site will not be available in the future (Rosenheim, 1999). However, as noted above, exactly how this tradeoff plays out depends upon the distribution of hosts in space, the landscape element in the problem.

Consider two types of agricultural pests each with different spatial distributions. The first is territorial and is uniformly spread across agricultural fields as in the dashed line in Fig. 1A. The second pest only attacks high quality plants and is generally very clumped in distribution (see the solid and dotted lines in Fig. 1A). Both pests are monophagous and are only found within fields and never in the matrix between fields, thus generating the oscillatory structure functions as shown in Fig. 1B. We assume that there is just one

susceptible life stage of the host though it would not be difficult to add an age structure to this problem e.g. Henry et al. (2009).

Recall that our focal parasitoid is solitary and pro-ovigenic and, as such, for each oviposition made there will be one less egg available for use in the future. Further, because of their solitary nature, normally only one offspring survives when superparasitism occurs, thus there is a clear relationship between number of ovipositions and fitness for a given size patch of hosts. In our example, below, we assume that a single oviposition delivers a fitness increment of 0.9 and that a host with a double-offspring load similarly delivers garners a fitness increment of 0.2 (i.e. occasionally, a second larvae survives) for a cumulative oviposition return of 1.1. The relationship between clutch size (oviposition number) and fitness for a patch of 5 hosts is given in Fig. 3.

Upon discovering a patch of a given size, the parasitoid must decide how many eggs to deposit at that patch, how many eggs to retain for future patches and how far to travel before seeking a new patch. We can describe this decision by modifying Eq. (2) to generate:

$$F_1(\varepsilon, t, T; k_0, k_1, r) = f(r) + (1 - m_{O,r})(1 - m)^{k_1/v}$$
$$\left[\begin{array}{l} p(k_1|1)F_1(\varepsilon - r, t + m_{O,r} + k_1/v, T; k_0, k_1, r) \\ + (1 - p(k_1|1)F_0(\varepsilon - r, t + m_{O,r} + k_1/v, T; k_0, k_1, r)) \end{array} \right] \quad (3)$$

Eq. (3) looks very similar to Eq. (2) except for the inclusion of an eggload term (ε). Notice that a decision to oviposit r number of eggs at the current patch means that there will only be $\varepsilon - r$ eggs available for use in the future, discounted by the probability of living into the future, which depends on the cost of ovipositing in the current patch $(1 - m_{O,r})$. (Note, we assume that the larger the clutch size, the more time it takes to lay those eggs, thus the parameter $m_{O,r}$). It is not clear how common egg limitation is in nature, however, there is considerable literature demonstrating eggload effects across a broad range of proovigenic parasitoids (Casas et al., 2000; Jervis et al., 2008; Minkenberg et al., 1992).

Here is where landscape and life history merge in an interesting way. Suppose, for example, that an older parasitoid has a very high eggload. In such cases (the life history part), it should pay to lay large clutches (i.e. superparasitize) at the current site but the degree to which it should do so will depend upon the ease of getting to new sites (the landscape part). At the extremes, we do not expect to see much effect of landscape (e.g. if very low egg load and lots of time, the decision should be: Never 'waste' eggs by superparasitizing unless the structure function is extremely steep)
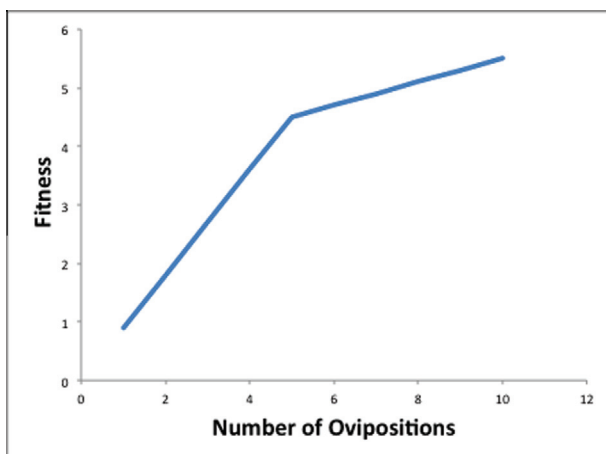

Fig. 3. The relationship between clutch size (oviposition number) and fitness for a hypothetical parasitoid exploiting a patch of 5 hosts.

however at intermediate values of eggload, expectation of life and structure function slope, then the details for those parameters come into play. For example, for parasitoids with intermediate eggloads, if hosts are very patchy (the steep fitness function) and the cost of moving through the landscape is high either because the time cost or the risk of predation is high, then superparasitism will be favoured (see Roitberg et al., 2010); this will not be the case when hosts are very evenly dispersed (the flat fitness function from above) and the cost of moving is low.

3.2. Incorporating synovigeny and pro-ovigeny

The discussion above provides a useful segue into an important life history classification, pro-ovigeny vs synovigeny (Jervis et al., 2001). Until now, we have focused on the former case, where the female emerges with all of the resources required to generate a lifetime supply of eggs. However the latter is equally interesting though more complex, as the female must acquire resources from the environment to generate eggs, for example, through pollen or host feeding. In order to capture egg dynamics across a landscape requires that we include another state variable (i) that will allow us to distinguish between immature and mature eggs (ε) along with another parameter (γ) that describes egg maturation rates. This gives:

$$F_1(i, \varepsilon, t, T; k_0, k_1, r) = f(r) + (1 - m_{O,r})(1 - m)^{k_0/v}$$
$$\left[\begin{array}{l} p(k_1|1)F_1(i - ((m_o + k_o)\gamma), \varepsilon - r + ((m_o + k_o)\gamma), t + m_o + k_0, T/v, T; k_0, k_1, r) \\ + (1 - p(k_1|1))F_0(i - ((m_{O,r} + k_o)\gamma), \varepsilon - r + ((m_{O,r} + k_o)\gamma), t + m_{O,r} + k_0/v, T; k_0, k_1, r) \end{array} \right] \quad (4)$$

where τ is the time required to lay a single egg. This model now allows for immature eggs to mature and replace mature eggs that are used to parasitize hosts during the time required to oviposit and move to new sites. The egg maturation parameter adds a new dynamic to the problem of how best to use eggs and time in space. Now, the parasitoid must manage its time budget to take into account egg availability for use in future hosts, including the notion of current–future tradeoff (see Peterson and Roitberg, 2010; Rosenheim et al., 1996). Once again, the landscape comes into play in terms of time investment in moving among sites and thus impacting eggload; for pro-ovigenic wasps this issue is moot.

In addition to foraging for hosts for oviposition, many parasitoids feed on nectar to fuel their somatic needs. Here, we see another tradeoff where parasitoids may spend time searching for hosts or for nectar but not both simultaneously (see Roitberg et al., 1992). In this context, landscape structure becomes very important. The nectar resource can easily be described by structure functions and we would not necessarily expect such functions to match those for hosts i.e. nectar-bearing plants will often be distributed differently than insect hosts. From the parasitoid's perspective, every time that it moves, its odds of encountering hosts and nectar change simultaneously though not necessarily at the same rate as noted above. What should the parasitoid do? Once again the optimal decision should depend upon the individual's state variable values in the landscape context. Additional terms could be added to the basic equations above to accommodate energy state, and other, landscape-derived factors, but the basic linkage between landscapes and patch exploitation by individuals will not change dramatically as a consequence.

In concluding this section on dynamic landscape models, it might appear that what we have done is to add further complexity to an already difficult problem. We argue otherwise. Rather than add more terms to descriptive, already-existing models of landscape, we took a different approach and built a theory of patch exploitation in a landscape context from first principles of evolutionary biology. In addition, our models incorporate the important assumption of environmental stochasticity, i.e. we calculate the

single best solution to living in a stochastic world (Mangel and Clark, 1988). Having such a theory, we can go beyond empirical data and predict how population and community dynamics will change in the face of change. Finally, one might argue that we do not need a model now that we understand the concept however from what we know from similar models, small changes in parameter values or interactions can engender large economic impacts at the farm level (see Roitberg, 2004). It is not clear without doing the calculations when this will be the case.

3.3. Biological control and landscapes

Finally, let us return to the major goal of this work, to link biological control to the landscape. Can we predict pest suppression by elucidating parasitoid life history at the landscape level? To evaluate killing rate by parasitoids, one can derive the functional response (Holling, 1966) i.e. the number of pests killed as a function of their density. A typical functional response for attacks (N_A) on healthy hosts by a solitary parasitoid with host discrimination is:

$$N_A = \frac{aN_t}{1 + aN_H T_h + aN_p \delta T_h + aN_P(1 - \delta)T_\delta} \tag{5}$$

where a is the search rate, N_t is the total number of hosts, N_H is the number of healthy hosts, N_P is the number of parasitized hosts, T_h is the handling time and δ is the probability of the parasitoid discriminating against a parasitized host and T_δ is the time to discriminate.

In classic functional response literature, it is generally assumed that parasitoid behavior is fixed (i.e. δ is a constant but see Barrette et al., 2009; Henry et al., 2009). Our spatial life history models however predict that within-patch exploitation rates will vary as a function of parasitoid state (e.g. age, eggload, energy state) and landscape, in other words, host acceptance will be dynamic. It is relatively easy to modify the classic functional response equation to take this into account. Essentially what is needed is to replace the host acceptance term (δ) with our rolling fulcrum model (Fig. 2). Roitberg (2004) describes implementation of a similar but aspatial model. Here, it is important to point out that the behavioral strategy that is optimal from the individual parasitoid's perspective need not be so from the biocontrol practitioner's perspective (Roitberg 2004). From this latter perspective, any superparasitism must be considered a waste on an egg even if it is evolutionarily advantageous to do so (van Alphen, 1990). It is the job of the practitioner to manage natural enemy behavior to minimize damage to crops. For example, 'proper placement' of alternate hosts could retain natural enemies within crops. In addition to the functional response there is the issue of the spatial distribution of parasitism. We will address this problem in a separate article to be published elsewhere.

4. Applications of the theory

In the discussion above, we developed a novel, functional landscape approach, a kind of rolling fulcrum model as a tool to facilitate biological control at a landscape level and further as a means to exploit biocontrol agents in changing landscapes. The value of this approach is illustrated in the following example. Canola, *Brassica napus ssp. oleifera* is widely grown in North America and Europe (Alford, 2003). The pests of canola in North America are largely invasive European species that were originally pests of cabbage production, and classical biological control is a strategy for management of these pests (Dosdall and Mason, 2010). If a new pest were to invade into this region from northern Europe, it might become a biological control target. We have in mind an insect similar to the pollen beetles, *Meligethes aneus* and *M. viridescens* (Coleoptera: Nitidulidae), which are important pests of canola in Europe and are

invasive in Canada (Alford et al., 2003). In northern Europe, these pests are managed in part by a landscape level application of conservation biological control that manages parasitoid communities (Ulber et al., 2010). Classical biological control of such a pest in Canada would involve selecting the most appropriate parasitoid(s) from that community. In the case of pollen beetles, there are a number of European parasitoids from which to choose (Nilsson, 2003).

We now consider the approaches and potential outcomes under the standard aspatial approach, and under our functional landscape approach. This is not simply a straw man. Although the record of biological control has not been one of high success rates (e.g. Beirne, 1985; Simberloff and Stiling, 1996), there are many examples of successful applications using standard approaches for selection of parasitoids (Mason and Gillespie, 2013; Mason and Huber, 2002).

Under the aspatial approach, the natural enemy community is surveyed in the native range. Using a life-table approach, one would select the parasitoids that have the biggest impact on target pest's reproduction for further study. Detailed study includes determining the potential for negative impacts on non-target organisms and the compatibility of the candidate natural enemies with the abiotic environment in the introduced range. Patch level experiments, along with life table analysis are needed to develop functional response curves, which indicate the capacity to reduce pests in patches, usually single patch experiments. All of these are both scientifically valid and are tried and true approaches that have a record of success. In aspatial approaches, the results of the experiments can be used to rank the parasitoids according to the above criteria and one or more species are selected for introduction.

However, additional details might be needed to make a choice of agent. The landscape of canola production differs dramatically between Canada and Europe. In Great Britain, in 2011, there were 13,700 holdings producing canola, on an area of 660,400 ha, for an average area per farm of 48.3 ha (data from https://www.gov.uk/government/statistical-data-sets/structure-of-the-agricultural-industry-in-england-and-the-uk-at-june, accessed 7 October 2013). In contrast, in the Canadian province of Saskatchewan in 2011, 8592 farms reported producing canola on 3,957,339 ha for an average per farm area of 460 ha (data from http://www29.statcan.gc.ca/ceag-web/eng/index-index, accessed 7 October 2013). The size of fields in Saskatchewan, where a natural enemy might be introduced, is at least 100 times larger than fields in Great Britain, from which the natural enemy might be obtained. Other aspects of the landscape clearly differ; in particular, the amount and nature of non-crop area adjacent to fields is necessarily less in Saskatchewan than in Great Britain, which may limit non-host resources that are necessary for parasitoids. In this context, we might need to know more about how the candidate natural enemies function on the landscape.

In our spatial approach, much of the above work still needs to be done. However through the following, we can provide added value and increased likelihood of success by including the following steps along with those from the above:

(1) For each biocontrol agent, structure functions need to be empirically measured for each of the key resources at both the sites of origin as well as their new location. For parasitoids, structure functions must be measured for hosts; this can easily be done using methods first described by Mangel and Adler (1994) and later Roitberg and Mangel (1997). For agents that maintain somatic function via nectar feeding, structure functions must be developed for feeding sites as well, again both in the native and the novel environments.

(2) Life history parameters must be empirically measured for employment within the state variable models. Some of these parameters may have been included in the aspatial approach

but should include: (i) longevity, (ii) fitness increments from oviposition (i.e. probability of success from an oviposition event, (iii) for pro-ovigenic parasitoids, eggload at ecolosion and for synovigenic species, a descriptor of egg maturation dynamics (see Jervis et al., 2008) is required.

(3) Choose and apply the appropriate state variable model from the set described above to the life history data and for the structure functions from the site of origin. Solve the model using backwards induction (see Mangel and Clark, 1988). This will generate a decision matrix i.e. the optimal strategy set for each and every combination of state variable for the site of origin. If not all data are available, employ a sensitivity analysis for those missing data to determine if accurate estimates are necessary and if not, employ ballpark values.

(4) Run a computer simulation for each candidate control agent in their novel habitat (see Roitberg and Mangel (2010) for a similar approach for controlling disease vectors). Here, one would apply the decision matrix from the site of origin in the new environment (e.g. with an eggload of x, and structure functions k_0 and k_1, exploit each host patch at rate r and move through the environment at rate m. This will generate kill rates and patterns of parasitism at the landscape level.

(5) Choose the optimal biocontrol agent based on simulated performance in the novel habitat. There may or may not be congruence with performance in the native habitat. For example, low eggload parasitoids may respond very differently to changes in landscape structure than high eggload species and as a result, generate very different killing rates. These differences could be substantial. For example, Roitberg and Mangel (1997) found differences of a magnitude or more in herbivore performance among habitats.

(6) Finally, perform an economic analysis to determine best candidate, which might include modification of new habitats (e.g. addition of nectar sources that more closely matches their expected distribution as defined by the structure function from the area of origin) or rearing procedures (e.g. Ode and Heinz, 2002) using a marginal analysis that would consider both marginal costs and benefits from release of biocontrol agents (see Roitberg, 2004). Without the spatial theory, it would be difficult to determine economic performance with such modifications.

Our 'recipe' does require more effort than the aspatial model however, it also provides greater benefits. In particular, the model can be applied to a broad range of organisms; only the parameter values change. In addition, this same model can be used to predict host breadth changes and non-target host attacks in novel environments based upon the same principles (see Roitberg, 2000).

The conceptual and mathematical models that we developed emphasize the often overlooked point that it is individual behavior and performance that determines the outcome of biological control processes at the landscape scale. These behaviors and performance are necessarily patch-level phenomena, and the problem is scaling those to the landscape. We achieved this by embedding landscape structure into individual life-history theory. This first cut shows how to build such a theory, and detailed analysis of our theory awaits. Regardless of the outcome of that analysis, we have followed the recommendation of one of our mentors, Bill Wellington (1977) who asked ecologists to "see the world from the organism's point of view".

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