

Spatial variability in ecosystem services: simple rules for predator-mediated pest suppression

F. J. J. A. BIANCHI,^{1,2} N. A. SCHELLHORN,^{1,5} Y. M. BUCKLEY,^{3,4} AND H. P. POSSINGHAM³

¹*Commonwealth Scientific and Industrial Research Organization (CSIRO), Entomology, 120 Meiers Road, Indooroopilly, Queensland 4068 Australia*

²*Cotton Catchment Communities Cooperative Research Centre, Australian Cotton Research Institute, Narrabri, New South Wales 2390 Australia*

³*University of Queensland, School of Biological Sciences, Queensland 4072 Australia*

⁴*CSIRO Sustainable Ecosystems, 306 Carmody Road, St Lucia, Queensland 4067 Australia*

Abstract. Agricultural pest control often relies on the ecosystem services provided by the predators of pests. Appropriate landscape and habitat management for pest control services requires an understanding of insect dispersal abilities and the spatial arrangement of source habitats for pests and their predators. Here we explore how dispersal and habitat configuration determine the locations where management actions are likely to have the biggest impact on natural pest control. The study focuses on the early colonization phase before predator reproduction takes place and when pest populations in crops are still relatively low. We developed a spatially explicit simulation model in which pest populations grow exponentially in pest patches and predators disperse across the landscape from predator patches. We generated 1000 computer-simulated landscapes in which the performance of four typical but different predator groups as biological control agents was evaluated. Predator groups represented trait combinations of poor and good dispersal ability and density-independent and density-dependent aggregation responses toward pests. Case studies from the literature were used to inform the parameterization of predator groups. Landscapes with a small nearest-neighbor distance between pest and predator patches had the lowest mean pest density at the landscape scale for all predator groups, but there can be high variation in pest density between the patches within these landscapes. Mobile and strongly aggregating predators provide the best pest suppression in the majority of landscape types. Ironically, this result is true except in landscapes with small nearest-neighbor distances between pest and predator patches. The pest control potential of mobile predators can best be explained by the mean distance between a pest patch and all predator patches in the landscape, whereas for poorly dispersing predators the distance between a pest patch and the nearest predator patch is the best explanatory variable. In conclusion, the spatial arrangement of source habitats for natural enemies of agricultural pest species can have profound effects on their potential to colonize crops and suppress pest populations.

Key words: biological control; habitat configuration; landscape ecology; predator–prey interaction; source–sink dynamics; spatial ecology.

INTRODUCTION

Arthropod natural enemies provide the important ecosystem service of pest control that is vital for agricultural production (Costanza et al. 1997, Losey and Vaughan 2006). As a consequence, there is increasing interest in management strategies aimed at their conservation (Landis et al. 2000). Although there is accumulating evidence that landscape context can influence pest control services (Bianchi et al. 2006), and there is a general consensus that conservation biological control should also consider spatial scales exceeding individual fields (e.g., Landis et al. 2000), in

practice the identification of priority areas where implementation of conservation biological control is most effective has received only limited attention. This can be explained in part by the fact that landholders base management decisions at convenient land management scales such as the field (Schellhorn et al. 2008), but there is also a lack of practical guidelines on spatial planning for ecosystem services (but see Bianchi and van der Werf 2003, Brosi et al. 2008). However, management strategies that recognize the importance of larger scale issues such as insect dispersal and the spatial arrangement of source habitats for pests and natural enemies in the landscape may be better suited to capitalize on the pest control services provided by natural enemies.

Agricultural landscapes are composed of patches of crop and non-crop habitats. Crops constitute a wide range of habitats that can differ in resource availability

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⁵ Corresponding author.

E-mail: nancy.schellhorn@csiro.au

(Forman 1995). Resource-rich habitats may act as sources of pests and/or predators (i.e., areas of population growth), whereas resource-poor habitats are likely to act as sinks (i.e., areas of population decline; Pulliam 1988). Due to factors such as the timing of reproduction of pests and their natural enemies and practices such as pesticide use and crop rotation, the spatial arrangement of source and sink habitats in the landscape is highly dynamic. As a consequence, the distance between source habitats of pest insects and their natural enemies changes within and between years, which has consequences for the timing of crop colonization by natural enemies and their potential to suppress pest populations (Bianchi et al. 2009). Therefore, the evaluation of interactions between the spatial arrangement of source habitats of pests and natural enemies and traits of natural enemies (e.g., dispersal ability) can contribute to a better understanding of what types of landscapes may benefit from substantial pest control services and which landscape metrics correlate with effective pest suppression by functional groups of natural enemies.

There is a wide diversity of natural enemies associated with natural pest control. In this study we will only consider arthropod predators. Generalist predators have been shown to be able to suppress pest populations in crops (Symondson et al. 2002), leading to yield increases (Östman et al. 2003). Predators can be placed in four functional groups according to their dispersal ability and response to prey aggregations. For instance, ground-dwelling predators are generally less mobile than flying predators and their movements are more likely to be affected by habitat transitions than flying predators (Duelli et al. 1990). Furthermore, the body size of predators is a trait that is expected to be positively correlated with dispersal capacity (Roland and Taylor 1997, Holland et al. 2005). Predators differ in their response to prey aggregations, which may be mediated by differences in diet breadth and preference for the prey type (Bryan and Wratten 1984, Schellhorn and Andow 2005a, b). Some predator species have the ability to effectively aggregate to prey patches through the use of olfactory cues (Raymond et al. 2000), vision (Henaut et al. 1999), or adapted movement patterns (Kareiva and Odell 1987). In contrast, there are also predators that do not show a strong aggregation response to prey patches and are often found in areas with low prey densities (Bryan and Wratten 1984). These traits are likely to affect how species move in landscapes and how effective they are in controlling pest populations in crops.

This study focuses on the early-season crop colonization process by predators as predation early in the season is considered key to preventing pest populations from reaching threshold levels (van der Werf 1995, Settle et al. 1996). We used a spatially explicit model (1) to investigate how the spatial arrangement of source habitats of arthropod predators and crops infested with

pests influences natural pest control, (2) to assess the potential of predators that differ in dispersal ability and aggregation behavior to suppress pest populations in crops in a wide range of landscape types, and (3) to identify landscape metrics that can be used to predict the pest suppressive potential of different landscapes.

MATERIALS AND METHODS

Functional groups of predators

Predators constitute a wide diversity of species, whereby each species can have specific responses to the spatial distribution of prey in the landscape. Classification of predators into functional groups can help with making generalizations among species responses to the landscape (Cole et al. 2002, Purtauf et al. 2005). We classified predators into four groups based on their dispersal ability (poor vs. good) and their response to prey aggregations (density dependent vs. density independent). A wide range of predator species can be positioned in this classification (Table 1).

Landscape generation

Landscapes served as spatial templates for a spatially explicit simulation model and are represented as grids containing 64×64 cells. Cells measure 100×100 m, hence each map represents a landscape of 6.4×6.4 km. Each landscape contains 10 pest and 10 predator patches that each consist of a single cell. Pest patches represent crops that are infested with pests and predator patches represent habitats from which predators of the pests emigrate and colonize the surrounding landscape. We generated a total of 1000 landscapes that contained a wide variety of spatial arrangements of pest and predator patches. The spatial distribution of pest patches varied from aggregated to uniform, and predator patches spanned a wide range from nearby to far from pest patches (Appendix). Pest and predator patches did not overlap. The landscapes were characterized by four metrics based on nearest-neighbor distances: the mean distance from pest (h for herbivore, which is the notation used to distinguish pests from predators) patches to the nearest predator (p) patch (n_{hp}) and its standard deviation ($\sigma_{n_{hp}}$), and the mean distance from predator patches to the nearest pest patch (n_{ph}) and its standard deviation ($\sigma_{n_{ph}}$). An example of the calculation of these metrics is given in Fig. 1. As each landscape contained 10 pest and 10 predator patches, these landscape metrics are based on 10 distances. In addition, we included three metrics using the mean distance between predator and pest patches: the average of the mean distance between each predator patch and the 10 pest patches (m), the standard deviation of the mean distance between pest and predator patches (σ_{mhp}), and the standard deviation of the mean distance between predator and pest patches (σ_{mph}). Note that the average of the mean distances from predator patches to pest patches is equal to the average of the mean

TABLE 1. Overview of predators with combinations of good and poor dispersal ability and that show density-dependent and density-independent aggregation toward prey.

Predator	Order and family	Prey	Reference
Group A, poor, density independent			
<i>Orius insidiosus</i>	Hemiptera: Anthorcoridae	aphids	Costamagna and Landis (2007)
<i>Amblyseus andersoni</i>	Acari: Phytoseiidae	spider mite eggs	Zhang and Sanderson (1993)
<i>Typhlodromus occidentalis</i>	Acari: Phytoseiidae	spider mite eggs	Zhang and Sanderson (1993)
<i>Loricera pilicornis</i>	Coleoptera: Carabidae	aphids	Bryan and Wratten (1984)
<i>Notiophilus biguttatus</i>	Coleoptera: Carabidae	aphids	Bryan and Wratten (1984)
<i>Nebria brevicollis</i>	Coleoptera: Carabidae	aphids	Bryan and Wratten (1984)
<i>Coleomegilla maculata</i> †	Coleoptera: Coccinellidae	aphids	Schellhorn and Andow (1999)
Group B, poor, density dependent			
<i>Pterostichus melanarius</i>	Coleoptera: Carabidae	aphids	Winder et al. (2001, 2005)
<i>Pterostichus melanarius</i>	Coleoptera: Carabidae	slugs	Bohan et al. (2000)
<i>Pterostichus madidus</i>	Coleoptera: Carabidae	aphids	Winder et al. (2005)
<i>Phytoseiulus persimilis</i>	Acari: Phytoseiidae	spider mite eggs	Zhang and Sanderson (1993)
<i>Agonum dorsale</i>	Coleoptera: Carabidae	aphids	Bryan and Wratten (1984)
<i>Bembidion lampros</i>	Coleoptera: Carabidae	aphids	Bryan and Wratten (1984)
<i>Bembidion obtusum</i>	Coleoptera: Carabidae	aphids	Bryan and Wratten (1984)
<i>Adalia bipunctata</i> †	Coleoptera: Coccinellidae	aphids	Schellhorn and Andow (1999)
<i>Hippodamia convergens</i> †	Coleoptera: Coccinellidae	aphids	Schellhorn and Andow (1999)
Group C, good, density independent			
<i>Coleomegilla maculata</i> ‡	Coleoptera: Coccinellidae	aphids	Elliott and Kieckhefer (2000), Schellhorn and Andow (2005a, b)
<i>Linyphiidae</i> spp.	Araae: Linyphiidae	collembola and other prey	Harwood et al. (2001)
<i>Linyphiidae</i> spp.	Araae: Linyphiidae	aphids and other prey	Harwood et al. (2003)
Group D, good, density dependent			
<i>Coccinella septempunctata</i> ‡	Coleoptera: Coccinellidae	aphids	Ives et al. (1993), Elliott and Kieckhefer (2000), Costamagna and Landis (2007)
<i>Hippodamia variegata</i> ‡	Coleoptera: Coccinellidae	aphids	Ives et al. (1993)
<i>Adalia bipunctata</i> ‡	Coleoptera: Coccinellidae	aphids	Schellhorn and Andow (2005a, b)
<i>Hippodamia convergens</i> ‡	Coleoptera: Coccinellidae	aphids	Elliott and Kieckhefer (2000)
<i>Harmonia axyridis</i> ‡	Coleoptera: Coccinellidae	aphids	Costamagna and Landis (2007)

† Larval stage of predators.

‡ Adult stage of predators.

distances from pest patches to predator patches (i.e., $m_{ph} = m_{hp}$), but the standard deviation is not. We therefore omit the subscript for the average of the mean distance and just use m . All calculations are based on distances between cell centers. The 1000 landscapes can be represented as points in the n_{hp} n_{ph} plane and classified in nine landscape groups (Fig. 2).

Simulation model

The model simulates the population increase of pests in pest patches (e.g., crops) and the colonization of pest patches and suppression of the pest populations by predators. The study focuses on the early colonization phase before predator reproduction takes place and pest populations in crops are still relatively low. Pests are not mobile and grow exponentially with relative growth rate r (d^{-1} ; Table 2). Predators are mobile and colonize the landscape from their patches, but show no population dynamics, which we assume is not relevant in the short term. The exponential power distribution was used to describe the dispersal kernel (Clark et al. 1999):

$$f(x) = \frac{1}{N} \exp \left[- \left(\frac{x}{a} \right)^b \right] \quad (1)$$

where $f(x)$ is the density of predators at distance x from the origin of dispersal, N is the normalization constant, a is the distance parameter (m), and b is a dimensionless shape parameter. This distribution can generate a family of distributions for specific parameter values, including the Laplace distribution ($b = 1$) and the normal distribution ($b = 2$). Edge effects are avoided by using a toroidal structure of the landscape, such that predators that move outside the map area reappear at the other side of the map. Predators move through the landscape and remove pests when they encounter pest patches. The per capita rate of predation y is modeled using the Holling type II functional response (Eq. 1):

$$y = \frac{sH}{1 + hsH} \quad (2)$$

where H is the pest density ($no./m^2$), s is the search rate (m^2/d), and h is the handling time (d). We consider two types of predator behavior when encountering pests: density-dependent and density-independent arrestment. For density-dependent arrestment, the tenure time u of predators in a cell is described as a linear function of the pest density:

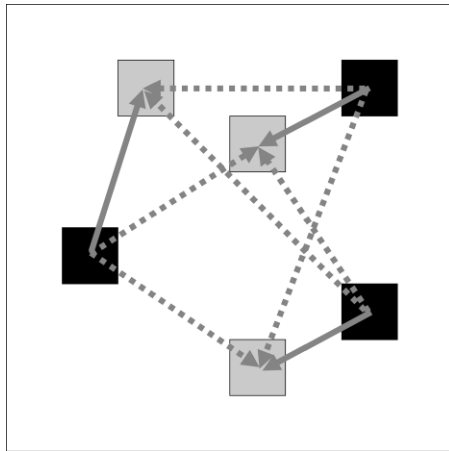


FIG. 1. Landscape with three pest patches (gray) and three predator patches (black), whereby solid arrows connect predator patches with the nearest pest patch and dotted arrows connect the predator patch with all remaining pest patches. The mean distance from predator patches to the nearest pest patch (n_{ph}) is calculated as the mean length of the three solid arrows and has standard deviation σ_{mph} . The average of the mean distance between predator and pest patches (m) is calculated by taking the mean arrow length of all three arrows (solid and dotted) pointing from a focal predator patch to each pest patch and averaging these values across the number of focal predator patches. The standard deviation of these three mean distances is σ_{mph} .

$$u = \begin{cases} kH & \text{for density-dependent arrestment} \\ c & \text{for density-independent arrestment} \end{cases} \quad (3)$$

where k is the residence coefficient ($d/[\text{no. pests}/\text{m}^2]$) and c is a constant (d). The residence coefficient k reflects the increase in pest density that is needed to increase the tenure time of predators with one unit of time. For density-independent arrestment it is assumed that a constant proportion $1/c$ of the predator population leaves the cell each time step. We assume that no predator reproduction and mortality takes place. Hereafter we will use the term “non-aggregating” as shorthand for density-independent aggregation and “aggregating” for density-dependent aggregation.

Parameterization

Parameter values were selected to be representative of aphids and their predators (Table 2). A relative growth rate $r = 0.25 \text{ d}^{-1}$ is typical for pest aphids on crops (e.g., Xia et al. 1999). Predator search rates $s = 0.01 \text{ m}^2/\text{d}$ and handling times $h = 0.01 \text{ d}$ pests are representative of adult stages of lady beetles (Xia et al. 2003). A Laplace dispersal kernel ($b = 1$) provides an accurate description for the movement of lady beetles (van der Werf et al. 2000). The distance parameters for well-dispersing ($a = 152.41$) and poorly dispersing predators ($a = 61.5 \text{ m}$) result in a mean dispersal distance of 140 and 40 m, respectively, which fall within the range of dispersal distances reported for predators in the literature. The residence coefficient $k = 0.1 \text{ d}/(\text{no. pests}/\text{m}^2)$ and relative

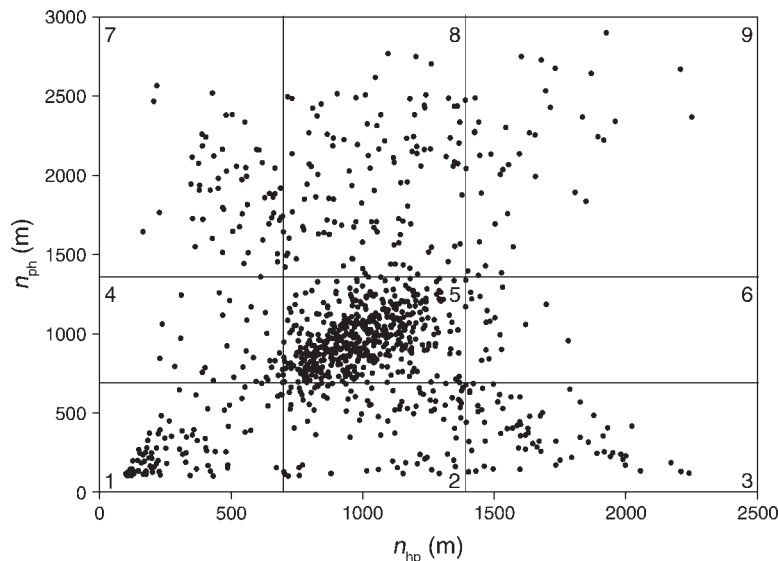


FIG. 2. Location of 1000 landscapes, containing 10 pest and 10 predator patches each, in the mean nearest-neighbor distance plane. The x -axis represents the mean distance from pest patches to the nearest predator patch (n_{hp}), and the y -axis represents the mean distance from predator patches to the nearest pest patch (n_{ph}). The plane is divided in nine landscape groups. In landscape group 1 pest and predator patches are both clumped together; in landscape group 3 predator patches are clumped, and most pest patches (but not all) are far from pest patches; in landscape group 7 pest patches are clumped and most predator patches (but not all) are far from pest patches; and in landscape group 9 pest and predator patches are spatially separated. Landscape groups 2, 4, 5, 6, and 8 have intermediate arrangements of pest and predator patches (see Appendix).

TABLE 2. Overview of model parameters.

Parameter	Description	Value	Unit	Reference
<i>r</i>	relative growth rate	0.25	d ⁻¹	Xia et al. (1999)
<i>s</i>	search rate	0.01	m ² /d	Xia et al. (2003)
<i>h</i>	handling time	0.01	d	Xia et al. (2003)
<i>b</i>	shape parameter of kernel	1	dimensionless	van der Werf et al. (2000)
<i>a</i>	distance parameter	61.5 or 152.41	m	
<i>k</i>	residence coefficient	0.1	d/(no. pests/m ²)	
<i>c</i>	tenure time	2	d	

emigration rate $1/c = 0.5 \text{ d}^{-1}$ are hypothetical but result in realistic aggregation dynamics.

Scenario studies

The model is used to study the potential of predators that exhibit different traits to suppress pest populations in the 1000 landscapes. A 30-d period is simulated with a time step of 0.01 d. We tested the performance of predators in a 2 × 2 factorial design: predators that are mobile (mean dispersal distance of 140 m) and less mobile (mean dispersal distance of 40 m) and predators that respond in a density-dependent and density-independent manner to pests (Table 1). Initially, we also considered two spatial redistribution functions, i.e., predators dispersing according to a Laplace ($b = 1$) and Gaussian dispersal kernel ($b = 2$), but as simulations with these parameters resulted in similar outcomes we report only results for the Laplace dispersal kernel. The initial density of pests is 1 pest/m², amounting to 100 000 individuals summed over the whole landscape, reflecting low early-season pest densities in crops (e.g., Karley et al. 2003). We used initial densities of predators of 100, 500, and 1000 predators/m², which translates to 10 million, 50 million, and 100 million predators per landscape. This predator density range corresponds to densities of several predator species including hibernating predators in beetle banks (ranging from 150 to 1500

predators/m²; Thomas et al. 1991), permanent field strips (400 to 600 predators/m²; Pffnner and Luka 2000, Geiger et al. 2009), orchards (1200 predators/m²; Pffnner and Luka 2000), sown wild flower strips (1200–1300 predators/m²; Lys and Nentwig 1994, Pffnner and Luka 2000), and sown meadow strips (100–200 predators/m²; Pffnner and Luka 2000). We evaluated the potential of predators to suppress pests in terms of pest load and relative pest load. Pest load is the integrated number of pests in the 10 patches over the 30-d simulation period. Relative pest load is the ratio of the pest load and the pest load in the absence of predators, which equals 7.18×10^8 pest-days.

Statistical analysis

Three sets of landscape metrics were evaluated as predictors for the pest-suppressive potential of landscapes: (1) n_{hp} and σ_{nhp} , (2) n_{ph} and σ_{nph} , and (3) m and σ_{mhp} . We did not include σ_{mhp} as preliminary exploration indicated that this metric explained less variation than σ_{mhp} and this way we had two metrics for sets 1, 2, and 3. We used logistic regression to model relative log pest load (the ratio between log pest load and log pest load without predators) at the high predator density with either n_{hp} and σ_{nhp} , n_{ph} and σ_{nph} , or m and σ_{mhp} as predictors. Statistical analyses were conducted in Genstat 10 (Payne et al. 2007).

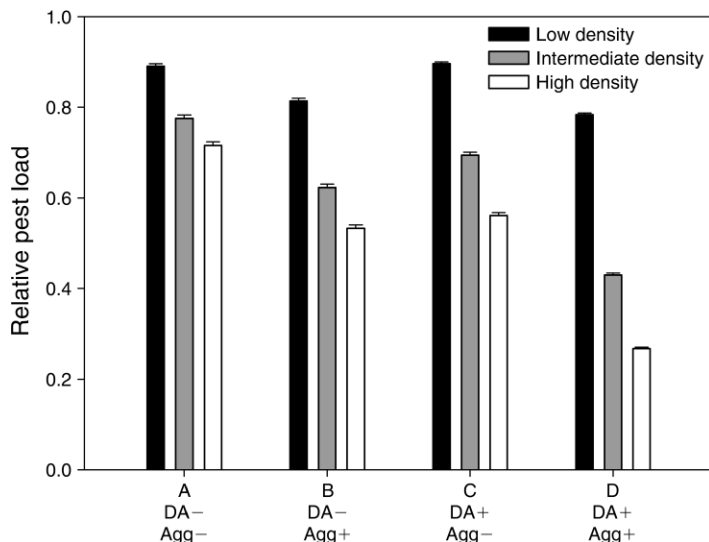


FIG. 3. Relative pest load in 1000 landscapes (mean and SE) for four predator groups (A–D) at three densities (black, 10 million; gray, 50 million; and white, 100 million predators/landscape). Species groups have poor (–) or good (+) dispersal ability (DA) and show density-independent (–) and density-dependent (+) aggregation (Agg) toward pests. Relative pest load is the ratio between the integrated number of pests in the landscape over time in the presence and in the absence of predators.

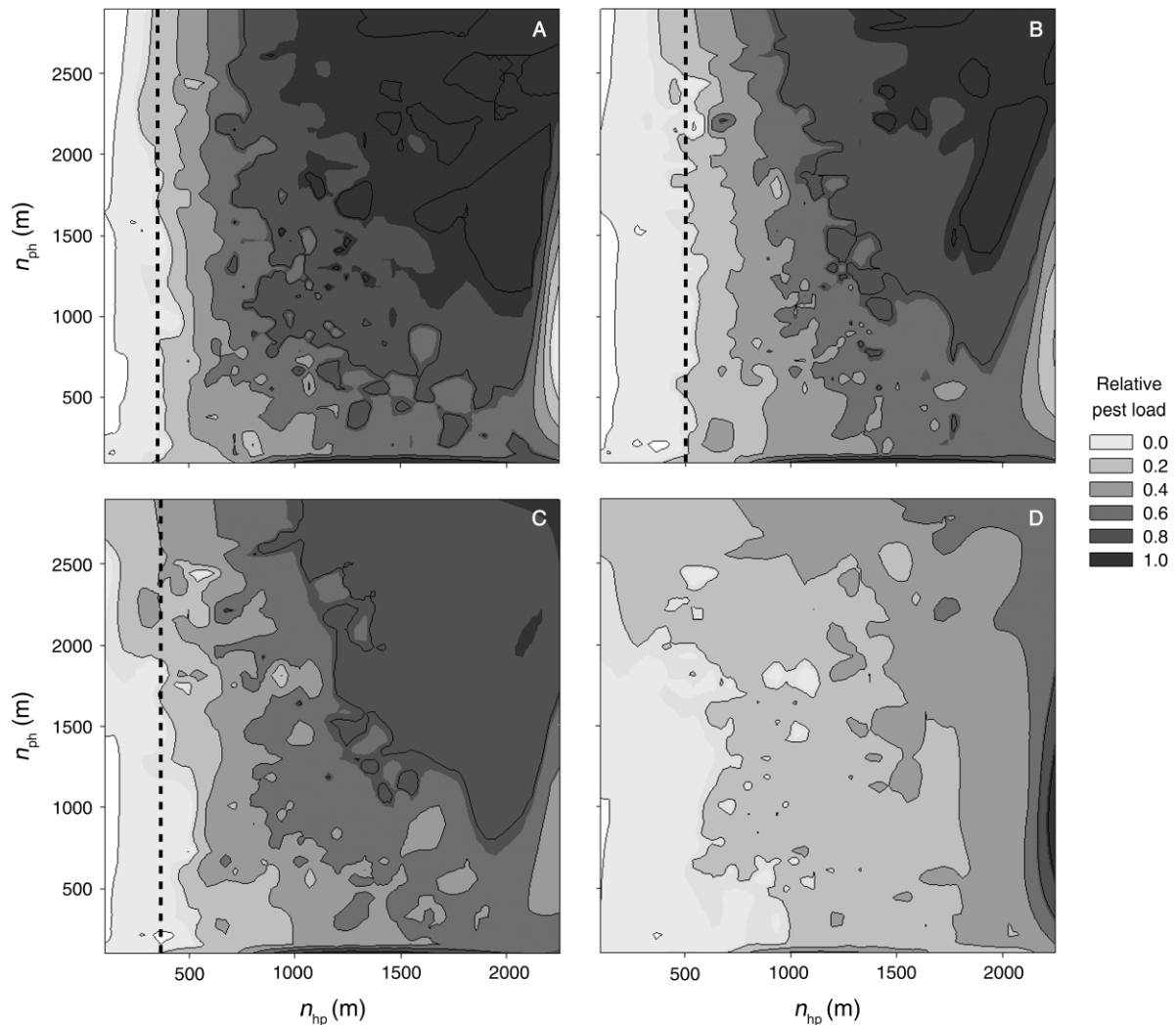


FIG. 4. Contour plots of relative pest load for (A) poorly dispersing and density-independent aggregating predators, (B) poorly dispersing and density-dependent aggregating predators, (C) well-dispersing and density-independent aggregating predators, and (D) well-dispersing and density-dependent aggregating predators. The areas left of the dashed lines indicate the $n_{hp} - n_{ph}$ space where the predator group can provide better pest control services than well-dispersing and strongly aggregating predators (D). Dark to light gray scales indicate high to low relative pest loads, respectively.

RESULTS

The four species groups (i.e., combinations of good and poor dispersers and aggregating and non-aggregating predators) differed in their potential to control pest populations averaged over all 1000 landscapes (Fig. 3). Poorly dispersing, non-aggregating predators (species group A) provided poor pest suppression at all three predator densities. Poorly dispersing, aggregating predators (species group B) and well-dispersing, non-aggregating predators (species group C) had a somewhat similar performance, except for the lowest predator density at which species group B were more effective than species group C. Well-dispersing, aggregating predators (species group D) provided the best pest suppression at all predator densities and also showed the

strongest reduction in pest load with increasing predator densities. This was in sharp contrast to species group A in which a 10-fold increase in predator density hardly resulted in a reduction of pest load.

The ability to suppress pest populations by the four functional groups of predators at the highest predator density was affected by spatial arrangement of predator and pest patches in the landscape (Fig. 4). In most landscapes species group D (Fig. 4D) gave rise to a lower pest load than species group A (better than group A in 957 out of 1000 landscapes; Fig. 4A), species group B (better than group B in 907 out of 1000 landscapes; Fig. 4B), and species group C (better than group C in 943 out of 1000 landscapes; Fig. 4C). In landscapes in which the mean nearest-neighbor distance from pest to predator patches, n_{hp} , exceeds 300 m, species group D

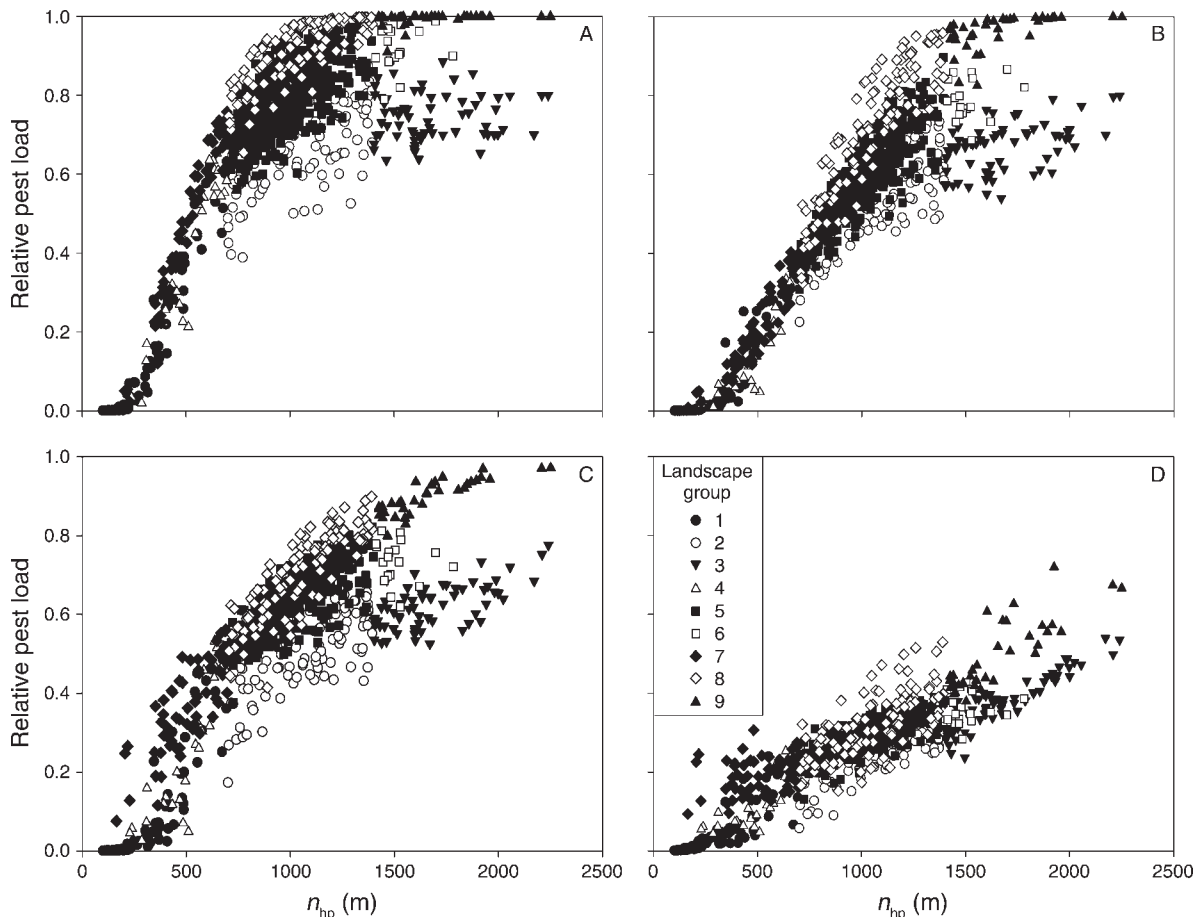


FIG. 5. Relationship between the mean nearest-neighbor distance from pest to predator patches (n_{hp}) and relative pest load for four predator groups that differ in mobility and aggregation behavior (A, poorly dispersing, density-independent aggregating; B, poorly dispersing, density-dependent aggregating; C, well-dispersing, density-independent aggregating; D, well-dispersing, density-dependent aggregating). Symbols indicate landscape groups; see Fig. 2 for a description. Relative pest load is the ratio between the integrated number of pests in the landscape over time in the presence and in the absence of predators.

always provided better pest control than species group A (area right of the dashed line in Fig. 4A). Species group D always provided better pest control than species groups B and C in landscapes in which the mean nearest-neighbor distances from pest to predator patches (n_{hp}) were 500 and 330 m, respectively (area right of the dashed line in Fig. 4B, C). Species group B provided better pest control in 666 out of 1000 landscapes than species group C. These were typically landscapes in which the mean nearest-neighbor distance from pest to predator patches (n_{hp}) was <1400 m. Species group A provided better pest control than species group B in only one landscape (n_{hp} 170 and n_{ph} 1640 m), whereas it provided better control than species group C in 44 landscapes. In the latter case, species group A only provided better pest control in landscapes in which the mean nearest-neighbor distance from pest to predator patches (n_{hp}) was less than 550 m. In summary, species group B provided the best pest control in 89 of the 1000 landscapes, species group C in three landscapes, and

species group A in one landscape. In the other 907 landscapes species group D performed best.

Evaluation of three types of landscape metrics to describe each predator groups' potential to suppress pest populations at the highest predator density indicated that the mean nearest-neighbor distance from pest to predator patches (n_{hp}) was a useful predictive metric that resulted in a restricted outcome domain (Fig. 5). In contrast, the mean nearest-neighbor distance from predator to pest patches (n_{ph}) resulted in a much wider outcome domain, indicating that this metric does not provide predictive power in explaining pest control at the landscape scale (data not shown). The average of the mean distance between predator and pest patches (m) provided a relatively wide outcome domain for poorly dispersing predators (Fig. 6A, B), but a more restricted domain for well-dispersing predators (Fig. 6C, D).

The ability of the four species groups to suppress pest populations in the nine landscape groups showed a similar pattern, even though the absolute level of

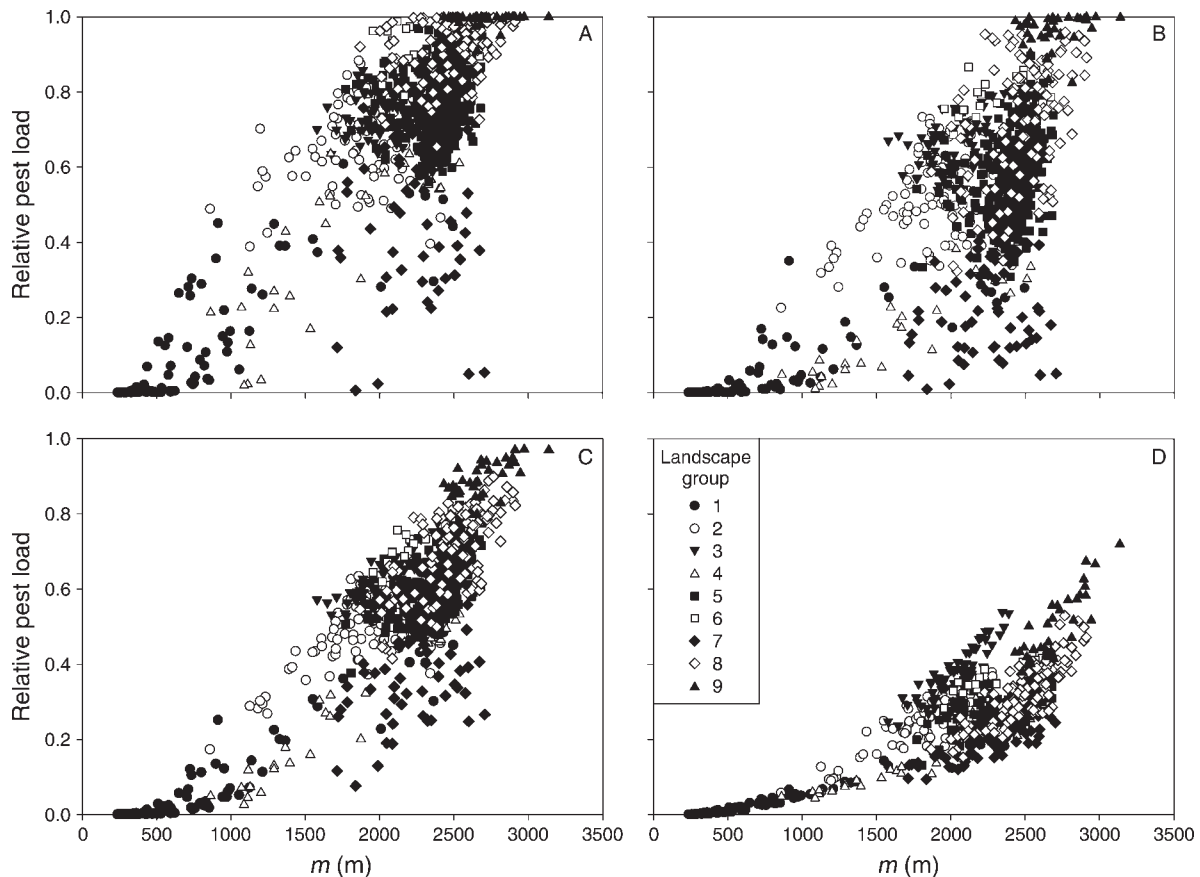


FIG. 6. Relationship between the average of the mean distance between predator and pest patches (m) and relative pest load for four predator groups that differ in mobility and aggregation behavior (A, poorly dispersing, density-independent aggregating; B, poorly dispersing, density-dependent aggregating; C, well-dispersing, density-independent aggregating; D, well-dispersing, density-dependent aggregating). Symbols indicate landscape groups; see Fig. 2 for a description. Relative pest load is the ratio between the integrated number of pests in the landscape over time in the presence and in the absence of predators.

suppression provided by the species groups varied (Figs. 5 and 6). Species group A (poorly dispersing, non-aggregating) kept pest loads below 40% of the maximum pest load in most landscapes of landscape group 1 (predator and pest patches clustered; Appendix), in some landscapes of group 4, and approximately half of the landscapes of group 7 (most predator patches far from pest patches; Figs. 5A and 6A). Relative pest loads in landscapes in group 9 (all predator patches far from pest patches) were in all cases close to the maximum pest load. The patterns for species group B (poorly dispersing, aggregating; Figs. 5B and 6B) and C (well-dispersing, non-aggregating; Figs. 5C and 6C) were similar to species group A (Figs. 5A and 6A), but the relative pest loads were generally lower than species group A. For species group D the variation in relative pest load in the nine landscape groups was relatively low as compared to the other species groups. Pest levels were kept below 40% of the maximum pest load in all landscapes except for landscapes in group 3 (predator patches close to a few pest patches), some landscapes in

groups 6 and 8, and almost all landscapes in group 9 (Figs. 5D and 6D).

Logistic regression analysis indicated that for well-dispersing predators the relative log pest load could best be described using landscape metrics based on the mean distance between pest and predator patches (m), whereas for poorly dispersing predators metrics derived from the nearest-neighbor distance between pest and predator patches (n_{hp}) provided a better description (Table 3). Landscape metrics based on the nearest-neighbor distance between predator and pest patches (n_{ph}) explained the lowest variation for all species groups.

In addition to variation in pest load between landscapes, there was variation in pest load within landscapes, i.e., variation in pest load among pest patches. The general trend among the four species groups was that the coefficient of variation (CV) of the pest load from patch to patch was largest for landscapes in group 1 and smallest in groups 6, 8, and 9 (Fig. 7). Predator groups with poor dispersal ability (Fig. 7A, B) created higher CVs of between-patch pest load than

TABLE 3. Multiple logistic regression models and adjusted correlation coefficient for relative log(pest load), Y , of four predator groups that differ in dispersal ability and aggregation behavior.

Dispersal ability	Aggregation	Regression model	R_{adj}^2
Good	density dependent	$Y = 0.916 + 0.179 n_{hp} + 0.135 \sigma_{nhp} - 0.0131 n_{hp} \cdot \sigma_{nhp}$	0.82
		$Y = 1.479 + 0.149 n_{ph} + 0.078 \sigma_{mph} - 0.0135 n_{ph} \cdot \sigma_{mph}$	0.44
		$Y = 0.546 + 0.087 m + 0.157 \sigma_{mhp} - 0.0051 m \cdot \sigma_{mhp}$	0.95
Good	density independent	$Y = 0.256 + 0.404 n_{hp} + 0.181 \sigma_{nhp} - 0.0280 n_{hp} \cdot \sigma_{nhp}$	0.92
		$Y = 1.110 + 0.354 n_{ph} + 0.084 \sigma_{mph} - 0.0282 n_{ph} \cdot \sigma_{mph}$	0.56
		$Y = -0.016 + 0.153 m + 0.278 \sigma_{mhp} - 0.0110 m \cdot \sigma_{mhp}$	0.95
Poor	density dependent	$Y = 0.033 + 0.421 n_{hp} + 0.151 \sigma_{nhp} - 0.0258 n_{hp} \cdot \sigma_{nhp}$	0.97
		$Y = 1.063 + 0.380 n_{ph} + 0.007 \sigma_{mph} - 0.0284 n_{ph} \cdot \sigma_{mph}$	0.51
		$Y = -0.171 + 0.147 m + 0.352 \sigma_{mhp} - 0.0125 m \cdot \sigma_{mhp}$	0.87
Poor	density independent	$Y = -0.081 + 0.611 n_{hp} + 0.114 \sigma_{nhp} - 0.0372 n_{hp} \cdot \sigma_{nhp}$	0.97
		$Y = 0.974 + 0.545 n_{ph} - 0.032 \sigma_{mph} - 0.0378 n_{ph} \cdot \sigma_{mph}$	0.58
		$Y = -0.222 + 0.191 m + 0.474 \sigma_{mhp} - 0.0203 m \cdot \sigma_{mhp}$	0.87

Notes: Regression models are based on predictors associated with the mean nearest-neighbor distance from pest to predator patches (n_{hp}), mean nearest-neighbor distance from predator to pest patches (n_{ph}), and mean distance between pest and predator patches (m). Relative log(pest load), Y , is the ratio between the logarithm of the cumulative pest density in the presence and the absence of predators. The highest R_{adj}^2 values for each predator group are indicated in boldface.

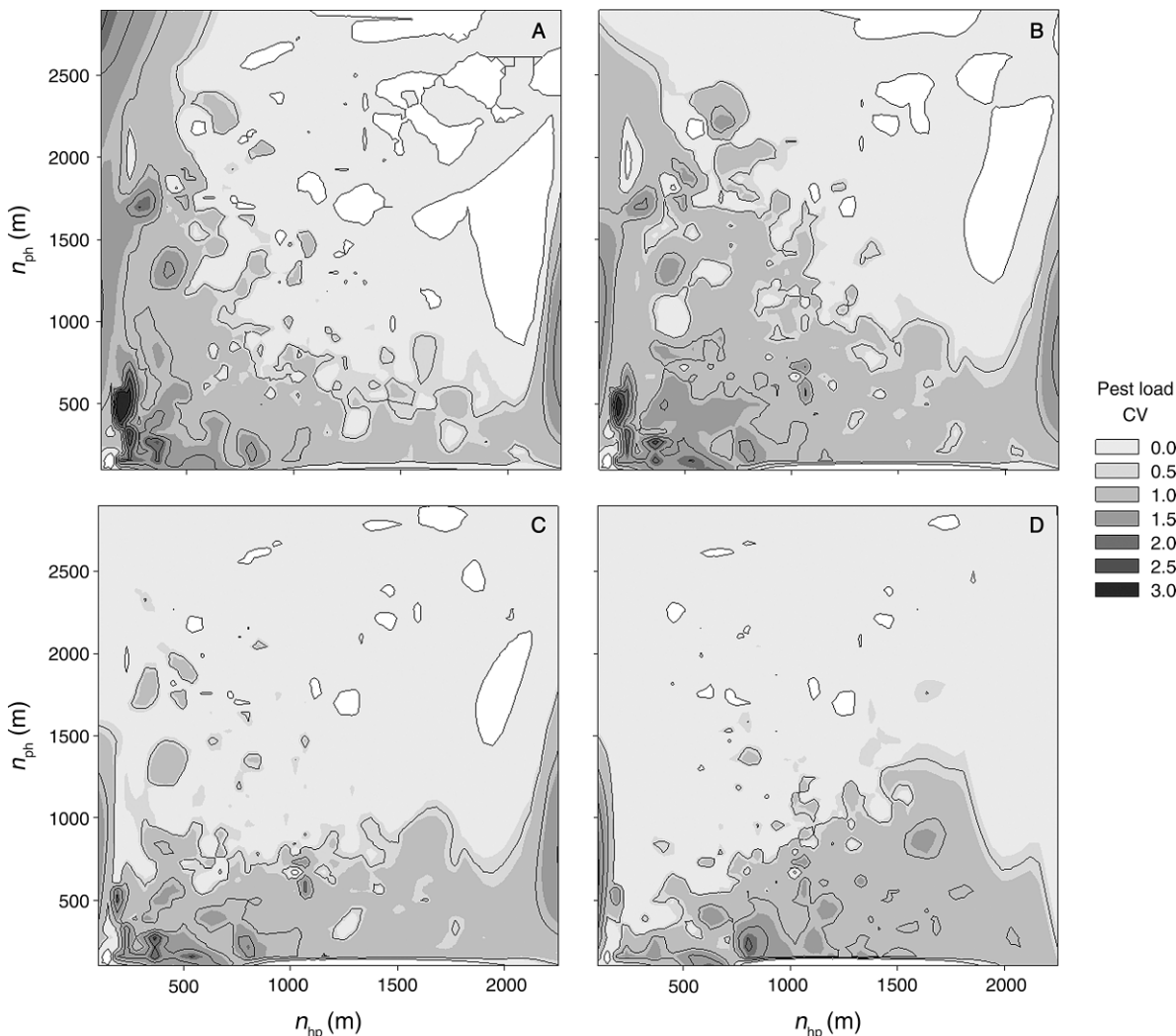


FIG. 7. Contour plots of the coefficient of variation of pest load for (A) poorly dispersing and density-independent aggregating predators, (B) poorly dispersing and density-dependent aggregating predators, (C) well-dispersing and density-independent aggregating predators, (D) well-dispersing and density-dependent aggregating predators. Dark and light gray scales indicate high and low coefficients of variation of pest load, respectively.

well-dispersing predators (Fig. 7C, D). This was most pronounced in landscapes with low n_{hp} values.

DISCUSSION

This study highlights the importance of the spatial arrangement of pest patches (e.g., crops) and predator patches from which predators colonize the surrounding landscape for effective pest suppression. We have three main findings: (1) landscapes with a small nearest-neighbor distance between pest and predator patches have the lowest pest load at the landscape scale for all predator groups, but the relative variation in pest load between pest patches in these landscapes can be high, (2) mobile and strongly aggregating predators provide the best pest control services in the majority of landscape types, but not necessarily in landscapes in which pest patches are close to the nearest predator patch, and (3) the pest control potential of mobile predators can best be explained by the mean distance between a pest patch and all predator patches, whereas for poorly dispersing predators the distance between a pest patch and the nearest predator patch is a more relevant metric.

The finding that all predator groups were effective in suppressing pest populations in landscapes in which pests had a close predator source (landscape group 1; Fig. 2) can be explained by two mechanisms. First, the short distance between predator and pest patches allows a timely arrival of predators in pest patches when pest densities are still low. Removal of pests at an early stage when their populations grow exponentially can prevent a potentially large number of offspring produced in future generations (van der Werf 1995, Ives and Settle 1997). This finding is in line with empirical studies on the early-season impact of predators on pest populations. For instance, Settle et al. (1996) showed that the presence of high densities of generalist predators early in the season can effectively suppress pest populations for over two months in tropical rice systems. Landis and van der Werf (1997) demonstrated that generalist predators reduced early-season aphid establishment and aphid-induced transmission of sugar beet yellow virus by 50%. Second, a larger proportion of the spreading predator population is likely to end up in nearby pest patches than in more distant patches because predator densities become more “diluted” when moving further away from their source. This may be one of the mechanisms underlying the findings of Kruess and Tschantke (1994), who found that parasitism rates in host patches declined with increasing distance from meadows that act as a source habitat of parasitoids.

As expected, well-dispersing, aggregating predators such as many species of lady beetles (species group D; Table 1) were most effective in suppressing pest populations in nearly all landscape types. However, in landscapes in which pest patches are close to the nearest predator patch (landscape groups 1, 4, and 7; Fig. 2) the other predator groups were, in a number of cases, superior control agents (Fig. 4). This phenomenon was

most pronounced in landscape groups 7 and 4 (Appendix). These landscapes are characterized by aggregations of pest patches around a few predator patches. Highly mobile predators will often disperse beyond (“overshoot”) the nearby pest patches and only a relatively small proportion of these predators will end up in nearby pest patches, whereas less mobile predators don’t show this behavior and more effectively colonize these pest patches. An example of “overshooting” predators is the rapid colonization of the landscapes by lady beetles from forest edges whereby adults cross 2000 m within a few days (Honěk 1982). These lady beetles are likely to disperse beyond at least a proportion of aphid patches. Species group B (poorly dispersing, aggregating predators that include some Carabidae and Staphylinidae spp.) provided better pest suppression than species group C (well-dispersing, non-aggregating predators such as ballooning spiders) in landscape groups 1, 4, and 7. Non-aggregating predators, such as some carabid beetle species, can result in better pest suppression than aggregating predators when pest patches are grouped in two clusters lined up with predator patches, potentially leading to shadowing effects (i.e., “shielding” of pest patches from predator patches by other pest patches). Aggregating predators will be arrested in the first pest patch cluster and hardly exploit the second cluster, whereas non-aggregating predators are not arrested by the first cluster and exploit both clusters.

Landscape metrics that can predict the potential of natural enemies to suppress pest populations can be instrumental for the development of pest control management strategies at the landscape scale. Our simulations suggest that the average of the mean distances between pest and predator sources (m) is a useful metric to predict the pest control potential of well-dispersing predators. For these predators, not only the predator patch nearest to a pest patch, but also patches further away are likely to provide predators that colonize the pest patch. In this case a metric that incorporates the distance of all predator patches to a focal pest patch (m) is a better predictor for predator-mediated pest control than a metric that only considers the distance to the single nearest predator patch (n_{hp}). In contrast, if predators have a poor dispersal capacity, pest patches are likely to be mainly colonized by predators from the nearest predator source and the contribution of predator patches further away will be small. In this case the mean nearest-neighbor distance from pest patches to predator patches (n_{hp}) is a more useful metric than a metric based on mean distances (m).

Variation in pest densities due to the activity of predators occurred between and within landscapes (i.e., variation in pest load between pest patches in the landscape). Metrics based on the nearest-neighbor distance (n_{hp}) and average distance between pest and predator patches (m) were good predictors for variation in pest densities between landscapes, but not for within-

landscape variation (data not shown). Variation in pest densities in pest patches within a landscape can be caused by shadowing effects, which are not captured by the three metric sets tested in this study. Within-landscape variation can have different implications for pest management depending on the economic pest density threshold level of the crop. For instance, low variation in pest load between fields (pest patches) in a landscape is positive when pest densities remain below the economic threshold, but negative when pest densities exceed the threshold, requiring large-scale intervention across the landscape. In the latter case, variation in pest densities among fields can be positive such that at least in some fields pest densities remain below the economic threshold level.

The findings of this study clearly demonstrate that integrated pest management (IPM) should consider larger spatial scales than the field and should incorporate knowledge about the ecological function of habitats in the surrounding landscape (e.g., sources, sinks) and their location relative to susceptible crops. There is also a need for information on biological traits of key natural enemies and pests (e.g., dispersal ability, aggregation behavior) to predict which areas are prone to pest attack and how effective natural enemies are likely to be in suppressing these pests. In addition to this, information about the source strength of habitats and their temporal dynamics is needed. For instance, which habitat or plant species support growing populations of pests and natural enemies at what time of the year? Although there is generally a good understanding about the key pests and natural enemies in crops, there is often surprisingly little known about ecology of these organisms and the habitats that support them. Even when this information is available it is generally not incorporated in pest management, although there is momentum growing for more ecologically based, scale-specific IPM (e.g., Schellhorn et al. 2008, Zalucki et al. 2009). Future work addressing these knowledge gaps may contribute to more effective, landscape context-specific IPM.

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APPENDIX

Spatial arrangements of patches (*Ecological Archives* A020-089-A1).