

Response by Specialist and Generalist Natural Enemies to Agroecosystem Diversification: A Selective Review

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ABSTRACT Effects of agroecosystem diversification on searching behavior and success of arthropod natural enemies are poorly understood. Crop diversification may increase generalist enemy effectiveness by increasing alternate food or prey availability, as predicted by the enemies hypothesis. But diversification may also reduce enemy searching efficiency and destabilize predator/prey interactions. Additionally, specialist enemies, often important in biological control programs, may be particularly sensitive to vegetation texture. Pest control by specialist enemies may be more effective in less diverse agroecosystems if concentration of host plants increases attraction or retention of these enemies.

AGRICULTURAL DIVERSIFICATION often leads to reduced pest populations (reviewed by Perrin & Phillips 1978, Way 1979, Cromartie 1981, Risch et al. 1983, Altieri & Letourneau 1984, Andow 1985), but the mechanisms involved are poorly understood. Root (1973) formulated two hypotheses to explain differences in herbivore populations in simple and diverse habitats. The resource concentration hypothesis predicts that monophagous or oligophagous herbivores are more likely to find, remain in, and build up populations in places such as monocultures where their host plants are concentrated. Polyphagous herbivores, on the other hand, are more likely to drift away from such patches into surrounding vegetation. The enemies hypothesis predicts that populations of natural enemies will be greater, and, consequently, herbivore populations lower, in diversified habitats due to the increased availability of alternate prey, nectar sources, and suitable microhabitats.

While the two hypotheses are neither comprehensive nor mutually exclusive, they have been the focus of recent experimental work in agricultural settings (Bach 1980, Risch 1981, Tukahirwa & Coaker 1982, Andow 1983, Salick 1983). These studies provided little support for the enemies hypothesis. Furthermore, a review by Risch et al. (1983) concluded that "herbivore movement patterns are more important than the activities of natural enemies in explaining the reduction of monophagous pest populations in diverse annual systems."

In this paper, I argue that one cannot rule out, on the basis of currently available information, the ability of natural enemies to limit herbivore populations in many situations. Additionally, I examine the consequences of resource concentration on natural enemies, and I propose that enemy foraging behavior and population dynamics be viewed in terms of concentration both of victims and of victim-containing vegetation (cf. Risch 1981). In

particular, consideration of responses by specialist enemies to such concentration suggests alternative hypotheses and predictions about natural enemy effectiveness in agroecosystems.

Definitions. Natural enemies of insect herbivores include insect parasitoids and arthropod predators. Pathogens and predators other than arthropods, although undoubtedly of importance, are not considered here. I use *victims* as shorthand for prey or hosts of natural enemies. *Foraging* refers to the activities of both predators hunting prey for food as well as adult female parasitoids hunting hosts on which to feed or in which to oviposit. Successful foraging ultimately results in death of victims in all cases. Diets of specific natural enemies may be restricted to 1) one or several related victim species (victim specialists), or to a number of victim species that exploit either; 2) a narrow range of plant species (plant specialists); or 3) specific plant structures, such as plant stems or leaf mines (niche specialists). Generalist enemies use more species or exploit more kinds of plants or plant structures. For clarity I use the terms *oligophagous* and *polyphagous* to describe herbivore diet breadth. Diet specialization is relative and may be affected by local ecological conditions (Fox & Morrow 1981), population density (Zwölfer 1971), or even individual experience (Arthur 1971, 1981, Vet 1983). Despite such difficulties, the concept of diet specialization is heuristic. Insect parasitoids tend on average to have narrower diets (attack fewer host species) than arthropod predators (Askew 1971, Price 1980, Vinson & Iwantsch 1980). Consequently, my discussion of specialist enemies emphasizes parasitoids.

Tests of the Hypotheses

To test the resource concentration and enemies hypotheses, one would like to directly measure, in simple and diverse systems, pest movement and

reproduction as well as mortality caused by natural enemies. Risch et al. (1983) examined 150 reports in the literature that describe pest abundance in both simple and diverse systems, yet they found only three studies that directly tested both of the hypotheses. Of these studies, those by Bach (1980) and Risch (1981) examined only the adult stage of herbivorous beetle species that have subterranean larval stages. Because differential mortality of larvae was not assessed, the overall role of natural enemies could not be determined. The third study mentioned (ICRISAT: see Bhatnagar and Davies [1982]) found both pest movement and natural enemies to be important in determining pest abundance patterns. Other recent studies that have examined both herbivore movement and enemy-caused mortality have suffered from insufficient sampling to determine enemy activity (Andow 1983), or inadequate replication and experimental control (Tukahirwa & Coaker 1982). In one study (Salick 1983), numbers of enemies were insignificant. However, in systems where enemies are present, studies to date do not allow for rejection of the enemies hypothesis.

Importance of Interactions Between Plants and Generalist Enemies

Consideration of enemy response both to victim concentration and to vegetation texture (Root 1975) suggests that predictions made by the enemies hypothesis are simplistic. Some factors appear to favor greater enemy abundance or effectiveness in diverse systems, but others may favor enemy success in simple systems. Most research on natural enemies has been limited to interactions between enemies and victims. Many authors believe that enemies tend to aggregate, on some scales at least, in areas of high victim density (reviewed by Hassell [1978, 1982], but see Morrison and Strong [1980]). By itself, a strong enemy aggregation response might be predicted in some situations to counteract concentration of oligophagous herbivores in simple habitats. However, a full understanding of the effects of enemies on herbivore populations, as well as of the effects of agricultural diversification on enemy/herbivore interactions, must incorporate an understanding of interactions between enemies and vegetation (Price et al. 1980).

Enemy response to vegetation factors has received less attention than enemy response to victim density and dispersion. The enemies hypothesis considers the importance of plant factors primarily through the effects of varied nectar sources and microhabitat complexity and quality in attracting and retaining those enemies that can use alternate prey species (Root 1973, Cromartie 1981, Risch 1981). These factors may indeed be important to the foraging success of many enemies, especially of generalist enemies (see reviews by Price et al. [1980], Vinson [1981], and Altieri & Letourneau [1982]). Furthermore, these factors

may lead to patterns of higher predation and parasitism in some diverse cultures (e.g., Altieri et al. [1981] and Letourneau & Altieri [1983]). However, two arguments suggest other possible predictions: 1) plant-related factors other than those considered by the enemies hypothesis may counteract generalist enemy success in diverse habitats (see below) and 2) the enemies hypothesis as currently formulated may be less applicable to specialist than to generalist natural enemies (see *Specialist Enemies*).

A largely neglected interaction is that between leaf surface area and foraging success of enemies that locate prey visually or by random contact. Need & Burbutis (1979) found that parasitism rates by *Trichogramma nubilale* Ertle and Davis varied inversely with leaf area of corn plants. Similarly, O'Neil (1984) demonstrated that predation rates on *Anticarsia gemmatalis* Hübner larvae are directly correlated with changes in host plant (soybean) leaf area. Apparently, as leaf surface area increases during the growing season, visually or tactilely searching enemies must search more area to find the same number of prey. Leaf surface area per unit soil area tends to be greater in diverse than in simple systems due to planting practices and to the closer spacing often possible with plants of different architecture (Andow 1985). Visually or tactilely searching enemies may therefore be less effective in reducing herbivore populations in dense, diverse systems than in sparser, simple systems, other factors being equal. Consistent with this hypothesis, Risch et al. (1982) found that foraging rates of *Coleomegilla maculata* (DeGeer) in laboratory cages were significantly reduced by increasing the density (but not diversity) of plants on which they foraged. The authors suggested that high plant density reduced enemy searching effectiveness and resulted in higher herbivore loads in the high density treatments.

Spatial dispersion of patches of plants containing potential victims in diverse agroecosystems, in conjunction with victim distribution, may exert strong effects on enemy/victim dynamics. Huffaker (1958), in a classic laboratory study, showed that the ability of predatory mites to coexist with their herbivorous mite prey was dependent on environmental complexity and dispersal rates of predator and prey. Until recently, spatial heterogeneity has been incorporated into models of enemy/victim dynamics only to the extent that internally homogeneous patches differ in prey density. Kaiser (1983) examined the effects of patch size, shape, and internal structure in laboratory experiments and found that these factors affected both encounter and predation rates of a mite predator that apparently searches randomly. In field experiments Kareiva (1983b) found that the placement of artificial barriers in strips of goldenrod altered the relative mobilities of a coccinellid beetle and its aphid prey and led to aphid outbreaks. Interestingly, patchiness at the scale studied by Kareiva

destabilized the predator/prey system, while in Huffaker's (1958) laboratory study patchiness was necessary to prevent prey extinction.

Specialist Enemies

The distinction between oligophagous and polyphagous herbivores is central to the resource concentration hypothesis: oligophagous herbivores are predicted to respond more strongly than polyphagous herbivores to resource concentration (Root 1973, Kareiva 1983a). A similar distinction has not been made for enemies, but in fact it is generalist enemies that are usually mentioned or implied in discussions of the enemies hypothesis. A primary tenet of the enemies hypothesis, as it has been developed by Pimentel (1961), Root (1973), Risch (1981), and Andow (1985), is that enemies should be more abundant and effective in diverse systems because of the greater availability of alternative prey, implying that effective enemies are generalists. Certainly maintenance of enemy populations on alternative prey is a characteristic that increases the effectiveness of many generalist enemies, especially in annual agroecosystems (Ehler & Miller 1978). However, specialist enemies may often be more effective than generalists in controlling herbivore populations, just as oligophagous herbivores are often more effective in exploiting host plants, and comprise the major portion of the herbivore load in many systems (Root 1973, Kogan 1981). The number of successes (Beddington et al. 1978, Waage & Hassell 1982) and the rates of success (Hall et al. 1980) of biological control introductions using specialist enemies indicate the widespread importance of specialist enemies in natural and agricultural systems. Considering their importance, it is of considerable interest to determine if specialist enemies respond to vegetation texture differently from generalist enemies, just as oligophagous herbivores often respond differently from generalist herbivores. Except for passing mention by some authors (e.g., by Root [1973], Perrin & Phillips [1978]), discussion of agroecosystem diversification has not considered the potential contribution of specialist enemies.

The results of three field studies are consistent with the hypothesis that specialist enemies, particularly parasitoids, may be equally or more abundant or effective in simple than in diverse systems. P. Gross (personal communication) controlled for host density and measured parasitism of Nantucket pine tip moth larvae, *Rhyacionia frustrana* (Comstock), in experimental weedy and mowed stands. Preliminary results suggested that parasitism by two generalist wasp parasitoids was higher in weedy stands, while parasitism by a tachinid specialist, *Lixophaga mediocris* Aldrich, was not significantly influenced by the presence of weeds. Smith (1976) compared the rates of parasitism of cabbage aphids by the crucifer-specialist parasit-

oid *Diaeretiella rapae* (M'Intosh) on weedy and tilled Brussels sprout plots. During 1 month when aphid densities were (coincidentally) equal in both treatments, she found 4-fold higher parasitism in the tilled monoculture plots. Finally, Richards (1940) recorded parasitism of *Artogeia* (= *Pieris*) *rapae* (L.) on potted cabbage plants placed in cabbage plots and old fields. He reared the specialist parasitoid *Apanteles rubecula* Marshall only from host larvae from cabbage monoculture plots, whereas he reared equal numbers of the generalist parasitoid *Phryxe vulgaris* (Fallén) from larvae from cabbage in uniform stands and in diverse vegetation.

Possibly contrary to the above results, D. Letourneau (personal communication) found that larval *Diaphania hyalinata* (L.) were attacked more often by parasitoids in squash/bean/corn triculture than in squash monoculture, despite higher host densities in monoculture plots. Assessment of parasitoid specialization in this case is hindered, however, by the fact that only one species (a generalist) was identified to species. Unfortunately, few experiments have been designed to determine enemy response to habitat factors, independent of enemy response to host density. Host density must be controlled in such experiments before the importance of particular habitat variables on enemy effectiveness can be assessed.

Mechanisms of Specialist Enemy Concentration

Vegetation texture may influence enemy searching behavior and population dynamics in ways analogous to its influence on herbivores (Vinson 1981, Kareiva 1983a, Stanton 1983). At least three general mechanisms can lead to increased populations of natural enemies in particular habitats: 1) high rates of immigration to patches of host or host plant concentration; 2) low rates of emigration; and 3) high survival and reproduction of successful immigrants within such patches. These mechanisms may operate in many situations to concentrate specialist enemies in patches of higher resource (host and host plant) concentration, and therefore in simple rather than in diverse habitats.

Patch Immigration. Plants provide visual, olfactory, and tactile stimuli that may be used as long-range attractants or as short-range arrestants by enemies in habitat or patch location (reviewed by Vinson [1976, 1984]; see Drost et al. 1986). However, evidence for distant (>10 m) olfactory orientation to plants is controversial for herbivores (Finch & Skinner 1982), and is entirely lacking for enemies. Specialist herbivores appear to use more specific chemical and visual cues than generalists in orienting to host plants (Städler 1977, Prokopy & Owens 1978); this may be true for enemies as well (Vinson 1976). Furthermore, when specific plant cues are used by insects to locate plant

patches, the presence of other plants in close association with these plants may disrupt orientation to the patch. Such disruption may be due to the masking of attractant or arrestment cues, to the presence of repellent cues, or to a combination of these (Tahvanainen & Root 1972, Dethier 1982). Olfactory disruption has been demonstrated more often for herbivores, but has been suggested for enemies as well (Monteith 1960, Cromartie 1981). If diverse vegetation has the effect of obscuring victim-containing plants, it is possible that specialist enemies will be more affected than generalists. Consequently, specialist enemies may colonize simple agroecosystems more readily than diverse systems.

Patch Emigration. The tendency of enemies to leave patches may also be influenced by plant population factors. Recognition of patch boundaries has been suggested to be critical for retaining certain herbivore species (Stanton 1983, Kareiva 1985), and Waage (1979) found that edge recognition in patches defined by host kairomones was a key determinant of patch time for the parasitoid *Nemeritis canescens* (Gravenhorst) attacking a grain moth. Although evidence is lacking, it is possible that enemy recognition of plant-defined patch boundaries (probably coupled with encounter rate with potential victims) may similarly affect patch time for some species, especially for specialist enemies that are adapted to search in dense, low-diversity stands. If so, then the alteration or obscuring of patch boundaries that may accompany agroecosystem diversification may adversely affect retention of those enemy species.

Within-patch Success. The presence in diverse systems of more nectar sources than in simple systems may indeed favor within-patch success of many enemies, as predicted by the enemies hypothesis. However, host feeding is often essential for adult parasitoids (Bartlett 1964, Sandlan 1979) and may account for a significant proportion (Van Driesche 1983) or even a majority (DeBach 1943) of parasite-inflicted mortality for some host species. For both specialist and generalist parasitoids, tenure time in patches may depend in some cases on availability of acceptable prey for feeding rather than on availability of nectar. The relative importance of nectar feeding versus host feeding to adult parasitoid reproductive success, and their effects on foraging behavior, deserves further study.

Scale. The question of spatial scale may also be relevant to the assessment of effects of cultural practices on enemy searching behavior. Concentration of host plants of herbivores may be effective in attracting or retaining enemies at intermediate scales, while less effective or ineffective at the scale of hectares. Enemies adapted to searching diverse natural habitats may at some point become habituated to superabundant plant cues and may tend to leave these areas after a limited time searching. However, evidence is insufficient.

Conclusions

An important result of experiments and analyses inspired by the resource concentration hypothesis (Root 1973) is that differential abundance of herbivores in simple and diverse agroecosystems may not in many cases be due to enemy-inflicted mortality. However, enemies clearly do inflict significant mortality on many herbivore pests. The hypothesis that natural enemies should be more abundant or effective where more alternative food sources are available (enemies hypothesis) is simplistic in several respects. Victim location by generalist enemies may be hindered by increased plant density or patchiness in diverse agricultural systems. More importantly, specialist enemies should not necessarily respond to habitat diversification in the same way as generalists. Factors that increase immigration to and decrease emigration from host plant areas by specialist enemies (e.g., large patch size, close plant spacing, the presence of specific chemical or visual stimuli, and lower chemical or structural diversity of associated vegetation) may cause those enemies to remain longer and hunt more effectively in simple than in diverse agroecosystems, at least in those that are not too extensive.

Several questions are raised by these speculations. How important is mortality caused by specialist versus generalist enemies in agroecosystems? Can behavioral modification (learning or switching) cause generalist enemies to function as specialists? Does the tendency of some enemies to limit search to specific plants or plant structures influence enemy foraging efficiency in diversified agroecosystems? Is diet specialization a useful concept at all? More generally, answers are needed to the following questions: How important is enemy-caused mortality relative to herbivore movement in influencing pest population response to agricultural diversification? Does the ecology of enemy/herbivore interactions differ fundamentally between agroecosystems and less disturbed or natural systems? Can the results of small-plot experiments be meaningfully extrapolated to large-scale agriculture? Finally, can useful generalizations be made about natural enemy response to agroecosystem diversification, or must each case be considered on an individual basis, as is suggested by Nordlund et al. (1984)? Clearly, more extensive and careful experimentation is needed to detect effects of agroecosystem diversification on both pest abundance and on pest control by natural enemies. Herbivore density must be controlled in these experiments. Observation and, preferably, experimentation in natural systems can also help elucidate ways in which agricultural practices can be altered to enhance enemy activity. Ultimately, perhaps, cultural practices can be manipulated to advantage with better knowledge of their effects on key enemy/victim combinations.

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