

Movement of Entomophagous Arthropods in Agricultural Landscapes: Links to Pest Suppression

N.A. Schellhorn,^{1,*} F.J.J.A. Bianchi,² and C.L. Hsu³

¹CSIRO Ecosystem Sciences, and Sustainable Agriculture Flagship, Brisbane, QLD 4001, Australia; email: nancy.schellhorn@csiro.au

²Farming Systems Ecology, Wageningen University, 6700 AN Wageningen, The Netherlands; email: felix.bianchi@wur.nl

³American Association for the Advancement of Science Fellow, Washington, DC; email: cynthia.hsu.33@gmail.com

Annu. Rev. Entomol. 2014. 59:559–81

The *Annual Review of Entomology* is online at ento.annualreviews.org

This article's doi:
10.1146/annurev-ento-011613-161952

Copyright © 2014 by Annual Reviews.
All rights reserved

*Corresponding author

Keywords

predator, parasitoid, biological control, population dynamics, disturbance, functional traits, spatial and temporal scales

Abstract

Entomophagous arthropods can provide valuable biological control services, but they need to fulfill their life cycle in agricultural landscapes often dominated by ephemeral and disturbed habitats. In this environment, movement is critical to escape from disturbances and to find resources scattered in space and time. Despite considerable research effort in documenting species movement and spatial distribution patterns, the quantification of arthropod movement has been hampered by their small size and the variety of modes of movement that can result in redistribution at different spatial scales. In addition, insight into how movement influences in-field population processes and the associated biocontrol services is limited because emigration and immigration are often confounded with local-scale population processes. More detailed measurements of the habitat functionality and movement processes are needed to better understand the interactions between species movement traits, disturbances, the landscape context, and the potential for entomophagous arthropods to suppress economically important pests.

Movement: a change in the spatial location of an individual

Dispersal: population redistribution that leads to spatial spread of organisms

Entomophagous arthropod (EA): an arthropod that consumes other arthropods in at least one developmental stage

Searching/foraging: a movement phase associated with locating prey or hosts and typically composed of short movement lengths, frequent stops, and a high frequency of turns

Habitat: an organism-preferred living environment that may or may not contain resource patches

INTRODUCTION

Movement is fundamental to the majority of organisms and necessary for their survival. The desire to understand the ultimate and proximate causes and consequences of movement and dispersal has resulted in a rich research domain across organisms and disciplines (25, 33, 41, 104, 178). For entomophagous arthropods (EAs) that live in dynamic agricultural landscapes, movement is critical to locate mates and food, find reproduction sites, and avoid mortality from agricultural practices. The distribution of EAs in agricultural landscapes has consequences for biocontrol services in food and fiber crops (71), with an estimated value of US\$400 billion per annum worldwide (39). Although predators and parasitoids have the potential to suppress pest populations in crops, as suggested by the occurrence of hundreds of species of herbivores in crops of which only a small fraction reach pest status, this requires the arrival of EAs of the right type, at the right times, and in sufficient numbers. Furthermore, few studies addressing EA movement quantify the impact of EAs on pest populations at the field level (66), and even fewer at the landscape level.

The mature and growing body of literature on movement, foraging, and dispersal of EAs has resulted in a broad interpretation, use, and interchange of terminology. More recently, there have been rapid advances in approaches, paradigms, and general understanding of individual-based movement (104). However, the small size of EAs limits the quantification of individual movement; therefore, the majority of studies quantify the outcome of movement in terms of population estimates at a location, rather than individual movement behavior. Emerging spatial patterns show that local-scale abundance and diversity of EAs in crops are related to habitats in the surrounding landscapes (133–135), yet our ability to link these patterns with pest suppression is limited by the lack of quantitative data on movement processes. By exploring the literature on movement and dispersal of EAs in agricultural landscapes, this review seeks to gain a better understanding of the relationship between spatial processes, landscape features, and the potential for pest suppression.

Here we focus on EAs interacting with field-based annual and perennial production landscapes with high spatiotemporal variability and the implications of their movement for pest suppression. In this review we (*a*) clarify relevant movement terminology; (*b*) identify the known proximate (or conditional) causes of movement and distinguish between different dispersal processes; (*c*) consider the consequences of movement related to the features of the agricultural landscape and the behavioral traits of EAs; and (*d*) explore the relationship between dispersal, landscape context, and implications for pest suppression. We do not address the evolutionary causes of movement, as excellent reviews on this topic are available (9, 25, 47, 125).

WHY, HOW, AND WHERE THEY MOVE

Terminology associated with movement of organisms varies across disciplines. The lack of standardization in expressions can be a barrier to identifying generalities regarding movement behavior and its consequences for population processes (25, 104). The term dispersal has been used in a rather narrow sense of “uni-directional movement of an organism away from its place of birth” (98). However, dispersal is also used synonymously with searching, foraging, ranging, and station keeping. These latter terms refer to movements that occur within a restricted geographic area (i.e. home range) to locate resources, but that may not result in spatial spread of the population (48, 159). From a population genetics perspective, dispersal is any movement with consequences for gene exchange (125). Often, dispersal is used to describe movement over different spatial and temporal scales even though the motivation for the movement can be quite different (25), such as migratory and nonmigratory movement (48, 83).

For the purpose of this review, we follow Turchin (159) and Nathan et al. (104) and use the term movement to refer to change in the spatial location of an individual and distinguish between the movement processes of emigration and immigration. The perceived spatial and temporal scales of a patch may be species specific, depending on species traits such as perceptual range and movement ability (99). We define dispersal as population redistribution that leads to spatial spread of organisms (159).

Why They Move: Motivation for Emigration and Immigration

Movement can be separated into three phases: emigration (leaving), interpatch movement, and immigration (arriving), each of which might be motivated by different factors (25, 83). Although movement can potentially result in fitness gain, it is also associated with different energetic, time, risk, and opportunity costs (24, 153). In practice, the phases of movement can be difficult to distinguish, particularly in field settings, and can be cyclical at the scale of hours to years (176). Many mechanisms underlying emigration and immigration have been identified for EAs, some of which are listed below, but there has been far less attention on the spatial scales at which EAs are attracted to or deterred from habitats (131).

Emigration involves patch leaving. In some cases, EAs emigrate immediately upon eclosion (e.g., oogenesis flight syndrome; 4, 83) or because of local biotic and abiotic conditions. While in transit they may engage in several bouts of arriving and leaving patches (48) and learn to recognize suitable prey or hosts along the way (167). Although numerous factors can initiate movement of EAs, in many cases a combination of factors triggers emigration. For example, patch leaving of the predatory bug *Orius minutus* L. (Hemiptera: Anthocoridae) was associated with the combination of temperature and presence of conspecifics (158). Such responses are often species specific (128).

Internal factors such as sex and mating status can influence emigration decisions (68, 165). For instance, unmated male and female parasitoids often postpone leaving until mating (88, 107). In addition, emigration propensity is influenced by numerous external factors. Crowding and cues from conspecifics or heterospecifics can influence EA emigration. For example, high densities of the female linyphiid spider *Erigone atra* Blackwall resulted in increased female rappelling, and the presence of silk threads increased leaving of both sexes (46). Emigration rates of immature and adult coccinellids are typically negatively related to prey density (57, 164), although this is more pronounced for oligophagous than for polyphagous species (128). In the spider *E. atra*, starvation of the mother resulted in emigration of her offspring (102). In contrast, the braconid parasitoid *Macrocentrus grandii* Goidanich was more likely to leave a concealed host site at high local host densities than at low densities (173).

Habitat attributes influence emigration of coccinellids. At the plant level, glandular trichomes repelled *Coleomegilla maculata* De Greer larvae, and the maturation stage of sorghum initiated emigration in *Hippodamia convergens* Guérin-Ménéville adults (40, 119). At the patch level, the lycosid spider *Hogna belluo* Walckenaer was more likely to leave no-till fields than mulched fields, but this had no influence on the leaving tendency of the lycosid *Pardosa milvina* Hentz (26). The braconid aphid parasitoid *Diaeretiella rapae* McIntosh was less likely to leave large patches of host plants than small patches, independent of aphid host density (137), whereas a higher proportion of coccinellids left patches with a high perimeter-to-area ratio than patches with a lower ratio (69).

Immigration involves the detection of, arrival at, and settlement on a patch. Immigration may operate at small temporal scales, for instance, when a patch is quickly explored for resources after which the patch is abandoned, but may also entail long-term settlement over multiple generations. Although the internal state of organisms (e.g., hunger level) is likely to be an important factor influencing immigration propensity, there are few reported cases. For instance, the parasitoid

Emigration:

the movement of an individual away from a patch or habitat

Immigration: the movement of an individual into a patch or habitat

Patch: an area containing resources that are spatially or temporally aggregated and separated in space and time from other areas containing that resource

Perceptual range: spatial extent for which information is available to the organism

Cotesia rubecula Marshall is attracted to flowers when it has low energy reserves, whereas well-fed parasitoids are not (138). Hence, hunger level could influence EA immigration decisions toward a patch with flowers or hosts (145).

A positive effect of prey or host density on immigration propensity has been shown for many EAs. For coccinellids, prey density is a key patch attribute that determines whether adults settle on agricultural crops (76). However, coccinellid species aggregate at varying prey densities and at different spatial scales (79, 129). Parasitoids are attracted to a range of infochemicals released by hosts and to herbivore-induced plant volatiles (61, 84, 131, 168). As yet, relatively few studies have investigated plant volatile effects under field conditions. Poelman et al. (116) showed that the release of volatiles is positively correlated to parasitism rates in small-scale field experiments, and Williams et al. (175) provide field evidence that parasitoids use upwind anemotaxis to arrive at patches of hosts and host plants. However, the spatial range of plant volatiles is unknown and evidence of effects on a landscape scale is lacking, hence further work in this area is needed.

How and Where They Move: Motion and Navigation Capacity

An organism's capacity to move defines its potential movement range (104) and is determined by phenotypic and genetic factors (25, 34, 49, 125). EAs use self-directed (e.g., walking, jumping, falling, and flying) and passive (wind, phoresy, and human-mediated transport) mechanisms for movement. Phoresy, whereby one organism acts as transport vector (i.e., host) and the other as passenger, is common in species of egg parasitoids (62), predatory mites (19), and a few species of Diptera, Coleoptera, and Neuroptera (32). Passive dispersal via anthropogenic transport can occur unintentionally, such as the movement of masses of spiders by trains, planes, and automobiles (9), or intentionally, such as the introduction of agents used in biological control programs.

The initiation or termination of movement is frequently influenced by weather and meteorological conditions. Movement of EAs can be affected by temperature, humidity, barometric pressure, and wind speed (8, 63, 86, 90, 100, 126, 158, 183). Flying arthropods can control their direction and speed within their flight boundary layer (FBL), i.e., the air layer above the ground or plant canopy where their flight speed exceeds wind speeds (144). Arthropods that rely on passive dispersal mediated by wind often use active behaviors to enter, stay in, and leave the wind stream above their species-specific FBL (49). For example, spiders use silk balloons to create drag-induced lift to become airborne (9), and predatory mites raise part of their body to increase their probability of wind dispersal (41). Ballooning spiders and predatory mites select meteorological conditions that maximize dispersal (9, 41).

The convective boundary layer (CBL) extends 1,000 m above the FBL. Wind speed increases with distance above the ground and once arthropods enter the CBL, transport is almost always downwind (29). In CBL netting studies in England, parasitic Hymenoptera were the third most abundant order found in aerial catches at 200 m above ground level (755 individuals) (28). Other EAs captured included minute pirate bugs (Hemiptera: Anthorcoridae), lacewings (Neuroptera: Chrysopidae, Hemerobiidae), hover flies (Diptera: Syrphidae), coccinellids (Coleoptera: Coccinellidae), and carabids (Coleoptera: Carabidae). Ichneumonids and carabids were primarily captured during the day, with a small portion of ichneumonids captured during dusk and night. Hence, a wide range of modes of movement can lead to displacement across a range of spatial scales.

Navigation capacity can be an important factor in emigration and immigration decisions. Navigation capacity involves the gathering of cues to inform movement decisions (34, 104) and is often expressed in terms of a detection distance or perceptual range, i.e., the spatial extent of the landscape for which information is available (58, 99). The perceptual range concept recognizes that insects can obtain reliable information from their surroundings only up to a critical distance,

which varies depending on the cue and the arthropod's perceptual ability. EAs can respond to a wide range of visual, olfactory, gustatory, and tactile cues (1, 84, 168, 170), and many EAs have the capacity to associate cues with resources and modify their behavior after perceiving a cue (45, 75). Some cues stimulate directional movement (taxes), whereas random movements are stimulated in response to cues that have no inherent direction (kineses) (70). Different cues are expected to operate at different spatial scales for long-range, intermediate-range, and short-range detection (61, 171). Interactions between the internal state of EAs that motivate movement and the spatial scales at which they respond to cues under field conditions remain ambiguous and need further study. A better qualitative and quantitative understanding of the factors that drive immigration and emigration and of the relevant distances associated with each factor can help prioritize those factors most relevant to understanding landscape-scale movements. In turn, this can inform and guide field studies investigating the impacts of landscape-scale movements on pest suppression.

Source: patches in which birth rates exceed death rates and emigration rates exceed immigration rates

IMMIGRATION AND EMIGRATION: IMPLICATIONS FOR IN-FIELD DYNAMICS

An emerging body of literature shows that local-scale patterns in abundance and diversity of EAs in crops are related to particular habitat types in the surrounding landscape (11, 120, 133–135, 147). Immigration to crops from surrounding habitats has been suggested as a driver of these spatial patterns, but few studies have quantified the timing, frequency, and intensity of immigration events of EAs into crops. In turn, immigration is often confounded with local reproduction, making inferences about the relative contribution of immigration and reproduction to population increase problematic, particularly when EAs can complete multiple generations in a crop cycle. Separating these processes can help researchers better understand the contribution of landscape-scale (immigration) and local-scale (reproduction) processes to population dynamics and their implications for pest suppression. **Table 1** summarizes studies that have quantified EA immigration and provides an overview with regard to timing (2, 36, 51, 74, 96, 106, 114, 150, 175), relationships with prey (2, 74), and adjacent habitats (2, 20, 36, 96, 105, 150). These studies highlight species-specific immigration dynamics and that EAs immigrating to a focal field are only sometimes found in adjacent habitats, suggesting that immigrants are recruited from both local and distant source habitats. An additional consequence of the lack of information on the timing, frequency, and intensity of immigration events is that the potential for EAs to reestablish after a disturbance is often unknown. Langhof et al. (94) indicated that the recolonization by *Aphidius colemani* Viereck (Hymenoptera: Braconidae) of potted kohlrabi plants (*Brassica oleracea*) treated with insecticides was extremely poor, whereas Stark et al. (142) found that spraying isolated trees in orchards with insecticide resulted in rapid recolonization by fruit flies and their parasitoids. In cases where in-field population increase of EAs is due primarily to local reproduction and immigration rates are low, broad-spectrum insecticide applications can result in the depletion of EA populations for extended periods in the growing season. For example, Topping & Sunderland (152) showed that with the exception of a single immigration event, in-field population growth of the Linyphiidae spider *Lepthyphantes tenuis* was due to reproduction.

Similarly, few studies have quantified season-long emigration patterns (**Table 2**) and distinguished between emigration and mortality. The limited information available suggests that emigration is not an end-of-cropping-season phenomenon, but a continuous process across the growing season and can vary between generations and in response to host density (**Table 2**). Work by Hirose et al. (74) showed that the second and subsequent generations of the Encyrtidae parasitoid *Ooencyrtus nezarae* Ishii left soybean crops while hosts were still present. However,

Table 1 Summary of open field studies of entomophagous arthropods that distinguish immigration from in-field reproduction, and/or links to adjacent habitats^a

Reference	Functional group	Species	Movement mechanism	Response variable measured	Frequency of immigration	Species relative immigration	Separate immigration and reproduction	EA and host/prey relative arrival time	EA occurs in adjacent habitats to focal field	EA in adjacent habitat linked to early or more EA in focal field	EA species composition similar in focal field and adjacent habitat
2	Predator (Hemiptera: Heteroptera)	Dt, Mc	Flight	Density	Cropping season	Dt > Mc	Yes	Predator < prey	+/-	+/-	n/a
20	Predator (Araneae)	Many families and species	Ballooning, cursorial	Density	Cropping season	n/a	n/a	n/a	+/-	+/-	Minority
36	Predator (Coleoptera: Carabidae)	5 species: Ad, Bl, Da, Th, Tc	Flight, cursorial	Counts	Cropping season	Ad = Bl > Da = Th > Tc	n/a	n/a	+	+/-	Majority
51	Predator (Acarina: Phytoseiidae)	Mo, Tp	Drift	Density	Cropping season	Mo > Tp	Yes	n/a	n/a	n/a	n/a
69	Predator (Coleoptera: Coccinellidae)	3 species (grouped in analysis)	Flight	Density, counts	Middle and late seasons	n/a	Yes	n/a	n/a	n/a	n/a
74	Parasitoid (Hymenoptera: Encyrtidae)	Encyrtidae: On, Scelionidae: Tt	Flight	Density, counts, percent parasitism	Cropping season	On > Tt	Yes	On: Parasitoid = host; Tt: Parasitoid < host	n/a	n/a	n/a
96	Predator (Araneae: Erigonidae)	Oa, Ea	Oa: cursorial; Ea: ballooning and cursorial	Density	Cropping season	Oa > Ea; Oa = Ea	n/a	n/a	Oa: +; Ea: +	Oa: +; Ea: +/-	n/a

(Continued)

105	Predator (Coleoptera: Carabidae)	5 species	Cursorial	Density	Early season	n/a	Yes	n/a	+	+	Majority
	Predator (Araneae: Lycosidae, Linyphiidae, Teragnathidae)	9 species	Cursorial	Density	Early season	n/a	Yes	n/a	+	+/-	Majority
106	Predator (Araneae: Lycosidae)	12 species	Ballooning	Density	Early season	Lycos < Liny	n/a	n/a	n/a	n/a	n/a
	Predator (Araneae: Linyphiidae)	34 species	Cursorial	Density	Early season	Liny > Lycos	n/a	n/a	n/a	n/a	n/a
114	Predator (Coleoptera: Carabidae)	Bl, Th	Bl: cursorial; Th: flight, cursorial	Counts	Early season	Bl > Th	Yes	n/a	n/a	n/a	n/a
150	Predator (Coleoptera: Carabidae)	Carabidae: Da, Staphylin- idae; Th	Da: cursorial; Th: flight, cursorial	Density	Early and middle seasons	Da < Th	Yes	n/a	+	+	n/a
152	Predator (Araneae: Linyphiidae)	Lt	Ballooning, cursorial	Density, counts	Cropping season	n/a	Yes	n/a	n/a	n/a	n/a
175	Parasitoid (Hymenoptera: Ichneumonidae)	Ichneumonidae: Pi, To; Playgasteridae: Ps	Flight	Counts	Cropping season	Pi > To > Ps	Yes	n/a	n/a	n/a	n/a

^aThe relative immigration time relates the arrival of one EA species to another and is expressed as species arriving at the same time (=), earlier (<), or later (>). The timing of EA immigration relative to hosts or prey is represented as equal (=), earlier (<), or later (>). Studies that separate the process of immigration and reproduction either directly or indirectly are indicated with "Yes." EA occurrence in focal fields and adjacent habitats and EA in adjacent habitat linked to early or more EA in focal field is characterized as often (+), sometimes (+/-), or never (-) present; EA species composition in a focal field and adjacent habitat is characterized as majority or minority.

Abbreviations: Ad, *Agonum dorsale*; Bl, *Bembidion lampros*; Da, *Demetrius atricapillus*; Dt, *Dicyphus tamaninii*; EA, entomophagous arthropod; Ea, *Erigone atra*; Lu, *Lepthyphantes tenuis*; Mc, *Macrolophus adiginosus*; Mo, *Metaseiulus occidentalis*; n/a, not applicable or did not measure; Oa, *Oedoborax apicatus*; On, *Ooencyrtus nezarae*; Pi, *Phradis interstitialis*; Ps, *Playgaster subuliformis*; Tc, *Tachyporus chrysomelinus*; Th, *Tachyporus hypnorum*; To, *Tersilochus obscurator*; Tp, *Typhlodromus pyri*; Tt, *Telenomus triptus*.

Table 2 Summary of open field studies of entomophagous arthropods that evaluate seasonal emigration and/or intergenerational leaving or leaving as a function of host/prey density

Reference	Functional group	Species	Movement mechanism	Response variable measured	Species relative emigration ^a	Intergenerational leaving	Leaving while host present	Hypothesized reason for leaving
74	Parasitoid (Hymenoptera)	Encyrtidae: On; Scelionidae: Tt	Flight	Counts	On > Tt	On: Strong; Tt: Weak	On > Tt	On: Strategy to exploit mobile host; Tt: n/a
81	Predator (Coleoptera: Coccinellidae)	Cc; Ct	Flight	Counts	Cc > Ct	Strong	Cc > Ct	Cc: Low aphid density and unknown reasons; Ct: High temperature and unknown reasons
109	Predator (Coleoptera: Coccinellidae)	<i>Harmonia axyridis</i>	Flight	Counts	n/a	Strong	n/a	Prey quantity and quality
152	Predator (Araneae: Linyphiidae)	<i>Leptyphantes tenuis</i>	Ballooning, cursorial	Density, counts	Females > males	n/a	n/a	Strategy to exploit ephemeral habitats
175	Parasitoid (Hymenoptera)	Ichneumonidae: Pi, To; Platygastridae: Ps	Flight	Counts	Pi ≥ To > Ps	n/a	n/a	n/a

^aThe relative emigration time relates to the leaving of one entomophagous arthropod species to another and is expressed as species leaving at the same time (=), earlier (<), or later (>).

Abbreviations: Cc, *Coccinella californica*; Ct, *Coccinella trifasciata*; n/a, not applicable or did not measure; On, *Ooencyrtus nezarae*; Pi, *Pbradis interstitialis*; Ps, *Platyaster subuliformis*; To, *Tersilochus obscurator*; Tt, *Telenomus triptus*;

the scelionid *Telenomus triptus* Nixon was less likely to leave. Ives (81) showed that 6–16% of coccinellids left alfalfa and oat fields per day, even at suitable prey levels (Table 2).

The outcome of emigration processes and associated spatial redistribution of emigrants can be quantified by mark-release, in-field marking, or self-marking methods. Although these approaches are often used to assess optimal release rates of biological control agents or average maximum distances moved, they can also provide insight into emigration as a function of host density, disturbance, and habitat type (10, 119, 130, 140). The wide array of approaches used to assess emigration and the subsequent interpretations hamper the derivation of broad generalizations, except that in most cases we are likely to underestimate the rate of emigration, distance traveled, and the variety of dispersal modes (5, 44, 90, 140, 164).

Immigration and emigration in cropping systems link dispersal processes operating at larger spatial scales to local in-field population dynamics (43). Although the surrounding landscape can influence the level of pest suppression (11, 27), less is known about the relationship between immigrants and their original source habitat (16), and the relationship between emigrants and their destination (121). For example, using spatially indexed regression techniques, researchers have suggested a functional spatial scale of 1–1.5 km for parasitoids—the ichneumonid *Pbradis interstitialis* Thomson and braconid *Tersilochus heterocerus* Thomson—and for the genera *Aphidius* and *Diadegma* (12, 146). However, these correlative studies based on land use classes do not

provide insights into the detailed characteristics of the source habitats, such as patch size, vegetation composition, and prey or host availability. The closely related concept of spillover (121) uses relative estimates of abundance of EAs in multiple habitats at different times to make inferences about emigration and immigration dynamics. However, these studies typically do not assess prey or host densities and the potential for EAs to remain in crops and contribute to pest suppression. As an example, there is solid empirical and theoretical work on searching efficiency and patch-leaving behavior (56, 167, 172), yet there is virtually no information available on how this is related to the phenology of the crop or economic pest density threshold levels. This knowledge gap demonstrates the lack of understanding of the relationships between EA behavior, their population-level response, and their ability to suppress pest populations in crops.

CONSEQUENCES OF POPULATION PROCESSES

EAs that are instrumental in providing biocontrol in crops must often persist year-round in agricultural landscapes and depend on life-support functions delivered by the landscape (7, 154). These life-support functions are often intimately linked to the vegetation present in the habitat patch, such as plant species that provide nectar or support suitable hosts or prey. The relevant features of a landscape depend on the ecological requisites of the species of interest. Following Tischen-dorf & Fahrig (151), agricultural landscape mosaics can be described in terms of structural features (e.g., shapes, sizes, spatial arrangements, and biophysical characteristics of habitats) and functional features (e.g., resources and threats present in habitats). This functional approach in particular may provide insight into how landscapes influence movement patterns, population processes (i.e., birth, death, immigration, and emigration), and spatial distributions of EAs.

Entomophagous Arthropods in a Landscape Context: The Spatial Dimension

Empirical evidence and theory suggest that movement patterns emerge from the interaction between landscape context and functional traits of the species with respect to movement (55, 59, 60, 155). The enormous differences in landscape contexts and the number of species living in these landscapes result in a bewildering array of emerging patterns.

Dunning et al. (52) identified four broad classes of landscape processes based on the physiog-nomy and composition of the landscape. First, landscape complementation occurs when species depend on at least two critical, nonsubstitutable resources that are found in different habitat types. The distance and functional connectivity between these habitat types can then influence the population size supported by the landscape. Second, landscape supplementation involves the enhancement of a population in a focal patch when there are patches with a substitutable resource present nearby. Third, source-sink relationships appear when productive patches serve as a source of emigrants that disperse to less productive patches, and populations in these less productive patches cannot persist without this immigration. Fourth, neighborhood effects occur when a population in a focal patch is more strongly affected by the characteristics of a nearby patch than patches farther away. Although this categorization of processes is useful to identify the relationships between habitats at the landscape scale, the categories are not mutually exclu-sive and multiple processes can apply to a particular population. For instance, the immigration of egg parasitoids in vineyards from nearby prune trees and more distant riparian habitats may involve landscape supplementation, source-sink relationships, and neighborhood effects (37). The establishment of flowering plants providing nectar resources adjacent to crops can affect EA pop-ulations via landscape complementation, source-sink relationships, and neighborhood effects (95, 160). Multiple categories can also be used to describe habitat-crossing behavior of EAs (50) and

Functional spatial scale: spatial scale experienced by an organism

Structural connectivity: habitat contiguity based on physical landscape features

Functional trait: a trait that strongly influences organism performance

Physiognomy: physical arrangement of landscape features relative to each other, such as patch isolation or connectivity

Functional connectivity: habitat contiguity defined by species-specific responses to landscape features

Sink: patches in which death rates exceed birth rates and immigration rates are higher than emigration rates

spillover effects from crop to noncrop habitats (21, 121, 157) as well as to identify EA source habitats (16, 108, 115).

The above four landscape processes have been developed for temporally stable conditions; however, the dynamic conditions in agricultural production landscapes may benefit from concepts that explicitly incorporate the effects of disturbance (166). For instance, crops supporting prey can be a source for EAs that reproduce in this habitat, but this could stop after a disturbance, leading to ephemeral source habitats. A low-quality rangeland may be a sink for EAs, but upon disturbance it may trigger emigration, leading to a propagating sink (166). To capture the reoccurring mortality and recolonization events in crop habitats in agricultural landscapes, approaches that explicitly distinguish between population changes due to local processes (birth and death) and processes associated with movement (emigration and immigration) can be advantageous. Using a process-based approach, Thomas & Kunin (148) describe the spatial structure of populations by positioning population units in two-dimensional demographic space according to the extent to which the population unit is dominated by local-scale population processes (birth and death) and by population processes associated with movement (immigration and emigration; **Figure 1**). This approach allows the visual characterization of structured populations in different habitat types that are linked via movement processes during critical periods in the growing season, such as the immigration of predators in a newly planted crop (36), the buildup of local predator populations in crops (181), and the recolonization of fields after a disturbance (149).

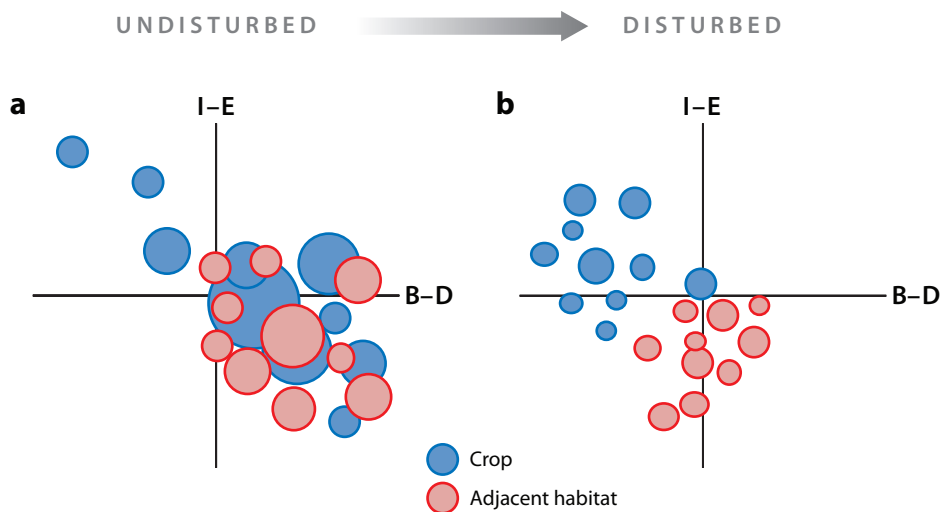


Figure 1

Hypothetical distribution of entomophagous arthropod (EA) population units on a local-scale population process axis (birth minus death, $B - D$) and a population process axis associated with movement (immigration minus emigration, $I - E$). Population units in crops and adjacent habitats are indicated in blue and red, respectively. The size of each circle represents the population size at a given sampling event. The undisturbed example (*a*) shows a landscape with mostly increasing EA population units in crops and adjacent habitats, due to local processes ($B > D$) and a net export of EAs ($E > I$). Such a landscape might represent the ideal for pest management where EAs are utilized. Disturbance events (*b*), such as extensive insecticide use or periodic harvesting, cause a transition to population units in crops with high mortality due to local processes ($D > B$), which now depend on immigration from adjacent habitats for survival ($I > E$). Population units in crops in this case cluster in the upper-left quadrant and have become effective sinks for EAs. Population units in adjacent habitats may suffer from insecticide drift resulting in increased mortality, reflected in a shift to the left on the $B - D$ axis. Schematic follows the concept of Thomas & Kunin (148).

Entomophagous Arthropods in a Landscape Context: The Temporal Dimension

The concepts discussed above focus on the spatial aspect of species-landscape interactions, but the temporal aspect has received far less attention. Agricultural landscapes are characterized by strong temporal changes in resource availability and arthropod population sizes. Both crop and noncrop habitats can provide resources for EAs, but crop habitats are inherently unstable because of management practices such as plowing, planting, weeding, insecticide applications, crop senescence, and harvest (87). As a consequence, EAs that live in these disturbed crop habitats are subject to frequent mortality events (108, 149) and often have traits to deal with these interventions, for instance, short life cycles or the ability to move to refuges outside the crop (141, 176). This implies that there is a selection pressure on species to cope with the harsh conditions in arable fields. Species that could contribute to biocontrol may not be present in crops (59), and EA species that are present in crops may show a high emigration propensity, even at suitable prey or host densities, which may compromise biological control (74). A small but growing body of literature is exploring the effects of periodic disturbance regimes and the ephemeral nature of crop habitats on population dynamics of EAs in agricultural landscapes (14, 30, 78, 80, 127, 166) and on the evolution of dispersal strategies (22).

Given the highly dynamic nature of agricultural landscapes, we propose that the functional categorization of agricultural landscapes for supporting EA populations should integrate the spatial (60) and temporal heterogeneity of the landscape and explicitly account for the disturbance regimes (Figure 2a–c). Because disturbances can differ in type, magnitude, frequency, and timing, many disturbance regimes are possible (127). Therefore, the interaction between disturbance regime and functional composition of the landscape is likely to influence emigration and immigration dynamics, although there is little empirical evidence for this. Mechanical and chemical disturbances associated with crop management can cause mortality in EA populations, in particular in those species that cannot fly (94, 131), and emigration of EAs that can move to other habitats (2, 130, 140). Although empirical support is lacking, insecticide applications may not only alter landscape

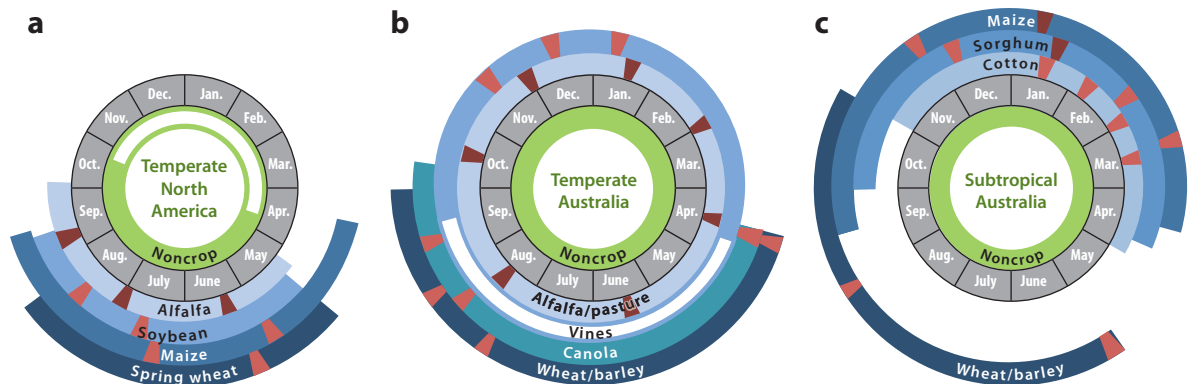


Figure 2

Agricultural landscape wheels representing compositional and temporal heterogeneity, and plausible scenarios of disturbance regimes from (a) temperate upper midwest North America, (b) temperate eastern Australia, and (c) subtropical eastern Australia. The visualization shows the periods when alternative habitats may be crucial for hosting entomophagous arthropods and influencing emigration and immigration dynamics within and between cropping seasons. Time is expressed clockwise in the inner circle. Seasonality of cropping systems is represented by each bar. Compositional heterogeneity is represented by the number of bars. Temporal heterogeneity is represented by the alignment of bars. Plausible disturbance from insecticides is represented by light red boxes, and periodic harvest is represented by dark red boxes. Late-successional noncrop habitat is represented by the innermost circle. White areas within bars represent deciduous habitats during leaf shed.

Colonization: the act of establishing a population in a new habitat via the reproduction of immigrants

functionality by creating sinks, but might also influence the functional connectivity of the landscape (60, 151). Depending on the landscape context, the activity period of the insecticide in the crop, and the timing and frequency of immigration events, the recovery period of EA populations in the disturbed habitat may vary. Disturbed habitats embedded in landscapes with a high functional connectivity and a high proportion of source habitats from which EAs are continuously emigrating are likely to show the greatest resilience (154). Whereas the landscape context can influence landscape-scale dispersal processes and the associated spatial distribution of EAs, the interaction between local-scale disturbances and landscape-scale dispersal processes are not well studied (but see 14). This knowledge gap creates a barrier to identifying local-scale mitigation strategies, such as providing refuges that may buffer the impact of disturbances and facilitate immigration and recolonization.

THE CONSEQUENCES OF MOVEMENT FOR PEST SUPPRESSION

The influence of movement on population processes, species distributions, and ultimately biodiversity patterns suggests that it can have implications for trophic interactions and pest suppression. Top-down natural biocontrol requires the establishment of effective EA communities that can keep herbivore populations below economic threshold levels. There are various ways in which the spatial context of crop production systems can influence the spatiotemporal distribution of biocontrol services by EAs.

Time to Colonization

An early arrival of EAs has been proposed as a key factor for the control of herbivore populations with high population growth rates (54, 80, 136). Empirical support for the importance of early predation by ground-dwelling predators for pest suppression comes from exclusion experiments whereby the time of predator arrival is manipulated in plots infested with aphids (31, 53, 92). For instance, Edwards et al. (53) showed that predator access postponed by one month increased aphid load by approximately 30–40%. Herbivore populations may also be controlled by flying predators that occasionally remove a limited number of herbivores as long as herbivore densities in crops are low (179). Several studies showed that exclusion of flying predators, including the coccinellids *Harmonia axyridis* Pallas, *Hippodamia variegata* Goeze, and *Coccinella septempunctata* L., resulted in a rapid buildup of aphid populations, whereas aphid densities in control plots remained low for several weeks (38, 64).

An early arrival of EAs in crops can be mediated by the interaction of species behavior (e.g., timing of emergence after hibernation, immigration propensity) and landscape features. On theoretic grounds the distance between source habitats and target (crop) sites has been suggested as a predictor for the arrival times of EAs (15, 17); however, the evidence for this is equivocal (2, 37, 105, 114).

Mass Action

Top-down control of herbivore populations can be enhanced by sheer numbers of EAs. As discussed above, various landscape processes can result in the buildup of EA populations. A key feature that allows this to occur is the provision of food resources for EAs (121). The availability of alternative prey or hosts during periods when pest densities in crops are low can be essential to sustain EA populations (93). For instance, thrips that appears in soybean fields soon after crop emergence allowed *O. insidiosus* populations to build up, resulting in effective suppression of soybean aphids that arrived later in the season (181). Mass action can also be related to the phenology of the life

cycle of EAs. For instance, mass immigration events have been reported for linyphiid spiders in cereal and grass fields during the summer reproduction period in July in the United Kingdom (149) and for the carabid beetle *Poecilus cupreus* L. in wheat fields in August in Austria (91).

Diversity of Entomophagous Arthropods

Emigration and immigration are the ultimate drivers of local species diversity. Many studies have examined the effect of the EA community on herbivore suppression (97) and the underlying mechanisms (77, 156). Although EA richness was associated with a greater level of herbivore suppression in 70% of 266 cases (97), there are also notable exceptions (103, 124). These contrasting findings could be explained by the level of heterogeneity of the study systems (162). Tylianakis & Romo (161) hypothesize that pest populations with high fluctuations in time and or spatially aggregated distributions are best controlled by a complex of EAs, whereas in cases when pest populations show little spatiotemporal variation, a single effective control agent might be more effective.

Whereas spatial patterns of EA diversity in agricultural landscapes have been extensively studied and show that late successional noncrop habitats are often reservoirs of EAs (35, 73, 132), the buildup of the EA community in crops during the growing season has received less attention. Kromp & Steinberger (91) show that the diversity of spiders and carabid beetles in winter wheat declines from May to September, whereas the diversity of harvestmen are stable across this period. Furthermore, little is known about the identity of source habitats from which immigrants are recruited (but see 36) and how habitat diversity influences local EA communities.

Species-Landscape Combinations

The combination of EA species traits and landscape features determines the functional connectivity of the landscape for the species of interest (60, 151, 177) and may in part determine where biocontrol services are provided (143). Habitats or edges may inhibit or facilitate movement (37, 42, 112, 123, 182). Whereas roads (50), hedgerows and grassy banks (65, 101), and tree lines (180) may act as barriers of EAs, there is much less evidence for landscape elements that facilitate EA movement (but see 89).

The species traits that historically have been associated with effective biocontrol include (a) reproductive capacity relative to that of the pest; (b) high dispersal capacity; (c) host specificity, preference, and synchrony; (d) superior competitive ability; and (e) searching capacity (85, 174). However, favorable traits for EAs operating in ephemeral or perennial habitats may not necessarily be the same (67). Given the experimental limitations to investigate the interaction between species traits with landscape features, modeling studies have been helpful to explore the potential outcomes of species-landscape interactions (3, 13–15, 18, 23, 118). For instance, Potting et al. (118) showed with a detailed, individual-based model for insect herbivores the importance of moving speed, search mode (contact, olfactory, or visual), and perceptual range for the spatial distribution of herbivores in diversified agroecosystems. A landscape-scale simulation study suggests that in landscapes in which fields are subject to recurrent mortality events, parasitoids with a low dispersal capacity may give rise to superior pest management outcomes compared with more mobile parasitoids (14). Although there is increasing evidence that edge-crossing behavior is a key factor determining how individuals disperse in landscapes (60, 151, 122), the incorporation of this behavior has been a long-standing challenge in modeling species-landscape interactions. In many modeling studies edge-effects are ignored, for instance by the use of fixed population redistribution functions (dispersal kernels). However, new approaches have been proposed to address this issue for diffusion models (110), individual-based models (118), and models using dispersal kernels (169). For instance, using a pattern-oriented individual-based modeling approach, Vinatier et al. (169)

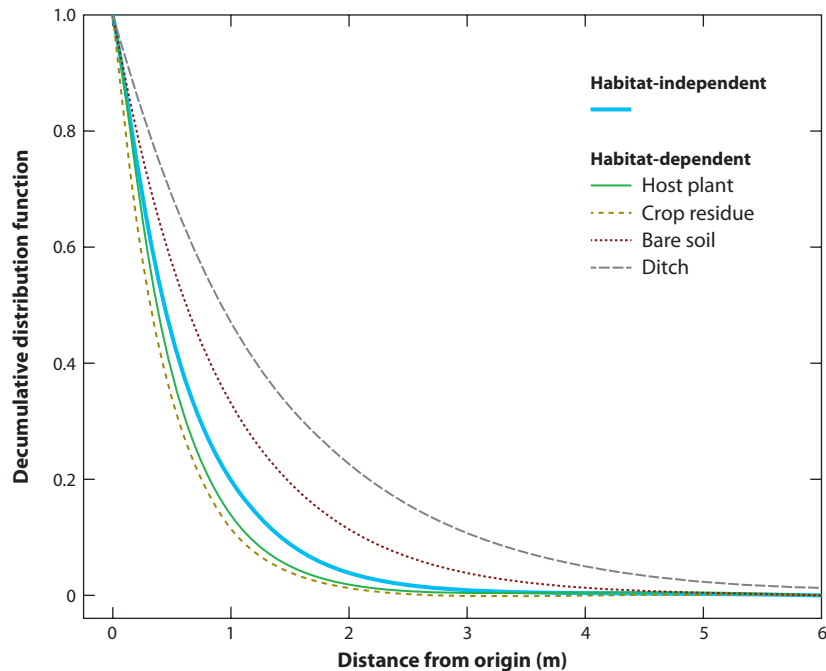


Figure 3

Habitat-specific spatial redistribution functions of the banana weevil *Cosmopolites sordidus* (Germar) (Coleoptera: Curculionidae). Reprinted with permission from Reference 169.

showed that a habitat-specific dispersal kernel approach received more support from empirical data than a model with a fixed (habitat-independent) dispersal kernel (**Figure 3**). This finding suggests that incorporating perceptual range, habitat-specific preferences, and mortality may improve inferences about the functional connectivity of landscapes (72) and the biocontrol potential of EAs (18).

REFLECTION AND OUTLOOK

Understanding top-down control of pest populations by EAs in dynamic cropping landscapes requires insight into the spatial ecology of pests and biocontrol service providers. In particular, more detailed information is needed on (a) the relative importance of the different population processes (emigration, immigration, birth, and death) in the habitat types present in agricultural landscape mosaics; (b) how these processes are affected by crop management practices; and (c) the timing, frequency, and spatial scale of movement between habitat and nonhabitat components of the landscape. Historically, the quantification of movement of EAs has been limited by their small size and high labor requirements. New approaches of marking EAs (140), landscape genetics (6), radar technologies (29), and wireless sensor networks (117) may be used to monitor population redistributions at larger spatial and temporal scales than before. Furthermore, recent advances in movement ecology highlight the generality of Lévy flight across a wide range of taxa (139; but see 82) and could be extended to farmland arthropods. However, the disturbed and ephemeral nature of crop habitats is likely to alter movements (59), such that potential dispersal ranges will not always be realized. The effect of habitat on EA movement underscores the need to consider movement within the context of species' traits and ecological requirements, as well as the functional properties

of the landscape (including disturbance) as perceived by the species (60, 99). Instead of descriptions of numbers of simple patterns, we need experiments that quantify the relative contributions of emigration, immigration, and reproduction and that estimate movement metrics at different spatial and temporal scales. This data can then be combined with novel quantitative tools (111, 113, 163) that can explore and extend empirical findings to provide a better understanding of the spatial distributions of EAs in agricultural landscapes and their potential to suppress pests.

SUMMARY POINTS

1. Standardization of terminology across disciplines in movement ecology can help develop unifying concepts.
2. The spatial scales at which cues are detected to initiate emigration or immigration under field conditions remain ambiguous and need further study.
3. The relative contribution of immigration and reproduction to in-field population increase of EAs is often confounded. Similarly, emigration and mortality are often confounded for in-field population decrease. Disentangling these processes offers insight into the seasonal dynamics of immigration and emigration in focal fields and the potential for re-establishment after disturbance.
4. Active and passive dispersal mechanisms used by the same EA can result in different spatial scales of movement, and more work is needed to connect movement mechanisms to local or landscape level dynamics.
5. The highly dynamic nature of agricultural landscapes demands a process-based approach to quantify the immigration and emigration rates of EAs in focal crops and to link local-scale and landscape-scale processes.
6. Functional categorization of agricultural landscapes for supporting EA populations should integrate the spatial and temporal heterogeneity of the landscape and explicitly account for the disturbance regimes. This approach allows for the identification of relevant landscape features and targeted mitigation strategies to buffer impacts of disturbance and facilitate recolonization.
7. The combination of EA species traits and landscape features determines the functional connectivity of the landscape and may in part determine where biocontrol services will be provided. Therefore, pest suppression is likely to depend on EA species traits and the spatial, temporal, and disturbance contexts.
8. The triad of laboratory, field experiments, and modeling provides a powerful approach to link species traits, landscape features, and pest suppression. Modeling overcomes some of the logistical limitations of empirical approaches for studying EA movement and can guide experimental studies by exploring processes and mechanisms and by identifying knowledge gaps.

FUTURE ISSUES

1. Tools are needed for the translation of individual movement to movement at the population level and for capturing movement patterns at various spatial scales.

2. Historically, quantifying the spatial extent and timing of EA movement has been constrained by intensive labor requirements. New technologies using small, cheap, and disposable tracking units and sampling stations may allow monitoring of individual behavior and population redistributions at larger spatial and temporal scales than before.
3. Spatially explicit simulation models provide a valuable exploratory tool to reveal the effects of mitigation strategies to buffer impacts of disturbance and landscape homogenization.
4. More studies are needed to investigate the interactions between species traits with regard to movement and the spatial distribution of resources and disturbances. This will enable a better understanding of species responses in realistic landscape settings.
5. Studies that assess the timing, number, and diversity of EAs in different landscape settings (e.g., varying disturbance levels, resource distribution) will contribute to a better mechanistic understanding of landscape-mediated biocontrol services.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank Anna Marcora and Andy Hulthen for support with literature search and graphics, and Sarina MacFadyen and Hazel Parry for useful comments on earlier versions of this article. FJJAB was supported in part by the Division for Earth and Life Sciences (ALW) with funding from the Netherlands Organization for Scientific Research (NWO). NAS is supported in part by Grains Research and Development Corporation and Cotton Research and Development Corporation.

LITERATURE CITED

1. Almohamad R, Verheggen FJ, Haubruge É. 2009. Searching and oviposition behavior of aphidophagous hoverflies (Diptera: Syrphidae): a review. *Biotechnol. Agron. Soc. Environ.* 13:467–81
2. Alomar Ò, Goula M, Albajes R. 2002. Colonisation of tomato fields by predatory mirid bugs (Hemiptera: Heteroptera) in northern Spain. *Agric. Ecosyst. Environ.* 89:105–15
3. Arrignon F, Deconchat M, Sarthou JP, Balent G, Monteil C. 2007. Modelling the overwintering strategy of a beneficial insect in a heterogeneous landscape using a multi-agent system. *Ecol. Model.* 205:423–36
4. Asplen MK, Hardin JA, Byrne DN. 2009. The relationship between pre-oviposition flight behaviour and reproductive timing in whitefly parasitoids. *Physiol. Entomol.* 34:350–58
5. Assefa Y, Mitchell A, Conlong DE, Muirhead KA. 2008. Establishment of *Cotesia flavipes* (Hymenoptera: Braconidae) in sugarcane fields of Ethiopia and origin of founding population. *J. Econ. Entomol.* 101:686–91
6. Balkenhol N, Landguth EL. 2011. Simulation modelling in landscape genetics: on the need to go further. *Mol. Ecol.* 20:667–70
7. Barbosa P. 1998. *Conservation Biological Control*. San Diego, CA: Academic
8. Bell JR, Aralimarad P, Lim KS, Chapman JW. 2013. Predicting insect migration density and speed in the daytime convective boundary layer. *PLoS One* 8:e54202
9. Bell JR, Bohan DA, Shaw EM, Weyman GS. 2005. Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. *Bull. Entomol. Res.* 95:69–114

10. Bellamy DE, Byrne DN. 2001. Effects of gender and mating status on self-directed dispersal by the whitefly parasitoid *Eretmocerus eremicus*. *Ecol. Entomol.* 26:571–77
11. Bianchi FJJA, Booij CJH, Tscharrntke T. 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proc. R. Soc. B* 273:1715–27
12. Bianchi FJJA, Goedhart PW, Baveco JM. 2008. Enhanced pest control in cabbage crops near forest in the Netherlands. *Landscape Ecol.* 23:595–602
13. Bianchi FJJA, Honěk AH, van der Werf W. 2007. Changes in agricultural land use can explain population decline in a ladybeetle species in the Czech Republic: evidence from a process-based spatially explicit model. *Landscape Ecol.* 22:1541–54
14. Bianchi FJJA, Ives AR, Schellhorn NA. 2013. Interactions between conventional and organic farming for biocontrol services across the landscape. *Ecol. Appl.* 23:1531–43
15. Bianchi FJJA, Schellhorn NA, Buckley YM, Possingham HP. 2010. Spatial variability in ecosystem services: simple rules for predator-mediated pest suppression. *Ecol. Appl.* 20:2322–33
16. Bianchi FJJA, Schellhorn NA, Cunningham SA. 2012. Habitat functionality for the ecosystem service of pest control: reproduction and feeding sites of pests and natural enemies. *Agric. For. Entomol.* 15:12–23
17. Bianchi FJJA, Schellhorn NA, van der Werf W. 2009. Predicting the time to colonization of the parasitoid *Diadegma semiclausum*: the importance of the shape of spatial dispersal kernels for biological control. *Biol. Control* 50:267–74
18. Bianchi FJJA, Schellhorn NA, van der Werf W. 2009. Foraging behaviour of predators in heterogeneous landscapes: the role of perceptual ability and diet breadth. *Oikos* 118:1363–72
19. Binns ES. 1982. Phoresy as migration—some functional aspects of phoresy in mites. *Biol. Rev.* 57:571–620
20. Bishop L, Riechart SE. 1990. Spider colonization of agroecosystems: mode and source. *Environ. Entomol.* 19:1738–45
21. Blitzer EJ, Dormann CF, Holzschuh A, Klein AM, Rand TA, Tscharrntke T. 2012. Spillover of functionally important organisms between managed and natural habitats. *Agric. Ecosyst. Environ.* 146:34–43
22. Bocedi G, Heinonen J, Travis MJ. 2012. Uncertainty and the role of information acquisition in the evolution of context-dependent emigration. *Am. Nat.* 179:606–20
23. Bommarco R, Firle SO, Ekbom B. 2007. Outbreak suppression by predators depends on spatial distribution of prey. *Ecol. Model.* 201:163–70
24. Bonte D, Van Dyck H, Bullock JM, Coulon A, Delgado M, et al. 2012. Costs of dispersal. *Biol. Rev.* 87:290–312
25. Bowler DE, Benton TG. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biol. Rev.* 80:205–25
26. Buddle CN, Rypstra AL. 2003. Factors initiating emigration of two wolf spider species (Araneae: Lycosidae) in an agroecosystem. *Environ. Entomol.* 32:88–95
27. Chaplin-Kramer R, Kremen C. 2012. Pest control experiments show benefits of complexity at landscape and local scales. *Ecol. Appl.* 22:1936–48
28. Chapman JW, Reynolds DR, Smith AD, Smith ET, Woiwood IP. 2004. An aerial netting study of insects migrating at high altitude over England. *Bull. Entomol. Res.* 94:123–36
29. Chapman JW, Drake VA, Reynolds DR. 2011. Recent insights from radar studies of insect flight. *Annu. Rev. Entomol.* 56:337–56
30. Childs DZ, Bonsall MB, Rees M. 2004. Periodic local disturbance in host-parasitoid metapopulations: host suppression and parasitoid persistence. *J. Theor. Biol.* 227:13–23
31. Chiverton PA. 1986. Predator density manipulation and its effects on populations of *Rhopalosiphum padi* (Hom.: Aphididae) in spring barley. *Ann. Appl. Biol.* 109:49–60
32. Clausen CP. 1976. Phoresy among entomophagous insects. *Annu. Rev. Entomol.* 21:343–68
33. Clobert J, Danchin E, Dhondt A, Nichols J, eds. 2001. *Dispersal*. New York: Oxford Univ. Press
34. Clobert J, Le Galliard JF, Cote J, Meylan S, Massot M. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol. Lett.* 12:197–209
35. Clough Y, Kruess A, Kleijn D, Tscharrntke T. 2005. Spider diversity in cereal fields: comparing factors at local, landscape and regional scales. *J. Biogeogr.* 32:2007–14
36. Coombes DS, Sotherton NW. 1986. The dispersal and distribution of polyphagous predatory Coleoptera in cereals. *Ann. Appl. Biol.* 108:461–74

37. Corbett A, Rosenheim JA. 1996. Impact of a natural enemy overwintering refuge and its interaction with the surrounding landscape. *Ecol. Entomol.* 21:155–64
38. Costamagna AC, Landis DA, Difonzo CD. 2007. Suppression of soybean aphid by generalist predators results in a trophic cascade in soybeans. *Ecol. Appl.* 17:441–51
39. Costanza R, d'Arge R, deGroot R, Farber S, Grasso M, et al. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387:253–60
40. Cottrell TE, Yeargan KV. 1999. Factors influencing dispersal of larval *Coleomegilla maculata* from the weed *Acalypha ostryaefolia* to sweet corn. *Entomol. Exp. Appl.* 90:313–22
41. Croft BA, Jung C. 2001. Phytoseiid dispersal at plant to regional levels: a review with emphasis on management of *Neoseiulus fallacis* in diverse agroecosystems. *Exp. Appl. Acarol.* 25:763–84
42. Cronin JT. 2003. Matrix heterogeneity and host-parasitoid interactions in space. *Ecology* 84:1506–16
43. Cronin JT. 2003. Patch structure, oviposition behavior, and the distribution of parasitism risk. *Ecol. Monogr.* 73:283–300
44. Darrrouzet-Nardi A, Hoopes MF, Walker JD, Briggs CJ. 2006. Dispersal and foraging behaviour of *Platygaster californica*: Hosts can't run, but they can hide. *Ecol. Entomol.* 31:298–306
45. de Boer JG, Dicke M. 2006. Olfactory learning by predatory arthropods. *Anim. Biol.* 56:143–55
46. De Meester N, Bonte D. 2010. Information use and density-dependent emigration in an agrobiont spider. *Behav. Ecol.* 21:992–98
47. Dingle H. 2001. The evolution of migratory syndromes in insects. See Ref. 178, pp. 159–81
48. Dingle H, Drake VA. 2007. What is migration? *BioScience* 57:113–21
49. Dudley R. 2001. The biomechanics and functional diversity of flight. See Ref. 178, pp. 19–41
50. Duelli P, Studer M, Marchand I, Jakob S. 1990. Population movements of arthropods between natural and cultivated areas. *Biol. Conserv.* 54:193–207
51. Dunley JE, Croft BA. 1990. Dispersal between and colonization of apple by *Metaseiulus occidentalis* and *Typhlodromus pyri*. *Exp. and Appl. Acarol.* 10:137–49
52. Dunning JB, Danielson BJ, Pulliam HR. 1992. Ecological processes that affect populations in landscapes. *Oikos* 65:169–75
53. Edwards CA, Sunderland KD, George KS. 1979. Studies on polyphagous predators of cereal aphids. *J. Appl. Ecol.* 16:811–23
54. Ekbom BS, Wiktelius S, Chiverton PA. 1992. Can polyphagous predators control the bird cherry-oat aphid (*Rhopalosiphum padi*) in spring cereals? A simulation study. *Entomol. Exp. Appl.* 65:215–23
55. Englund G, Hambäck PA. 2007. Scale dependence of immigration rates: models, metrics and data. *J. Anim. Ecol.* 76:30–35
56. Evans EW. 2003. Searching and reproductive behavior of female aphidophagous ladybirds (Coleoptera: Coccinellidae): a review. *Eur. J. Entomol.* 100:1–10
57. Ewert MA, Chiang HC. 1966. Dispersal of three species of coccinellids in corn fields. *Can. Entomol.* 98:999–1003
58. Fahrig L. 1988. A general model of populations in patchy habitats. *Appl. Math. Comput.* 27:53–66
59. Fahrig L. 2007. Non-optimal animal movement in human-altered landscapes. *Funct. Ecol.* 21:1003–15
60. Fahrig L, Baudry J, Brotons L, Burel FG, Crist TO, et al. 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecol. Lett.* 14:101–12
61. Fatourous NE, Dicke M, Mumm R, Meiners T, Hilker M. 2008. Foraging behavior of egg parasitoids exploiting chemical information. *Behav. Ecol.* 19:677–89
62. Fatourous NE, Huigens ME. 2012. Phoresy in the field: natural occurrence of *Trichogramma* egg parasitoids on butterflies and moths. *BioControl* 57:493–502
63. Fournier F, Boivin G. 2000. Comparative dispersal of *Trichogramma evanescens* and *Trichogramma pretiosum* (Hymenoptera: Trichogrammatidae) in relation to environmental conditions. *Environ. Entomol.* 29:55–63
64. Fox TB, Landis DA, Cardoso FF, Difonzo CD. 2004. Predators suppress *Aphis glycines* Matsumura population growth in soybean. *Environ. Entomol.* 33:608–18
65. Frampton GK, Cilgi T, Fry GLA, Wratten SD. 1995. Effects of grassy banks on the dispersal of some carabid beetles (Coleoptera: Carabidae) on farmland. *Biol. Conserv.* 71:347–55

66. Furlong MJ, Zalucki MP. 2010. Exploiting predators for pest management: the need for sound ecological assessment. *Entomol. Exp. Appl.* 135:225–36
67. Gilstrap FE. 1997. Importation biological control in ephemeral crop habitats. *Biol. Control* 10:23–29
68. Godfray HCJ. 1994. *Parasitoids: Behavioural and Evolutionary Ecology*. Princeton, NJ: Princeton Univ. Press
69. Grez AA, Prado E. 2000. Effect of plant patch shape and surrounding vegetation on the dynamics of predatory coccinellids and their prey *Brevicoryne brassicae* (Hemiptera: Aphididae). *Environ. Entomol.* 29:1244–50
70. Hardie J, Gibson G, Wyatt TD. 2001. Insect behaviours associated with resource finding. See Ref. 178, pp. 87–109
71. Hawkins BA, Mills NJ, Jervis MA, Price PW. 1999. Is the biological control of insects a natural phenomenon? *Oikos* 86:493–506
72. Hein S, Poethke HJ, Hovestadt T. 2005. Computer-generated null models as an approach to detect perceptual range in mark-re-sight studies: an example with grasshoppers. *Ecol. Entomol.* 30:225–33
73. Hendrickx F, Maelfait J-P, Van Wingerden W, Schweiger O, Speelmans M, et al. 2007. How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *J. Appl. Ecol.* 44:340–51
74. Hirose Y, Takasu K, Takagi M. 1996. Egg parasitoids of phytophagous bugs in soybean: mobile natural enemies as naturally occurring biological control agents of mobile pests. *Biol. Control* 7:84–94
75. Hoedjes KM, Kruidhof HM, Huigens ME, Dicke M, Vet LE, Smid HM. 2011. Natural variation in learning rate and memory dynamics in parasitoid wasps: opportunities for converging ecology and neuroscience. *Proc. R. Soc. B* 278:889–97
76. Honěk A. 1980. Population density of aphids at the time of settling and ovariole maturation in *Coccinella septempunctata* (Coleoptera, Coccinellidae). *Entomophaga* 25:427–30
77. Ives AR, Cardinale BJ, Snyder WE. 2005. A synthesis of subdisciplines: predator-prey interactions, and biodiversity and ecosystem functioning. *Ecol. Lett.* 8:102–16
78. Ives AR, Gross K, Jansen VAA. 2000. Periodic mortality events in predator-prey systems. *Ecology* 81:3330–40
79. Ives AR, Kareiva P, Perry R. 1993. Response of a predator to variation in prey density at three hierarchical scales: lady beetles feeding on aphids. *Ecology* 74:1929–38
80. Ives AR, Settle WH. 1997. Metapopulation dynamics and pest control in agricultural systems. *Am. Nat.* 149:220–46
81. Ives PM. 1981. Estimation of coccinellid numbers and movement in the field. *Can. Entomol.* 113:981–97
82. James A, Plank MJ, Edwards AM. 2011. Assessing Lévy walks as models of animal foraging. *J. R. Soc. Interface* 8:1233–47
83. Johnson CG. 1969. *Migration and Dispersal of Insects by Flight*. Suffolk, UK: Chaucer Press
84. Kaplan I. 2012. Attracting carnivorous arthropods with plant volatiles: the future of biocontrol or playing with fire? *Biol. Control* 60:77–89
85. Kean J, Wratten S, Tylianakis J, Barlow N. 2003. The population consequences of natural enemy enhancement and implications for conservation biological control. *Ecol. Lett.* 6:604–12
86. Keller MA, Lewis WJ, Stinner RE. 1985. Biological and practical significance of movement by *Trichogramma* species: a review. *Southwest. Entomol.* 8:138–55
87. Kennedy GG, Storer NP. 2000. Life systems of polyphagous arthropod pests in temporally unstable cropping systems. *Annu. Rev. Entomol.* 45:467–93
88. King B. 1993. Flight activity in the parasitoid wasp *Nasonia vitripennis* (Hymenoptera, Pteromalidae). *J. Insect Behav.* 6:313–21
89. Krewenka KM, Holzschuh A, Tscharnkte T, Dormann CF. 2011. Landscape elements as potential barriers and corridors for bees, wasps and parasitoids. *Biol. Conserv.* 144:1816–25
90. Kristensen NP, De Barro PJ, Schellhorn NA. 2013. The initial dispersal and spread of an intentional invader at three spatial scales. *PLoS One* 8:e62407
91. Kromp B, Steinberger KH. 1992. Grassy field margins and arthropod diversity: a case study on ground beetles and spiders in eastern Austria (Coleoptera: Carabidae; Arachnida: Aranei, Opiliones). *Agric. Ecosyst. Environ.* 40:71–93

92. Landis DA, Van der Werf W. 1997. Early-season predation impacts the establishment of aphids and spread of beet yellows virus in sugar beet. *Entomophaga* 42:499–516
93. Landis DA, Wratten SD, Gurr GM. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* 45:175–201
94. Langhof M, Gathmann A, Poehling HM, Meyhofer R. 2003. Impact of insecticide drift on aphids and their parasitoids: residual toxicity, persistence and recolonisation. *Agric. Ecosyst. Environ.* 94:265–74
95. Lavandero B, Wratten S, Shishehbor P, Worner S. 2005. Enhancing the effectiveness of the parasitoid *Diadegma semiclausum* (Helen): movement after use of nectar in the field. *Biol. Control* 34:152–58
96. Lemke A, Poehling H-M. 2002. Sown weed strips in cereal fields: overwintering site and “source” habitat for *Oedothorax apicatus* (Blackwall) and *Erigone atra* (Blackwall) (Araneae: Erigonidae). *Agr. Ecosys. Environ.* 90:67–80
97. Letourneau DK, Jedlicka JA, Bothwell SG, Moreno CR. 2009. Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial ecosystems. *Annu. Rev. Ecol. Evol. Syst.* 40:573–92
98. Levin SA, Muller-Landau HC, Nathan R, Chave J. 2003. The ecology and evolution of seed dispersal: a theoretical perspective. *Annu. Rev. Ecol. Evol. Syst.* 34:575–604
99. Lima SL, Zollner PA. 1996. Towards a behavioral ecology of ecological landscapes. *Trends Ecol. Evol.* 11:131–35
100. Liu Z, McNeil JN, Wu K. 2011. Flight mill performance of the lacewing *Chrysoperla sinica* (Neuroptera: Chrysopidae) as a function of age, temperature, and relative humidity. *J. Econ. Entomol.* 104:94–100
101. Mauremooto JR, Wratten SD, Worner SP, Fry GLA. 1995. Permeability of hedgerows to predatory carabid beetles. *Agric. Ecosyst. Environ.* 52:141–48
102. Mestre L, Bonte D. 2012. Food stress during juvenile and maternal development shapes natal and breeding dispersal in a spider. *Behav. Ecol.* 23:759–64
103. Myers JH, Higgins C, Kovacs E. 1989. How many insect species are necessary for the biological control of insects? *Environ. Entomol.* 18:541–47
104. Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, et al. 2008. A movement ecology paradigm for unifying organismal movement research. *Proc. Natl. Acad. Sci. USA* 105:19052–59
105. Öberg S, Ekbohm B. 2006. Recolonisation and distribution of spiders and carabids in cereal fields after spring sowing. *Ann. Appl. Biol.* 149:203–11
106. Öberg S, Mayr S, Dauber J. 2008. Landscape effects on recolonisation patterns of spiders in arable fields. *Agr. Ecosys. Environ.* 123:211–18
107. Ode PJ, Antolin MF, Strand MR. 1998. Differential dispersal and female-biased sex allocation in a parasitic wasp. *Ecol. Entomol.* 23:314–18
108. Opatovsky I, Lubin Y. 2012. Coping with abrupt decline in habitat quality: effects of harvest on spider abundance and movement. *Acta Oecol.* 41:14–19
109. Osawa N. 2000. Population field studies on the aphidophagous ladybeetle *Harmonia axyridis* (Coleoptera: Coccinellidae): resource tracking and population characteristics. *Popul. Ecol.* 42:115–27
110. Ovaskainen O. 2004. Habitat-specific movement parameters estimated using mark-recapture data and a diffusion model. *Ecology* 85:242–57
111. Ovaskainen O, Rekola H, Meyke E, Arjas E. 2008. Bayesian methods for analyzing movements in heterogeneous landscapes from mark-recapture data. *Ecology* 89:542–54
112. Pasek JE. 1988. Influence of wind and windbreaks on local dispersal of insects. *Agric. Ecosyst. Environ.* 22–23:529–54
113. Patterson TA, Thomas L, Wilcox C, Ovaskainen O, Matthiopoulos J. 2008. State-space models of individual animal movement. *Trends Ecol. Evol.* 23:87–94
114. Petersen MK. 1999. The timing of dispersal of the predatory beetles *Bembidion lampros* and *Tachyporus hypnorum* from hibernating sites into arable fields. *Entomol. Exp. Appl.* 90:221–24
115. Pluess T, Opatovsky I, Gavish-Regev E, Lubin Y, Schmidt-Entling MH. 2010. Non-crop habitats in the landscape enhance spider diversity in wheat fields of a desert agroecosystem. *Agric. Ecosyst. Environ.* 137:68–74
116. Poelman EH, Oduor AMO, Broekgaarden C, Hordijk CA, Jansen JJ, et al. 2009. Field parasitism rates of caterpillars on *Brassica oleracea* plants are reliably predicted by differential attraction of *Cotesia* parasitoids. *Funct. Ecol.* 23:951–62

117. Porter J, Arzberger P, Braun HW, Bryant P, Gage S, et al. 2005. Wireless sensor networks for ecology. *BioScience* 55:561–72
118. Potting RPJ, Perry JN, Powell W. 2005. Insect behavioural ecology and other factors affecting the control efficacy of agro-ecosystem diversification strategies. *Ecol. Model.* 182:199–216
119. Prasifka JR, Heinz KM, Sansone CG. 2004. Timing, magnitude, rates, and putative causes of predator movement between cotton and grain sorghum fields. *Environ. Entomol.* 33:282–90
120. Prasifka JR, Heinz KM, Minzenmayer RR. 2004. Relationship of landscape, prey and agronomic variables to the abundance of generalist predators in cotton (*Gossypium hirsutum*) fields. *Landsc. Ecol.* 19:709–17
121. Rand TA, Tylanakis JM, Tscharrntke T. 2006. Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecol. Lett.* 9:603–14
122. Ricketts TH. 2001. The matrix matters: effective isolation in fragmented landscapes. *Am. Nat.* 158:87–99
123. Ries L, Sisk TD. 2004. A predictive model for edge effects. *Ecology* 85:2917–26
124. Rodriguez MA, Hawkins BA. 2000. Diversity, function and stability in parasitoid communities. *Ecol. Lett.* 3:35–40
125. Ronce O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annu. Rev. Ecol. Evol. Syst.* 38:231–53
126. Rousse P, Gourdon F, Roubaud M, Chiroleu F, Quilici S. 2009. Biotic and abiotic factors affecting the flight activity of *Popillia arisanus*, an egg-pupal parasitoid of fruit fly pests. *Environ. Entomol.* 38:896–903
127. Sabatier R, Meyer K, Wiegand K, Clough Y. 2013. Non-linear effects of pesticide application on biodiversity-driven ecosystem services and disservices in a cacao agroecosystem. *Basic Appl. Ecol.* 2:93–186
128. Schellhorn NA, Andow DA. 1999. Mortality of coccinellid (Coleoptera: Coccinellidae) larvae and pupae when prey become scarce. *Environ. Entomol.* 28:1092–100
129. Schellhorn NA, Andow DA. 2005. Response of coccinellids to their aphid prey at different spatial scales. *Popul. Ecol.* 47:71–76. Erratum. 2005. *Popul. Ecol.* 47:281
130. Schellhorn NA, Bellati J, Paull CA, Maratos L. 2008. Parasitoid and moth movement from refuge to crop. *Basic Appl. Ecol.* 9:691–700
131. Schellhorn NA, Harmon JP, Andow DA. 2000. Using cultural practices to enhance insect pest control by natural enemies. In *Insect Pest Management: Techniques for Environmental Protection*, ed. JE Rechcigl, NA Rechcigl, pp. 147–70. Boca Raton, FL/London: Lewis
132. Schmidt MH, Roschewitz I, Thies C, Tscharrntke T. 2005. Differential effects of landscape and management on diversity and density of ground-dwelling farmland spiders. *J. Appl. Ecol.* 42:281–87
133. Schmidt MH, Tscharrntke T. 2005. Landscape context of sheetweb spider (Araneae: Linyphiidae) abundance in cereal fields. *J. Biogeogr.* 32:467–73
134. Schmidt-Entling MH, Dobeli J. 2009. Sown wildflower areas to enhance spiders in arable fields. *Agric. Ecosyst. Environ.* 133:19–22
135. Schweiger O, Maelfait JP, Van Wingerden W, Hendrickx F, Billeter R, et al. 2005. Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales. *J. Appl. Ecol.* 42:1129–39
136. Settle WH, Ariawan H, Astuti ET, Cahyana W, Hakim AL, et al. 1996. Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. *Ecology* 77:1975–88
137. Sheehan W, Shelton AM. 1989. Parasitoid response to concentration of herbivore food plants: finding and leaving plants. *Ecology* 70:993–98
138. Siekmann G, Keller MA, Tenhumberg B. 2004. The sweet tooth of adult parasitoid *Cotesia glomerata*: ignoring hosts for nectar? *J. Insect Behav.* 17:459–76
139. Sims DW, Southall EJ, Humphries NE, Hays GC, Bradshaw CJ, et al. 2008. Scaling laws of marine predator search behaviour. *Nature* 451:1098–102
140. Sivakoff FS, Rosenheim JA, Hagler JR. 2012. Relative dispersal ability of a key agricultural pest and its predators in an annual agroecosystem. *Biol. Control* 63:296–303
141. Southwood TRE. 1988. Tactics, strategies, templets. *Oikos* 52:3–18
142. Stark JD, Vargas RI, Walsh WA. 1994. Temporal synchrony and patterns in an exotic host-parasitoid community. *Oecologia* 100:196–99
143. Taylor AD. 1993. Heterogeneity in host parasitoid interactions: ‘aggregation of risk’ and the ‘CV²’ greater than 1 rule. *Trends Ecol. Evol.* 8:400–5

144. Taylor LR. 1974. Insect migration, flight periodicity and the boundary layer. *J. Anim. Ecol.* 43:225–38
145. Tenhumberg B, Siekmann G, Keller MA. 2006. Optimal time allocation in parasitic wasps searching for hosts and food. *Oikos* 113:121–31
146. Thies C, Steffan-Dewenter I, Tscharnkte T. 2003. Effects of landscape context on herbivory and parasitism at different spatial scales. *Oikos* 101:18–25
147. Thies C, Tscharnkte T. 1999. Landscape structure and biological control in agroecosystems. *Science* 285:893–95
148. Thomas CD, Kunin WE. 1999. The spatial structure of populations. *J. Anim. Ecol.* 68:647–57
149. Thomas CFG, Jepson PC. 1997. Field-scale effects of farming practices on linyphiid spider populations in grass and cereals. *Entomol. Exp. Appl.* 84:59–69
150. Thomas MB, Wratten SD, Sotherton NW. 1991. Creation of ‘island’ habitats in farmland to manipulate populations of beneficial arthropods: predator densities and emigration. *J. Appl. Ecol.* 28:906–17
151. Tischendorf L, Fahrig L. 2000. On the usage and measurement of landscape connectivity. *Oikos* 90:7–19
152. Topping CJ, Sunderland KD. 1998. Population dynamics and dispersal of *Lepthyphantes tenuis* in an ephemeral habitat. *Entomol. Exp. Appl.* 87:29–41
153. Travis JMJ, Mustin K, Barton KA, Benton TG, Clobert J, et al. 2012. Modelling dispersal: an eco-evolutionary framework incorporating emigration, movement, settlement behaviour and the multiple costs involved. *Methods Ecol. Evol.* 3:628–41
154. Tscharnkte T, Bommarco R, Clough Y, Crist TO, Kleijn D, et al. 2007. Conservation biological control and enemy diversity on a landscape scale. *Biol. Control* 43:294–309
155. Tscharnkte T, Brandl R. 2004. Plant-insect interactions in fragmented landscapes. *Annu. Rev. Entomol.* 49:405–30
156. Tscharnkte T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C. 2005. Landscape perspectives on agricultural intensification and biodiversity—ecosystem service management. *Ecol. Lett.* 8:857–74
157. Tscharnkte T, Rand TA, Bianchi FJJA. 2005. The landscape context of trophic interactions: insect spillover across the crop-noncrop interface. *Ann. Zool. Fenn.* 42:421–32
158. Tuda M, Shima K. 2002. Relative importance of weather and density dependence on the dispersal and on-plant activity of the predator *Orius minutus*. *Popul. Ecol.* 44:251–57
159. Turchin P. 1998. *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants*. Sunderland, MA: Sinauer
160. Tylianakis JM, Didham RK, Wratten SD. 2004. Improved fitness of aphid parasitoids receiving resource subsidies. *Ecology* 85:658–66
161. Tylianakis JM, Romo CM. 2010. Natural enemy diversity and biological control: making sense of the context-dependency. *Basic Appl. Ecol.* 11:657–68
162. Tylianakis JM, Tscharnkte T, Lewis OT. 2007. Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature* 445:202–5
163. Urban DL, Minor ES, Trembl EA, Schick RS. 2009. Graph models of habitat mosaics. *Ecol. Lett.* 12:260–73
164. Van der Werf W, Evans EW, Powell J. 2000. Measuring and modelling the dispersal of *Coccinella septempunctata* (Coleoptera: Coccinellidae) in alfalfa fields. *Eur. J. Entomol.* 97:487–93
165. Van Roermund HJW, Hemerik L, Van Lenteren JC. 1994. Influence of intrapatch experiences and temperature on the time allocation of the whitefly parasitoid *Encarsia formosa* (Hymenoptera, Aphelinidae). *J. Insect Behav.* 7:483–501
166. Vandermeer J, Perfecto I, Schellhorn N. 2010. Propagating sinks, ephemeral sources and percolating mosaics: conservation in landscapes. *Landsc. Ecol.* 25:509–18
167. Vet LEM. 2001. Parasitoid searching efficiency links behaviour to population processes. *Appl. Entomol. Zool.* 36:399–408
168. Vet LEM, Dicke M. 1992. Ecology of infochemical use by natural enemies in a tritrophic context. *Annu. Rev. Entomol.* 37:141–72
169. Vinatier F, Lescourret F, Duyck PF, Martin O, Senoussi R, Tixier P. 2011. Should I stay or should I go? A habitat-dependent dispersal kernel improves prediction of movement. *PLoS One* 6:e21115
170. Virant-Doberlet M, King RA, Polajnar J, Symondson WO. 2011. Molecular diagnostics reveal spiders that exploit prey vibrational signals used in sexual communication. *Mol. Ecol.* 20:2204–16

171. Volkl W. 2000. Foraging behaviour and sequential multisensory orientation in the aphid parasitoid, *Pauesia picta* (Hym., Aphidiidae) at different spatial scales. *J. Appl. Entomol.* 124:307–14
172. Wajnberg E. 2006. Time allocation strategies in insect parasitoids: from ultimate predictions to proximate behavioral mechanisms. *Behav. Ecol. Sociobiol.* 60:589–611
173. White JA, Andow DA. 2007. Foraging for intermittently refuged prey: theory and field observations of a parasitoid. *J. Anim. Ecol.* 76:1244–54
174. Wiedenmann RN, Smith JW. 1997. Attributes of natural enemies in ephemeral crop habitats. *Biol. Control* 10:16–22
175. Williams IH, Frearson DJT, Barari H, McCartney A. 2007. First field evidence that parasitoids use upwind anemotaxis for host-habitat location. *Entomol. Exp. Appl.* 123:299–307
176. Wissinger SA. 1997. Cyclic colonization in predictably ephemeral habitats: a template for biological control in annual crop systems. *Biol. Control* 10:4–15
177. With KA, Crist TO. 1995. Critical thresholds in species' responses to landscape structure. *Ecology* 76:2446–59.
178. Woiwod IP, Reynolds DR, Thomas CD, eds. 2001. *Insect Movement: Mechanisms and Consequences*. Wallingford, UK: CABI
179. Woltz JM, Landis DA. 2013. Coccinellid immigration to infested host patches influences suppression of *Aphis glycines* in soybean. *Biol. Control* 64:330–37
180. Wratten SD, Bowie MH, Hickman JM, Evans AM, Sedcole JR, Tylianakis JM. 2003. Field boundaries as barriers to movement of hover flies (Diptera: Syrphidae) in cultivated land. *Oecologia* 134:605–11
181. Yoo HJS, O'Neil RJ. 2009. Temporal relationships between the generalist predator, *Orius insidiosus*, and its two major prey in soybean. *Biol. Control* 48:168–80
182. Zeller KA, McGarigal K, Whiteley AR. 2012. Estimating landscape resistance to movement: a review. *Landsch. Ecol.* 27:777–97
183. Zhang Y, Shipp JL. 1998. Effect of temperature and vapor pressure deficit on the flight activity of *Orius insidiosus* (Hemiptera: Anthocoridae). *Environ. Entomol.* 27:736–42

Contents

Nancy E. Beckage (1950–2012): Pioneer in Insect Host-Parasite Interactions <i>Lynn M. Riddiford and Bruce A. Webb</i>	1
Emerald Ash Borer Invasion of North America: History, Biology, Ecology, Impacts, and Management <i>Daniel A. Herms and Deborah G. McCullough</i>	13
Invasion Biology of <i>Aedes japonicus japonicus</i> (Diptera: Culicidae) <i>Michael G. Kaufman and Dina M. Fonseca</i>	31
Death Valley, <i>Drosophila</i> , and the Devonian Toolkit <i>Michael H. Dickinson</i>	51
Mosquito Diapause <i>David L. Denlinger and Peter A. Armbruster</i>	73
Insect Mitochondrial Genomics: Implications for Evolution and Phylogeny <i>Stephen L. Cameron</i>	95
Response of Native Insect Communities to Invasive Plants <i>T. Martijn Bezemer, Jeffrey A. Harvey, and James T. Cronin</i>	119
Freshwater Biodiversity and Aquatic Insect Diversification <i>Klaas-Douwe B. Dijkstra, Michael T. Monaghan, and Steffen U. Pauls</i>	143
Organization and Functional Roles of the Central Complex in the Insect Brain <i>Keram Pfeiffer and Uwe Homberg</i>	165
Interactions Between Insect Herbivores and Plant Mating Systems <i>David E. Carr and Micky D. Eubanks</i>	185
Genetic Control of Mosquitoes <i>Luke Alphey</i>	205
Molecular Mechanisms of Phase Change in Locusts <i>Xianbui Wang and Le Kang</i>	225

Traumatic Insemination in Terrestrial Arthropods <i>Nikolai J. Tatarnic, Gerasimos Cassis, and Michael T. Siva-Jothy</i>	245
Behavioral Assays for Studies of Host Plant Choice and Adaptation in Herbivorous Insects <i>Lisa M. Knolhoff and David G. Heckel</i>	263
Biology and Management of Psocids Infesting Stored Products <i>Manoj K. Nayak, Patrick J. Collins, James E. Throne, and Jin-Jun Wang</i>	279
Chemical Ecology of Bumble Bees <i>Manfred Ayasse and Stefan Jarau</i>	299
Model Systems, Taxonomic Bias, and Sexual Selection: Beyond <i>Drosophila</i> <i>Marlene Zuk, Francisco Garcia-Gonzalez, Marie Elisabeth Herberstein,</i> <i>and Leigh W. Simmons</i>	321
Insect Speciation Rules: Unifying Concepts in Speciation Research <i>Sean P. Mullen and Kerry L. Shaw</i>	339
Neural and Hormonal Control of Postecdysial Behaviors in Insects <i>Benjamin H. White and John Ewer</i>	363
Using Semifield Studies to Examine the Effects of Pesticides on Mobile Terrestrial Invertebrates <i>S. Macfadyen, J.E. Banks, J.D. Stark, and A.P. Davies</i>	383
The Development and Functions of Oenocytes <i>Rami Makki, Einat Cinnamon, and Alex P. Gould</i>	405
Sexual Selection in Complex Environments <i>Christine W. Miller and Erik I. Svensson</i>	427
Significance and Control of the Poultry Red Mite, <i>Dermanyssus gallinae</i> <i>O.A.E. Sparagano, D.R. George, D.W.J. Harrington, and A. Giangaspero</i>	447
Evolutionary Interaction Networks of Insect Pathogenic Fungi <i>Jacobus J. Boomsma, Annette B. Jensen, Nicolai V. Meyling, and Jørgen Eilenberg</i> ...	467
Systematics, Phylogeny, and Evolution of Orb-Weaving Spiders <i>Gustavo Hormiga and Charles E. Griswold</i>	487
Advances in Silkworm Studies Accelerated by the Genome Sequencing of <i>Bombyx mori</i> <i>Qingyou Xia, Sheng Li, and Qili Feng</i>	513
The Role of Mites in Insect-Fungus Associations <i>R.W. Hofstetter and J.C. Moser</i>	537
Movement of Entomophagous Arthropods in Agricultural Landscapes: Links to Pest Suppression <i>N.A. Schellhorn, F.J.J.A. Bianchi, and C.L. Hsu</i>	559