

# Local variation in plant quality influences large-scale population dynamics

Maria A. Riolo, Pejman Rohani and Mark D. Hunter

*M. A. Riolo (mariolo@umich.edu), Mathematics, Univ. of Michigan, 4852 East Hall 530 Church Street, Ann Arbor, MI 48105, USA. – P. Rohani and M. D. Hunter, Ecology and Evolutionary Biology, Univ. of Michigan, Ann Arbor, MI 48109-1048, USA.*

Spatial variation in ecological systems can arise both as a consequence of variation in the quality and availability of resources and as an emergent property of spatially structured interactions. We used a spatially explicit model to simulate populations of herbivore hosts and their parasitoids in landscapes with different levels of variance in plant patch quality and different spatial arrangements of high- and low-quality plant patches.

We found that even small variation in patch quality at a fine spatial scale decreased overall herbivore populations, as parasitoid populations on low-quality plant patches were subsidized by those from high-quality neighbors. On landscapes with large, homogeneous regions of high- and low-quality plant patches, herbivore populations increased with variation in patch quality.

Overall, our results demonstrate that local variation in resource quality profoundly influences global population dynamics. In particular, fine-scale variation in plant patch quality enhanced biological control of herbivores by parasitoids, suggesting that adding back plant genetic variation into perennial production systems may enhance the biological control of herbivores by their natural enemies.

Spatial variation in ecological systems can arise both as a consequence of underlying variation in the quality and availability of resources (Denno and McClure 1983, Pulliam 1988) and as an emergent property of spatially structured trophic interactions (Huffaker 1958, Hassell 2000). Although there have been many exceptions (Roughgarden 1974, Cantrell and Cosner 1991, Oksanen et al. 1992, Bjørnstad and Hansen 1994, Holt and Barfield 2003, Underwood 2004, Helms and Hunter 2005), mathematical models of spatial heterogeneity have largely focused on spatial and temporal variation in organism abundance caused by top–down mechanisms rather than resource heterogeneity. For example, effects of spatially structured host–parasitoid interactions on spatial and temporal host dynamics have been studied for some years (Hassell and May 1974, Hassell et al. 1991, Comins et al. 1992, Rohani et al. 1994), demonstrating how spatial heterogeneity may facilitate the persistence of otherwise unstable systems and generate spatial patterns that include spirals and traveling waves (Hassell et al. 1991, Rohani and Miramontes 1995, Bjørnstad et al. 2002). This body of work has also identified the destabilizing impact of asymmetry in the dispersal traits of hosts and parasitoids on systems which, in isolation, would be stable (Allen 1975, Reeve 1988, Rohani and Ruxton 1999).

In these classic metapopulation models, spatial variation in abundance emerges because populations are not well-mixed; there is always some degree of asynchrony between growth and decline in local but weakly coupled populations.

These top–down mechanisms can induce spatial heterogeneity even among populations living in a network of identical habitat patches.

However, in the real world, habitat patches are rarely identical. Predator–prey interactions are superimposed upon landscapes that vary dramatically in their quality for herbivores (Hunter and Price 1992). For example, insect herbivore populations are affected by very local, bottom–up forces such as the chemistry (Hunter et al. 1996) and genotype (Underwood and Rausher 2000, McIntyre and Whitham 2003, Evans et al. 2012b) of their host plants. At larger spatial scales, the local plant community (Pimentel 1961, Murdoch et al. 1972, Andow 1991) and surrounding landscape (Cappuccino et al. 1998) affect both the diversity and abundance of herbivores and of their natural enemies (Root 1973).

Given that both trophic interactions and underlying resource heterogeneity are important drivers of spatial and temporal dynamics, there is growing interest in understanding how they interact to influence the dynamics of species (Hunter et al. 1997). The impact of resource heterogeneity can depend on the scale of variation in resource quality (Oksanen et al. 1992, Roland and Taylor 1997, Thies et al. 2003), and may affect population dynamics at different spatial scales (Murdoch et al. 1972). Further, the effects of resource heterogeneity have been found to interact with the top–down forces acting on populations both in field (Batch 1984) and modeling studies (Foster et al. 1992).

While linking studies of spatial variation in resource quality and trophic interactions is of significant theoretical interest, such studies also may inform management, particularly in agricultural ecosystems where pest organisms attack crops that are planted in well defined spatial arrays (Andow 1991). Managing the species and genotypes of crops and their arrangements in space provide opportunities to minimize pest attack and maximize biological control by the natural enemies of pests (Belyea 1923, Pimentel 1961, Root 1973). Intercropping, planting multiple agricultural products together in fields, has shown some success as a method of enhancing top-down control of insect herbivores by their natural enemies (Bickerton 2011, Chen et al. 2011). At larger spatial scales, increased predation and parasitism of insect herbivores in agricultural systems have also been associated with landscape features such as close proximity to uncultivated land, higher proportions of non-crop area in the surrounding region, and more diversity in nearby habitat patches (Thies and Tschardt 1999, Cronin and Reeve 2005). Long-term effects of variation in plant patch quality on herbivore–enemy interactions may be particularly likely in perennial cropping systems (fruit orchards, tea, coffee, plantation forestry) in which the consequences of variation in patch structure and quality may emerge over multiple generations of the pest herbivore and its natural enemies.

In field studies, the effects of variation in plant quality on herbivore populations depends not only on mean plant quality but on the distribution of plant qualities (Underwood 2004, 2009, Helms and Hunter 2005) as well as the spatial arrangement of high and low quality plants (Evans et al. 2012b, Thies et al. 2003). Consequently, we explored the effects of variability around a constant mean plant patch quality on the outcome of spatially structured host–parasitoid interactions.

We modified an existing spatially-explicit model of host–parasitoid dynamics (Rohani and Miramontes 1995) to simulate host and parasitoid populations on landscapes with different variance and spatial layout of plant patch quality. We aimed to determine the extent to which a combination of local variation in resource quality and simple parasite–host interactions can give rise to the kind of complex spatial and temporal dynamics observed in field studies.

Specifically, we tested the following two hypotheses:

- Mean patch hypothesis – large scale population dynamics in landscapes of heterogeneous patch quality differ from those in homogeneous landscapes with the same mean patch quality.
- Patch architecture hypothesis – effects of variation in habitat quality on dynamics are contingent on the arrangement of high and low quality patches in space.

## Mathematical model and simulation methods

Our model of host–parasitoid dynamics is similar to previous models (Hassell et al. 1991, Rohani and Miramontes 1995) with the addition of spatial heterogeneity in patch quality. In this framework, herbivore hosts (hereafter, ‘hosts’) and parasitoids with synchronized generations grow and disperse in alternating steps according to a coupled map lattice. Each position on the lattice represents a habitat patch of known

plant quality for hosts. What a single habitat patch represents depends on the particular organism of study and its scale of movement. For example, with gall-forming insects that can spend many generations on the same perennial plant, the appropriate definition for a habitat patch might be a single individual plant (Abrahamson et al. 2003). Much larger habitat patches would be needed to capture the spatial variation in plant quality regularly encountered by elk (Hebblewhite and Merrill 2009). Within a habitat patch, populations are assumed to be well-mixed.

During the growth phase, populations on each patch grow according to a simple Nicholson–Bailey model (Nicholson and Bailey 1935). In the absence of parasitoids, the host population grows at a fixed rate  $\lambda$ . Throughout our study, we will use  $\lambda$  as a proxy for plant patch quality. Because homogeneous landscapes where host fecundity  $\lambda = 2.0$  have been studied previously (Hassell et al. 1991, Rohani and Miramontes 1995), we will use  $\bar{\lambda} = 2.0$  as the mean patch quality in our heterogeneous fields.

For simplicity, we assume each host attacked results in an average of one adult parasitoid in the next generation. Thus, given the densities of hosts ( $H_t$ ) and parasitoids ( $P_t$ ) during generation  $t$ , the population densities after reproduction are given by

$$H'_t = \lambda H_t f(H_t, P_t) \quad (1)$$

$$P'_t = H_t (1 - f(H_t, P_t)) \quad (2)$$

where  $f(H_t, P_t)$  is the fraction of hosts escaping parasitoid attack given the current densities of hosts and parasitoids.

Our model uses a linear parasitoid functional response with attacks distributed at random among hosts, as in (Nicholson and Bailey 1935) and (Comins et al. 1992). Assuming that populations within plant patches are well-mixed and parasitoids search over some area  $a$  for hosts to oviposit in, we expect a total of  $aH_tP_t$  encounters between hosts and parasitoids. With parasitoid attacks distributed at random among hosts, the number of attacks on each host follows a Poisson distribution with mean  $aP_t$  attacks per host. Thus, the expected fraction of hosts to escape parasitism is  $f(H_t, P_t) = e^{-aP_t}$ . Because  $a$  does not qualitatively effect the dynamics of the model, but rather acts as a scaling parameter (Hassell et al. 1991), we arbitrarily fix  $a$  at 0.2 throughout our simulations. Given host and parasitoid populations  $H_t$  and  $P_t$  during generation  $t$ , their populations after reproduction will thus be given by

$$H'_t = \lambda H_t e^{-aP_t} \quad (3)$$

$$P'_t = H_t (1 - e^{-aP_t}) \quad (4)$$

On a single plant patch or a small lattice of plant patches coupled by dispersal, these growth dynamics result in rapidly growing oscillations of both host and parasitoid populations (Nicholson and Bailey 1935). However, if the size of the total arena of coupled sites (hereafter, ‘landscape’) is large compared to the distance hosts and parasitoids are able to disperse, long-term coexistence can occur (Hassell et al. 1991, Comins et al. 1992). Our simulations all take place on 60 patch by 60 patch square lattices (landscapes) with

absorbing boundaries, which was a sufficiently large arena that neither hosts nor parasitoids experienced global extinctions in any of our runs. Reflecting boundaries were examined in our sensitivity analysis but did not qualitatively affect our results.

Hosts and parasitoids disperse to nearby plant patches with probabilities  $m_H$  and  $m_P$  respectively. Previous studies have found that the spatial patterns of host and parasitoid populations depend on  $\lambda$ ,  $m_H$ ,  $m_P$ , and the size of the landscape (Hassell et al. 1991, Comins et al. 1992). Our preliminary sensitivity analyses found that the dispersal traits of herbivores and parasitoids strongly modulated the effects of spatial variation in resource quality. To cope with the nonlinear, interacting effects of these parameters on the interplay between habitat heterogeneity and host–parasitoid interactions in the absence of an existing body of theory, we have chosen to focus our current study on a single, biologically plausible region of parameter space, where parasitoids disperse more frequently than their hosts (Briggs and Latto 2000, Taylor 1991). Our main body of results fixes  $m_H$  and  $m_P$  at 0.2 and 0.8, respectively, with other values explored in our sensitivity analyses.

We set the dispersal range of both hosts and parasitoids to be their home patch and the eight surrounding plant patches in the landscape, which has been the dispersal range typically used in studies of hosts and parasitoids in homogeneous landscapes (Hassell et al. 1991, Comins et al. 1992, Rohani and Miramontes 1995). We denote this neighborhood of plant patch  $i$  by  $N(i)$ .

We model hosts as dispersing uniformly among plant patches in range, so that after dispersal the host density at plant patch  $i$  becomes

$$H_{t+1}(i) = (1 - m_H)H'_t(i) + m_H\bar{H}(i) \quad (5)$$

where  $\bar{H}(i)$  is the mean density of hosts in the neighborhood of plant patch  $i$ . Instead of diffusing uniformly like hosts, we allow parasitoids to preferentially disperse to plant patch with a higher density of hosts as modeled in (Hassell and May 1973), so that the density of parasitoids on plant patch  $i$  after dispersal is

$$P_{t+1}(i) = (1 - m_P)P'_t(i) + m_P \sum_{j \in N(i)} \beta(j, i) P'_t(j) \quad (6)$$

The fraction of dispersing parasitoids from plant patch  $j$  that land in plant patch  $i$ ,  $\beta(j, i)$ , is determined by nearby host populations according to

$$\beta(j, i) = v \left( \frac{H'_t(i)}{\sum_{k \in N(j)} H'_t(k)} \right)^\mu \quad (7)$$

where  $v$  is a normalization constant so that  $\sum_{i \in N(j)} \beta(j, i) = 1$ . The parameter  $\mu$  controls the strength of the aggregation, with  $\mu = 0$  resulting in uniform diffusion like the host population,  $\mu = 1$  resulting in parasitoid dispersal proportional to the relative host populations of nearby plant patches, and parasitoids increasingly ignoring all but the most host rich plant patch in range as  $\mu$  approaches infinity. In our main body of

simulations,  $\mu$  is fixed at 1.0, so as to qualitatively approximate the preferential dispersal of parasitoids to nearby plant patches with high host density as observed in the field (Fischbein et al. 2012). Our sensitivity analyses included values of  $\mu$  from 0.0 (pure diffusion) to 2.0 (strong aggregation).

Within this framework, we can model spatial variation in habitat quality by varying the intrinsic growth rate of the local host population  $\lambda$  on each plant patch. For example, to construct an environment with source–sink dynamics, we could give plant patches in our desired source regions  $\lambda > 1$  and plant patches in our sink regions  $\lambda < 1$ . Hirzel et al. (2007) explored an extreme case of a similar host parasitoid model in which patches were either habitable (with fixed  $\lambda > 1$ ) or completely hostile ( $\lambda = 0$ ) (Hirzel et al. 2007).

For simplicity, we will consider landscapes where half of the plant patches are high quality, with host fecundity  $\lambda_+$ , and half are low quality, with host fecundity  $\lambda_-$ . This allows us to vary the difference in plant quality ( $\lambda_+ - \lambda_-$ ), while keeping the mean plant quality  $\bar{\lambda} = \frac{1}{2} (\lambda_+ + \lambda_-)$  fixed. Even

restricting our choices to the set of landscapes with equal numbers of high and low quality plant patches, we are still left with over  $10^{1080}$  possible arrangements of patches. In our current study, we consider two arrangements of high and low quality plant patches: a landscape where one half contains all high quality plant patches and the other contains all low quality plant patches (hereafter, the ‘half-and-half landscape’), and a landscape of high and low quality plant patches alternating in a checkerboard pattern (hereafter, the ‘checkerboard landscape’). Figure 1 shows a schematic of these landscape types.

These two arrangements both approximate plausible agricultural landscapes, where two species or genotypes are intercropped at a coarse (e.g. whole field) or fine (e.g. within-field) spatial scale. They also represent two extremes of spatial correlation in plant quality. In the half-and-half landscape, the vast majority of plant patches share the same patch quality as all of their neighbors, with the only exceptions occurring at the border between the high and low quality sides of the landscape. At the opposite extreme, each plant patch in the checkerboard matches only half of its neighbors in patch quality.

In order to test the extent to which a heterogeneous landscape’s dynamics could be captured by simply aggregating the behavior of high and low quality plant patches, we constructed an ‘additive’ base case to compare with each heterogeneous landscape. Specifically, we independently simulated population dynamics on one homogeneous, high fecundity landscape and one homogeneous, low fecundity landscape. For the purposes of calculating population statistics, we then treated the left half of the high fecundity landscape and the right half of the low fecundity landscape as a single run, giving us a time series of host and parasitoid populations in a field with the appropriate distribution of plant qualities but none of the connections between high and low quality plant patches (Fig. 1C). We constructed checkerboard patterned ‘additive landscapes’ in an analogous fashion, by first creating homogeneous landscapes of high or low quality plant patches, and then sampling every second plant patch from each of those landscapes to give the same average plant quality (Fig. 1D).

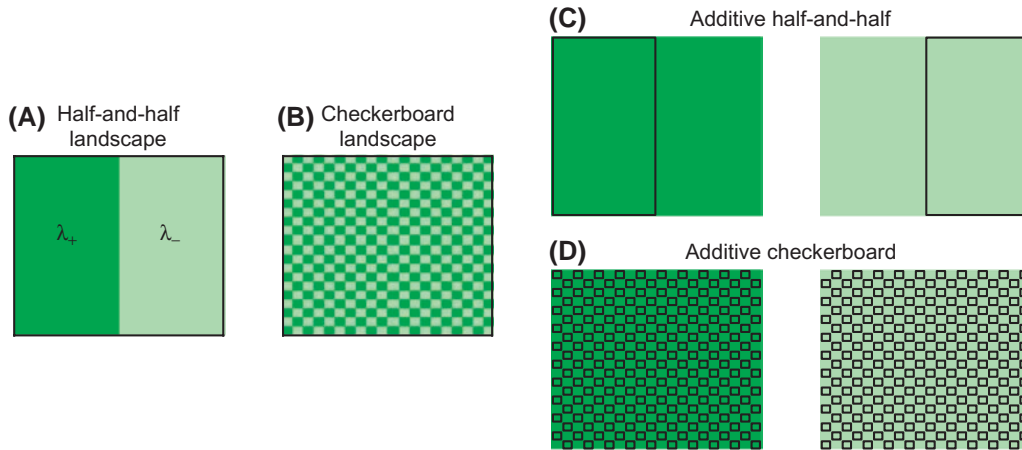


Figure 1. Plants of high (dark green) and low (light green) quality arranged in (A) a ‘half-and-half’ landscape containing one large patch of high fecundity plants and one large patch of low quality plants, (B) a ‘checkerboard’ landscape of alternating high and low quality plants, (C) an ‘additive’ half-and-half landscape, and (D) an ‘additive’ checkerboard landscape, using plants from two homogeneous landscapes (outlined by black rectangles).

We fixed mean quality  $\bar{\lambda}$  at 2.0, and varied the difference in qualities so that  $\lambda_- = 1.0, 1.05, 1.1, \dots, 1.95, 2.0$  (homogeneous) for a total of 21 different levels of variation in plant quality, all with the same global average. For each case, we constructed heterogeneous landscapes and associated pairs of high and low quality homogeneous landscapes. We ran 20 replicate simulations of each, with randomly generated initial populations, and simulated populations for 1000 generations. The initial populations on each plant patch were independently drawn from uniform distributions from 50% to 150% of what would be (unstable) equilibrium populations of the Nicholson–Bailey equation on that plant patch alone. All temporal means and variances were calculated over the last 200 generations of the run, which we found to be much longer than the dominant periods at which populations in homogeneous landscapes oscillated. All populations in heterogeneous landscapes persisted until the end and global extinctions of hosts or parasitoids occurred only in homogeneous fields with  $\lambda = 1$ .

## Results

Figure 2 shows snapshots of host and parasitoid density in homogeneous landscapes of high and low quality plant patches (panels A and C), a half-and-half landscape (panel E), and a checkerboard landscape (panel H). The spatial patterns of host and parasitoid populations in the high and low quality regions of the half-and-half landscape were generally similar to those in homogeneous landscapes of the same quality. However, the spatial patterns in the checkerboard landscape are organized over a larger spatial scale than the variation in plant patch quality, so that one traveling wave of hosts and parasitoids would pass through many patches of both high and low quality. This difference in spatial population dynamics between half-and-half and checkerboard landscapes can also be observed in the way local populations oscillate over time. While the populations on a high quality patch in the half-and-half landscape (panel D) oscillate with a higher frequency and amplitude than those on a low

quality patch in the same landscape (panel F), the oscillations of populations on high and low quality patches at the same locations in a checkerboard landscape (panels G and H) are more similar in frequency.

In additive landscapes, where high and low quality plant patches were not connected by any dispersal, both host and parasitoid populations increased with increasing variance in patch quality. However, populations in half-and-half and checkerboard landscapes differed both from additive landscapes and from each other (Fig. 3A–B). Half-and-half landscapes consistently supported slightly larger populations than did the unconnected, additive landscapes. In contrast, herbivore populations in checkerboard landscapes were lowest at intermediate levels of variation in patch quality. Parasitoid populations in checkerboard landscapes, however, did not undergo a corresponding decrease as variance in patch quality increases, but rather stayed roughly constant until increasing along with host densities when variance in patch quality was large.

In fact, checkerboard landscapes had more parasitoids per host than other landscapes (Fig. 4). While the ratio of parasitoids to hosts increased with the difference in plant patch quality in all landscapes, the most dramatic increase occurred in the checkerboard landscape. The half-and-half landscape also had more parasitoids to hosts than either additive landscape, although the difference was less extreme as long as low quality patches could support growth in host populations ( $\lambda_- > 1$ ).

The temporal variance in population densities also differed with the spatial arrangement of high and low quality plant patches (Fig. 4C–D). In all cases, the variance in both host and parasitoid populations increased relative to the mean population as the variance in patch quality increased. However, each type of landscape showed a different pattern of increase. The coefficient of variation of host and parasitoid populations (calculated by dividing the standard deviation of the population in time by the mean population) increased gradually with variance in patch quality in both heterogeneous and additive half-and-half landscapes. Meanwhile, the coefficients of variation of populations in both

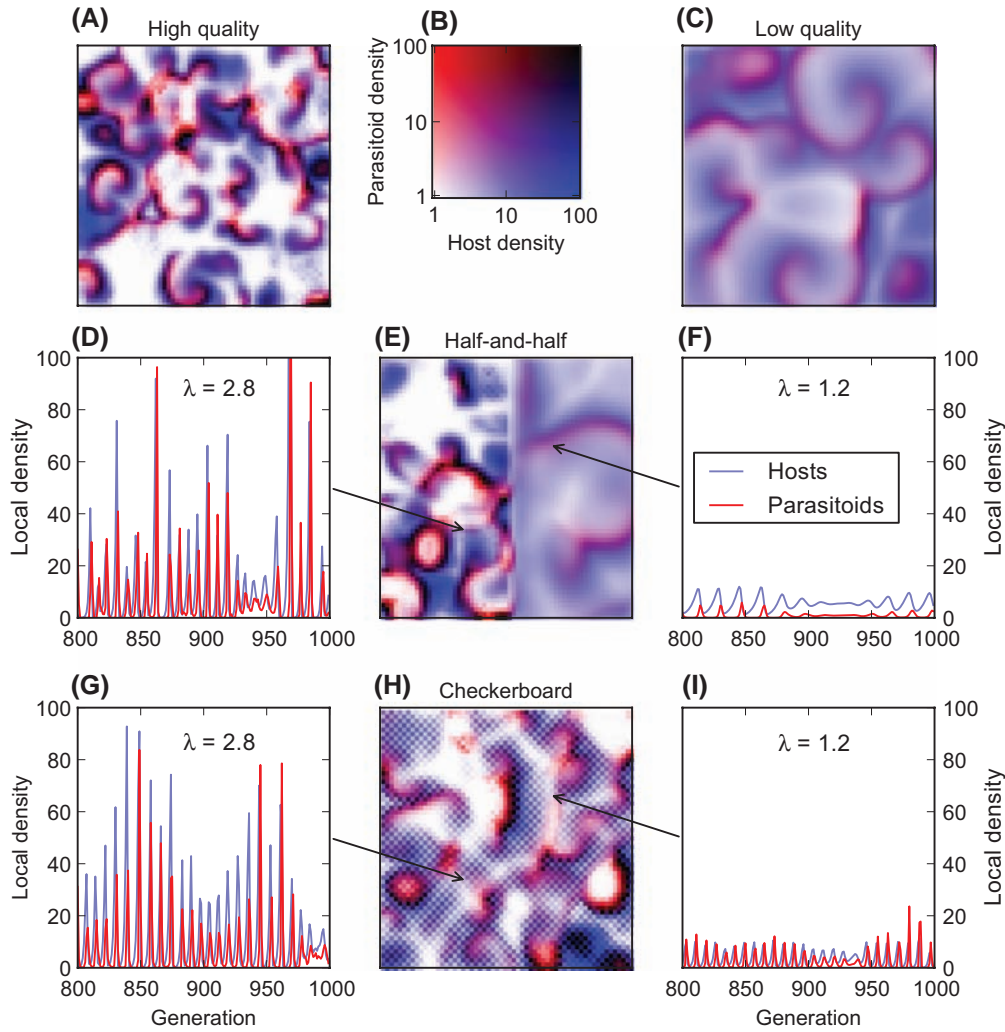


Figure 2. Snapshots of host and parasitoid densities in space after 1000 generations in single realizations of (A) a homogeneous high fecundity ( $\lambda = 2.8$ ) landscape (C) a homogeneous low fecundity ( $\lambda = 1.2$ ) landscape (E) a half-and-half landscape ( $\lambda_+ = 2.8, \lambda_- = 1.2$ ) and (H) a checkerboard landscape ( $\lambda_+ = 2.8, \lambda_- = 1.2$ ). Higher host densities are indicated by more blue and higher parasitoid densities by more red (see colormap in panel B). Local populations of hosts (in blue) and parasitoids (in red) are plotted over the last 200 of 1000 generations on (D) a high quality plant in the half-and-half landscape (F) a low quality plant in the half-and-half landscape (G) a high quality plant in the checkerboard landscape and (I) a low quality plant in the checkerboard landscape.

heterogeneous and additive checkerboard landscapes were lower, particularly for the additive checkerboard.

These differences between populations on checkerboard landscapes, on half-and-half landscapes, and on their additive counterparts were not evenly distributed among high and low quality plant patches (Fig. 5). As one might expect on a landscape where every patch has some neighbors of the opposite quality and there is plenty of dispersal between high and low quality patches, high quality patches on checkerboard landscapes had lower densities of parasitoids than did high quality patches on additive landscapes (Fig. 5B), while parasitoid densities were higher on low quality patches on checkerboard landscapes than on additive landscapes (Fig. 5D). These differences became more pronounced as the difference in host fecundity on high and low quality plant patches increased. However, host populations on checkerboard landscapes did not follow this same pattern. On low quality patches, host populations were even lower on checkerboard landscapes than on additive landscapes, likely due

to the higher parasitoid density (Fig. 5C). At the same time, high quality patches on checkerboard landscapes supported at most slightly larger host populations than did high quality patches on additive landscapes (Fig. 5A), even with their substantially lower parasitoid densities.

Populations on half-and-half landscapes also differed from those on additive landscapes. On both high quality and low quality plant patches on half-and-half landscapes, parasitoid populations were slightly higher than on the corresponding additive landscapes (Fig. 5B, D). However, populations of hosts on high quality patches were even higher (Fig. 5A) and populations of hosts on low quality patches even lower (Fig. 5C) than on high and low quality patches, respectively, in additive landscapes.

In order to understand why host populations in half-and-half landscapes differ even more between high- and low-quality plant patches than do host populations in additive landscapes, we examined local populations along a transect of individual patches from the high fecundity side of the

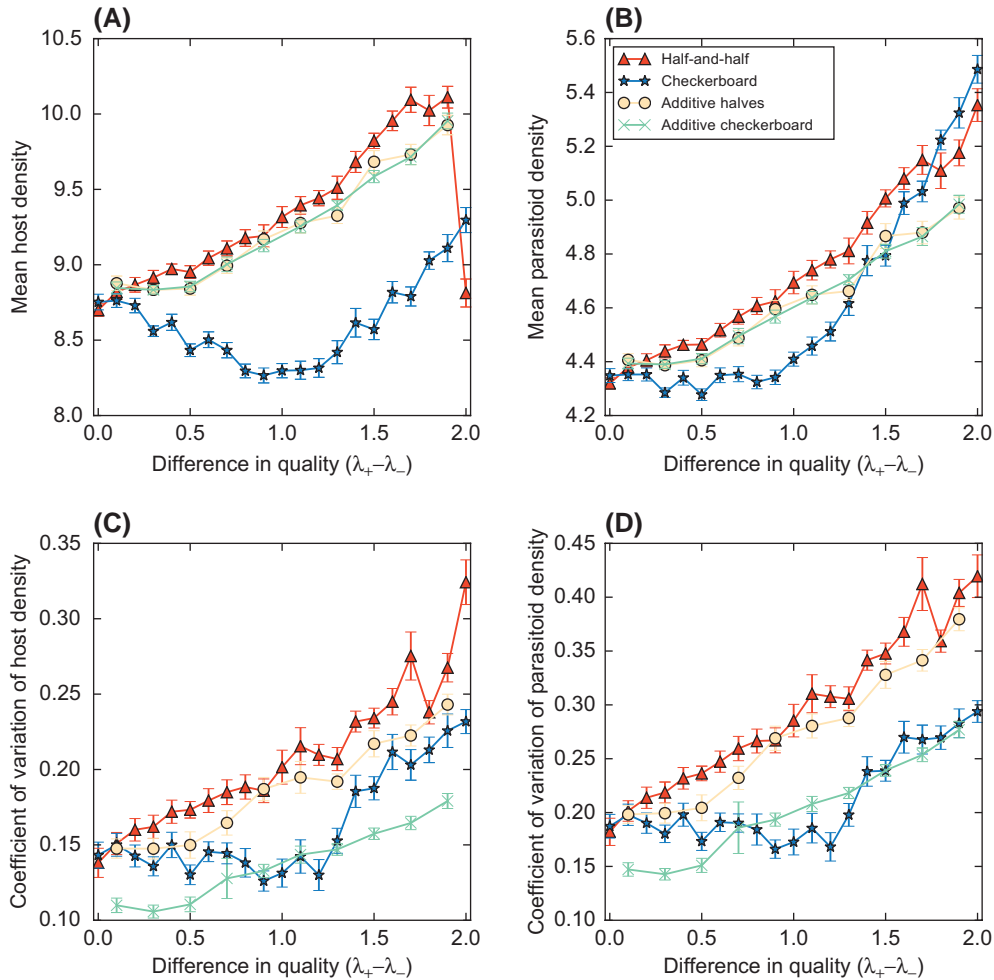


Figure 3. Plots of (A) mean host density, (B) mean parasitoid density, (C) coefficient of variation (mean / standard deviation) of host density, (D) coefficient of variation (mean / standard deviation) of parasitoid density during the last 200 of 1000 generations plotted against the difference in plant quality. Error bars show one standard error above and below the mean value for twenty replicate fields.

field to the low fecundity side (Fig. 6A–B). The difference between populations on the half-and-half field and those on its non-interacting, additive counterpart seems to stem from the patches near the boundary between high and low quality patches. The low quality patches that are situated near high quality patches have especially low host populations while those high quality patches, as well as those near the absorbing boundary of the landscape, have especially high populations. When we look at the frequency at which these local host populations oscillate, we see that the low quality border patches share the rapid oscillations of the high fecundity region, rather than the slower, long period outbreak cycle of the low fecundity side (Fig. 6C–D).

This pattern seems to be driven by fast, high density periodic traveling waves from the high fecundity side crossing the border to the low quality side (Supplementary material Appendix 7 video). At a lower per capita host fecundity, the high densities of hosts and parasitoids are no longer sustainable, so a rapid crash occurs. Because these crashes on the low fecundity side are driven by the same traveling waves dominating the dynamics on the high fecundity side, they share the same periodicity. This phenomenon can be seen in an example run in the Supplementary material Appendix 7 video.

## Sensitivity

We varied the fraction of hosts and parasitoids dispersing each generation,  $m_H = 0.1, 0.15, 0.2, 0.25, 0.3$  and  $m_p = 0.7, 0.75, 0.8, 0.85, 0.9$ , and the aggregation of the parasitoids,  $\mu = 0.0, 0.5, 1.0, 1.5, 2.0$ . For each set of dispersal parameters, we fixed the mean patch quality at 2.0 and simulated 4 replicate landscapes each with checkerboard and half-and-half arrangements at  $(\lambda_+ - \lambda_-) = 0.0$  (homogeneous), 0.5, 1.0, 1.5, 2.0 ( $\lambda_- = 1$ ).

Our results throughout this region of parameter space were qualitatively similar (Supplementary material Appendix 1, 2), with the exception of the case where parasitoids did not aggregate to patches with more hosts ( $\mu = 0$ ). When parasitoids preferentially dispersed to patches with more herbivore hosts ( $\mu > 0$ ), herbivore populations in checkerboard landscapes decreased steadily (at  $\mu = 2$ ) or decreased and then increased as variance in patch quality increased (Supplementary material Appendix 1). In all half-and-half landscapes, herbivore populations increased or stayed constant as variance in patch quality increased, until decreasing sharply when the lower quality patches became unable to sustain growth in host populations ( $\lambda_- = 1$ ).

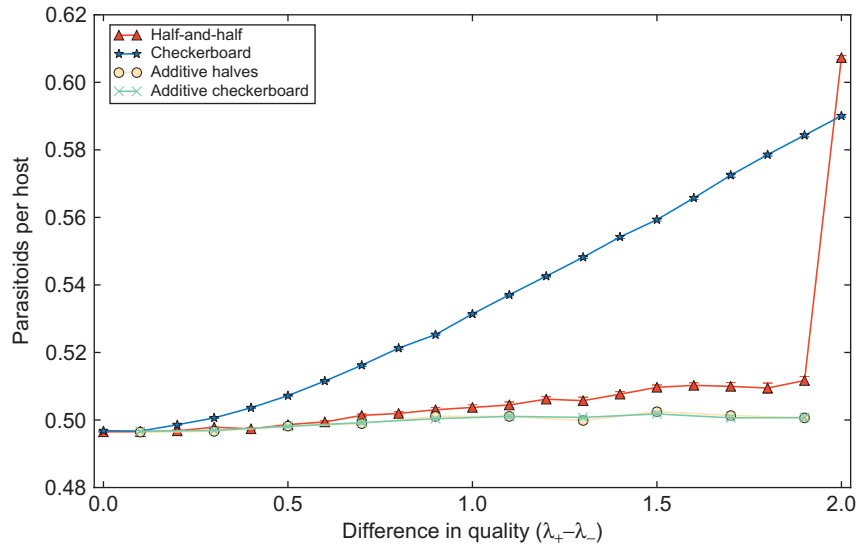


Figure 4. The mean parasitoids per host during the last 200 of 1000 generations plotted against the difference in plant quality. Error bars show one standard error above and below the mean value for twenty replicate fields. However, the standard deviations in each case were consistently small enough that the error bars are not visible.

When parasitoids were non-aggregating ( $\mu = 0$ ), checkerboard landscapes had higher densities of herbivores than half-and-half landscapes, and the herbivore populations in checkerboard landscapes increased rapidly with variance in patch quality (Supplementary material Appendix 2), suggesting that some degree of aggregation is necessary to produce the suppression of host populations on low-quality patches in the checkerboard landscape observed in Fig. 5.

We further examined the effects of our boundary assumptions by repeating the simulation experiment presented in the main body of text with reflecting rather than absorbing boundaries (Supplementary material Appendix 3–6). We find that, although local populations at the edges of the landscapes are affected by the choice of boundary conditions (Supplementary material Appendix 6), our overall conclusions are not altered.

## Discussion

We used a spatially explicit model of host–parasitoid dynamics to explore the interaction between variation in resource quality and spatially structured trophic interactions. Even in very simple landscapes, we found that local variation in resource quality influences global population dynamics dramatically.

When either the spatial scale of variation in plant patch quality or the magnitude of that variation was large, both the mean and variance of host and parasitoid populations in heterogeneous landscapes were substantially greater than those in homogeneous landscapes with the same mean patch quality. The ratio of parasitoids to hosts also increased with the variance in patch qualities present in the landscape. This confirms that the spatially structured interaction between herbivores and their natural enemies can combine with the effects of variable patch quality to generate spatial and temporal dynamics observed previously in field studies

(Underwood 2004, 2009, Helms and Hunter 2005). Moreover, field studies have found that the shape and spatial arrangement of high quality plant patches can also affect herbivory (Evans et al. 2012a). In our model, landscapes with different spatial arrangements of patches also gave rise to differences in population dynamics.

Most strikingly, we found that small variations in plant patch quality occurring on a small spatial scale led to decreased herbivore density. The frequent dispersal of parasitoids between high and low quality patches led to strong suppression of herbivore populations on the lower quality patches, without a corresponding increase in herbivore populations on higher quality patches, an effect that Oksanen et al. (1992) found for predator–prey interactions in habitats where the scale of heterogeneity is smaller than the home-range of an individual predator. This enhancement of parasitism by small-scale variation in patch quality may have particularly important consequences for populations in productive patches. Because herbivore fecundity is, in many cases, affected by plant genotype (Underwood and Rausher 2000, McIntyre and Whitham 2003, Evans et al. 2012b), we might expect the genetic variation in natural plant populations to lead to more local variation in plant quality and higher parasitism than we would see in agricultural and forestry systems that use single genotypes or low genetic diversity. Although our results may be less applicable to annual production systems, which experience large management disturbances each season, long-term patterns in herbivore populations described here may be more relevant in perennial production systems such as orchards, managed forests, and tropical coffee farms. Adding genetic variation in plant quality back into such agricultural ecosystems might serve to increase rates of parasitism on pest insects.

We see a similar effect in landscapes composed of two large, homogeneous patches of different quality, where host populations were suppressed on low-quality patches that were near the boundary between low- and high-quality

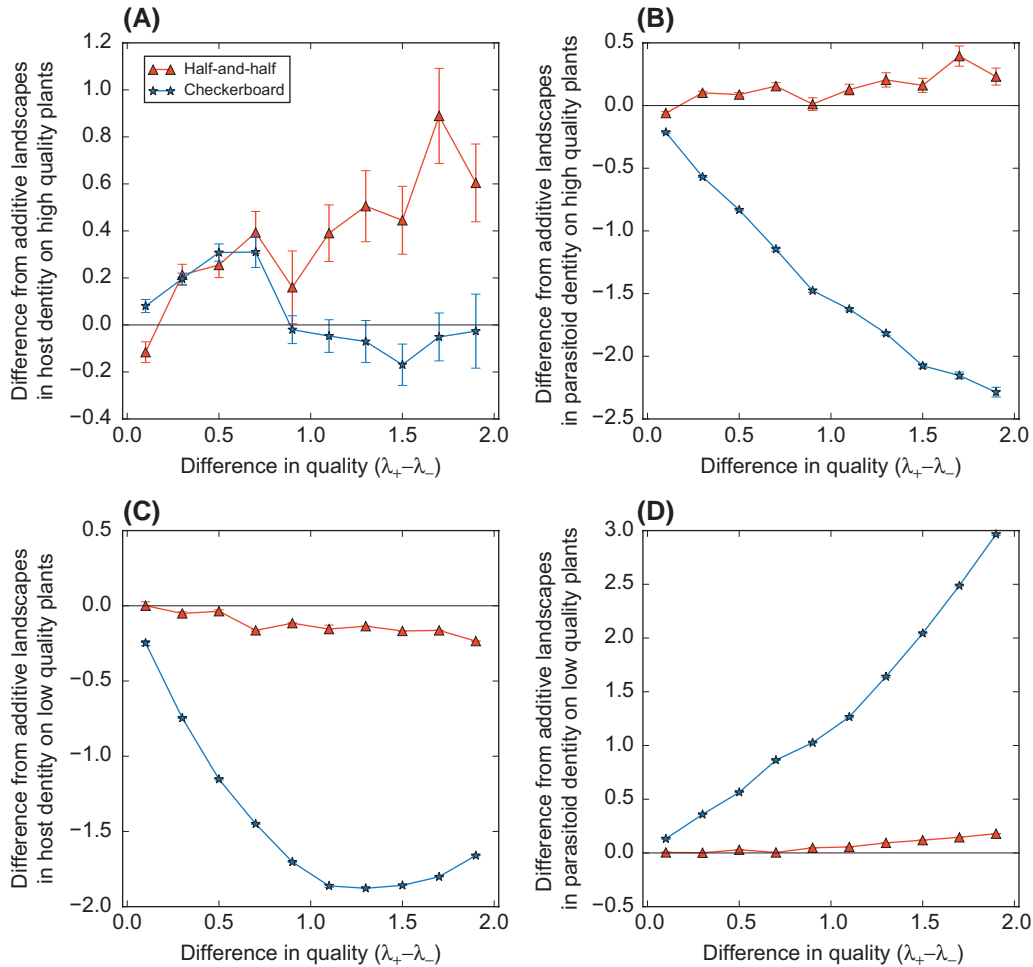


Figure 5. Plots of the difference between connected and additive landscapes in the (A) mean host density on high quality plants, (B) mean parasitoid density on high quality plants, (C) mean host density on low quality plants, and (D) mean parasitoid density on low quality plants during the last 200 of 1000 generations, plotted against the difference in plant quality. For clarity, the horizontal line where the difference equals zero is plotted in black.

regions, resembling the spillover effect observed at crop-noncrop boundaries (Rand and Louda 2006). In their study of predatory coccinellid beetles in crops and grassland sites in Nebraska, Rand and Louda found that coccinellid densities were 2.6–9.0 times higher in grassland sites in landscapes containing mostly crops than in grassland sites surrounded by more grassland (Rand and Louda 2006). At the same time, they found that aphid density increased significantly when predators were excluded from experimental aphid colonies via a mesh sleeve, suggesting that the coccinellids could indeed suppress aphid populations and that the spillover of beetles from cultivated areas could lead to lower aphid populations in the surrounding grasslands.

The sharp delineation between high and low plant patch quality in our simulated landscapes may reasonably approximate production landscapes, but natural systems often contain smoother gradients in plant quality and arthropod population density over space (Salmore and Hunter 2001, Pennings et al. 2007). For example, Salmore and Hunter (2001) found that the concentration of defensive alkaloids in *Sanguinaria canadensis* (bloodroot) tended to decrease with elevation along an elevational gradient from Georgia

to North Carolina. Pennings et al. (2007) reported a latitudinal gradient of plant palatability in their study of plant–herbivore interactions in European salt-marshes. Leaves and plant litter from higher latitudes were more palatable to several insect species than were their low-latitude congeners. Several of the plant taxa studied also tended to suffer more herbivory at lower latitudes than higher, suggesting that the latitudinal gradient in plant palatability might result from differing selective pressure from herbivory.

Such resource gradients, coupled with herbivore–natural enemy interactions, have the potential to drive patterns in insect herbivore populations over large spatial and temporal scales. In their investigation of the periodic traveling waves of larch budmoths *Zeiraphera diniana* across the European Alps, Bjørnstad et al. (2002) simulated the populations of an herbivore host and its parasitoid along a resource gradient. They found that, under a wide range of parameter values, the addition of a spatial gradient in resource quality caused the emergence of periodic traveling waves of hosts and parasitoids similar to those observed in larch budmoth populations or to the winter moth *Operphthera brumata* outbreaks that periodically move across Europe (Tenow et al. 2013).



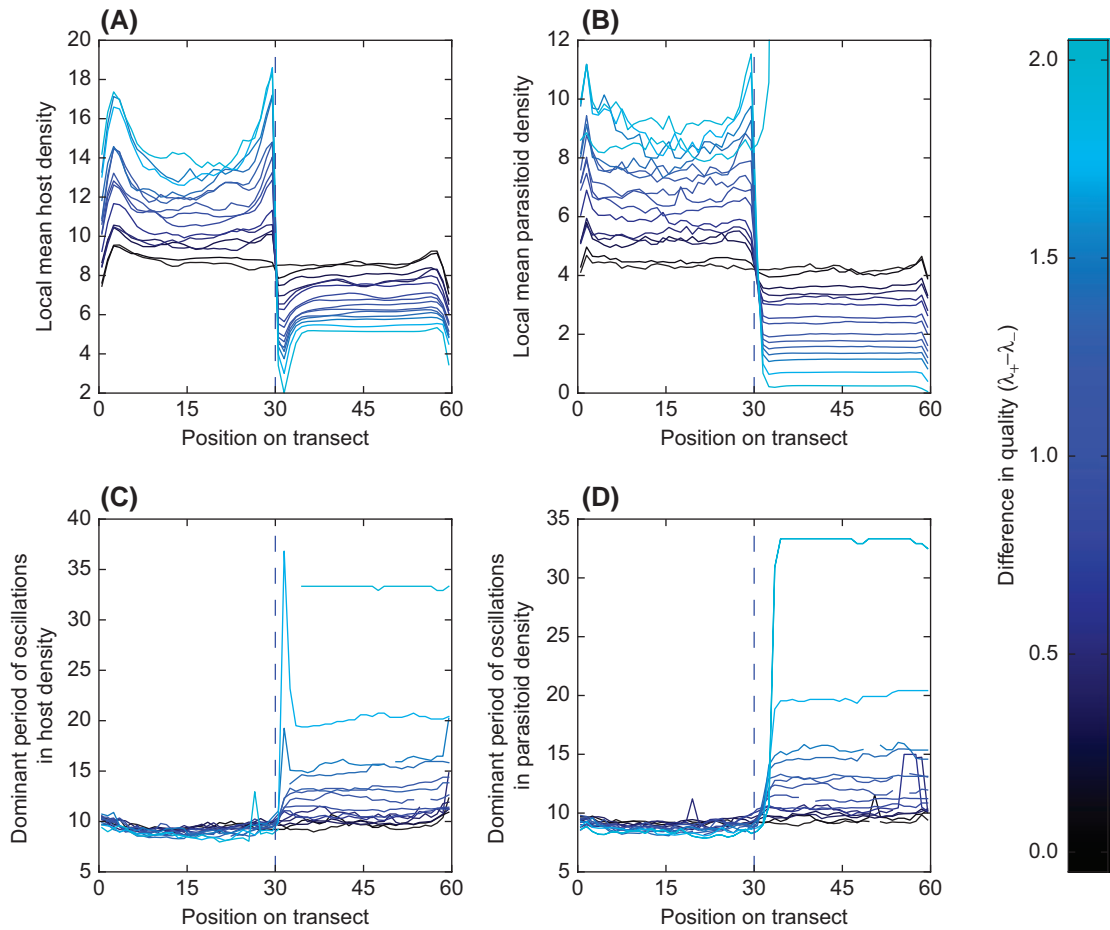


Figure 6. Plots of (A) mean host density, (B) mean parasitoid density, (C) dominant period of oscillations in host density, (D) dominant period of oscillations in parasitoid density during the last 200 of 1000 generations at each plant along a transect. Each line shows the average of 20 runs on identical fields starting from random initial conditions. Line color indicates the difference in host fecundity ( $\lambda_+ - \lambda_-$ ) between the high and low quality plants. The border between high quality plants to the left of the boundary (host fecundity  $\lambda_+$ ) and low quality plants to the right of the boundary (host fecundity  $\lambda_-$ ) is indicated with a blue, dashed line.

The magnitude and spatial scale of variation in plant quality can depend on both abiotic factors, such as variation in altitude and moisture, and life-history and dispersal traits of plants (Loveless and Hamrick 1984). Different parasitoid species respond to variation in host habitat quality at different spatial scales, and it is likely that these differences stem at least in part from differences in the dispersal patterns of the parasitoids and their hosts (Roland and Taylor 1997). Both in models (Comins et al. 1992, Rohani and Miramontes 1995) and in the field (Cronin and Reeve 2005), dispersal of hosts and parasitoids can have strong effects on the stability and spatiotemporal patterns of abundance. Not only do host and parasitoid dispersal patterns have profound effects on their population dynamics, but landscape structure and diversity has been found to affect both herbivore (Hill et al. 1996) and parasitoid dispersal (Cronin 2003). Further, the structure of spatial heterogeneities in resource quality may influence the evolution of dispersal strategies, with different landscapes selecting for different dispersal strategies (Johst et al. 2002).

In previous studies on homogeneous landscapes, the choice of dispersal parameters has been found to strongly affect the stability of host–parasitoid interactions, the effi-

ciency of parasitoid control of hosts, and the emergent spatial patterns of host and parasitoid populations (Hassell and May 1973, Hassell et al. 1991, Comins et al. 1992, Rohani and Miramontes 1995, Bjørnstad et al. 2002, Hirzel et al. 2007). Though we have found that our main results hold for a range of parameters where parasitoids disperse much more frequently than their hosts and parasitoids preferentially disperse to patches with higher host populations, our preliminary exploration of a wider range of dispersal behaviors suggest that host and parasitoid populations with different dispersal may have qualitatively different responses to environmental heterogeneity. The interplay between host and parasitoid dispersal behaviors and spatial variation in patch quality remains a rich avenue for future study.

Models similar to the one used here have been used to simulate a variety of processes in homogenous landscapes. These include a wide variety of demographic processes acting on herbivores and their parasitoids, and the attack behavior of foraging enemies (Ruxton and Rohani 1996, Hassell 2000). We suggest that exploring such interactions on landscapes that differ in resource quality for herbivores could provide interesting insights into population dynamics of natural and agricultural systems. For example, the combined effect of

demographic stochasticity and a strong spillover effect might make a low quality region effectively impermeable to hosts, even if a deterministic model allowed very small densities of hosts and parasitoids to colonize it.

The large scale consequences of other plant quality effects on hosts and parasitoids also remain open to exploration. For simplicity, we only modeled spatial heterogeneity in host fecundity, but there is strong evidence to suggest that the size and growth rate of hosts, which also vary with plant quality, can affect parasitoid reproductive success (Hunter 2003). Additional factors contributing to parasitoid fecundity, such as availability of overwintering sites or alternate food sources, may also vary spatially (Cronin and Reeve 2005), but need not correlate with plant quality. Further, plant quality is, in turn, influenced by host and parasitoid populations. In the short term, damage from host herbivory may reduce plant quality for the next generation of hosts. In the longer term, high levels of herbivory select for plants with stronger defenses against hosts. Another potential extension of our model would be to incorporate some of these tritrophic interactions between plants, herbivore hosts and parasitoids.

Even without the additional complexity of these mechanisms, we find that large scale population dynamics of hosts and parasitoids depend both on the distribution of plant qualities and their behaviors in space. Our results suggest that fine-scale variation in plant quality may be particularly important for supporting populations of parasitoids and predators and that plant genetic variation in perennial production systems could be managed to enhance biological control of herbivores.

*Acknowledgements* – Statement of authorship: MDH, PR and MAR designed the study. MAR implemented the models, analyzed the results, and wrote the first draft of the report. MDH and PR contributed to the writing of the report.

## References

- Abrahamson, W. G. et al. 2003. Sequential radiation of unrelated organisms: the gall fly *Eurosta solidaginis* and the tumbling flower beetle *Mordellistena convicta*. – *J. Evol. Biol.* 16: 781–789.
- Allen, J. C. 1975. Mathematical models of species interactions in time and space. – *Am. Nat.* 109: 319–342.
- Andow, D. A. 1991. Vegetational diversity and arthropod population response. – *Annu. Rev. Entomol.* 36: 561–586.
- Batch, C. E. 1984. Plant spatial pattern and herbivore population dynamics: plant factors affecting the movement patterns of a tropical cucurbit specialist (*Acalymma innubum*). – *Ecology* 65: 175–190.
- Belyea, H. C. 1923. The control of white pine weevil (*Pissodes strobi*) by mixed planting. – *J. For.* 21: 384–390.
- Bickerton, M. W. 2011. Intercropping for conservation biological control of European corn borer *Ostrinia nubilalis* Hübner (Lepidoptera: Crambidae) in bell peppers. – PhD thesis, Rutgers Univ.-Graduate School, New Brunswick.
- Bjørnstad, O. N. and Hansen, T. F. 1994. Individual variation and population dynamics. – *Oikos* 69: 167–171.
- Bjørnstad, O. N. et al. 2002. Waves of larch budmoth outbreaks in the European Alps. – *Science* 298: 1020–1023.
- Briggs, C. J. and Latto, J. 2000. The effect of dispersal on the population dynamics of a gall-forming midge and its parasitoids. – *J. Anim. Ecol.* 69: 96–105.
- Cantrell, R. S. and Cosner, C. 1991. The effects of spatial heterogeneity in population dynamics. – *J. Math. Biol.* 29: 315–338.
- Cappuccino, N. et al. 1998. Spruce budworm impact, abundance and parasitism rate in a patchy landscape. – *Oecologia* 114: 236–242.
- Chen, B. et al. 2011. Effect of intercropping pepper with sugarcane on populations of *Liriomyza huidobrensis* (Diptera: Agromyzidae) and its parasitoids. – *Crop Protection* 30: 253–258.
- Comins, H. N. et al. 1992. The spatial dynamics of host–parasitoid systems. – *J. Anim. Ecol.* 61: 735–748.
- Cronin, J. T. 2003. Patch structure, oviposition behavior, and the distribution of parasitism risk. – *Ecol. Monogr.* 73: 283–300.
- Cronin, J. T. and Reeve, J. D. 2005. Host–parasitoid spatial ecology: a plea for a landscape-level synthesis. – *Proc. R. Soc. B* 272: 2225–2235.
- Denno, R. F. and McClure, M. S. 1983. Variability: a key to understanding plant–herbivore interactions. – In: Denno, R. and McClure, M. (eds), *Variable plants and herbivores in natural and managed systems*. Academic Press, pp. 1–12.
- Evans, D. M. et al. 2012a. Habitat patch shape, not corridors, determines herbivory and fruit production of an annual plant. – *Ecology* 93: 1016–1025.
- Evans, L. M. et al. 2012b. The relative influences of host plant genotype and yearly abiotic variability in determining herbivore abundance. – *Oecologia* 168: 483–489.
- Fischbein, D. et al. 2012. Patch choice from a distance and use of habitat information during foraging by the parasitoid *Ibalia leucospoides*. – *Ecol. Entomol.* 37: 161–168.
- Foster, M. A. et al. 1992. Modeling gypsy moth–virus–leaf chemistry interactions: implications of plant quality for pest and pathogen dynamics. – *J. Anim. Ecol.* 61: 509–520.
- Hassell, M. P. 2000. The spatial and temporal dynamics of host–parasitoid interactions. – Oxford Univ. Press.
- Hassell, M. P. and May, R. M. 1973. Stability in insect host–parasite models. – *J. Anim. Ecol.* 43: 693–726.
- Hassell, M. P. and May, R. M. 1974. Aggregation of predators and insect parasites and its effect on stability. – *J. Anim. Ecol.* 43: 567–594.
- Hassell, M. P. et al. 1991. Spatial structure and chaos in insect population dynamics. – *Nature* 353: 255–258.
- Hebblewhite, M. and Merrill, E. H. 2009. Tradeoffs between predation risk and forage differ between migrant strategies in a migratory ungulate. – *Ecology* 90: 3445–3454.
- Helms, S. E. and Hunter, M. D. 2005. Variation in plant quality and the population dynamics of herbivores: there is nothing average about aphids. – *Oecologia* 145: 197–204.
- Hill, J. K. et al. 1996. Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: implications for metapopulation structure. – *J. Anim. Ecol.* 65: 725–735.
- Hirzel, A. H. et al. 2007. Host–parasitoid spatial dynamics in heterogeneous landscapes. – *Oikos* 116: 2082–2096.
- Holt, R. D. and Barfield, M. 2003. Impacts of temporal variation on apparent competition and coexistence in open ecosystems. – *Oikos* 101: 49–58.
- Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predator–prey oscillations. – *Hilgardia* 27: 343–383.
- Hunter, M. D. 2003. Effects of plant quality on the population ecology of parasitoids. – *Agric. Fore. Entomol.* 5: 1–8.
- Hunter, M. D. and Price, P. W. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom–up and top–down forces in natural communities. – *Ecology* 73: 724–732.
- Hunter, M. D. et al. 1996. Population–level variation in plant secondary chemistry, and the population biology of herbivores. – *Chemoecology* 7: 45–56.

- Hunter, M. D. et al. 1997. Estimating the relative roles of top-down and bottom-up forces on insect herbivore populations: a classic study revisited. – *Proc. Natl Acad. Sci. USA* 94: 9176–9181.
- Johst, K. et al. 2002. Metapopulation persistence in dynamic landscapes: the role of dispersal distance. – *Oikos* 98: 263–270.
- Loveless, M. D. and Hamrick, J. L. 1984. Ecological determinants of genetic structure in plant populations. – *Annu. Rev. Ecol. Syst.* 15: 65–95.
- McIntyre, P. J. and Whitham, T. G. 2003. Plant genotype affects long-term herbivore population dynamics and extinction: conservation implications. – *Ecology* 84: 311–322.
- Murdoch, W. et al. 1972. Diversity and pattern in plants and insects. – *Ecology* 53: 819–829.
- Nicholson, A. J. and Bailey, V. A. 1935. The balance of animal populations. Part 1. – *Proc. Zool. Soc. Lond.* 105: 551–598.
- Oksanen, T. L. et al. 1992. Exploitation ecosystems in heterogeneous habitat complexes. II. Impact of small-scale heterogeneity on predator–prey dynamics. – *Evol. Ecol.* 6: 383–398.
- Pennings, S. C. et al. 2007. Latitudinal variation in plant–herbivore interactions in European salt marshes. – *Oikos* 116: 543–549.
- Pimentel, D. 1961. Species diversity and insect population outbreaks. – *Ann. Entomol. Soc. Am.* 54: 76–86.
- Pulliam, H. R. 1988. Sources, sinks and population regulation. – *Am. Nat.* 132: 652–661.
- Rand, T. A. and Louda, S. M. 2006. Spillover of agriculturally subsidized predators as a potential threat to native insect herbivores in fragmented landscapes. – *Conserv. Biol.* 20: 1720–1729.
- Reeve, J. D. 1988. Environmental variability, migration, and persistence in host–parasitoid systems. – *Am. Nat.* 132: 810–836.
- Rohani, P. and Miramontes, O. 1995. Host–parasitoid metapopulations: the consequences of parasitoid aggregation on spatial dynamics and searching efficiency. – *Proc. R. Soci. B* 260: 335–342.
- Rohani, P. and Ruxton, G. D. 1999. Dispersal-induced instabilities in host–parasitoid metapopulations. – *Theor. Popul. Biol.* 55: 23–36.
- Rohani, P. et al. 1994. Aggregation and the dynamics of host–parasitoid systems: a discrete-generation model with within-generation redistribution. – *Am. Nat.* 144: 491–509.
- Roland, J. and Taylor, P. D. 1997. Insect parasitoid species respond to forest structure at different spatial scales. – *Nature* 386: 710–713.
- Root, R. B. 1973. Organization of a plant–arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). – *Ecol. Monogr.* 43: 95–124.
- Roughgarden, J. 1974. Population dynamics in a spatially varying environment: how population size “tracks” spatial variation in carrying capacity. – *Am. Nat.* 108: 649–664.
- Ruxton, G. D. and Rohani, P. 1996. The consequences of stochasticity for self-organized spatial dynamics, persistence and coexistence in spatially extended host–parasitoid communities. – *Proc. R. Soc. B* 263: 625–631.
- Salmore, A. K. and Hunter, M. D. 2001. Elevational trends in defense chemistry, vegetation and reproduction in *Sanguinaria canadensis*. – *J. Chem. Ecol.* 27: 1713–1727.
- Taylor, A. D. 1991. Studying metapopulation effects in predator–prey systems. – *Biol. J. Linn. Soc.* 42: 305–323.
- Tenow, O. et al. 2013. Geometrid outbreak waves travel across Europe. – *J. Anim. Ecol.* 82: 84–95.
- Thies, C. and Tschardtke, T. 1999. Landscape structure and biological control in agroecosystems. – *Science* 285: 893–895.
- Thies, C. et al. 2003. Effects of landscape context on herbivory and parasitism at different spatial scales. – *Oikos* 101: 18–25.
- Underwood, N. 2004. Variance and skew of the distribution of plant quality influence herbivore population dynamics. – *Ecology* 85: 686–693.
- Underwood, N. 2009. Effect of genetic variance in plant quality on the population dynamics of a herbivorous insect. – *J. Anim. Ecol.* 78: 839–847.
- Underwood, N. and Rausher, M. 2000. The effects of host–plant genotype on herbivore population dynamics. – *Ecology* 81: 1565–1576.

Supplementary material (available online as Appendix oik.01759 at <[www.oikosjournal.org/readers/appendix](http://www.oikosjournal.org/readers/appendix)>). Appendix 1–8