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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.

Keywords: *Anagrus columbi*; Dispersal; Landscape; Metapopulation; *Prokelisia crocea*

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.