



Edge-biased distributions of insects. A review

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Abstract

Spatial ecology includes research into factors responsible for observed distribution patterns of organisms. Moreover, the spatial distribution of an animal at a given spatial scale and in a given landscape may provide valuable insight into its host preference, fitness, evolutionary adaptation potential, and response to resource limitations. In agro-ecology, in-depth understanding of spatial distributions of insects is of particular importance when the goals are to (1) promote establishment and persistence of certain food webs, (2) maximize performance of pollinators and natural enemies, and (3) develop precision-targeted monitoring and detection of emerging outbreaks of herbivorous pests. In this article, we review and discuss a spatial phenomenon that is widespread among insect species across agricultural systems and across spatial scales—they tend to show “edge-biased distributions” (spatial distribution patterns show distinct “edge effects”). In the conservation and biodiversity literature, this phenomenon has been studied and reviewed intensively in the context of how landscape fragmentation affects species diversity. However, possible explanations of, and also implications of, edge-biased distributions of insects in agricultural systems have not received the same attention. Our review suggests that (1) mathematical modeling approaches can partially explain edge-biased distributions and (2) abiotic factors, crop vegetation traits, and environmental parameters are factors that are likely responsible for this phenomenon. However, we argue that more research, especially experimental research, is needed to increase the current understanding of how and why edge-biased distributions of insects are so widespread. We argue that the fact that many insect pests show edge-biased distribution patterns may be used to optimize both pest monitoring practices and precision targeting of pesticide applications and releases of natural enemies.

Keywords Spatial distribution · Insect sampling · Pest management · Precision agriculture

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1 Introduction

An “ecological or environmental edge” can be defined as the transition between two landscape elements (Fischer and Lindenmayer 2007), and it can be permanent (i.e., geographical feature, such as border between two types of vegetation), or it may be more temporary (i.e., between anthropogenic elements, such as junctions between a natural forest and a cultivated farmland) (Thomas et al. 1979) Fig. 1. Generally, the effects of ecological and environmental edges on spatial distributions of animals and plants have been described and discussed mostly from the perspective of how ecosystem fragmentation affects biodiversity (Stangler et al. 2015; Rossetti et al. 2014; Altamirano et al. 2016; Valladares et al. 2006; Weathers et al. 2001; Saunders et al. 1991; Murphy et al. 2016; Ries and Sisk 2004; Ries et al. 2004). “Habitat islands,” originating from the process of landscape fragmentation, are characterized by differences in physical environments (e.g., radiation fluxes, wind, microclimate, and soil characteristics) between edges and interior, leading to biogeographic changes in original wildlife communities (Weathers et al. 2001; Valladares et al. 2006; Yahner 1988). For example, a study of five groups of carabid species in the Aggtelek National Park, Hungary, revealed greater carabid species diversity near forest edges as compared to forest interiors due to increase in the number of edge-preferring carabid species and higher herb cover near forest edges (Magura 2002). Gall-forming insects in natural forest patches in the Brazilian Pantanal also showed different species composition between edge and interior with one third of 113 species only sampled along forest edges and with another third sampled exclusively in the interior (Julião et al. 2004). Similarly, Altamirano et al. (2016) showed that the spatial distribution of galling insects sampled at transects in nine forests in Central Argentina were most predominant along forest edges and that many species benefitted from unspecified forest edge conditions. In broader terms, it has been reported that there is an increase in richness and abundance of insect generalist species near ecological or environmental edges, while the interior of fragmented habitats tend to favor specialized and competitor

insects (Didham 1997). The topic of biographic changes in insect communities as the result of ecosystem fragmentations and edge-biased distributions has been discussed and reviewed by several ecologists (Tschamtkke et al. 2002; Harris 1988; Yahner 1988; Saunders et al. 1991; Fagan et al. 1999; Fischer and Lindenmayer 2007; Weathers et al. 2001; Valladares et al. 2006; Ries and Sisk 2004; Ries et al. 2004; Murphy et al. 2016).

In addition to a rich body of literature on relationships between biodiversity and ecological or environmental edges in natural and semi-natural ecosystems, there are numerous reports of similar edge-biased distributions of insects in agricultural systems. However, this specific topic has never been reviewed, and it has not been emphasized how this unique aspect of spatial distribution patterns is highly relevant to both insect monitoring and pest management in agricultural systems. Here, we describe published reports of insect distributions with edge-biased distributions across a wide range of agricultural systems. We discuss the following two questions: (1) What are the potential mechanisms responsible for an edge-biased distribution of insect populations in agricultural systems? (2) How can increased knowledge about edge-biased distributions and their governing mechanisms help to enhance the efficiency of agricultural pest management practices?

2 Edge-biased distributions in agricultural systems

The following sections are not meant to provide exhaustive reviews but aim to provide an insight into the prevalence of edge-biased insect distributions in a range of agricultural systems and across a wide range of spatial scales.

2.1 Edge-biased distributions in open field systems

An edge-biased distribution of insects in agricultural systems was first reported in 1950 in a study on black bean aphids, *Aphis fabae* Scop. (Hemiptera: Aphididae) on twigs of

Fig. 1 A canola field showing tree lines and isolated tree island which serve as environmental edges



Euonymus europaeus L. (Celastrales: Celastraceae) and *Viburnum opulus* L. (Dipsacales: Adoxaceae) (Johnson 1950). The author noted that the onset of infestations by black bean aphids was near field edges and eventually spread throughout the field, although field edges would be the areas with the highest aphid density. Winder et al. (1999) conducted a large-scale study of the effect of grid size on the analysis of the spatial distribution of English grain aphids, *Sitobion avenae* Fabricius (Hemiptera: Aphididae) and found that significant edge effect was detected for large grid size with higher count of aphids along field edges. However, the edge-biased distribution was not evident at small grid sizes. Thus, sampling unit size was highlighted as a critical aspect of the ability to detect and quantify spatial trends, such as edge-biased distributions. Another large-scale spatial distribution study of common farmland arthropods in winter wheat fields also demonstrated higher density of species along edges (Holland et al. 1999). The studies by Winder et al. (1999) and Holland et al. (1999) noted the effervescent occurrence of edge-biased distributions. These findings agree with Wilson and Morton (1993) who showed that edge-biased distribution of two-spotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae), in cotton was only prominent early in the growing season but eventually diminished as the season progressed. Studying the spatial distribution of cabbage aphids, *Brevicoryne brassicae* L. (Hemiptera: Aphididae) in commercial canola field sites, Severtson et al. (2015) also found significantly higher counts of this important pest within 20–30 m from field edges compared to further inwards into canola fields. Based on logistic regression, the population density of cabbage aphids was found to be negatively correlated with the distance from field edges in dryland canola host plants. Besides aphids, cabbage seed weevils, *Ceutorhynchus assimilis* Paykull (Coleoptera: Curculionidae), displayed a similar spatiotemporal pattern of distribution in winter oilseed rape (Ferguson et al. 2000). A study describing the distribution of Andean potato weevils, *Premnotrypes* spp. (Coleoptera: Curculionidae), showed heavier infestation of potato tubers along field edges (Parsa et al. 2012). Edge-biased distribution was also reported regarding wheat stem sawflies, *Cephus cinctus* Norton (Hymenoptera: Cephidae), in dryland wheat fields (Nansen et al. 2005a, 2005b).

2.2 Edge-biased distributions in orchard systems

The distribution of wild bees in high bush blueberry, *Vaccinium corymbosum* L. (Ericales: Ericaceae), orchards showed significantly higher abundance of bees [*Ceratina calcarata* Robertson (Hymenoptera: Apoidea), *Ceratina dupla* Say (Hymenoptera: Apoidea), *Augochlorella aurata* Smith (Hymenoptera: Apoidea), and *Lasioglossum pilosum* Smith (Hymenoptera: Apoidea)], especially along the edges

of orchards as compared to the interior (Tuell et al. 2009). In addition, it was found that distance to orchard edge was an important predictor of abundance of red mason bees, *Osmia bicornis* L. (Hymenoptera: Megachilidae), in apple orchards (Gruber et al. 2011). Higher bee activity and greater preference for nesting of bees were noted along orchard edges compared to orchard interior. Such distribution pattern, especially that of *O. lignaria*, was linked to the presence of big leaf lupine, *Lupinus polyphyllus* Lindley (Fabales: Fabaceae), planted along field edges (Sheffield et al. 2012). In addition, a study of the spatial distribution of Asian citrus psyllids, *Diaphorina citri* Kuwayama (Hemiptera: Liviidae), in citrus groves (grapefruit and orange) showed strong season-long edge-biased distributions (Setamou and Bartels 2015).

2.3 Edge-biased distributions in stored product systems

In the context of stored products, warehouse walls can be considered as physical or environmental edges. Insects associated with stored products have been shown to aggregate along warehouse walls and near physical edges. A study of the spatial distribution of red flour beetles, *Tribolium castaneum* Herbst (Coleoptera: Tenebrionidae), in stored wheat warehouse showed consistent aggregations along warehouse walls (Athanassiou et al. 2005). This wall-biased distribution has also been observed regarding other stored product pests, such as *Trogoderma variabile* Ballion (Coleoptera: Dermestidae) (Campbell et al. 2002). Similarly, a study of the distribution of insect pests in a botanical warehouse in Florida found higher abundance of both moths and beetles [*Cadra cautella* Walker (Lepidoptera: Pyralidae), *Lasioderma serricornis* Fabricius (Coleoptera: Anobiidae), *Oryzaephilus mercator* Fauvel (Coleoptera: Silvanidae), *Typhaea stercorea* L. (Coleoptera: Mycetophagidae), and Indianmeal moths, *Plodia interpunctella* Hübner (Lepidoptera: Pyralidae)] along the walls and corners of the warehouse (Arbogast et al. 2002). In an experimental study with pheromone traps placed in 1-m intervals along a vertical gradient from the floor level to the ceiling in a 6-m tall warehouse, most Indian meal moths were caught predominantly either near the ground level or near the ceiling (Nansen et al. 2004), thus showing a vertical edge-biased distribution. Interestingly, the same study showed that the moths' preference for vertical edges could be eliminated through addition of landing surfaces to pheromone traps or by placing traps near walls. Thus, the study by Nansen et al. (2004) showed important ways to enhance moth trap captures through a combination of manipulation (addition of landing platform) and targeted placements of traps near walls, and both improvements hinged on the importance of recognizing edge bias of moth captures.

2.4 Edge-biased distributions in small-scaled laboratory experiments

Several small-scale laboratory studies have indicated the occurrence of edge-biased distributions of insects. As an example, female almond moths, *C. cautella*, were released into a 120-cm-square arena with uniform layers of intact or cracked peanuts, and the spatial distribution of eggs laid by these female was recorded after 48 h (Mankin et al. 2014). The results indicated that when peanuts filled the entire arena, female almond moths significantly aggregated their oviposition along arena edges. Moreover, when only the central 25% of the arena was filled with peanuts, the majority of the eggs were found along the edges of the peanut patches instead of the edge of the arena. Similarly, the infestation pattern of the red flour beetles, *T. castaneum*, also showed insect aggregations along arena edges (Campbell and Hagstrum 2002).

3 Theoretical models of edge-biased insect distributions

Given the prevalence of edge-biased distributions of insects in agricultural systems, it seems of considerable importance to unravel the driving mechanisms of the phenomenon. One of the common approaches used in the study of edge-biased distributions is the development of models that can simulate the edged-biased pattern of insect distributions. Although these models are theoretical and based on assumptions that are difficult to validate, they have been used widely on a conceptual basis and also to produce meaningful predictions of insect distributions.

3.1 Simple diffusion model

The most simplistic model of insect distribution is the basic diffusion model, which considers insects as independent particles whose dispersal is completely random and independent of external factors. The random dispersal (also known as Brownian motion) is modeled as particles in a fluid whose collisions with fluid molecules result in a three-dimensional spread of particles (insects) (Hida 1980). In an ecological context, the simple diffusion model combines both the exponential function of animals' population growth and the probability function of animals' locations to predict their dispersal and distribution over time (Skellam 1991). The model is described by the following Eq. (1):

$$\frac{\delta N(x, y, t)}{\delta t} = D \left[\frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2} \right] \quad (1)$$

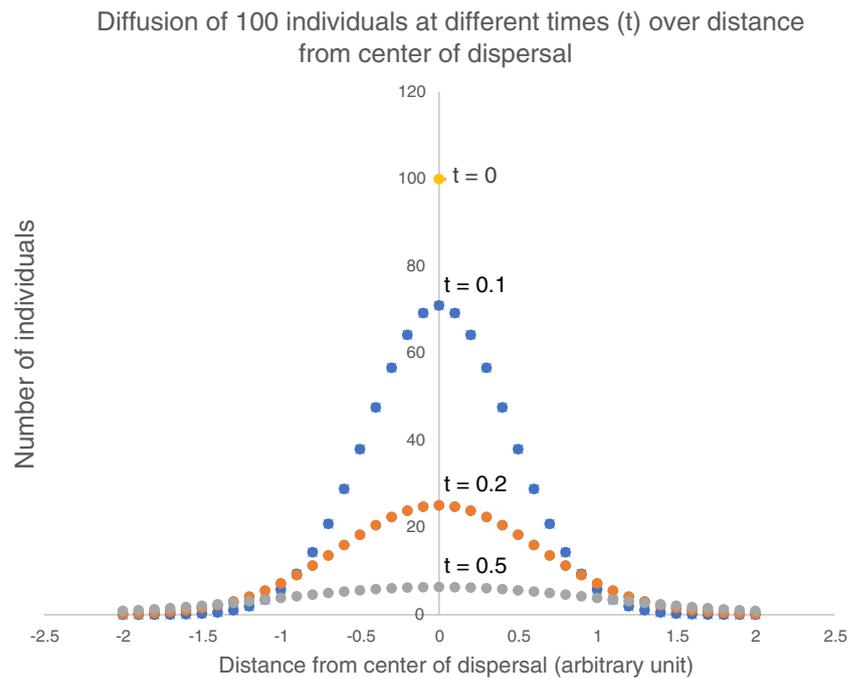
in which N refers to population density, t refers to time, and x and y refer to the coordinates of organisms on a two-

dimensional plane (Okubo 1980). In Eq. (1), the factor D is known as the diffusion coefficient, which can be estimated through the mean square difference of displacement of insects over time (Okubo 1980; Kareiva 1983). Predicted dispersal distributions based on Eq. 1 are presented in Fig. 2, and it is seen that they follow a normal distribution with population density being highest at the center of dispersal and gradually decreasing over distance. Based on simple diffusion, an animal is predicted to have highest abundance near edges due to spillover (Shmida and Wilson 1985), as individuals transition from one habitat into other and unlikely move far into the new habitat (Ries and Sisk 2004). A series of mark release and recapture experiments with multiple insect pest species [*Phyllotreta cruciferae* Goeze (Coleoptera: Chrysomelidae), *Phyllotreta striolata* Fabricius (Coleoptera: Chrysomelidae), and *Trirhabda sericotrachyla* Blake (Coleoptera: Chrysomelidae)] displayed distribution patterns characterized by highest population density at the point of release and gradual decrease over distance away from the original point of release (Kareiva 1983). In addition, Severtson et al. (2015) conducted an experimental release study with alate cabbage aphids released into centers of small plots of canola and found that the distribution of cabbage aphids also followed a diffusive pattern. These experiments, as well as the predicted frequency distributed depicted in Fig. 2, assume dispersal from a single point. In reality, the actual insect distribution in agricultural systems would more likely involve multiple points of dispersal which, depending on their relative distances to each other and relative positions to field edges, can result in different distribution patterns. If centers of dispersal are located outside an agricultural system, simple diffusion models will predict that the colonization of insects will lead to higher population densities along field edges as compared to inwards into an agricultural system. However, if dispersal centers are located within an agricultural field, the bell-shaped curve distribution of insects will result in lower population density along field edges and higher population density in the interior. Such a counter-edge effect distribution pattern has been noted in nymphs of potato psyllid, *Bactericera cockerelli* Sulz (Hemiptera: Trioziidae), in commercial fields of potato (Martini et al. 2012).

3.2 Stratified diffusion model

Despite support for the simple diffusion model, this model does not explain the initial aggregation point and therefore what is driving the establishment of insect populations near edges. In addition, Liebhold and Tobin (2008) argue that the relevance of simple diffusion models to predict spatial distributions of insects is limited to small spatial scales and fails to account for greater rate of diffusion at large spatial scales. In addition, large-scale insect distributions show a certain degree of aggregation and patchiness that varies over time (Winder et al. 1999;

Fig. 2 Population density over distance from the point of dispersal at various times t for 100 individuals with $D = 1$ in three dimensions. Graph was reconstructed based on Rudd and Gandour (1985)



Holland et al. 1999; Dean 1973). To account for the patchiness of insect distributions and the faster speed of insect dispersal at a large spatial scale, Liebhold and Tobin (2008) propose stratified diffusion model to consider the effects of stochastic events, such as accidental spread of insects due to human activities and prevailing wind (Helson 1958). That means there will be groups of insect colonies leaping ahead of the main population front line. Each of these new groups become new centers of dispersal. Although stratified diffusion model has been shown to improve predictions of insect distributions compared to simple diffusion models, they are also known to have limitations. Stratified diffusion models, just like simple diffusion models, rely on the concept of insect population density over distance as a time-dependent function. As time elapses, insects will eventually spread randomly and evenly across crop fields with little population density variance, failing to account for the aggregation and patchiness in insect distribution in many agricultural systems in the long term.

3.3 Influential edge models

To overcome the limitations of simple and stratified diffusion models, there is a need to revisit the major assumptions of these two models. Both models rely on the assumption that insect movement and dispersal, to a large extent, are intrinsic to their biological processes, such as their natural mobility and population growth rate. Thus, the complex influences of external environment have been simplified. Although stratified diffusion model does factor in the effects of stochastic events on insect distribution, these events often occur at irregular frequencies and within very short duration of time. After these

short events, pockets of insects are still expected to spread via simple diffusion mechanism. Therefore, in relation to edge effect, the interest of modeling would be to directly address the question: How far does an edge environment affect the spatial distribution of insects in agricultural systems? The theoretical response to such a question entails three possibilities: Edges have (1) no effect, (2) repelling effect, and (3) aggregating effect on insect spatial distribution. Several influential edge models have been developed to reflect the abovementioned possibilities of edge influence, including null-edge, attractive-edge, and reflective-edge models by Olson and Andow (2008); absorptive-edge model by Fagan et al. (1999); and the edge resource model (Ries and Sisk 2004). The null-edge model assumes that edges have no effect on insect movement and spatial distribution. Therefore, null-edge model is essentially a simple diffusion model, which predicts a bell-shaped distribution of insects within an agricultural system (Fig. 3a). Unlike null-edge model, reflective-edge model considers edges as unfavorable environments that directly bounce insects back into the interior by altering their direction of movement (Fig. 3b). Meanwhile, absorptive-edge model assumes that the environment outside an edge is lethal for insects, resulting in declining population density towards the edge. Similarly, attractive-edge model assumes the ability of an edge to pull insects and/or trap them, leading to their aggregation along the edge (Fig. 3c). Although both absorptive-edge and attractive-edge models produce mathematical simulations for the aggregation of insects along edges, their difference lies in whether or not insects are lost to the adjacent habitat. In absorptive-edge model, once insects cross the edge boundary to the lethal habitat, they are lost from the

original habitat. Meanwhile, in attractive-edge model, insects crossing the boundary to less favorable habitat can return to the original and more favorable habitat, leading to their accumulation along edges. Ries and Sisk (2004) argued that accumulation of species at habitat edges is widely accepted to be driven by three mechanisms: (1) spillover, (2) edges as enhanced habitats, and (3) complementary resource distributions. Moreover, they argued that a conceptual model based on resource availability and quality of bordering habitats can be used to predict the likelihood of edge-biased distributions. Of all the influential edge models, the attractive-edge model

(Olson and Andow 2008) and the edge resource model (Ries and Sisk 2004) most closely resemble the discussed edge-biased distribution of insects, providing conceptual basis for the understanding of edge-biased distributions. The strength of attractive-edge modeling approach, as compared to simple diffusion modeling approaches, is its consideration of the constraints imposed by edge environment on insect spatial distribution. These constraints most likely stem from the inherent features of the edge environment (e.g., landscape, vegetation, and microclimate), which are relatively stable. Therefore, the attractive-edge model can potentially provide the explanation of edge-biased distribution of insects in the long term as seen from certain case studies of edge effect.

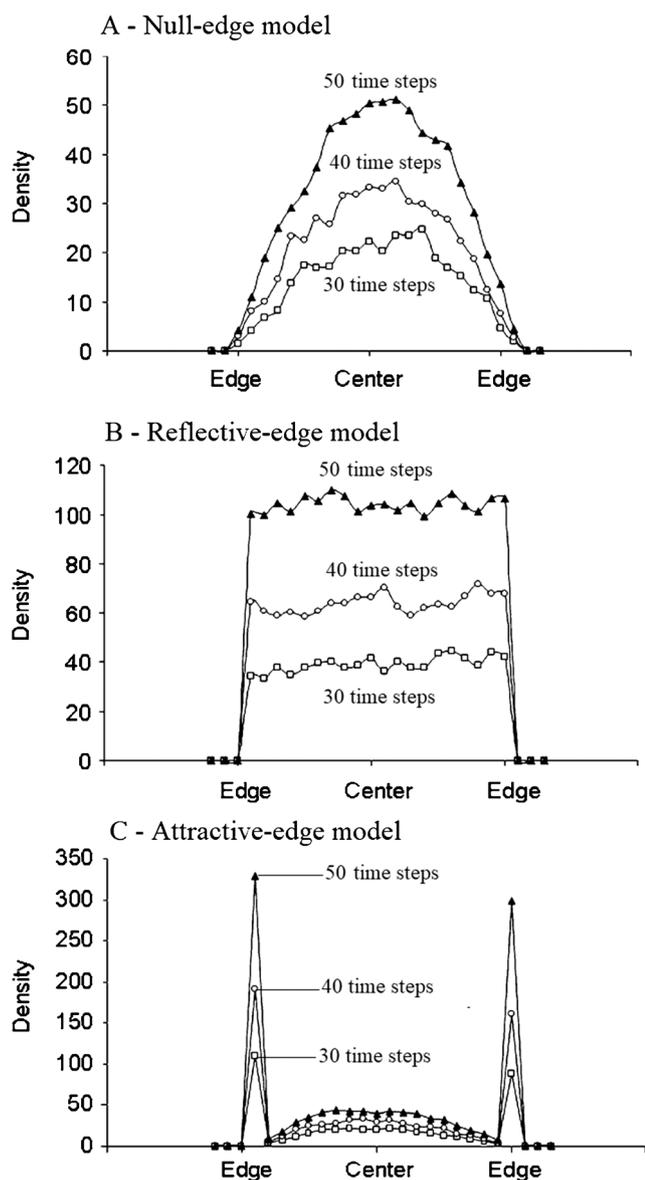


Fig. 3 Simulation of insect distribution for different models and time steps within homogenous habitat. For each homogenous habitat, the area is divided into 20 transect rows each of which is represented as a data point in the graphs. Picture adapted from Olson and Andow (2008)

4 Potential driving factors of edge-biased distributions

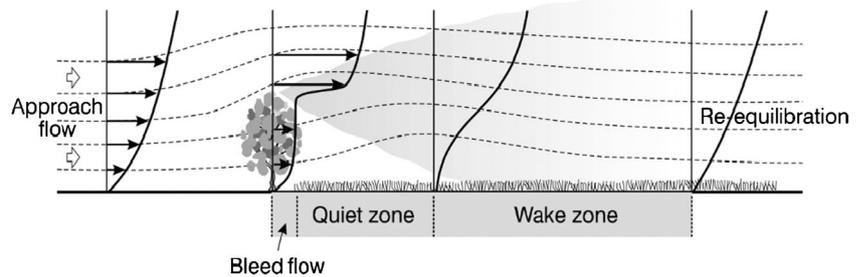
In light of an attractive edge as a potential explanation for the occurrence of edge-biased insect distributions in agricultural systems, the following question needs to be discussed: What set(s) of conditions would make an agricultural edge attractive? Before further discussion of this question, it is worth mentioning that the term “attractive edge,” as described by Olson and Andow (2008), should be broadly understood as an edge environment that leads to higher insect density than further inwards into agricultural systems. Therefore, an attractive edge does not necessarily act as favorable environment that attracts insects, but it can also or simply act as a trapping environment that reduces insects’ dispersal.

4.1 Mobility-altering factors

4.1.1 Wind patterns

Within the large body of literature on factors affecting insect movement, wind has been investigated extensively. Small-bodied, weak flying, or airborne insect pests (e.g., aphids) often rely on air flows for their dispersal and colonization of crop fields (Pasek 1988). Studies of small-bodied flies (Peng et al. 1992) and bark beetles (Lanier and Burns 1978) showed less likelihood of dispersal under strong winds. However, in a study of fruit flies [*Ceratitis capitata* Wiedemann (Diptera: Tephritidae)] dispersal into an area of 3600 ha which was treated with chemosterilant bait stations, Navarro-Llopis et al. (2014) concluded that the fruit flies showed an edge effect but traveled over 1 km into the treated area. Wind patterns are relevant to a discussion about edge-biased insect distributions in agricultural landscapes, because the presence of hedgerows and artificial windbreaks along field edges has been shown to create a triangular region right behind it known as the “quiet zone” whose length extends to around twice the height of the barriers (Fig. 4) (Cleugh and Hughes 2002). This region is characterized by

Fig. 4 Model of airflow through a windbreak. Picture adapted from Cleugh and Hughes (2002)



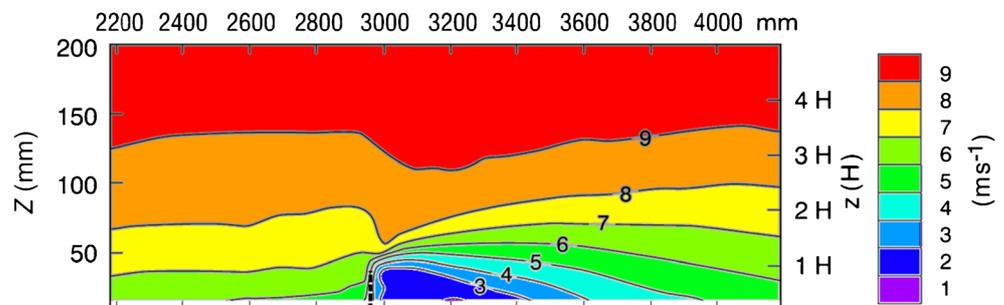
very weak or no winds (Fig. 5). Right next to the quiet zone is the “wake zone” where wind speed starts to increase to its original value (Figs. 4 and 5). Accordingly, Lewis (1965a) conducted a series of studies to quantify the distribution of insects in relation to distance from artificial windbreaks in fields. The studies found that there were several fold higher densities of gall midges (Diptera: Cecidomyiidae), moth flies (Diptera: Psychodidae), and seven times more fruit flies (Diptera: Drosophilidae) and day-flying thrips (Thysanoptera: Thripidae) on the leeward side at a distance equivalent to one-windbreak height away from the windbreak as compared to unsheltered fields. A similar windbreak-skewed distribution was observed in the lettuce root aphid, *Pemphigus bursarius* L. (Hemiptera: Aphididae) (Lewis 1965b). An accumulation of insect pest near windbreaks is more evident in windy weather as compared to calm weather conditions (Lewis 1969). The shelter capability of artificial windbreaks is also influenced by their permeability. Higher permeability of artificial windbreaks leads to higher wind speed in the leeward side, lower sheltering effects for insect pests, and lower insect pest density near the artificial windbreaks (Lewis and Stephenson 1966). Furthermore, higher windbreak permeability also shifts the positions of the highest insect pest density further away from the windbreak. Instead of maximal insect pest density at one-windbreak height for 0% permeable windbreak, the highest density was observed at distance equivalent to 2 to 3 windbreak height for thrips (Thysanoptera: Thripidae), aphids (Hemiptera: Aphididae), fungus gnats (Diptera: Mycetophilidae), and gall midges (Diptera: Cecidomyiidae) (Lewis and Stephenson 1966). Besides artificial windbreaks, natural hedgerows also exert similar effects on insect pest distribution (Lewis 1969). In another experiment, using trace of rubidium element to mark

egg parasitoids in the genus *Aragus* (Hymenoptera: Mymaridae) overwintering in French prune trees, Corbett and Rosenheim (1996) showed that the peak in *Aragus* density did not coincide with the original points of dispersal but some distance downwind, displaying certain degree of windbreak effect. Therefore, it can be inferred from these studies that the wake zone, which, in this case, can be considered as edge environment, traps insects along edges, resulting in their higher density along edges as compared to field interior.

4.1.2 Microclimate

Several studies have examined effects of the combination of natural landscape fragmentation and microclimatic conditions and how such variables affect insect communities in non-agricultural habitats (Stangler et al. 2015). The spatial distribution of a butterfly, *Lopinga achine* Scopoli (Lepidoptera: Nymphalidae), showed distinct edge-biased distribution, which was explained by specific microclimatic conditions leading to the ground cover of *Carex montana* L. (Cyperaceae) having the highest abundance near forest edges (Bergman 1999). In a study of bark beetle [*Ips typographus* L. (Coleoptera: Curculionidae)] infestations, Kautz et al. (2013) investigated the risk of infestation in three types of forest edges and compared the results of trees from the interior of the same forests. They concluded that the risk of bark beetle infestation was highest in forest patches cleared by sanitary logging measures, in particular along south-facing edges. Thus, the combination of a particular edge management practice and ambient temperature was highlighted as a key driver of bark beetle infestations. Although exclusively based on analyses of data derived from

Fig. 5 Changes of wind speed as it passes through a wind break (represented as dotted vertical line of height $1H$). Picture adapted from Cleugh and Hughes (2002)



natural habitats, such studies strongly suggest that edge-biased distributions are often explained by microclimatic differences between edge and interior locations. Using different types environmental sensors, it has been demonstrated how abiotic variables, including ground surface temperature and soil temperature, show considerable with-field variation and in particular vary between edges and inwards into fields (Bense et al. 2016). Such microclimatic variation can lead to spatial variation in crop growth and relative suitability of host plants and therefore lead to edge-biased distribution of herbivorous insects in agricultural systems.

4.1.3 Terrain property

Although windbreaks and hedgerows are common features in many agricultural systems, sole reliance on the shelter effect and microclimate promoted by these features does not provide encompassing account for the occurrence of edge-biased distributions, especially for agricultural systems in which they are not present. Other factors that are more intrinsic to the agricultural environment, such as the nature of landscape matrix, have been shown to affect insect rate of dispersal and emigration and result in their aggregation along edges. In a marked release and re-captured experiment on movement of delphacid planthopper, *Prokelisia crocea* Van Duzee (Hemiptera: Delphacidae), in patches of prairie cordgrass, the rate of emigration from cordgrass patches bordered with brome grass matrix was higher than that from cordgrass patches bordered with mudflat (Haynes and Cronin 2003). The same study also noted the accumulation of planthoppers along cordgrass-mudflat edges, but no such aggregation of planthoppers was observed along cordgrass-brome edges. It was later confirmed that the lower permeability of cordgrass-mudflat edges makes this type of edges a barrier to emigration since planthoppers behaviorally avoid crossing highly contrast border between vegetated cordgrass matrix to sparsely vegetated mudflat matrix (Haynes and Cronin 2006). Moreover, the cordgrass-mudflat border was clearly not a reflective edge, as planthoppers did not show edge-avoidance behavior. Meanwhile, the distribution of planthoppers within a homogenous patch of cordgrass was found to be random (Cronin 2003). Therefore, although landscape matrix permeability may explain why insects can be contained in their original patches, it does not directly explain the aggregation of insects along edges, especially for the case of delphacid planthoppers.

4.2 Vegetational factors contributing to edge-biased distributions

4.2.1 Vegetation heterogeneity

In cases where agricultural systems are adjacent to natural forests, the edges can be described as an “ecotone” that marks

the ecological change between two environments (Marshall and Moonen 2002). The adjacency of vegetation of two different habitats (agricultural fields and natural forests) results in an increase in floral diversity and vegetation heterogeneity (Marshall 1989; Yahner 1988). The increase in heterogeneity of vegetation along field edges has been shown to increase carabid species richness along field edges (Magura 2002). For example, boreal forests with sparse ground vegetation were found to have lower numbers of herbivorous invertebrate prey for carabids (Niemelä and Spence 1994). The interspersed between grasses, shrubs, and boreal trees as seen in the edges between farming lands and boreal forests can effectively increase the density of ground vegetation, resulting in greater abundance of herbivorous invertebrates which, in turn, leads to higher carabid abundance along edges (Magura 2002). Similarly, the interspersed of vegetation types between the forest edges and urban habitat in north Ohio has been attributed to the increase in ant (Hymenoptera: Formicidae) species richness (Ivanov and Keiper 2010). Therefore, the ecotone environment observed along field edges could serve as a preferential habitat for some insect species.

4.2.2 Plant quality

In the discussion of edge-biased distributions in relation to the vegetation heterogeneity, there seems to be an underlying assumption that vegetation homogeneity exists within a given habitat or agricultural system. Therefore, the heterogeneity of vegetation observed in the ecotone along edges is mainly caused by the interspersed between the vegetation types of two environments, while the within-system variation of vegetation is often ignored. However, despite cropping systems predominantly being monocultures and under a quasi-homogeneous management regime, there is broad evidence of significant vegetational heterogeneity within agricultural fields. That means individual crop plants within an agricultural field may have differential growth rates, phenotypes, and quality. This issue was highlighted above as microclimatic conditions may vary within fields and show distinct gradients between edges and locations further inwards into fields (Bense et al. 2016). Edge-biased crop development has been observed and reported for almost 100 years in winter wheat fields, where wheat rows along the borders showed higher yields than those in the center (Arny 1922). Over the years, rice (Wang et al. 2013), maize and climbing beans (Davis et al. 2008; Tiegu et al. 2012), wheat (Wu and Li 2002; Bulinski and Niemczyk 2015), millets, Sudan grass (Drapala and Johnson 1961), soybean (Teng et al. 2008), cotton (Luckett et al. 1992), rapeseed (Buliński and Niemczyk 2010), carrots, cabbages, and onions (Peach et al. 2000) have been shown to display edge-biased distribution of growth. In rice, the increase in yield of border rows compared to central portions of fields or plots ranged from 63 to 68% (Bulinski and

Niemczyk 2015). The difference can be as large as 394% between edge and center crops (Hadjichristodoulou 1993). The major factors accounting for such edge-biased growth difference have been attributed to competition for nutrients and light among crop plants (Peach et al. 2000).

The body of research documenting edge-biased distributions of crop development often regards the phenomenon as undesirable and seeks ways to curb the effect to avoid overestimation in yield calculations (Wang et al. 2013; Miller and Mountier 1955; Arny 1922). However, from an entomological perspective, the research focus would be to study how within-field vegetational heterogeneity contributes to the edge-biased distribution of insects in agricultural systems. We are unaware of any published study addressing this question directly, but the edge resource model by Ries and Sisk (2004) could partially explain this, as microclimatic conditions near edges may affect host plant growth and quality (suitability as a host plant for insect herbivores). Nonetheless, given that edge crops can have significantly higher yield than center crops, it is reasonable to hypothesize that there are physiological, and therefore nutritional, differences between edge and center crops. If such physiological differences are linked to differences in suitability as hosts and insects are able to—via volatiles or visual cues—perceive such differences among crop plants, then vegetational heterogeneity may partially explain observed edge-biased distributions of insects. That is, vegetational heterogeneity may drive selection by favoring both behavioral attraction and oviposition behavior by insects to certain plants. In addition, difference in suitability of crop plants will likely lead to differential growth and survival rates of insects. As an example, longevity and fecundity of *Sitobion avenae* and *Rhopalosiphum padi* L. (Hemiptera: Aphididae) have been shown to increase with the level of nitrogen fertilizer applied to wheat host plants (Aqueel and Leather 2011). Meanwhile, poor-quality host plants can cause many female insects to resorb their own eggs to mobilize nutrients for their survival (Awmack and Leather 2002). In broader term, female insects have been shown to vary their oviposition and number of eggs laid in accordance to the suitability of host plants for the performance of future progeny (Gripenberg et al. 2010). Therefore, the better-quality edge crops may be preferred by insects or provide better growing conditions for insects and their larval stages, resulting in a skewed distribution towards crop edges. However, using plant vigor to explain edge-biased distribution of insects may also involve important trade-offs. On one hand, more vigorous plants may provide insects and their larvae with more nutrients for their development. On the other hand, healthier plants can also produce more defensive chemicals such as alkaloids, glucosinolates, and phenolics to protect themselves from insect herbivores (Awmack and Leather 2002). Furthermore, the idea of plant quality as potential explanation for insect aggregation along edges is also contested by the data reported by Haynes and

Cronin (2003). Their study found that the nitrogen content of plants along mudflat-cordgrass edges and brome-cordgrass edges was both higher than that of plants in the interior. Interestingly, delphacid planthoppers aggregated along mudflat-cordgrass edges but not along brome-cordgrass edges, implying that host plant quality may not be the main driving factor of edge effect. Thus, we argue that considerable research is needed to investigate the complex of factors affecting plant growth along edges compared to inwards into cropping systems and how differential plant growth may affect their role as suitable hosts for associated insect communities.

5 Potential applications of edge-biased distributions into insect monitoring and pest management

Originally, skewed distributions of agricultural insects towards field edges were mostly regarded as a source of error when developing insect sampling plans. Therefore, the data collected along field edges were not considered representative of the actual insect population (Fleischer et al. 1999). However, edge-biased distributions of insects in agricultural systems can potentially provide opportunities to optimize sampling efforts. Currently, sampling units employed in sampling plans are often randomized and spread across the field. Such an approach can be highly labor intensive. Given the prevalence of edge effects in many insect species, stratified sampling plans with a greater focus along field edges than field interiors can reduce sampling efforts as well as increase sampling accuracy if a stable spatial pattern of insect distribution within an agricultural system is well studied and established. For example, increased performance (less sampling needed) of such a spatially targeted sampling approach was demonstrated for the wheat stem sawfly (Nansen et al. 2012). In addition, Severtson et al. (2016) described a spatially optimized sequential sampling plan for cabbage aphids in canola fields. In their study, canola fields were divided into two types of sampling grids: inner grids and edge grids. Edge grids were defined as the areas within 20 m of the field edge, while inner grids were the rest of the sampling grids. Their sampling results showed that 9 out of 20 edge grids displayed infestation level above threshold while only 2 out of 20 inner grids showed infestation level above threshold. Taking the proposed edge effect distribution of aphids into account, Severtson et al. (2016) conducted stratified sampling analysis and managed to reduce spatial variability as well as to increase accuracy of infestation level. Nonetheless, we also acknowledge that edge effect distribution of insects in many agricultural systems can be highly seasonal and temporally dependent (Corbett and Rosenheim 1996; Winder et al. 1999; Holland et al. 1999; Wilson and Morton 1993).

Furthermore, applications of insecticides in agricultural fields have been proven to greatly change the edge-biased distribution of insects to random distribution across agricultural fields (Trumble 1985; De Jiu and Waage 1990; Maredia et al. 2003). Therefore, the mentioned limitations may jeopardize the robustness of edge-stratified sampling methods and highlight the importance of timing in proposed edge-stratified sampling methods.

Broadly speaking, increased understanding of the mechanisms responsible for edge-biased distributions can be used to improve the practices of precision agriculture. As compared to conventional agriculture, precision agriculture focuses more on timely and targeted application of treatments to control insect pest infestations rather than field-wide and calendar-based spraying of chemicals (Council 1997). The knowledge of edge-biased distributions can help create targeted sampling plans to generate more reliable mapping of insect distributions and enable more targeted application of pesticides used in IPM programs (Weisz et al. 1995). Targeted application of insecticide has the potential to reduce pesticide usage in conventional farming systems yet maintain an effective control over agricultural pests. Focusing spray along field borders can also potentially address the issue of spray coverage, one of the main problems faced in field-wide treatment of pesticides that severely reduce the efficacy of applied chemicals (Nansen and Ridsdill-Smith 2013). An example of successful targeted application of insecticides would be the recent efforts to control brown marmorated stink bug, *Halyomorpha halys* Stål (Hemiptera: Pentatomidae), in Northeastern USA by focus spraying along edges in peach orchards instead of orchard-wide application (Blaauw et al. 2015). The results are promising as pesticide usage was reduced by 25–61% using this method and the damage on peach caused by brown marmorated stink bugs was also reduced when compared with the common standard practices. In addition, better understanding of edge-biased distributions may be used to optimize deployments of anti-insect nets in the orchard industry (Castellano et al. 2008). Finally, there is a growing body of literature on the potential use of banker plant systems (Zheng et al. 2017; Gurr et al. 2004, 2012, 2015, 2016; Lu et al. 2015; Zehnder et al. 2007; Hossain et al. 2002). In these agricultural systems, the agro-ecological landscape is manipulated through integration of special plants along crop banks. These banker plants serve several purposes, including (1) nectar and pollen for natural enemies, (2) host plants for alternative prey of natural enemies, and (3) shelter and oviposition sites for natural enemies. Thus, banker plant systems represent ways to enhance the performance of biological control of crop pest. A very important aspect of banker plant systems is that the landscape manipulation is conducted along field edges, so edge-biased distributions of many insect pests are a contributing factor to the growing interest in this type of agricultural systems.

6 Conclusion

As discussed in this review, edge-biased insect distributions represent a significant phenomenon that is observed in both natural and agricultural systems and across a wide range of spatial scales. Although there have been very important modeling studies attempting to explain edge-biased distributions (Ries and Sisk 2004; Ries et al. 2004), the phenomenon has not been studied extensively on the basis of manipulative/experimental research, and we wish to highlight this important research gap. Agricultural systems lend themselves nicely to such manipulative/experimental research, so we argue that the broader community of landscape ecologists should consider agricultural systems when testing their theories on how biodiversity is affected by landscape fragmentation and environmental edges. Improved knowledge and appreciation of edge-biased distributions can greatly facilitate the development and implementation of precision agriculture, such as optimization of sampling efforts and creation of more accurate insect distribution maps that enable targeted application of treatments. Finally, edge-biased distributions of insects are one of the underlying reasons why ecological engineering (Gurr et al. 2012, 2015) and banker plant systems are being recognized as sustainable alternatives to a growing number of conventional farming systems.

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References

- Altamirano A, Valladares G, Kuzmanich N, Salvo A (2016) Galling insects in a fragmented forest: incidence of habitat loss, edge effects and plant availability. *J Insect Conserv* 20(1):119–127. <https://doi.org/10.1007/s10841-016-9845-2>
- Aqueel MA, Leather SR (2011) Effect of nitrogen fertilizer on the growth and survival of *Rhopalosiphum padi* (L.) and *Sitobion avenae* (F.) (Homoptera: Aphididae) on different wheat cultivars. *Crop Prot* 30(2):216–221. <https://doi.org/10.1016/j.cropro.2010.09.013>
- Arbogast RT, Kendra PE, Mankin RW, McDonald RC (2002) Insect infestation of a botanicals warehouse in north-central Florida. *J Stored Prod Res* 38(4):349–363. [https://doi.org/10.1016/S0022-474X\(01\)00037-6](https://doi.org/10.1016/S0022-474X(01)00037-6)
- Amy A (1922) Border effect and ways of avoiding it. *Agron J*
- Athanassiou CG, Kavallieratos NG, Palyvos NE, Sciarretta A, Trematerra P (2005) Spatiotemporal distribution of insects and mites in horizontally stored wheat. *J Econ Entomol* 98(3):1058–1069. <https://doi.org/10.1603/0022-0493-98.3.1058>

- Awmack CS, Leather SR (2002) Host plant quality and fecundity in herbivorous insects. *Annu Rev Entomol* 47(1):817–844. <https://doi.org/10.1146/annurev.ento.47.091201.145300>
- Bense VF, Read T, Verhoef A (2016) Using distributed temperature sensing to monitor field scale dynamics of ground surface temperature and related substrate heat flux. *Agric For Meteorol* 220(Supplement C):207–215. <https://doi.org/10.1016/j.agrformet.2016.01.138>
- Bergman K-O (1999) Habitat utilization by *Lopinga achine* (Nymphalidae: Satyrinae) larvae and ovipositing females: implications for conservation. *Biol Conserv* 88(1):69–74. [https://doi.org/10.1016/S0006-3207\(98\)00088-3](https://doi.org/10.1016/S0006-3207(98)00088-3)
- Blaauw BR, Polk D, Nielsen AL (2015) IPM-CPR for peaches: incorporating behaviorally-based methods to manage *Halyomorpha halys* and key pests in peach. *Pest Manag Sci* 71(11):1513–1522. <https://doi.org/10.1002/ps.3955>
- Bulinski J, Niemczyk H (2010) Edge effect in winter rape cultivation technology with traffic paths. EDITORIAL BOARD:5
- Bulinski J, Niemczyk H (2015) Assessment of border effect in wheat cultivation with tramlines. *Annals of Warsaw University of Life Sciences-SGGW Agriculture* (65 Agric. Forest Eng)
- Campbell JF, Hagstrum DW (2002) Patch exploitation by *Tribolium castaneum*: movement patterns, distribution, and oviposition. *J Stored Prod Res* 38(1):55–68. [https://doi.org/10.1016/S0022-474X\(00\)00042-4](https://doi.org/10.1016/S0022-474X(00)00042-4)
- Campbell JF, Mullen MA, Dowdy AK (2002) Monitoring stored-product pests in food processing plants with pheromone trapping, contour mapping, and mark-recapture. *J Econ Entomol* 95(5):1089–1101. <https://doi.org/10.1603/0022-0493-95.5.1089>
- Castellano S, Gm S, Russo G, Briassoulis D, Mistriotis A, Hemming S, Waaijenberg D (2008) Plastic nets in agriculture: a general review of types and applications. *Appl Eng Agric* 24(6):799–808. <https://doi.org/10.13031/2013.25368>
- Cleugh HA, Hughes DE (2002) Impact of shelter on crop microclimates: a synthesis of results from wind tunnel and field experiments. *Aust J Exp Agric* 42(6):679. <https://doi.org/10.1071/ea02005>
- Corbett A, Rosenheim JA (1996) Impact of a natural enemy overwintering refuge and its interaction with the surrounding landscape. *Ecol Entomol* 21(2):155–164. <https://doi.org/10.1111/j.1365-2311.1996.tb01182.x>
- Council NR (1997) Precision agriculture in the 21st century: geospatial and information technologies in crop management. *Natl Academy Pr.* doi:<https://doi.org/10.17226/5491>
- Cronin JT (2003) Movement and spatial population structure of a prairie planthopper. *Ecology* 84(5):1179–1188. [https://doi.org/10.1890/0012-9658\(2003\)084\[1179:MASPSO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[1179:MASPSO]2.0.CO;2)
- Davis JHC, AmÉZquita MC, MuÑoz JE (2008) Border effects and optimum plot sizes for climbing beans (*Phaseolus vulgaris*) and maize in association and monoculture. *Exp Agric* 17(2):127–135. <https://doi.org/10.1017/S0014479700011364>
- De Jiu G, Waage JK (1990) The effect of insecticides on the distribution of foraging parasitoids, *Diaeretiella rapae* [Hym.: Braconidae] on plants. *Entomophaga* 35(1):49–56. <https://doi.org/10.1007/bf02374300>
- Dean BG (1973) Aphid colonization of spring cereals. *Ann Appl Biol* 75(2):183–193. <https://doi.org/10.1111/j.1744-7348.1973.tb07298.x>
- Didham R (1997) The influence of edge effects and forest fragmentation on leaf litter invertebrates in central Amazonia. *Tropical forest remnants: ecology, management, and conservation of fragmented communities.* University of Chicago Press, Chicago, pp 55–70
- Drapala W, Johnson CM (1961) Border and competition effects in millet and sudangrass plots characterized by different levels of nitrogen fertilization. *Agron J* 53(1):17–19. <https://doi.org/10.2134/agronj1961.00021962005300010006x>
- Fagan WF, Cantrell RS, Cosner C (1999) How habitat edges change species interactions. *Am Nat* 153(2):165–182. <https://doi.org/10.1086/303162>
- Ferguson AW, Klukowski Z, Walczak B, Perry JN, Muggleston MA, Clark SJ, Williams IH (2000) The spatio-temporal distribution of adult *Ceutorhynchus assimilis* in a crop of winter oilseed rape in relation to the distribution of their larvae and that of the parasitoid *Trichomalus perfectus*. *Entomol Exp Appl* 95(2):161–171. <https://doi.org/10.1046/j.1570-7458.2000.00654.x>
- Fischer J, Lindenmayer DB (2007) Landscape modification and habitat fragmentation: a synthesis. *Glob Ecol Biogeogr* 16(3):265–280. <https://doi.org/10.1111/j.1466-8238.2007.00287.x>
- Fleischer S, Blom P, Weisz R (1999) Sampling in precision IPM: when the objective is a map. *Phytopathology* 89(11):1112–1118. <https://doi.org/10.1094/PHYTO.1999.89.11.1112>
- Gripenberg S, Mayhew PJ, Parnell M, Roslin T (2010) A meta-analysis of preference–performance relationships in phytophagous insects. *Ecol Lett* 13(3):383–393. <https://doi.org/10.1111/j.1461-0248.2009.01433.x>
- Gruber B, Eckel K, Everaars J, Dormann CF (2011) On managing the red mason bee (*Osmia bicornis*) in apple orchards. *Apidologie* 42(5): 564–576. <https://doi.org/10.1007/s13592-011-0059-z>
- Gurr GM, Heong KL, Cheng JA, Catindig J (2012) Ecological engineering strategies to manage insect pests in rice. In: Gurr GM, Wratten SD, Snyder WE, Read DMY (eds) *Biodiversity and insect pests: key issues for sustainable management.* Wiley-Blackwell, Chichester, pp 214–229. <https://doi.org/10.1002/9781118231838.ch13>
- Gurr GM, Lu Z, Zheng X, Xu H, Zhu P, Chen G, Yao X, Cheng J, Zhu Z, Catindig JL, Villareal S, Van Chien H, Cuong LQ, Channoo C, Chengwattana N, Lan LP, Hai LH, Chaiwong J, Nicol HI, Perovic DJ, Wratten SD, Heong KL (2016) Multi-country evidence that crop diversification promotes ecological intensification of agriculture. *Nat Plants* 2(3):16014. <https://doi.org/10.1038/nplants.2016.14> <http://www.nature.com/articles/nplants201614#supplementary-information>
- Gurr GM, Scarratt SL, Wratten SD, Berndt L, Irvin N (2004) Ecological engineering, habitat manipulation and pest management. In: Gurr GM, Wratten SD, Alteiri MA (eds). *CSIRO Publishing, Collingwood, Australia*
- Gurr GM, Zhu ZR, You MS (2015) The big picture: prospects for ecological engineering to guide the delivery of ecosystem services in global agriculture. In: Heong KL, Cheng J, Escalada MM (eds) *Rice planthoppers: ecology, management, socio economics and policy* Springer Science and Business Media. Netherlands, Dordrecht, pp 143–160
- Hadjichristodoulou A (1993) Edge effects on yield, yield components and other physiological characteristics in cereals and oilseed crops. *J Agric Sci* 120(01):7–12. <https://doi.org/10.1017/S0021859600073536>
- Harris LD (1988) Edge effects and conservation of biotic diversity. *Conserv Biol* 2(4):330–332. <https://doi.org/10.1111/j.1523-1739.1988.tb00196.x>
- Haynes KJ, Cronin JT (2003) Matrix composition affects the spatial ecology of a prairie planthopper. *Ecology* 84(11):2856–2866. <https://doi.org/10.1890/02-0611>
- Haynes KJ, Cronin JT (2006) Interpatch movement and edge effects: the role of behavioral responses to the landscape matrix. *Oikos* 113(1): 43–54. <https://doi.org/10.1111/j.0030-1299.2006.13977.x>
- Helson G (1958) Aphid populations: ecology and methods of sampling aphids *Myzus persicae* (Sulz.) and *Aulacorthum solani* (Kltb.) *N Z Entomol* 2(3):20–23. <https://doi.org/10.1080/00779962.1958.9722768>
- Hida T (1980) Brownian motion. In: Hida T (ed) *Brownian motion.* Springer US, New York, pp 44–113. https://doi.org/10.1007/978-1-4612-6030-1_2

- Holland JM, Perry JN, Winder L (1999) The within-field spatial and temporal distribution of arthropods in winter wheat. *Bull Entomol Res* 89(06):499–513. <https://doi.org/10.1017/s0007485399000656>
- Hossain Z, Gurr GM, Wratten SD, Raman A (2002) Habitat manipulation in lucerne *Medicago sativa*: arthropod population dynamics in harvested and ‘refuge’ crop strips. *J Appl Ecol* 39(3):445–454. <https://doi.org/10.1046/j.1365-2664.2002.00729.x>
- Ivanov K, Keiper J (2010) Ant (Hymenoptera: Formicidae) diversity and community composition along sharp urban forest edges. *Biodivers Conserv* 19(14):3917–3933. <https://doi.org/10.1007/s10531-010-9937-3>
- Johnson C (1950) Infestation of a bean field by *Aphis fabae* Scop. in relation to wind direction. *Ann Appl Biol* 37(3):441–450. <https://doi.org/10.1111/j.1744-7348.1950.tb00967.x>
- Julião G, Amaral M, Fernandes G, Oliveira E (2004) Edge effect and species–area relationships in the gall-forming insect fauna of natural forest patches in the Brazilian Pantanal. *Biodivers Conserv* 13(11):2055–2066. <https://doi.org/10.1023/B:BIOC.0000040006.81958.f2>
- Kareiva PM (1983) Local movement in herbivorous insects: applying a passive diffusion model to mark-recapture field experiments. *Oecologia* 57(3):322–327. <https://doi.org/10.1007/BF00377175>
- Kautz M, Schopf R, Ohser J (2013) The ‘sun-effect’: microclimatic alterations predispose forest edges to bark beetle infestations. *Eur J For Res* 132(3):453–465. <https://doi.org/10.1007/s10342-013-0685-2>
- Lanier GN, Burns BW (1978) Barometric flux. *J Chem Ecol* 4(2):139–147. <https://doi.org/10.1007/bf00988050>
- Lewis T (1965a) The effects of an artificial windbreak on the aerial distribution of flying insects. *Ann Appl Biol* 55(3):503–512. <https://doi.org/10.1111/j.1744-7348.1965.tb07963.x>
- Lewis T (1965b) The effect of an artificial windbreak on the distribution of aphids in a lettuce crop. *Ann Appl Biol* 55(3):513–518. <https://doi.org/10.1111/j.1744-7348.1965.tb07964.x>
- Lewis T (1969) The distribution of flying insects near a low hedgerow. *J Appl Ecol* 6(3):443. <https://doi.org/10.2307/2401510>
- Lewis T, Stephenson J (1966) The permeability of artificial windbreaks and the distribution of flying insects in the leeward sheltered zone. *Ann Appl Biol* 58(3):355–363. <https://doi.org/10.1111/j.1744-7348.1966.tb04395.x>
- Liebold AM, Tobin PC (2008) Population ecology of insect invasions and their management. *Annu Rev Entomol* 53(1):387–408. <https://doi.org/10.1146/annurev.ento.52.110405.091401>
- Lu ZX, Zhu PY, Gurr GM, Zheng XS, Chen GH, Heong KL (2015) Rice pest management by ecological engineering: a pioneering attempt in China. In: Heong KL, Cheng JA, Escalada MM (eds) *Rice planthoppers: ecology, management, socio economics and policy*. Springer Science and Business Media, Dordrecht, pp 163–180
- Luckett D, Williams E, Reid P, Thomson N (1992) Irrigated plot trials in cotton: quantifying end effects and the influence of plot size upon intergenotypic competition. *Aust J Agric Res* 43(1):181–190. <https://doi.org/10.1071/AR9920181>
- Magura T (2002) Carabids and forest edge: spatial pattern and edge effect. *For Ecol Manag* 157(1):23–37. [https://doi.org/10.1016/S0378-1127\(00\)00654-X](https://doi.org/10.1016/S0378-1127(00)00654-X)
- Mankin RW, Hagstrum DW, Nansen C, Meikle WG (2014) Almond moth oviposition patterns in continuous layers of peanuts. *J Stored Prod Res* 59:48–54. <https://doi.org/10.1016/j.jspr.2014.05.002>
- Maredia KM, Dakouo D, Mota-Sanchez D (2003) *Integrated Pest Management in Mexico*. In: *Integrated pest management in the global arena*. CABI, pp 273–284. doi:<https://doi.org/10.1079/9780851996523.0000>
- Marshall EJP (1989) Distribution patterns of plants associated with arable field edges. *J Appl Ecol* 26(1):247–257. <https://doi.org/10.2307/2403665>
- Marshall EJP, Moonen AC (2002) Field margins in northern Europe: their functions and interactions with agriculture. *Agric Ecosyst Environ* 89(1–2):5–21. [https://doi.org/10.1016/s0167-8809\(01\)00315-2](https://doi.org/10.1016/s0167-8809(01)00315-2)
- Martini X, Seibert S, Prager SM, Nansen C (2012) Sampling and interpretation of psyllid nymph counts in potatoes. *Entomol Exp Appl* 143(2):103–110. <https://doi.org/10.1111/j.1570-7458.2012.01235.x>
- Miller J, Mountier N (1955) The border row effect in wheat trials with different spacings between plots. *NZJ Sci Tech* 37:287–299
- Murphy SM, Battocletti AH, Tinghitella RM, Wimp GM, Ries L (2016) Complex community and evolutionary responses to habitat fragmentation and habitat edges: what can we learn from insect science? *Curr Opin Insect Scie* 14(Supplement C):61–65. <https://doi.org/10.1016/j.cois.2016.01.007>
- Nansen C, Macedo TB, Weaver DK, Peterson RKD (2005) Spatio-temporal distributions of wheat stem sawfly, *Cephus cinctus* Norton, eggs and larvae in dryland wheat fields. *Can Entomol* 137(04):428–440. <https://doi.org/10.4039/n04-094>
- Nansen C, Payton ME, Runyon JB, Weaver DK, Morrill WL, Sing SE (2012) Preharvest sampling plan for larvae of the wheat stem sawfly, *Cephus cinctus* (Hymenoptera: Cephidae), in winter wheat fields. *Can Entomol* 137(5):602–614. <https://doi.org/10.4039/n04-087>
- Nansen C, Phillips TW, Sanders S (2004) The effects of height and adjacent surfaces on captures of the Indianmeal Moth, *Plodia interpunctella* (Lepidoptera: Pyralidae) in pheromone-baited traps. *J Econ Entomol* 97(4):1284–1290. <https://doi.org/10.1093/jee/97.4.1284>
- Nansen C, Ridsdill-Smith JT (2013) The performance of insecticides—a critical review. INTECH Open Access Publisher doi:<https://doi.org/10.5772/53987>
- Nansen C, Weaver DK, Sing SE, Runyon JB, Morrill WL, Grieshop MJ, Shannon CL, Johnson ML (2005) Within-field spatial distribution of *Cephus cinctus* (Hymenoptera: Cephidae) larvae in Montana wheat fields. *Can Entomol* 137(02):202–214. <https://doi.org/10.4039/N04-036>
- Navarro-Llopis V, Vacas S, Zarzo M, Primo J (2014) Dispersal ability of *Ceratitis capitata* (Diptera: Tephritidae): edge effect in area-wide treatments. *J Appl Entomol* 138(6):403–408. <https://doi.org/10.1111/jen.12029>
- Niemelä JK, Spence JR (1994) Distribution of forest dwelling carabids (Coleoptera): spatial scale and the concept of communities. *Ecography* 17(2):166–175. <https://doi.org/10.1111/j.1600-0587.1994.tb00090.x>
- Okubo A (1980) *Diffusion and ecological problems: mathematical models*. Springer-Verlag, New York. <https://doi.org/10.1002/bimj.4710240311>
- Olson D, Andow D (2008) Patch edges and insect populations. *Oecologia* 155(3):549–558. <https://doi.org/10.1007/s00442-007-0933-6>
- Paras S, Ccanto R, Olivera E, Scurrah M, Alcázar J, Rosenheim JA (2012) Explaining Andean potato weevils in relation to local and landscape features: a facilitated ecoinformatics approach. *PLoS One* 7(5):e36533. <https://doi.org/10.1371/journal.pone.0036533>
- Pasek JE (1988) Influence of wind and windbreaks on local dispersal of insects. *Agric Ecosyst Environ* 22:539–554. [https://doi.org/10.1016/0167-8809\(88\)90044-8](https://doi.org/10.1016/0167-8809(88)90044-8)
- Peach L, Benjamin LR, Mead A (2000) Effects on the growth of carrots (*Daucus carota* L.), cabbage (*Brassica oleracea* var. capitata L.) and onion (*Allium cepa* L.) of restricting the ability of the plants to intercept resources. *J Exp Bot* 51(344):605–615. <https://doi.org/10.1093/jexbot/51.344.605>
- Peng R, Fletcher C, Sutton S (1992) The effect of microclimate on flying dipterans. *Int J Biometeorol* 36(2):69–76. <https://doi.org/10.1007/BF01208916>
- Ries L, Fletcher RJ, Battin J, Sisk TD (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annu Rev Ecol Evol Syst* 35(1):491–522. <https://doi.org/10.1146/annurev.ecolsys.35.112202.130148>

- Ries L, Sisk TD (2004) A predictive model of edge effects. *Ecology* 85(11):2917–2926. <https://doi.org/10.1890/03-8021>
- Rossetti MR, González E, Salvo A, Valladares G (2014) Not all in the same boat: trends and mechanisms in herbivory responses to forest fragmentation differ among insect guilds. *Arthropod Plant Interact* 8(6):593–603. <https://doi.org/10.1007/s11829-014-9342-z>
- Rudd WG, Gandour RW (1985) Diffusion model for insect dispersal. *J Econ Entomol* 78(2):295–301. <https://doi.org/10.1093/jee/78.2.295>
- Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. *Conserv Biol* 5(1):18–32. <https://doi.org/10.1111/j.1523-1739.1991.tb00384.x>
- Setamou M, Bartels DW (2015) Living on the edges: spatial niche occupation of Asian citrus psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Liviidae), in citrus groves. *PLoS One* 10(7):e0131917. <https://doi.org/10.1371/journal.pone.0131917>
- Severtson D, Flower K, Nansen C (2015) Nonrandom distribution of cabbage aphids (Hemiptera: Aphididae) in dryland canola (Brassicales: Brassicaceae). *Environ Entomol* 44(3):767–779. <https://doi.org/10.1093/ee/nvv021>
- Severtson D, Flower K, Nansen C (2016) Spatially-optimized sequential sampling plan for cabbage aphids *Brevicoryne brassicae* L. (Hemiptera: Aphididae) in canola fields. *J Econ Entomol* 109(4):1929–1935. <https://doi.org/10.1093/jee/tow147>
- Sheffield CS, Westby SM, Smith RF, Kevan PG (2012) Potential of bigleaf lupine for building and sustaining *Osmia lignaria* populations for pollination of apple. *Can Entomol* 140(05):589–599. <https://doi.org/10.4039/n08-011>
- Shmida A, Wilson MV (1985) Biological determinants of species diversity. *J Biogeogr* 12(1):1–20. <https://doi.org/10.2307/2845026>
- Skellam J (1991) Random dispersal in theoretical populations. *Bull Math Biol* 53(1–2):135–165. <https://doi.org/10.1007/bf02464427>
- Stangler ES, Hanson PE, Steffan-Dewenter I (2015) Interactive effects of habitat fragmentation and microclimate on trap-nesting Hymenoptera and their trophic interactions in small secondary rainforest remnants. *Biodivers Conserv* 24(3):563–577. <https://doi.org/10.1007/s10531-014-0836-x>
- Teng W-l, Han Y-p, Li W-b (2008) Marginal effect index on the yield characters of soybean cultivars with different leaf shape [J]. *Soybean Sci* 3:013
- Thomas JW, Maser C, Rodiek JE (1979) Edges, vol 553. *Wildlife habitats in managed forest: the Blue Mountains of Oregon and Washington*. U.S. Department of Agriculture, Forest Service, Washington, D.C.
- Tiegu W, Xinliang Z, Huaisheng Z, Juan M, Shilin C (2012) Marginal effect of yield and correlation analysis with main agricultural traits in maize. *Chin Agric Sci Bull* 28(18):122–126
- Trumble JT (1985) Implications of changes in arthropod distribution following chemical application. *Res Popul Ecol* 27(2):277–285. <https://doi.org/10.1007/bf02515466>
- Tscharntke T, Steffan-Dewenter I, Kruess A, Thies C (2002) Characteristics of insect populations on habitat fragments: a mini review. *Ecol Res* 17(2):229–239. <https://doi.org/10.1046/j.1440-1703.2002.00482.x>
- Tuell JK, Ascher JS, Isaacs R (2009) Wild bees (Hymenoptera: Apoidea: Anthophila) of the Michigan highbush blueberry agroecosystem. *Ann Entomol Soc Am* 102(2):275–287. <https://doi.org/10.1603/008.102.0209>
- Valladares G, Salvo A, Cagnolo L (2006) Habitat fragmentation effects on trophic processes of insect-plant food webs. *Conserv Biol* 20(1):212–217. <https://doi.org/10.1111/j.1523-1739.2006.00337.x>
- Wang K, Zhou H, Wang B, Jian Z, Wang F, Huang J, Nie L, Cui K, Peng S (2013) Quantification of border effect on grain yield measurement of hybrid rice. *Field Crop Res* 141:47–54. <https://doi.org/10.1016/j.fcr.2012.11.012>
- Weathers KC, Cadenasso ML, Pickett STA (2001) Forest edges as nutrient and pollutant concentrators: potential synergisms between fragmentation, forest canopies, and the atmosphere. *Conserv Biol* 15(6):1506–1514. <https://doi.org/10.1046/j.1523-1739.2001.01090.x>
- Weisz R, Fleischer S, Smilowitz Z (1995) Site-specific integrated Pest Management for High Value Crops: sample units for map generation using the Colorado potato beetle (Coleoptera: Chrysomelidae) as a model system. *J Econ Entomol* 88(5):1069–1080. <https://doi.org/10.1093/jee/88.5.1069>
- Wilson L, Morton R (1993) Seasonal abundance and distribution of *Tetranychus urticae* (Acari: Tetranychidae), the two spotted spider mite, on cotton in Australia and implications for management. *Bull Entomol Res* 83(2):291–303. <https://doi.org/10.1017/S0007485300034787>
- Winder L, Perry JN, Holland JM (1999) The spatial and temporal distribution of the grain aphid *Sitobion Avenae* in winter wheat. *Entomol Exp Appl* 93(3):275–288. <https://doi.org/10.1046/j.1570-7458.1999.00588.x>
- Wu W, Li X (2002) Research on the marginal effect of wheat experimental plot. *Acta Botan Boreali-Occiden Sin* 23(12):2167–2171
- Yahner RH (1988) Changes in wildlife communities near edges. *Conserv Biol* 2(4):333–339. <https://doi.org/10.1111/j.1523-1739.1988.tb00197.x>
- Zehnder G, Gurr GM, Kühne S, Wade MR, Wratten SD, Wyss E (2007) Arthropod pest management in organic crops. *Annu Rev Entomol* 52(1):57–80. <https://doi.org/10.1146/annurev.ento.52.110405.091337>
- Zheng X, Lu Y, Zhu P, Zhang F, Tian J, Xu H, Chen G, Nansen C, Lu Z (2017) Use of banker plant system for sustainable management of the most important insect pest in rice fields in China. *Sci Rep* 7:45581. <https://doi.org/10.1038/srep45581>