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An integrative approach to understanding host–parasitoid population dynamics in real landscapes

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Abstract

Many of our advances regarding the spatial ecology of predators and prey have been attributed to research with insect parasitoids and their hosts. Host–parasitoid systems are ideal for spatial-ecological studies because of the small size of the organisms, the often discrete distribution of their resources, and the relative ease with which host mortality from parasitoids can be determined. We outline an integrated approach to studying host–parasitoid interactions in heterogeneous natural landscapes. This approach involves conducting experiments to obtain critically important information on dispersal and boundary behavior of the host and parasitoid, large-scale manipulations of landscape structure to reveal the impacts of landscape change on host–parasitoid interactions and temporal population dynamics, and the development of spatially realistic, behavior-based landscape models. The dividends from such an integrative approach are far reaching, as is illustrated in our research on the prairie planthopper *Prokelisia crocea* and its egg parasitoid *Anagrus columbi* that occurs in the tall-grass prairies of North America. Here, we describe the population structure of this system which is based on a long-term survey of planthoppers and parasitoids among host–plant patches. We also outline novel approaches to experimentally quantify and model the movement and boundary behavior of animals in general. The value of this information is revealed in a landscape-level field experiment that was designed to test predictions about how landscape change affects the spatial and temporal population dynamics of the host and parasitoid. Finally, with these empirical data as the foundation, we describe novel simulation models that are spatially realistic and behavior based. Drawing from this integrated approach and case study, we identify key research questions for the future.

Zusammenfassung

Viele unserer Fortschritte bezüglich der räumlichen Ökologie von Räubern und Beute sind der Forschung an Parasitoiden und ihren Wirten zugeschrieben worden. Wirt-Parasitoid-Systeme sind ideal für Studien zur räumlichen Ökologie: wegen der geringen Größe der Tiere, der oft diskreten Verteilung ihrer Ressourcen und der relativen Einfachheit, mit der von Parasitoiden verursachte Wirtsmortalität festgestellt werden kann.

Wir skizzieren einen integrierten Ansatz zur Untersuchung von Wirt-Parasitoid-Intertaktionen in heterogenen natürlichen Landschaften. Diese Herangehensweise beinhaltet Experimente, um unabdingbare Informationen zum Verhalten von Wirt und Parasitoid bei der Ausbreitung und an Habitatgrenzen zu erhalten, großskalige Manipulationen der Landschaftsstruktur, um die Auswirkungen von Änderungen der Landschaft auf die Wirt-Parasitoid-Interaktionen und die Populationsdynamik zu ergründen, sowie die Entwicklung von räumlich realistischen, verhaltensbasierten Landschaftsmodellen.

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Die Erträge eines solchen integrierten Ansatzes sind weitreichend, wie am Beispiel unserer Forschung an der Spornzikade *Prokelisia crocea* und ihres Parasitoiden *Anagrus columbi*, die in den Tallgrass-Prärien Nordamerikas auftreten, dargestellt wird. Hier beschreiben wir die Populationsstruktur dieses Systems basierend auf einer langfristigen Erfassung von Zikaden und Parasitoiden in den Patches der Wirtspflanze.

Wir skizzieren außerdem neuartige Ansätze zur experimentellen Quantifizierung und Modellierung des Bewegungs- und Grenzverhaltens von Tieren im Allgemeinen.

Der Wert dieser Informationen wird bei einem Freilandexperiment auf Landschaftsebene aufgezeigt, welches angelegt war, um Vorhersagen dazu zu testen, wie Änderungen der Landschaft die räumliche und zeitliche Populationsdynamik von Wirt und Parasitoid beeinflussen. Mit diesen empirischen Ergebnissen als Grundlage beschreiben wir schließlich neuartige Simulationsmodelle, die räumlich realistisch und verhaltensbasiert sind. Ausgehend von diesem integrierten Ansatz und der Fallstudie identifizieren wir Schlüsselfragen für die zukünftige Forschung.

Introduction

Since the publication of the seminal paper by Huffaker (1958) on herbivorous and predatory mites, spatial heterogeneity and its effects on predator–prey interactions has captivated the interests of ecologists. For most of this time, spatial heterogeneity was simplified to a dichotomy involving suitable patches and the homogeneously inhospitable space between them (the matrix). The prevailing heuristic and operational models for understanding this heterogeneity were the island biogeography and metapopulation models (Hanski 1999; Levins 1969, 1970; MacArthur & Wilson 1967). These models, and the empirical data that followed, strongly suggested that spatial considerations such as the size, spatial arrangement, and connectivity of habitat patches can impact animal foraging behavior, population dynamics, interactions within and among trophic levels, and community structure (e.g., Cooper, Li, & Montagnes 2012; Kareiva 1990; Tscharntke & Brandl 2004; Wieters, Gaines, Navarrete, Blanchette, & Menge 2008). In fact, larger-scale processes can potentially dominate local-scale processes (e.g., Cronin 2004, 2007; Thies, Steffan-Dewenter, & Tscharntke 2003).

The field of landscape ecology eschews the simple dichotomous view of landscapes inherent in classic island-biogeographic and metapopulation theory and embraces the real complexity that exists in nature (Turner 2005; Wiens 1997). In real landscapes, habitat patches may have indistinct boundaries, their geometry and occurrence may be transient, and the matrix may be quite heterogeneous in terms of composition or suitability for the focal species (Cronin & Reeve 2005; Turner 2005; Wiens 1997). In addition, patch quality can depend on local edaphic and topographic conditions and on their proximity to other landscape elements (Haynes & Cronin 2004; Lange, Diekotter, Schiffmann, Wolters, & Durka 2012; With 2004). From the perspective of a population or interacting species, theoretical and empirical landscape studies often focus on how the spatial arrangement and composition of landscape elements (i.e., landscape context) influence within-patch dynamics, boundary or edge responses, spillover among adjacent elements, functional connectivity, and the distribution of organisms (Cronin & Reeve 2005; Lange et al. 2012; Tscharntke & Brandl 2004; Turner 2005; Zeller, McGarigal, & Whiteley 2012).

The purview of landscape ecology extends beyond theoretical and basic scientific investigations. In the field of conservation biology, the loss and fragmentation of suitable habitat (Baguette, Blanchet, Legrand, & Stevens 2012; Fahrig 2003) is a phenomenon that is often best understood at the landscape level (e.g., Aune, Jonsson, & Moen 2005; Bascompte & Rodriguez 2001; Tscharntke, Steffan-Dewenter, Kruess, & Thies 2002). Moreover, as landscape ecology has matured as a field of study, its influence also has begun to permeate into a variety of applied fields including biological pest management, invasion biology, fisheries and infectious disease management and urban planning (e.g., Baguette et al. 2012; Cronin 2007; Liu & Taylor 2002; MacNeale, Kiffney, & Scholz 2010; Ramalho & Hobbs 2012; Roland 2000).

Although we have made great strides in our understanding of how the mosaic structure of real landscapes can affect populations, communities, and ecosystem functions, quantifying these effects remains a challenging empirical problem. Here, we highlight what we consider to be some of the main gaps in our understanding of predator–prey interactions at the landscape level. Drawing from our research experience with a host–parasitoid system, the planthopper *Prokelisia crocea* and its egg parasitoid *Anagrus columbi*, we describe a mechanistic approach that integrates experimentation and modeling to address the gaps in our knowledge of this subject. Our aim is to provide guidance for broadening research on predator–prey spatial ecology to the landscape level. It is not our intention to provide an exhaustive review of the field of landscape ecology as it pertains to predators and their prey. It is also beyond the scope of this review to address spatial-pattern formation in relatively homogeneous landscapes (e.g., traveling waves; Sherratt 2001) or broader community-level issues; e.g., diversity, structure, succession.

Predator–prey landscape ecology: a synopsis of the progress and gaps

Most of the research at the landscape level has focused on single species or collections of species within the same guild or assemblage (e.g., Haynes & Cronin 2003; Moilanen & Hanski 1998; Schultz, Franco, & Crone 2012). In contrast, studies of predator–prey/parasitoid–host interactions in a landscape context are relatively uncommon. Although theoretical work has been at the forefront of the field, predator–prey models generally have been very simplistic in their treatment of spatial heterogeneity and dispersal. For example, classic host–parasitoid models included variation in parasitoid densities among host patches, but also assumed random redistribution of the host and parasitoid populations each generation (e.g., Hassell & May 1974; Hassell, May, Pacala, & Chesson 1991). More recent models linked collections of local populations through a dispersal pool or to their nearest neighbors in a two-dimensional lattice (e.g., Hirzel, Nisbet, & Murdoch 2007; Lee 2010; Reeve 1988; Rodrigues, Mistro, & Petrovskii 2012). Predator–prey models incorporating reaction–diffusion provide a more realistic depiction of dispersal behavior, but space is generally treated as a continuum (Okubo, Hastings, & Powell 2001). More recent spatial models have incorporated behavior at patch boundaries within the diffusion framework (e.g., Ovaskainen & Cornell 2003; Reeve & Cronin 2010; Reeve, Cronin, & Haynes 2008; Xiao, Xu, & Cronin 2013) but these are typically single-species models. Alternative approaches that focus on tracking the movement of individuals (i.e., Lagrangian models) are rich in behavioral mechanisms, but typically are limited to single species and generally fall well short of encapsulating the spatial heterogeneity associated with real landscapes (Fronhofer, Hovestadt, & Poethke 2013; Holyoak, Casagrandi, Nathan, Revilla, & Spiegel 2008; Van Gils 2010). True landscape models that explore the interplay of spatial heterogeneity, realistic aspects of the movement of both species, and its consequences for their regional population dynamics are currently unavailable.

Empirical research at the landscape level points to the important role of landscape heterogeneity on predator and/or prey connectivity among patches. Measures of geographic isolation such as nearest-neighbor distance (i.e., structural connectivity) only partly explain rates of inter-patch movement. In most cases, connectivity was functionally dependent on the composition of the matrix (for reviews, see Baguette et al. 2012; Eycott et al. 2012). The cause for this functional dependence has been attributed to differential rates of movement, tortuosity of paths, propensity to traverse boundaries, or survival among landscape elements. Matrix heterogeneity has been shown to not only affect connectivity, but also patterns of patch occupancy, density and local extinction risk – in some cases, it can be of overriding importance relative to traditional measures of patch geography such as patch size and isolation (e.g., Haynes & Cronin 2003; Kennedy, Grant,

Neel, Fagan, & Marra 2011; but see Moilanen & Hanski 1998).

Detailed data on the dispersal behavior of a species in a heterogeneous landscape have grown in recent years, but the number of cases in which this level of data are available for both a predator and its prey is exceedingly rare (Cronin & Reeve 2005). This is disappointing because differences in dispersal have long been recognized as being important to predator–prey stability (Huffaker 1958). In a number of predator–prey models, stability is achieved in instances where the prey is more dispersive than the predator (e.g., Hassell 2000; McCauley, Wilson, & de Roos 1996). However, unequal dispersal rates are not necessary, nor are they sufficient for interaction persistence (Briggs & Hoopes 2004; Kleinhans & Jonsson 2011). Based on a review of the literature, Cronin & Reeve (2005) found that in 92% of the studies, a prey and its predator(s) differ significantly in the scales at which they disperse or respond to spatial subdivision. This finding underlies a potentially serious issue in the study of predator–prey spatial ecology – the spatial scales at which the species move and interact with each other and the environment are almost always different. Despite the near ubiquity of this discrepancy in scale, mathematical models and, to a lesser extent empirical research, often assume that both predator and prey operate on comparable spatial scales (but see e.g., Cronin & Haynes 2004; de Roos, McCauley, & Wilson 1998; Wieters et al. 2008).

To date, empiricists have only scratched the surface in understanding how landscape structure influences predator–prey interactions. Most of the available studies are non-experimental and have focused on short-term effects of the landscape on parasitism of hosts by parasitoids. For example, spillover from non-crop habitat often results in higher parasitism rates near the crop edge than interior (e.g., Thies & Tscharntke 1999; Tylianakis, Didham, & Wratten 2004). Consequently, effective top–down control of plant pests may be contingent upon the composition of adjacent matrix habitats (e.g., Casini et al. 2012; Gladbach et al. 2011).

The lack of manipulative studies that seek to provide a causal link between changes in landscape structure, habitat connectivity and the local and regional population-dynamics of predators and their prey remains a key impediment to the advancement of this field (e.g., Bowne & Bowers 2004; Cronin & Haynes 2004; Cronin & Reeve 2005; Donahue, Holyoak, & Feng 2003). To date, there are relatively few field studies that have manipulated the spatial structure of patches and examined its consequences to predator–prey dynamics at multiple spatial scales (but see e.g., Braschler, Lampel, & Baur 2003; Cronin & Haynes 2004; Kruess & Tscharntke 2000). Additionally, we need studies that change other aspects of the landscape such as the composition of the matrix, the type or nature of element boundaries, and the relative abundances of different elements.

Integrative approach to studying predator–prey landscape ecology

Here, we describe the advantages of an integrative approach to studying predator–prey landscape ecology. This approach entails conducting experiments to obtain critically important information on dispersal and boundary behavior of the prey and predator, large-scale manipulations of landscape structure to reveal the impacts of landscape change on predator–prey interactions and temporal population dynamics, and the development of spatially realistic, behavior-based landscape models. At present, there are only a few study systems for which ecologists have amassed this kind of data. The dividends from such an integrative approach are far reaching, insightful and are likely to reveal novel interactions among predators and their prey.

For approximately 16 years, we have been studying the spatial and landscape ecology of the planthopper *P. crocea* (Hemiptera: Delphacidae) and its facultative specialist egg parasitoid *A. columbi* (Hymenoptera: Mymaridae) that are distributed among host–plant patches (prairie cordgrass, *Spartina pectinata* [Poaceae]) in tall-grass prairie fragments. We use this study system to illustrate how this integrative approach has greatly facilitated our understanding of predator–prey interactions.

The prairie planthopper – egg parasitoid system

P. crocea is a dominant specialist herbivore of prairie cordgrass (Cronin 2003a, 2003b, 2003c), a common plant associated with grasslands of the North American Great Plains (Cronin 2003a). *A. columbi* is a facultative specialist of *P. crocea* eggs at our field sites and singularly causes the highest rate of mortality of the planthopper (Cronin 2003b, 2003c; Cronin, Haynes, & Dillemuth 2004). Parasitism of hosts within a patch is spatially and temporally density independent (Cronin 2003c). However, the distribution of parasitism is strongly aggregated among hosts within cordgrass patches (Cronin 2003c) which is theoretically stabilizing for the host–parasitoid interaction (Hassell et al. 1991).

Spatial population structure

From the perspective of the planthopper and its egg parasitoid, the tall-grass prairie is quite fragmented and consists of numerous discrete host-plant patches (Cronin 2003b). Host-plant patches have a heavily skewed size distribution such that a few large patches (>4 ha) are intermixed with many small patches (<10 m^2). The intervening matrix consists of three distinct types: (1) mudflat, (2) a mixture of native grasses (primarily *Andropogon scoparius* Michx., *A. gerardii* Vitman, and *Agropyron smithii* Rydb.), and (3) the exotic grass, smooth brome (*Bromus inermis* Leyss) (Haynes & Cronin 2003).

Contrary to the basic assumptions of metapopulation theory (Hanski 1999), this landscape is quite dynamic. Smooth brome was introduced into North America in the late 1880s from Hungary and Russia and subsequently spread and became established in native remnant prairies (Larson, Anderson, & Newton 2001). The invasion of smooth brome appears to be an important driver of landscape change, affecting cordgrass patch dynamics and matrix composition (Dillemuth, Rietschier, & Cronin 2009). Dillemuth et al. (2009) found that cordgrass patch growth was two times greater in areas not invaded by smooth brome versus areas that were heavily infested with smooth brome. In addition, the probability of establishment of a new cordgrass patch was 23% higher and the probability of extinction of an existing cordgrass patch was 87% lower in areas of low brome coverage (<25%) as compared to areas of high brome coverage (>75%). These results suggest that the host and parasitoid are unlikely to be in a dynamic equilibrium, and that models developed for this system will ultimately need to account for the dynamic nature of this landscape brought about by the invasion of smooth brome.

Based on a census spanning 3.5 years (7 host–parasitoid generations), we were able to assess the factors that influence extinction–colonization dynamics and characterize the spatial population structure of *P. crocea* and *A. columbi* (Cronin 2003b, 2004, 2007; Haynes & Cronin 2004). Despite strong local density-dependence in the planthopper and parasitoid population growth rates (Cronin 2007), local populations were quite extinction prone. The extinction rate for the planthopper was $23 \pm 5\%$ per generation, decreased significantly with increasing patch size, and decreased with an increase in the proportion of the matrix that was mudflat (Cronin 2004). Because cordgrass patches embedded in mudflat are richer in nitrogen than patches embedded in brome (Haynes & Cronin 2003), patch nutritional quality for the host, as mediated by matrix composition, may be an important determinant of extinction dynamics in this system. We also discovered that populations in large patches (>1 ha), irrespective of matrix composition, were never observed to go extinct, suggesting the possibility of mainland-island metapopulation dynamics (Cronin 2003a, 2003b, 2004). Interestingly, planthopper extinction risk was unaffected by parasitoid density in the previous generation suggesting that the parasitoids may not be a driving force in the extinction dynamics of its host. At present, we also see no evidence that planthoppers are driving host-plant extinctions. Therefore, extinctions in this tri-trophic system are not likely controlled from the top down.

For the parasitoid, the local population extinction rate was almost twice that of the host ($39 \pm 16\%$ per generation) and the primary determinant of extinction was the local abundance of hosts. An increase in plant density, decrease in host density within the patch and decrease in parasitoid density within the patch (lagged one generation) all increased the likelihood of *A. columbi* extinction within a patch. The dependency on multiple trophic levels may explain the higher extinction risk for the parasitoid than its host (see also Holt

1996). As with the host, local extinctions were asynchronous and populations of *A. columbi* in large patches never went extinct during the study.

Vacant patches were colonized at rates of 53% and 34% per generation for the planthopper and parasitoid, respectively (Cronin 2004). For both species, colonization probabilities decreased with an increase in isolation from neighboring sources. High host densities in a patch also favored high rates of colonization by *A. columbi*. We have concluded that the population structure of *P. crocea* and *A. columbi* most closely approximates a mainland-island metapopulation (see also e.g., Berendonk & Bonsall 2002). It remains an open question whether the ensemble of extinction prone smaller patches could persist without the inputs from the larger, mainland patches. Although few in number, surveys of the spatial structure of host–parasitoid systems have revealed a diversity of structures, ranging from classic metapopulations (e.g., Van Nouhuys & Hanski 1999), to mainland-island metapopulations (Cronin 2003a, 2003b, 2004), to patchy populations (Dempster, Atkinson, & Cheesman 1995).

Movement and boundary behavior

Movement or connectivity among habitat patches is a key process influencing spatial population structure and the regional persistence of subdivided populations (e.g., Hanski 1999; Holyoak & Lawler 1996; Ims & Yaccoz 1997). Using fluorescent powders to mark adult planthoppers, we found that their within-patch movement was well described by a diffusion process, with median displacement distances that were quite short, ≈1 m per day (Cronin 2003b; Haynes & Cronin 2006; Reeve et al. 2008). Movement among patches declined exponentially with distance between patches (Cronin & Haynes 2004; Cronin 2003b), but the rate of movement and the tortuosity of their pathways was strongly dependent on matrix composition (Cronin & Haynes 2004; Haynes & Cronin 2006; Reeve et al. 2008). In a mudflat matrix, planthopper movement was highly linear and averaged ≈1 m/h; whereas in brome matrix or host patch (cordgrass), movements were very tortuous and averaged only ≈1 m/d (Haynes & Cronin 2006). Linear patterns of movement are likely to be less effective for discovering a new patch if patches tend to be clumped (Conradt, Zollner, Roper, Frank, & Thomas 2003; Zollner & Lima 1999), as is the case in our study system (unpublished data).

More recently, Reeve et al. (2008) conducted mark-release-resight experiments to quantify planthopper movement in association with a cordgrass-brome and cordgrass-mudflat boundary (Fig. 1A and B). The size of the experimental arena was 1 m × 2 m, sufficiently large given the mean net displacement of planthoppers per day (see above). The diffusion equations used to describe planthopper movements were numerically solved using COMSSOL (2007). The solution process consisted of choosing the diffusion module within COMSOL, drawing a rectangular domain that surrounded
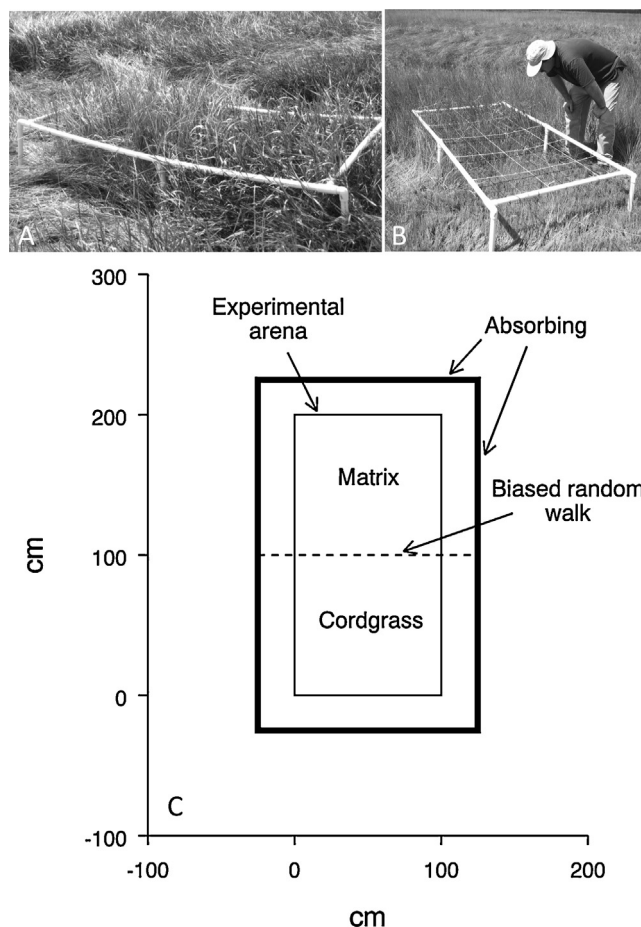
Fig. 1. Photograph of a (A) cordgrass-brome or (B) cordgrass mudflat edge in which planthoppers were released 25 cm into the cordgrass, at the patch edge, and 25 cm in the matrix. The overlaying grid (200 cm × 100 cm) provides a reference for determining the location of each planthopper over time. (C) The landscape drawn in COMSOL depicting the experimental arena surrounded by a rectangular area with boundary conditions.
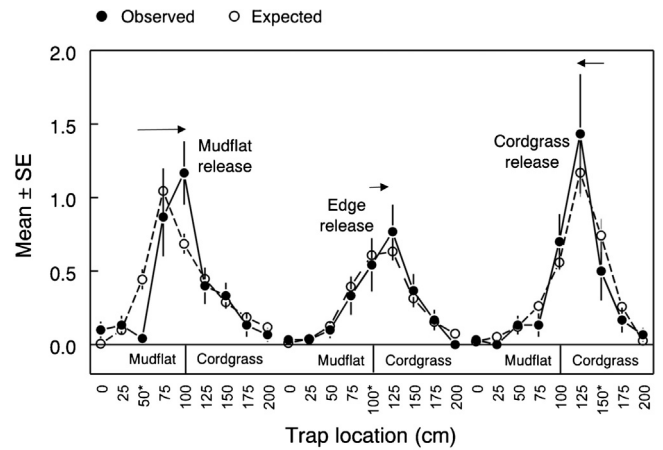
the arena used in the experiments (Fig. 1C). We used absorbing boundary conditions for the outer edges of the rectangle. An interior boundary representing the cordgrass-matrix edge was modeled as a biased random walk, where a parameter k_1 describes the probability of the planthopper on the cordgrass-matrix boundary moving toward cordgrass, while $k_2 = 1 - k_1$ is the probability of entering the brome or mudflat matrix (Harrison, Hanski, & Ovaskainen 2011; Ovaskainen & Cornell 2003). Values of k_1 near 1 indicate that movement is strongly biased toward cordgrass, while $k_1 = 0.5$ implies no bias in movement and thus no edge behavior. A proportion of the planthoppers were sedentary throughout the experiment, and this was modeled by dividing the insects into sessile and mobile classes. The model parameters were estimated using maximum likelihood.

In fitting the diffusion model to our data, we found clear support for models incorporating both heterogeneity among planthoppers in their propensity to move as well as
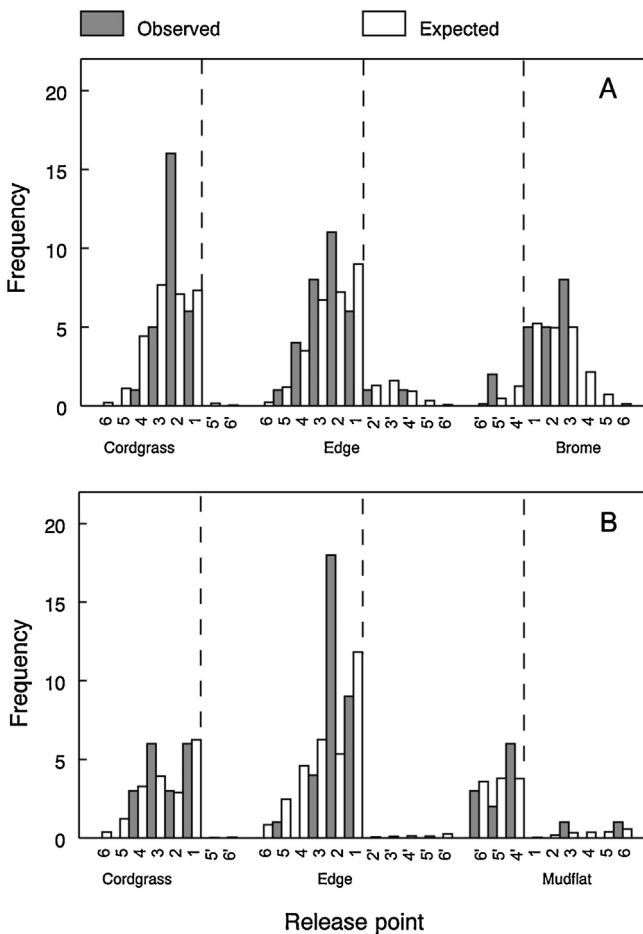
Fig. 2. Observed and expected frequencies of marked planthoppers (*P. crocea*) 2 h after their release in a cordgrass-brome (A) or cordgrass-mudflat (B) arena. Planthoppers were released at three points in association with the cordgrass-matrix boundary: in cordgrass (25 cm from the edge), at the cordgrass-matrix edge, and in the matrix (25 cm from the edge). The edge is denoted by a dashed vertical line. Numerals on the *x*-axis represent concentric squares surrounding each release point. Square 1 is the release point (10 cm × 10 cm), square 2 consists of the eight squares surrounding the first square, and so on. Squares labeled as 2′, 3′, etc. are the portions of the squares on the far side of the cordgrass-matrix boundary from the release point
From Reeve et al. (2008) and re-drawn with permission from the British Ecological Society.

Fig. 3. Mean observed and expected frequencies (±SE) of marked *A. columbi* at trap locations extending from mudflat into cordgrass perpendicular to the cordgrass-mudflat edge. Data are shown for releases in mudflat, at the edge, and within cordgrass. Similar patterns were observed in the cordgrass-brome replicates. The expected frequencies were generated using an advection–diffusion model fitted to the trap data (see text for details). The release locations are denoted with an asterisk. Arrows indicate the magnitude and direction of advective movement from the release point.
From Reeve and Cronin (2010) and re-drawn with permission from the British Ecological Society.

strong edge behavior (see also e.g., Ovaskainen 2004; Skorka et al. 2013). Planthoppers readily crossed the cordgrass-brome edge in either direction ($k_1 \approx 0.83$), but traversed the cordgrass-mudflat edge in primarily one direction, mudflat to cordgrass ($k_1 \approx 0.98$) (Fig. 2A and B). As compared to the cordgrass-brome boundary, the cordgrass-mudflat boundary is very distinct which may explain the reluctance to emigrate into mudflat (see also Eycott et al. 2012). The high permeability of the cordgrass-brome boundary may explain why interpatch movement rates were so much higher when the matrix was brome than when it was mudflat in the

experiments by Cronin & Haynes (2004) and Haynes & Cronin (2003).

Parallel dispersal studies with the tiny *A. columbi* (0.7 mm) demonstrated that recaptures of fluorescent-marked adults declined exponentially with distance and the interpatch dispersal rate was an order of magnitude higher when the matrix was composed of brome than of mudflat (Cronin 2003a; Cronin & Haynes 2004). The main difference between the two species was that the inter-patch dispersal rate of *A. columbi* was 10–100 times lower than that of its host (depending on distance from the source).

Another important difference in the dispersal behavior between the host and parasitoid regards their boundary behavior. We (Reeve & Cronin 2010) conducted a movement study with the parasitoid at patch boundaries that was meant to complement the experiment with its host (Reeve et al. 2008). We initially fitted a model with boundary behavior similar to the planthopper, but this model poorly matched the observed data. We then fitted an advection–diffusion model to these data using COMSOL. The redistribution of parasitoids was well fit by the advection–diffusion model ($R^2 > 0.65$) and the overall pattern suggests that parasitoids strongly biased their movements toward the edge when released in either matrix type, and to a lesser extent when released in cordgrass (Fig. 3). When released at the edge, parasitoids showed biased movement toward the patch interior when the matrix was mudflat but not brome. Unlike the planthoppers, there was little difference in response to the two edge types. Moreover, there was no evidence for differences in
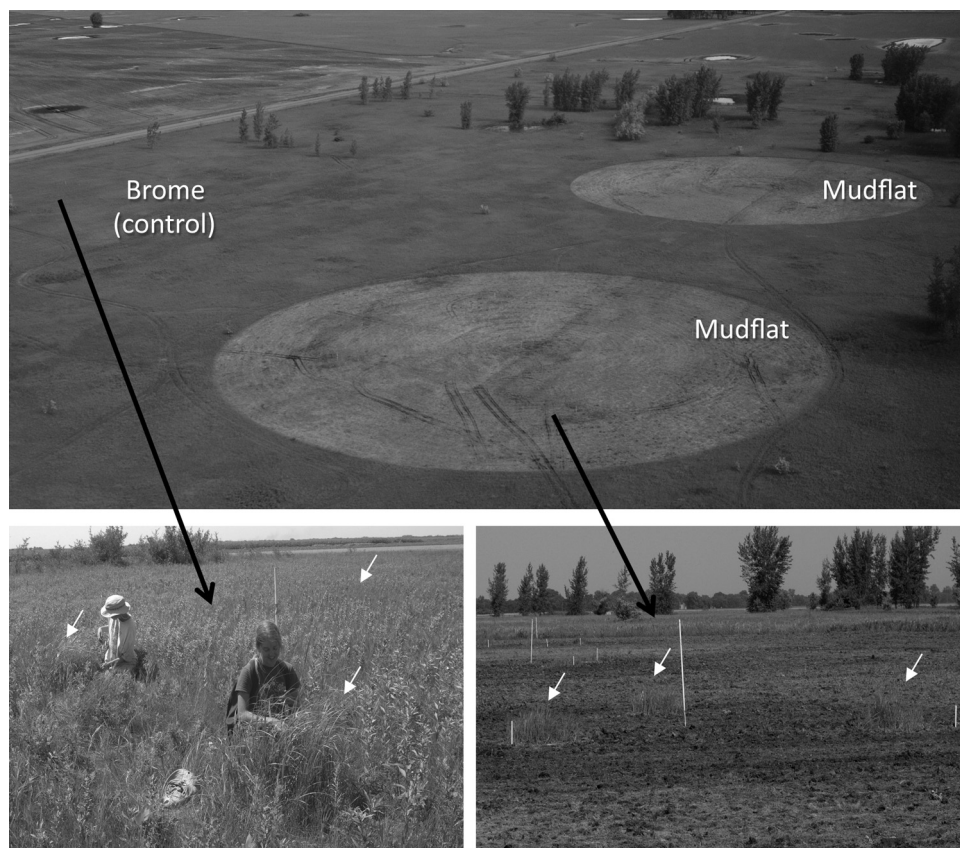
Fig. 4. Aerial photograph of large-scale experimental landscapes. Insets are closeups of a brome (lower left) or mudflat (lower right) landscape and several cordgrass patches (of the fifteen patches in each landscape). White arrows indicate cordgrass patches (each 0.66 m^2).

diffusion rate for the different substrates. These results suggest that *A. columbi* may be attracted to cordgrass patches from short distances (≈ 50 cm) regardless of the matrix within which they are moving. Greater retention of *A. columbi* in mudflat-embedded patches arises, in part, because of the bias in movement toward the interior of the patch when at the patch boundary. This edge behavior is potentially adaptive given that planthopper densities are significantly higher at the cordgrass-mudflat edge than the interior (Haynes & Cronin 2003).

Armed with this extensive information about *P. crocea* and its parasitoid's dispersal behavior, it becomes possible to develop informed hypotheses with regard to how manipulations of landscape structure can affect movement directly, and population dynamics indirectly. Very few studies, to date, have made these connections (but see e.g., Burgess, Treml, & Marshall 2012; Cronin & Haynes 2004; Cronin 2007; Dempster et al. 1995; Hein & Gillooly 2011; Huffaker 1958).

Local and regional population dynamics

The benefits of having a detailed understanding of the dispersal behavior of a predator and its prey are clearly revealed from a large-scale experiment conducted by Cronin and Haynes (2004) and Cronin (2007). We hypothesized, a priori, that connectivity among local planthopper and parasitoid populations in a landscape consisting of an ensemble of cordgrass patches embedded in a mudflat matrix would be quite low. Emigration rates would be low in those patches, and if individuals did emigrate, the likelihood of successfully immigrating to a new patch would also be quite low. An important consequence would be that local populations would have a low probability of being rescued from extinction or re-colonized following an extinction event (Brown & Kodric-Brown 1977). We would also expect that local populations would exhibit relatively independent (i.e., asynchronous) fluctuations in density, a critically important factor affecting metapopulation persistence (Hanski 1999). Alternatively, we hypothesized that a brome-dominated landscape would have high connectivity among cordgrass patches for both the planthopper and parasitoid. Emigration rates would be high and unless the combined effects of immigration and reproduction exceeded this rate, local patch densities likely would be lower than in a mudflat-dominated landscape. Also, the high connectivity would likely favor increased spatial synchrony in densities and a relatively high risk of extinction for the whole ensemble of patches (Hanski 1999; Levins 1969, 1970).
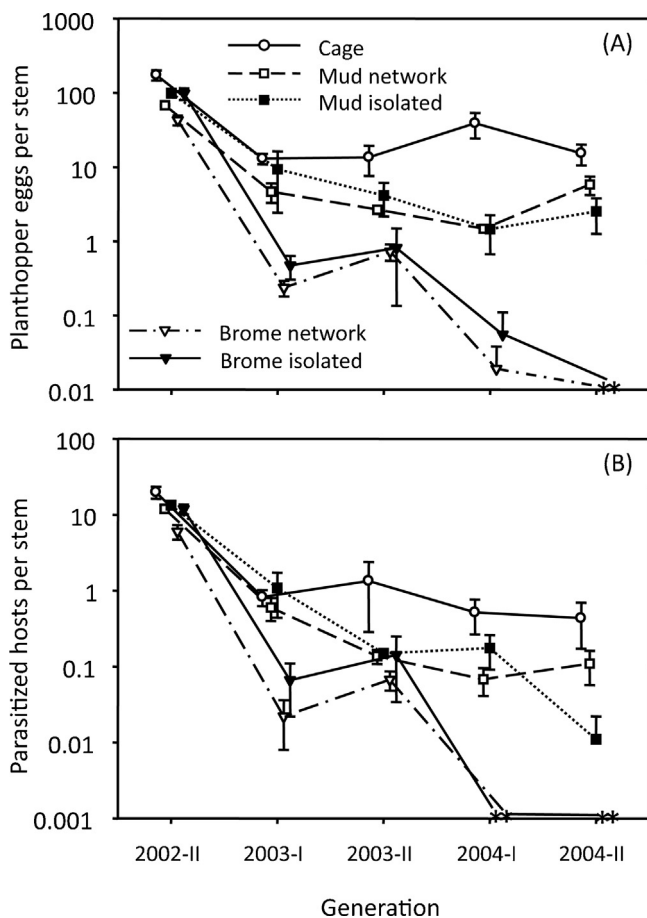
Fig. 5. Change in (A) planthopper or (B) parasitoid density (mean numbers per stem per patch ± SE) over time in experimental cordgrass patches from five different patch treatments. * indicates zero mean population density.
From Cronin (2007) and re-drawn with permission from the Ecological Society of America.

We tested these predictions by creating replicate cordgrass networks (identical in number, size, quality and distribution of cordgrass patches) that were embedded in either a smooth brome or mudflat matrix (Fig. 4). To further explore the importance of connectivity to local population dynamics, we also established an additional subset of individual cordgrass patches that were far from other potential sources of hosts and parasitoids (emigration possible but no immigration; either brome or mudflat matrix), and caged (no emigration or immigration). Following the creation of these treatments, cordgrass patches were seeded with planthoppers and parasitoids and then monitored for five generations.

Our a priori predictions about the effects of changing connectivity on the local and regional population dynamics of the planthopper and parasitoid were well supported by this experiment. The caged patches had host and parasitoid populations that achieved high equilibrial densities (Fig. 5), had strong density-dependent growth rates (Cronin 2007), and rarely went extinct. These data suggested that the small

experimental cordgrass patches were inherently self-sustaining sources (birth rate > death rate) (Cronin 2007).

Populations in cordgrass networks exhibited very different local and regional dynamics depending on the matrix composition. Open patches in mudflat (in isolation or within a cordgrass network) had dynamics similar to caged patches with the exception that densities were 2–3 times lower. In contrast, planthoppers and parasitoids in all brome-embedded patches had densities that were on average 50% lower, spatially 50–90% more variable, and had a local extinction rate that was 4–5 times higher than those in mudflat. At the scale of the whole network of patches (i.e., the metapopulation), the complete extinction of parasitoids and hosts took place within 4–5 generations. No regional extinctions occurred in the replicate mudflat landscapes. We suggest that the mudflat-bounded patches functioned similarly to caged patches; i.e., a closed system. Extinction in the brome-embedded patches resulted because cordgrass-brome boundaries are so permeable to planthoppers and (to a lesser extent) parasitoids that emigration losses greatly exceeded gains from reproduction and immigration. Thomas and Kunin (1999) referred to these types of populations as "population sieves". This study provided the first experimental evidence to suggest that inherent source populations can be changed into extinction–prone sieves by altering matrix composition.

Also of interest was the finding that the host and parasitoid generally exhibited the same response to our manipulations of landscape structure, although the parasitoids appear to be much more sensitive, in terms of effects on density and extinction risk, than the hosts. This latter finding is consistent with the expectation that predators are more prone to extinction than their prey in the face of landscape change (Holt 1996).

Integrating the two approaches

With the exception of a few laboratory systems (e.g., Bull, Pickup, Pickett, Hassell, & Bonsall 2007; Cooper et al. 2012; Holyoak & Lawler 1996; Huffaker 1958), modeling has been the only avenue through which the long-term effects of changes in habitat heterogeneity and dispersal on populations and species interactions can be understood. Recent modeling efforts have combined spatially realistic landscape structure with individual dispersal behavior (e.g., Fronhofer et al. 2013; Harrison et al. 2011; Ovaskainen & Cornell 2003; Tischendorf 1997). We suggest that continued advancement in the fields of spatial/landscape ecology and conservation biology requires that this modeling approach be extended to include important interactions with other species (i.e., predators or competitors). These models also need to be flexible, i.e., easily modifiable to fit the movement behavior of a wide range of species, and reflect real landscapes. Individual-based movement models represent one possible approach and have clear advantages in being mechanistic, capable of accounting for animal cognitive ability, and capable of assessing the adaptiveness of different dispersal

strategies (Nathan et al. 2008). The alternative approach that we describe below, which emphasizes population redistribution, trades off behavioral flexibility for greater realism of the landscape and more tractable population-dynamic consequences.

Our approach involves using COMSOL (COMSOL 4 2012) to model the dispersal component of the population model. This software package is particularly advantageous for landscape modeling because it has drawing tools that allow the creation of any arrangement of elements (patches, different matrix types) in a two-dimensional landscape. Each element can be assigned different systems of equations and parameter values for diffusion within an element, and different boundary conditions (reflecting, absorbing, biased random walk) can be assigned to any edge of an element. Interactions between different species can be incorporated in the model by adding reaction terms.

The *P. crocea–A. columbi* system also has two features that simplify model development: (1) adult planthoppers and parasitoids are the only life history stages with significant mobility, and (2) both organisms have discrete generations that are synchronized in the field. We can therefore model the dispersal phase of both life cycles using diffusion equations similar in form to the ones in our dispersal experiments, with the addition of oviposition and adult mortality terms. In particular, adult planthoppers lay eggs at rate λ in cordgrass areas while adult parasitoids attack them at rate a, generating juvenile parasitoids. Dispersal (emigration) can be made density dependent but to date, we have no evidence to suggest that this is the case (Cronin 2003b, 2007). Adult mortality also occurs during the dispersal phase, and the numerical solutions (using COMSOL) are continued through time until the remaining densities are negligible. The spatial distributions of unparasitized and parasitized planthopper eggs after dispersal are then used as the initial distributions of adult planthoppers and parasitoids in the next dispersal phase, after adjusting them for mortality during the juvenile stages. Cronin and Reeve (2005) demonstrated a model of this form with five cordgrass patches of various sizes and showed its dynamics were strongly influenced by edge behavior. Here, we examine the dynamics of the planthopper in relation to cordgrass patch size and matrix type, using our experimentally-derived estimates of the diffusion rates, edge parameters (k_1) and mortality rates on cordgrass, brome, and mudflat, as well as an estimate of the daily oviposition rate (female eggs per female) for the planthopper (Fig. 6). The simulations used five different sized cordgrass patches (0.32–2.52 m^2) embedded in either brome or mudflat. The cordgrass patch was initiated with a uniform distribution of adult planthoppers, and then the system was iterated for 10 generations. For each patch size and matrix type, the population growth rate per generation, r, was calculated using just the last two generations, to eliminate transient behavior. The mean value of r increased with patch size for both matrix types. Mean r was always positive for cordgrass-mudflat patches, even for small patch sizes. Based on the 95% confidence intervals, r was
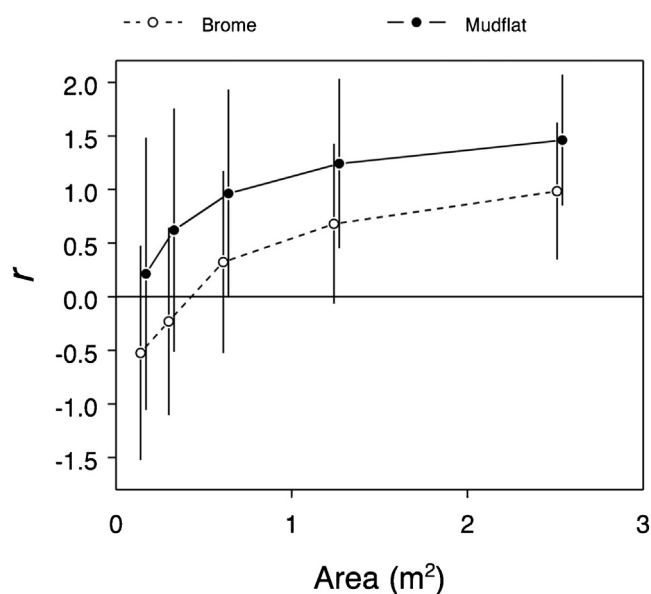
Fig. 6. Simulated population growth rates (r) vs. area for square cordgrass patches of five different sizes, surrounded by a matrix of brome or mudflat. Estimated diffusion rates D for cordgrass, brome, and mudflat, the proportion of sessile insects p, and the edge behavior parameter k_1 were taken from Reeve et al. (2008). The simulations used an average diffusion rate obtained by combining the rates for mobile and sessile individuals, i.e., $\bar{D} = (1 - p)D + p(0)$. We also assumed a per capita fecundity of $\lambda = 2.25$ female eggs/day, and mortality rates of $\delta = 0.0625$/day for cordgrass, and $\delta = 0.36$/day for brome and mudflat (Haynes and Cronin, unpublished data). The error bars represent 95% confidence intervals for r (see text for other details).

significantly greater than zero for the three largest patch sizes. For cordgrass-brome patches, mean r was negative for the two smallest patch sizes and significantly different from zero for only the largest patch size. The model corroborates the conclusions from our landscape-level experiment that boundary behavior may drive the differences in planthopper and parasitoid persistence in cordgrass patches surrounded by either brome or mudflat. Finally, the code for this model is available on request from the authors.

Further refinements of the *P. crocea–A. columbi* model will be needed to facilitate more quantitative comparisons of its output with experimental and observational data. Because the parasitoid is attracted to the patch edge (Reeve & Cronin 2010), advection terms will need to be added to the parasitoid dispersal model. In addition, much of the data available for evaluating the model involves extinction rates for patches of different sizes, arrangements, and matrix types. For comparison with these data, it would be useful to add some form of demographic stochasticity so that patches can genuinely go extinct (see Bonsall & Hastings 2004). The refined model could then be used to address various applied problems in this system, including the effects of fragmentation, the function of corridors or stepping stones, and the invasion and spread of exotic species such as brome.

Summary and new directions

Landscape ecology, as a formal field of study, is less than three decades old (Turner 2005). The extension of this field to predator–prey interactions is presently quite limited. We suggest that an integrative research approach, one that combines experiments on movement behavior, manipulation of landscape structure, and spatially realistic models is the key to advancement of this area of study. As we can attest, the work involved is daunting but we hope that the findings we have uncovered make a strong case for the value of this approach.

Quality dispersal data represent the biggest hurdle to this approach. At present, there is no substitute for these critical data. We simply need more dispersal studies involving both predators and their prey to begin to comprehend the range of possibilities that exists out there. Our study of *P. crocea* and *A. columbi*, and a review of the literature (Cronin & Reeve 2005), strongly suggest that it is very likely predators and their prey will differ in both the scale of movement and responses to boundaries between landscape elements. These idiosyncratic differences may critically affect local or regional population dynamics in ways that we have not envisioned yet.

The upshot is that new methods are becoming available that not only make it easier to mark and track the movements of species, but also simplify the experimental approach and computational requirements for quantifying dispersal and boundary behavior. With the availability of various marking techniques (e.g., immunomarking; Jones, Hagler, Brunner, Baker, & Wilburn 2006), satellite tracking of mobile animals (e.g., Macandza, Owen-Smith, & Cain 2012), and the miniaturization of tracking devices (e.g., Whitehead & Peakall 2012), movement data are now much easier to obtain for species of a broad range of sizes and dispersal capabilities. Also, Xiao et al. (2013) recently developed an alternate approach to estimating diffusion parameters in reaction–diffusion models. Traditional methods involve a mass release of marked individuals and then recording positions over time across a grid, or extended observation of movements for individuals. These approaches can be laborious to set up and run in the field. Another important drawback to these methods is that estimates of diffusion rates are essentially averages over the entire trapping or observational grid. In comparison, Xiao et al.'s (2013) method involves estimating diffusion, dispersal mortality, and edge behavior based on the mean occupancy time within a defined area (including on the boundary between two elements). Much less trapping/observation time is necessary as you only need to know when the animal has left the area. This approach also provides diffusion estimates for a more precise location which is more conducive to heterogeneous landscapes comprised of numerous elements and boundary types.

As more data are collected, and patterns begin to emerge, it may become less imperative that detailed dispersal data be collected for each species to construct landscape models. In fact, it may be possible to make inferences about the dispersal behavior of a species based on simple characteristics of the species in question or the landscape within which it resides. For example, the scale of dispersal is known to be related to body size, morphology, physiology or various life-history traits (e.g., Jenkins et al. 2007; Stevens, Trochet, Van Dyck, Clobert, & Baguette 2012). Relative dispersal ability may also be predicted from records of occurrence of the species outside of its normal range (Stevens, Turlure, & Baguette 2010). Also, movement within a landscape element or across element boundaries may be a simple function of the structural similarity between elements (see Eycott et al. 2012). It is possible, then, that with baseline data on the movement within the host habitat (using the new method by Xiao et al. 2013), and easily obtainable measures of the structural differences among landscape elements, you could roughly approximate the movement behavior of a species.

Lastly, it is also critical that we create models that can account for realism and complexity of landscape. These models will be most useful if they are flexible enough that they can be easily modified to suit different landscape structures and species. Better yet, they also should allow for the possibility that the landscape is dynamic, as has been shown to occur in nature (e.g., Dillemuth et al. 2009; Ramalho & Hobbs 2012; Turner 2010). At a minimum, parameterization of the spatial component of these models is likely to require some idea of the landscape structure (easily obtainable with GIS, satellite imagery, etc.), permeability of edges, and approximate estimates of spatial spread. The methodology we described above is just one approach to achieve this goal. By integrating behavioral ecology with spatially realistic models, it becomes much more feasible to experimentally test model predictions and expand the scope of questions from the purely heuristic to the applied. Finally, with information about the movement behavior of novel predators or alternate prey species, these models could be expanded to include larger components of the community. The future of predator–prey landscape ecology shows much promise and host–parasitoid systems, which are so amenable to manipulation, are likely to be at the forefront of this work.

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