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Enemies Hypothesis: A Review of the Effect of Vegetational Diversity on Predatory Insects and Parasitoids

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ABSTRACT The enemies hypothesis holds that predatory insects and parasitoids are more effective at controlling populations of herbivores in diverse systems of vegetation than in simple ones. Eighteen studies that tested the enemies hypothesis are reviewed. Of those studies reporting mortality from predation or parasitism, nine found higher mortality rates in diverse systems; two found a lower mortality rate; and two found no difference. The mechanisms that are thought to underlie the enemies hypothesis and directions for future research are discussed. Evidence suggests that the enemies hypothesis and the resource concentration hypothesis (which predicts that herbivores more easily find, stay in, and reproduce in monocultures of host plants than in polycultures) are complementary mechanisms in reducing numbers of herbivores in diverse agricultural systems.

KEY WORDS Insecta, enemies hypothesis, resource concentration, predators

THEORIES ABOUT THE FACTORS that control the abundance of herbivorous insects have figured prominently in the history of ecology, occasioning several of the discipline's seminal papers (Andrewartha & Birch 1954, Hairston et al. 1960, Ehrlich & Raven 1964). Recently, particular attention has been paid to the effect of vegetational diversity on phytophagous insects (Feeny 1976, Rhoades & Cates 1976, Scriber 1984) and their natural enemies (Price et al. 1980, Sheehan 1986). Agricultural systems, where variables such as density and patch size can be controlled, have proved especially useful in testing hypotheses about diversity and insects.

Studies have commonly, though not universally, found that populations of herbivorous insects reach higher levels in simple agroecosystems than in diverse ones (reviewed by Andow 1983b, Risch et al. 1983, Altieri & Letourneau 1984, Vandermeer 1989). Root (1973) proposed two possible explanations for this pattern. (1) The enemies hypothesis: Predators and parasites are more effective in diverse systems than in simple ones. (2) The resource concentration hypothesis: Specialist herbivores more easily find, stay in, and reproduce in simple systems (monocultures) of their host plants.

This paper reviews the enemies hypothesis; the resource concentration hypothesis has been reviewed by Kareiva (1983) and Stanton (1983). In the first part, I examine whether predators and parasites inflict significantly higher mortality on insect herbivores in diverse than simple systems and thereby reduce herbivore populations. I review the mechanisms proposed for greater predator and parasite effectiveness in diverse systems and directions for future research in the second section. In the last section, I discuss the relationship between the enemies and resource concentration hypotheses.

For the purposes of this paper, a diverse agricultural system, or polyculture, is one in which two or more plant species grow simultaneously. A simple system, or monoculture, consists of one plant species. Enemies are predatory arthropods or insect parasitoids. Victims are their prey or hosts. Generalists consume a variety of species. Specialists consume one or several related species.

Testing the Enemies Hypothesis

Root's (1973) formulation of the enemies hypothesis makes one essential prediction: "predators and parasites are more effective in [complex environments than simple ones]" (114). That prediction can be broken into two components: predators and parasites kill herbivores at higher rates in polycultures than in monocultures, and the higher mortality rates in polycultures significantly reduce herbivore populations.

Table 1 lists studies that explicitly test the enemies hypothesis or that compare predation or parasitism rates in agricultural monocultures and polycultures. All controlled tests of the hypothesis that I found were done in agroecosystems. Some studies measured only mortality rates; others also did censuses of herbivore populations. I did not include studies that deduced enemy-caused mortality from inverse correlations between enemy and victim abundances, except for the studies in which the author said he or she was testing the enemies hypothesis. Such correlations do not prove that enemies caused the reductions in herbivore numbers. I included only studies that compared the effects of within-field diversification. Diversity on a larger scale is an important part of the enemies hypothesis, but to my knowledge controlled comparisons

Table 1. Tests of the enemies hypothesis in polyculture versus monoculture

Researcher	Predation/parasitism rate	Victim stage examined	Sampling method	Enemy abundance	Herbivore abundance	Enemy/herbivore ratio
Altieri & Schmidt 1986	Higher	Egg predation	Predation on eggs on cards	Higher	Lower	Higher
Andow 1983a	Same	Egg, larval predation or parasitism	Visual	NA	Varied	NA
Andow 1983b	NA	NA	Review	Usually higher	Usually lower	Usually higher
Andow & Risch 1985	Lower	Egg predation	Predation on eggs on cards	Lower (1 spp.)	Higher	Lower
Andow & Risch 1987	Lower	Egg parasitism	Parasitism on eggs on cards	NA	NA	NA
Bach 1980a	NA	NA	Visual; pitfall; sticky traps	Same	Lower	Higher
Bach 1980b	NA	NA	Visual	Higher	Lower	Higher
Dempster 1969	Higher	Larval predation or parasitism[a]	Visual; pitfall	Higher	Lower	Higher
Dempster & Coaker 1974	Higher	Larval predation	Visual; pitfall	Higher	Lower	Higher
Hansen 1983	Higher	Egg predation	Eggs on cards	Higher[b]	Lower	Higher[c]
Leius 1967	Higher	Egg, larval, pupal parasitism	Collected all stages from orchards	NA	NA	NA
Letourneau 1987	Higher	Egg parasitism	Collected eggs	Mixed[d]	Higher	NA
Letourneau & Altieri 1983	Higher	All stages: predation	Visual; cages	Higher	Lower	Higher
Risch 1981	Same	Adult parasitism; egg predation or parasitism	Visual; eggs collected	Same	Lower	Higher
Risch et al. 1983	NA	NA	Review	Usually higher	Usually lower	Usually higher
Root 1973	NA	Adult: neither	Vacuum; bags	Same	Higher	Higher
Ryan et al. 1980	Higher	Egg, larval predation	Pitfall; visual	Same	Lower	Higher
Speight & Lawton 1976	Higher	Pupal predation	Pitfall; pupae on cards	Higher	NA	NA
Tukahirwa & Coaker 1982	Same	Egg predation	Visual; pitfall; yellow traps	Higher	Lower	Higher

[a] Predation rate higher. No difference in parasitism rate.
[b] Non-ant enemies significantly higher in polycultures all season. Early in the season, ants were more abundant in squash monoculture, but that pattern reversed itself by the end of the season.
[c] Number of herbivores not reported. However, Risch's (1981) study on same plots at same time reported fewer beetle pests in polycultures. Given that the number of enemies increased and the number of beetles, the major pests, decreased, the ratio of enemies to herbivores must have been higher.
[d] More parasites were found in polycultures and in maize monoculture. Predators were unaffected by cropping pattern.

with monocultures of comparable size have not been made.

Most studies verify the prediction of the enemies hypothesis that enemies cause higher herbivore mortality in polycultures than in monocultures. Nine studies found higher mortality rates from predation or parasitism in diverse systems and two found no difference. It is interesting that only 2 studies out of 13 found lower mortality in polycultures than in monocultures given predictions that predators (Risch et al. 1982) and parasitoids (Monteith 1960, Sheehan 1986) should display reduced searching efficiency in more dense or diverse systems. If this occurs for individual enemies, their greater numbers in polycultures (Andow 1983b) may compensate.

Published studies generally support the second part of the prediction, that enemies cause smaller herbivore populations in polycultures, especially for slow-moving apterous larvae (Cain et al. 1985). Drawing the same conclusions about adult populations is more difficult, because alates can move in and out of patches easily. The one manipulative study that controlled for such adult movement (Letourneau & Altieri 1983) found that predators effectively controlled all life stages of herbivorous thrips. More manipulative studies are clearly needed.

Three studies (Root 1973; Bach 1980a,b) and two reviews (Andow 1983b, Risch et al. 1983) that tested the enemies hypothesis by comparing insect abundances in simple and diverse systems found little or no evidence for the hypothesis, almost the opposite result from the studies that measured mortality rates. Enemy abundances often correlate inversely with victim abundances (Coaker 1965; Smith 1969, 1976; Speight & Lawton 1976; Mayse & Price 1978; Andow & Risch 1985), but the correlation is not a sure index of mortality rates. Mortality rates can vary between treatments with equal enemy densities (Ryan et al. 1980), or be equal despite differences in enemy density (Tukahirwa & Coaker 1982). Mortality during egg and larval stages is significant (Price 1984) but often unmeasured.

I found only two experiments that manipulated enemy density. Letourneau & Altieri (1983) used cages and Tukahirwa & Coaker (1982) erected barriers of bituminized felt to exclude ground-dwelling carabids. We need more such manipulations, despite their disadvantages in changing microclimates (DeBach et al. 1976) and in limiting movement by victims and enemies. Barriers to ground-dwelling predators (Tukahirwa & Coaker 1982) do not prevent immigration by alate enemies, which may have contributed to equalizing predation rates in that study.

Another striking pattern in Table 1 is that the predator/herbivore ratios rise in all but one of the polycultures. What are the implications of this change? We might predict more search movement by enemies, more enemy emigration, or higher enemy effectiveness. I found no studies that test predictions based on this ratio.

Mechanisms Underpinning the Enemies Hypothesis

Root (1973) presents five reasons why enemies should control populations of herbivores more effectively in polycultures than in monocultures.

"*A greater diversity of prey/host [victim] species and microhabitats is available within complex environments, such as most natural, compound communities*" (114). Several studies have found a correlation between the diversity of plant species and the diversity of herbivorous insects. This relationship has been reported for Homoptera (Murdoch et al. 1972); for Hemiptera, Homoptera, and Thysanoptera (Brown & Southwood 1983); and for communities of herbivores in agricultural fields (Mayse & Price 1978). A review by Lawton & Strong (1981) concluded that this pattern holds for insect communities in general.

However, none of these studies mentions how the investigators determined appropriate sampling effort, a crucial methodological question. In any community, we expect the number of sampled species to rise with sampling effort, reaching an asymptote at the total number of species. Risch (1979) found higher species diversity in a tropical diculture than in monoculture, but an increase in parasitic Hymenoptera, not herbivores, accounted for the difference. In fact, the number of herbivorous species was lower in the diculture. More importantly, Risch noted that the species-sweep curve did not level after 600 sweeps. Risch used the formula developed by Stout & Vandermeer (1975) to estimate the number of species in the community. The pattern reversed itself, with more total species expected in the monoculture than in the polyculture. Bach et al. (1982) found no difference in species numbers in secondary succession near and far from tropical rainforest after a few sweeps. Further sampling found the number of herbivorous species the same in both habitats, but the number of entomophagous species increased with distance from the forest.

The studies finding a positive correlation between vegetational diversity and the number of herbivorous species were done in temperate regions, whereas those finding other patterns were done in the tropics. Further studies are needed before we can conclude whether the differences are due to the regions studied or to the sampling methods.

"*As a result, relatively stable populations of generalized predators and parasites can persist in these habitats because they can exploit the wide variety of herbivores which become available at different times or in different microhabitats*" (114). Do generalist enemy populations fluctuate less in diverse than in simple systems? A subjective inspection of graphs in the studies listed in Table 1 revealed no clear or consistent differences. Perfecto et al. (1986) did the only study of enemy movement patterns, which would largely determine population fluctuations. They found no consistent response to plant diversity, but carabids did stay longer in plots with ground cover. We need more studies of the specific factors to which enemies respond in polycultures, because "diversity" is actually a shorthand description of a number of factors that change in intercrops, including number of species, density, architecture, moisture, and wind patterns.

Does increasing the diversity of prey species result in populations of predators persisting longer? Many ecologists have argued that increasing diversity leads to greater stability for communities in general (Odum 1953, MacArthur 1955, Elton 1958, Margalef 1968, Armstrong 1982) and for agricultural systems in particular (Pimentel 1961, van Emden & Williams 1974, Murdoch 1975). The doctrine came under question when May (1973) and others (reviewed in May [1976]) showed that increased diversity leads to decreased stability in some mathematical models. Definitions of stability (Pimm 1984) and assumptions (reviewed by Begon et al. 1986) often determine whether a model is stable. For example, Vandermeer (personal communication) has found that increased diversity theoretically results in increased species persistence when indirect interactions (Vandermeer 1980, Vandermeer et al. 1985) are taken into account.

Indirect interactions may prove more significant than previously realized. Price et al. (1980) noted that plants and enemies function as indirect mutualists, because plants "provide" victims for the enemies, and enemies presumably help the plants by eliminating herbivores. Similarly, herbivores and enemies on the fourth trophic level should be considered mutualistic. Parasites and predators can kill a significant number of natural enemies (Spencer 1926; van Emden 1965, 1966; Iperti 1966; Kirk 1974), but their effect in the field has seldom been assessed (Doutt et al. 1976, Orr & Boethel 1986). If diverse systems attract greater numbers of enemies on the fourth as well as third trophic level, the effect of the third trophic level on herbivores may be reduced.

"*Specialized predators and parasites are less likely to fluctuate widely because the refuge provided by a complex environment enables their prey/host species to escape widespread annihilation*" (114). The generalization that refuges prevent annihilations and thus "stabilize" predator-prey interactions grew out of laboratory studies (Huffaker 1958, Pimentel et al. 1963, Luckenbill 1974, Glesener 1978). Unstable community models can achieve global stability by adding a migration component (Levins & Culver 1971, MacArthur 1972, Vandermeer 1973, Horn & Levin 1974, Slatkin 1974, Hassell 1978).

Few field tests of the role of refuges in population dynamics have been done. Reeve & Murdoch (1986) found that effective control of the California red scale had been achieved by a parasitoid because the scale was able to find a spatial refuge in the interior of trees, thus preventing extinction of both species. In Australia, Myers et al. (1981) found that refuges are important in continued control of the prickly pear cactus by enemies. Kareiva (1985, 1987) found that vegetational patchiness leads to increased outbreaks of aphid populations in the field, apparently by interfering with searching and aggregation behavior of predatory coccinellids. The experiment did not run long enough to draw conclusions about persistence of the system.

Classical biological control theory has focused on specialist enemies and how to keep them from eliminating themselves along with their prey (DeBach 1974, Huffaker & Messenger 1976). The same concern has not traditionally been voiced for generalist predators, but questions have been raised about the assumption that specialists more often drive themselves to extinction than do generalists. Introduced predators (which tend to generalize) and parasites (which tend to specialize) have been found to establish themselves at the same rate (Hall & Ehler 1979). More importantly, a review by Murdoch et al. (1985) of successful biological control programs found that local annihilation of prey did not threaten long-term control.

"*(D)iverse habitats offer many important requisites for adult parasitoids and predators, such as nectar and pollen sources, that are not available in a monoculture*" (114). Many monocultures do produce nectar and pollen, but more kinds of pollen generally are available, and at more times in the season, in polycultures. Eating nectar and pollen increases predator and parasite longevity and fecundity (Leius 1963, Bombosch 1966, Hodek 1966, Shahjahan 1974, Syme 1975, Hagen et al. 1976, Vinson 1981). Indeed, syrphid ovarioles do not mature unless the female feeds on pollen (Bombosch 1966). Different species of pollen affect fecundity and longevity differently (Leius 1963), so access to a diversity of plant species might well prove advantageous to enemies. Nectar and pollen appear to be important in keeping parasites (Leius 1963, Shahjahan 1974, Hansen 1983) and predators (Smith 1966, Bentley 1977) in certain vegetation. This often leads to higher herbivore mortality (Leius 1963, van Emden 1965, Shahjahan 1974, Tilman 1978, Barton 1986).

Discussion of the availability of alternative victims, nectar, and pollen raises questions about the scale on which enemies operate. Flaherty (1969) found that weeds growing within a field harbored alternative prey for predatory phytoseiids, which led to more effective control of Willamette mites, *Eotetranychus willamettei* Ewing, in weedy than weedless fields. Perrin (1975) argued that nettles growing next to fields support alternative victims for enemies, including entomophagous fungi. Enemies can colonize cultivated fields from uncultivated land near fields (van Emden 1962, Galecka 1966). Parasitization rates on sugar cane weevils increased within 200 ft of nectar sources in field margins in Hawaii (Topham & Beardsley 1975). Bombosch (1966) inferred from population measurements that syrphids move in a constant pattern from woodland edges to distant sugar beet and potato fields to roadsides and weedy ditchbanks over an area of 10 km^2. Doutt & Nakata (1973) found that control of leafhoppers declined in vineyards more than 6 km from *Rubus* bushes, which support an essential alternative host.

All of these studies show that vegetational diversity benefits enemy populations, but what is the appropriate scale for the enemies hypothesis? Such questions assume great significance in experimental tests, which rarely are done on plots 6 km wide. Highly mobile species with diverse requirements probably benefit from diversity over a large area, whereas less mobile enemies with fewer needs probably operate on a smaller scale. The explicit tests of the enemies hypothesis (Table 1) have generally used test plots 10 or 15 m on a side, usually located within 10 m of each other. This has at least two important implications.

First, enemies may regard the sum of the test plots as one large polyculture, moving freely between individual monocultures and polycultures. Altieri & Whitcomb (1980) found that predatory communities did not differ between monocultures and polycultures when test plots were located 8 m from each other. In contrast, they found significantly more predators in polycultures when test plots were 50 m from each other. Finding the same enemy abundance or herbivore mortality between treatments might mean a lack of evidence for the enemies hypothesis, or it might mean that the test plots are too close together. Small, juxtaposed plots constitute a conservative design, because their proximity tends to reduce differences between plots.

Second, a "fine-grained" field to one enemy (e.g., a specialist parasitoid that spends a great deal of time flying) might appear more "coarse-grained" to another enemy (e.g., a sit-and-wait predator). Van Emden (1965) found exactly this pattern when he charted predation and parasitism rates in different parts of a 1.75-acre monoculture surrounded by diverse vegetation. Parasitism rates remained virtually constant over the whole field, but predation rates were significantly higher near the edges. Enemies operate on different spatial scales even within the same system.

"*Thus incipient outbreaks of herbivores are checked early by the functional response of enemies whose numbers have been maintained by the diverse resources available in complex environments*" (114). The biological control literature indicates that predators and parasites can control pest populations by their functional or numerical response to pest populations (reviewed in DeBach 1974, Huffaker & Messenger 1976, Hall et al. 1980). Generalist enemies do exploit different victims at different times (Evenhuis 1966, Hodek 1966, Flaherty 1969, Burleigh et al. 1973, Doutt & Nakata 1973, Hagen et al. 1976, Mayse & Price 1978, Carroll & Hoyt 1986). Murdoch (1969, 1973) and Murdoch & Marks (1972) found that insect predators demonstrate the predicted Type 3 functional response and control population outbreaks. However, switching occurs when predators possess only a weak preference for one prey over the other. We do not know whether generalist enemies require a diversity of prey, nor whether they become functional specialists in the field (Fox & Morrow 1981). We need more research on the behavior of individual arthropod enemies, especially in the field, to determine when and why they switch their choice of victim species.

Foraging theory might provide a useful framework to explore these issues (reviewed by Hassell & Southwood 1978, Stephens & Krebs 1986). The results of the few studies on arthropod foraging are sometimes consistent with predictions from foraging theory (e.g., Charnov 1976) and sometimes not (e.g., Eveleigh & Chant 1982a–c). Energy is commonly used as currency in foraging models, but herbivores often sequester secondary chemicals of their host plants (Duffey 1980), so toxicity is an important variable that is not reflected in caloric content.

Little quantitative work has been done on predicting arthropod habitat choice based on costs and benefits of different habitats. The work of Werner & Mittelbach (1981) and Werner et al. (1983a,b) with sunfish indicates that such approaches might yield useful results. A few studies have attempted to quantify the importance of various environmental variables such as nectar, pollen, and prey availability (Hansen 1983, Andow & Risch 1985). More are needed.

Most work on habitat shifts has focused on how well shifts correlate with changes in prey density. Many authors have concluded that predators stay in a habitat until the food supply drops below the level needed to maintain them (Perrin 1975, Frazer & Gilbert 1976, Wheeler 1977, Hassell & Southwood 1978, Baumgartner et al. 1981, Best et al 1981, Horn 1981, Ives 1981). The finer the scale of diversity, the more likely enemies will be near the place they are needed. If enemies live in weeds surrounding a field, their functional response will likely not prove so fast or effective as when weeds grow in the field itself. This would probably be less of a problem for species that seem to switch habitats when they can get a higher return in another patch (Skuhravy & Novak 1966, Burleigh et al. 1973, Ives 1981).

Are enemy populations maintained at higher levels in polycultures, thus making the functional response effective? Andow's (1983b) review shows that enemies usually do maintain higher populations in polycultures than in monocultures.

Relationship Between the Enemies Hypothesis and the Resource Concentration Hypothesis

Root (1973) described the enemies hypothesis as "one of the hypotheses most frequently offered to explain smaller herbivore populations in complex environments" (114). Root proposed an alternative hypothesis, the resource concentration hypothesis, which stimulated a number of excellent studies (Cromartie 1975; Bach 1980a,b, 1984, 1986; Risch 1980, 1981; Kareiva 1982). "Plant apparency" (Feeny 1976, Rhoades & Cates 1976) and "associational resistance" (Tahvanainen & Root 1972; Altieri & Letourneau 1982, 1984) are other terms emphasizing the importance of plant spatial patterns for herbivore movement and reproduction.

The resource concentration and enemies hypotheses are neither exhaustive nor mutually exclusive (Sheehan 1986). In the first part of this review, I showed that enemies often inflict significantly higher mortality on insects in polycultures than in monocultures, whereas studies of the resource concentration hypothesis (cited above) found that movement patterns play a significant role in determining specialist insect population patterns. The enemies and resource concentration hypotheses are complementary, not competing, mechanisms.

Field studies confirm that the two mechanisms can function simultaneously. Dempster & Coaker (1974) found that enemies reduced the populations of some pests, while movement patterns reduced the populations of others. The caterpillar *Pieris rapae* (L.) lays eggs at the same rate in monocultures and polycultures, but ground beetles and harvest spiders prey on larvae in the polyculture at a significantly higher rate, verifying the enemies hypothesis. But cabbage aphids, *Brevicoryne brassica* (L.), and *Erioischia brassicae* (Bouche) immigrated at a significantly lower rate in the intercrop, verifying the resource concentration hypothesis. Likewise, Ryan et al. (1980) found both mechanisms at work in the same place, but on one species. *E. brassicae* lay fewer eggs in polycultures than monocultures, but predators reduce their numbers even more by preying at a higher rate in the polycultures.

Comparisons of the enemies and resource concentration hypotheses echo the longstanding debate over the factors that control populations (Nicholson 1933, Andrewartha & Birch 1954, Hairston et al. 1960, Ehrlich & Birch 1967, Murdoch 1975). Are herbivores limited by the trophic level below, the trophic level above, or by abiotic factors? It eventually became clear that different factors operate at different times and in different places (Begon et al. 1986). Similarly, I predict that a single factor will not be found that explains why herbivores are often less abundant in diverse than simple systems. In agroecosystems, the challenges are to enhance the effect of each mechanism to control pests by developing quantitative, mechanistic approaches with greater predictive power, and to explain the many exceptions to both hypotheses (Table 1; Andow 1983b). It is likely that by finding reasons for the exceptions we will come closer to understanding the rules.

Conclusions

The relatively few studies that have been done generally bear out the prediction that predators and parasites kill herbivores at higher rates in polycultures than in monocultures. This results in fewer herbivore eggs and larvae in polycultures, but a lack of adequate control in all but one study prevents us from concluding that this difference in mortality is what reduces the number of adult herbivores in complex systems.

The mechanisms postulated to underlie the enemies hypothesis largely remain intuitively reasonable, but need more testing. We do not know for certain that diversity of herbivorous insects increases with vegetational diversity in agroecosystems. Enemies generally achieve larger populations in polycultures than in monocultures, but we do not know whether this is due to increased tenure time or more frequent visits. We have only general, qualitative notions of which environmental variables draw or keep enemies in polycultures. Switching behavior by predators, one of the keystones of the theory, seems to fit predictions only when predators have no preference for different species of prey, an assumption that is not always appropriate. The importance of refuges has come under question recently. Researchers have yet to agree on what we mean by diversity and stability and how one affects the other.

It is clear that herbivore populations are controlled by enemies and by their ability to find and stay on host plants. The relevant question in pest management should not be whether one or the other is at work, but how to enhance both to achieve maximum control. The next step for the enemies hypothesis will be to move beyond qualitative studies and into quantitative ones. We need to predict and test the relative importance of various factors that control enemy effectiveness and response to vegetational patterns. That should allow us to move into a more predictive theory of enemy activity in diverse systems.

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