Could increased understanding of foraging behavior help to predict the success of biological control?

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Importation biological control, the introduction of a specialist natural enemy from the region of origin of an invasive pest or weed, has been practiced for more than 100 years and has provided some iconic success stories, but also a number of failures. To improve both the success and safety of biological control in the future it is important to consider all opportunities that can help to transform biological control into a more predictive science. Once established, whether or not an imported natural enemy can reduce the abundance and distribution of an invasive host, likely depends on a suite of life history and behavioral traits that include phenological synchronization and foraging efficiency among many others. One key aspect of foraging efficiency is how individuals respond to the patchy distribution of hosts in a spatially fragmented environment when facing potential competition and predation risk. Another is what distributions of natural enemy foraging effort lead to the greatest temporal reduction in mean host density among patches. Here we explore the current theoretical framework for natural enemy foraging behavior and find some evidence that a weak resource dilution distribution of natural enemies among patches might be an important trait for improving the success of importation biological control.

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Introduction

Biological control is a component of pest and weed management that is based on manipulation of interactions between natural enemies (here limited to consideration of insect predators, parasitoids and herbivores) and their hosts (used here to refer to either insect pests or weeds) [1•]. Importation biological control (hereafter referred to simply as biological control) focuses on the control of an invasive species through the deliberate introduction of a specialist natural enemy from its geographic region of origin. It has a long history of application in both managed and natural ecosystems [2–4] and provides a valuable alternative to pesticides as a long-term management strategy for exotic pests and weeds. Although there have been many successes in biological control there have also been failures, and our inability to predict the outcomes and safety of natural enemy introductions and to improve on past success rates present important challenges for the future [5•,6,7].

Biological control has contributed substantially to population ecology and the development of consumer-resource models [8], but such models have contributed little to improving the success of biological control programs due to a focus on stability and persistence rather than a reduction of host densities [9••]. Many other aspects of ecology can also inform the practice of biological control, however, and so it is perhaps surprising that behavioral ecology has only rarely been considered in this context [10,11,12•] as behavior contributes to all foraging, oviposition and sex allocation decisions made by natural enemies in the exploitation of their hosts. On the other hand, as animal behavior operates on a shorter time scale than population dynamics, it remains unclear to what extent individual behavior is likely to affect population dynamics [13].

One of the most important aspects of behavioral ecology for biological control is the linkage between the foraging behavior of natural enemies and the population dynamics of their hosts [14,15]. The foraging behavior of a natural enemy is a multi-scale process that depends on its dispersal ability and on a sequence of behavioral decisions that it makes as it moves among host patches in a fragmented environment. While consideration of spatial processes in consumer-resource models has almost exclusively focused on the stability, there remains the observation that natural enemies that aggregate in patches of higher host density are more effective in reducing mean host density, due to their greater search efficiency across a spatially-explicit environment [8]. Thus the distribution and size of habitat patches and the foraging responses of natural enemies determine not only the fitness consequences of patch use for natural enemies, but also the impact of the natural enemies on the temporal dynamics of mean host density across the landscape. Consequently increased knowledge of the movement behavior of

natural enemies could be of critical importance to improving the success of biological control [9[•][•],11,16[•][•],17,18]. Here we ask how movement behavior affects the spatial distribution of natural enemies among habitat patches and how the spatial distribution of natural enemies influences the temporal dynamics of host populations, before considering the implications for improvement of biological control and future research directions
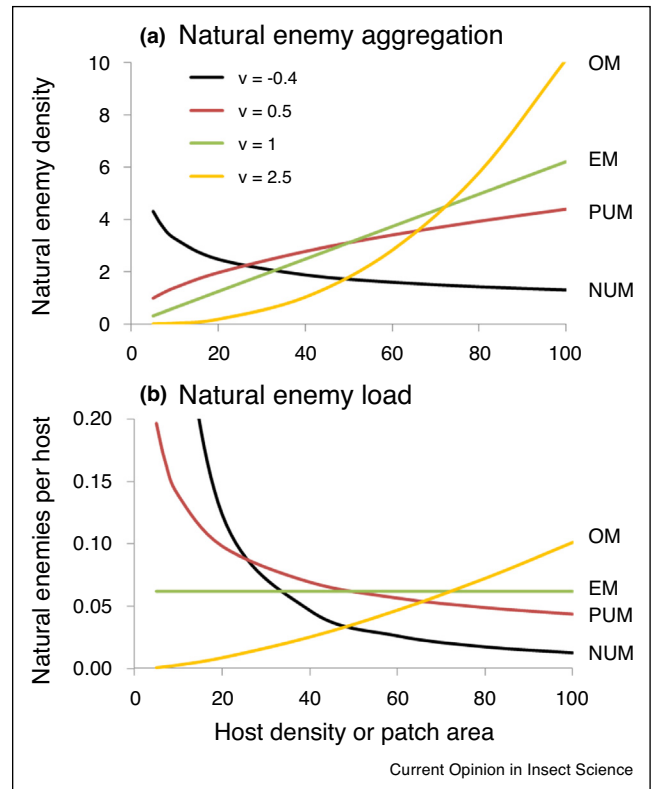
How movement behavior affects the spatial distribution of natural enemies

Hosts are distributed in fragmented environments in habitat patches that can differ in area, isolation, host density and host quality. To maximize their fitness in a fragmented environment, natural enemies should forage optimally by maximizing their lifetime reproductive success or more generally by maximizing their reproductive value at each stage in the life cycle when tradeoffs such as mortality risk apply [19,20]. The simplest optimal strategy of habitat patch selection is represented by the ideal free distribution (IFD) and is achieved when the net rate of resource gain is equal among host patches [21,22,23]. The interference IFD model [24] is represented by:

$$\frac{e_i}{E} = c * \left(\frac{h_i}{H}\right)^v \tag{1}$$

where e_i and h_i are the number of natural enemies and hosts in patch i respectively, E and H are the total number of natural enemies and hosts in all patches respectively, $v = 1/m$ with m the interference coefficient as a measure of the level of competition between natural enemies, and c is a normalizing constant such that the proportions of natural enemies (e_i/E) in each patch sum to unity. This model predicts the optimal distribution of natural enemies among patches from a balance between the positive effect of host density and the negative effect of interference competition (Figure 1a). If patches vary in area but not in host density then, the optimal proportion of natural enemies in a patch should exactly match the proportion of hosts in that patch for all values of the interference coefficient, but if host density varies among patches of constant area then the optimal distribution of natural enemies should be sensitive to the level of interference [25]. In the latter case, exact matching is expected only when the interference coefficient is 1, with overmatching (greater aggregation of natural enemies in higher host density patches and less in lower host density patches) when interference is weak ($m < 1$) and undermatching (the reverse of overmatching) when interference is strong ($m > 1$) (Figure 1a). When extended to a multitrophic perspective allowing for movement among patches by both herbivores and natural enemies, herbivore populations are expected to undermatch their plant resources due to predation risk by matching the plant density to predation risk ratio, and natural enemy populations are

predicted to overmatch their herbivore hosts by matching plant density rather than herbivore density [23,26]. IFD models assume that natural enemies have 'ideal' knowledge of the profitability (host density and quality) of each patch, are 'free' from any costs of travel between patches, and have equal competitive ability. While the 'ideal' and 'free' assumptions of these models are unlikely to apply to natural populations, the substitution of more realistic movement behavior and patch leaving rules shows that the optimal distribution of natural enemies among patches is fairly robust to violations of these initial assumptions [27,28].

Figure 1

(a) Natural enemy aggregation

- v = -0.4
- v = 0.5
- v = 1
- v = 2.5

Natural enemy density

OM
EM
PUM
NUM

(b) Natural enemy load

Natural enemies per host

OM
EM
PUM
NUM

Host density or patch area

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Spatial distributions of natural enemies in response to host density or patch area from patch selection models in relation to (a) natural enemy aggregation and (b) natural enemy load. The power function exponent of the models v represents the reciprocal of the interference coefficient for the interference IFD model [24], the balance of the scaling coefficients for migration rates for the patch area model [33], and the curvature coefficient for the resource concentration model [32]. The number of natural enemies $E = 20$ and the number of hosts and total patch area $H = A = 230$. Resource concentration occurs with (a) overmatching (OM) aggregation and (b) a resultant increase in natural enemy load (OM) when $v > 1$. Exact matching requires (a) proportional aggregation (EM) and (b) a constant natural enemy load (EM) when $v = 1$. Weak resource dilution results from (a) positive but undermatching (PUM) aggregation and (b) a weaker decrease in natural enemy load (PUM) when $v = 0.5$. Strong resource dilution results from (a) negative undermatching (NUM) aggregation and (b) a stronger decrease in natural enemy load (PUM) when $v = -0.4$.