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AN GENERALIST PREDATORS BE EFFECTIVE OCONTROL AGENTS?*

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■ **Abstract** Theoretical developments are helping us to comprehend the basic parameters governing the dynamics of the interactions between generalist predators and their many pest and nonpest prey. In practice, however, inter- and intraspecific interactions between generalist predators, and between the predators and their prey, within multispecies systems under the influence of rapidly changing biotic and abiotic variables are difficult to predict. We discuss trade-offs between the relative merits of specialists and generalists that allow both to be effective, and often complementary, under different circumstances. A review of manipulative field studies showed that in ~75% of cases, generalist predators, whether single species or species assemblages, reduced pest numbers significantly. Techniques for manipulating predator numbers to enhance pest control at different scales are discussed. We now need to find ways of disentangling the factors influencing positive and negative interactions within natural enemy communities in order to optimize beneficial synergies leading to pest control.

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INTRODUCTION

Mortality caused by invertebrate predators and parasitoids is a major biotic factor determining the numbers of any invertebrate prey (host) species and fluctuations in those numbers. It can sometimes be exploited for biological control, which is seen as a key component of sustainable, integrated pest-management strategies that permit reductions in the use of chemical pesticides. To date, theory and practice have concentrated mainly on "classical" biocontrol by specialist natural enemies, especially parasitoids. This is for good reasons. There is now, unfortunately, a growing list of disastrously unwise introductions of generalist predators that have gone on to decimate indigenous fauna (reviewed in 70, 107, 115). The European *Coccinella septempunctata* L. has, for example, completely replaced some native species of coccinellid in parts of the United States (65). It has been suggested that attacks by stenophagous insects on nontarget species are unlikely because of their

tendency to attack the most abundant prey available (the pests) (92). However, detailed tracing of food webs has shown that among parasitoids interactions between biological control agents and nontarget native hosts are relatively frequent (140). As target-pest density increases so will numbers of the natural enemy, which in turn may have a negative effect on numbers of the nontarget natives, especially if they are less-competitive nonpest species.

It is still assumed by some (49, 116) that an effective biocontrol agent should be highly prey or host specific. Specialists have evolved to seek out their specific targets (in space and time) and will not be diverted by the presence of alternative prey. Such an approach may be appropriate for exotic introductions but may not be applicable to native natural enemies. Although there has long been a debate as to the merits of specialists versus generalists (49, 56, 94, 119; see "Specialists versus Generalists"), it is perhaps only recently that analyses of past successes in biological control, as well as advances in many areas of predation theory, have started to strengthen seriously the case for generalists (32, 150).

We review research into the pest control potential of arthropod generalist predators, particularly through the conservation and exploitation of native natural enemies. We do not cover generalist parasitoids, although the literature on these and their interactions with specialists is relevant to the debate on predators (97, 242). We concentrate instead on the potential of individual generalist predator species, on species assemblages and guilds to control pests in the field, and on methods of enhancing control.

There is no doubt that assemblages or guilds of generalist predators can effectively suppress populations of both indigenous and exotic pests (209, 210, 229). DeBach & Rosen (49) review experiments demonstrating how the use of broad-spectrum insecticides can lead directly to the proliferation of pests once they have been freed from the controlling influence of their natural enemies. DeBach (47) showed that generalist predators could be more important than parasitoids at controlling pests in citrus trees. Other experiments using insecticide-soaked barriers have managed to separate the effects of mainly nonflying, epigeal, and highly generalist predators from those of more stenophagous flying insects and parasitoids (36). Since then there have been numerous examples of control by guilds or assemblages of such generalist predators (see "Experimental Evidence from Manipulative Field Studies"). If communities of generalists are controlling pests, then key groups, or even species, within such communities must be having an effect, too (179). There is good evidence, for example, that native predators such as mirid and anthocorid bugs (73, 146, 195), spiders (80, 208), and carabids (64, 209, 216) can reduce prey populations.

Recently, the lessons taught by the early practitioners of integrated pest management are being relearned, as farmers begin to realize that the economic cost of multiple applications of pesticide on a crop can be greater than the losses caused by pests in untreated fields. Overuse of pesticides can result in environmental damage and the development of both insecticide resistance and secondary pest problems (137). At the same time invertebrate ecologists need to develop

a better understanding of the dynamic interactions between generalist predators and their prey within complex ecosystems, both in theory and practice. We still have a limited understanding of how pest regulation is affected (or not) by intraguild competition, behavioral interference, predation and cannibalism among predators (105, 172, 173, 182, 185, 186, 199, 200, 210), interactions between specialists and generalists (97, 242), and disruption by generalists of biocontrol by parasitoids (156, 198). In some instances such generally negative interactions may be counterbalanced by synergistic factors leading to enhanced control. For example, coccinellids and carabids both feed on aphids within a crop (additive), but dislodgement of aphids by the coccinellids in the canopy also causes them to fall to the ground where they are more vulnerable to the carabids (synergistic) (130). Until we comprehend the basic parameters governing the population dynamics of generalist predators and their prey within multispecies and/or multitrophic systems, biocontrol of pests by generalist predators will remain an uncertain and empirical art.

DEFINITIONS

For the purposes of this paper we consider the terms generalist and polyphagous predator to be synonymous and resist the suggestion that the term polyphagous should only be applied to herbivores. Many stenophagous and generalist predators, such as coccinellids (91), mites (201), carabids (76) and staphylinids (51), also eat plants and fungi and can even be pests [certain carabids (133)], and thus might reasonably be called generalist omnivores. The main difficulty is defining exactly where on the continuum from monophagous specialist to ultra-generalist an individual predator lies. An unspecialized predator, such as *Pterostichus melanarius* Illiger (Coleoptera: Carabidae), which is common in arable fields in northern Europe and North America, is a good example of an ultra-generalist, eating almost anything it can subdue including a wide range of arthropods, mollusks, annelid worms, and even vertebrates (90, 163, 206, 209, 215–217). Many other species of carabid and staphylinid beetle and ants are similarly catholic in their feeding habits. However, most predators are physically, physiologically, or behaviorally restricted to some degree in their prey choice. Most spiders eat any nontoxic insect prey they can subdue (178) but only occasionally eat mollusks or earthworms (158, 159). Body size is a powerful determinant of the prey range of a predator (190). Thus, mites are often effectively restricted to preying on other mites or, when these are not available, plant material (201). Other predators are adapted to feed only on prey within a limited size range. Thus, larvae of the green lacewings *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae) have a preference for aphids but will eat other small insects or their eggs (201). Aphidophagous ladybirds (Coleoptera: Coccinellidae), such as *C. septempunctata*, feed mainly on different species of aphid but also on other insects (especially Thysanoptera), fungal spores, and pollen (223). Some coccinellids, such as *Coleomegilla maculata* (DeGeer), are more generalist in their prey choices (91, 183), whereas others, such as *Rodolia* (=*Vedelia*) *cardinalis* (Mulsant), are less so (see below). Probably

the majority of predators labelled generalists are in fact stenophagous to varying degrees. Assigning a particular nonspecialized predator to a particular category (stenophagous, oligophagous, polyphagous) is an uncertain process, given our restricted knowledge of the dietary breadth of most species. Unfortunately, the dynamic relationship between a predator and any particular target prey is not simply governed by functional and numerical responses to prey density. It is also profoundly affected by the availability of acceptable nontarget food resources, by prey choice, and by the degree of polyphagy. That is why development of monoclonal antibody and new molecular techniques, which help us to analyze accurately, quantitatively and qualitatively, the diets of predators, are so important (reviewed in 214).

Throughout this paper we make little distinction between biological and natural control. The latter refers to control by predators and pathogens as one element among many natural control factors, biotic and abiotic, that affect invertebrate populations (49). The former often refers specifically to introduced natural enemies rather than to those that already exist in the field, but this creates an artificial distinction. Introduced predators and parasitoids, bred elsewhere and augmentatively released, may exist in the field already at low density, while enemies already found in the field may be the descendants of exotic or indigenous species accidentally or deliberately introduced many years previously. The important factor is control by predators, defined as their ability to reduce significantly numbers of a pest on a crop to a lower mean level that leads to an effective reduction in crop damage, ideally below an acceptable economic damage threshold.

CHANGING ATTITUDES TO GENERALIST PREDATORS

Historical Perspectives

There are many excellent reviews of the history of biological control (48, 49, 82, 117, 229). Here we wish to focus briefly and more specifically on the changing attitudes toward generalist predators.

Indigenous generalist predators have been controlling pests on crops since the dawn of agriculture, and it is probable that early farmers appreciated this. For many centuries, the Chinese have brought ant nests into citrus orchards to control pests, constructing bamboo walkways for the ants between the trees, while date growers used similar practices in the Yemen (55). However, some species of ant protect aphids, psyllids, and leafhoppers in return for honeydew or other nutritious rewards (e.g., 77, 204). Current manipulation of ants in biocontrol must take account of and circumvent such negative attributes.

Erasmus Darwin suggested the deliberate introduction of ladybirds to control aphids in hothouses, while in nineteenth century England women and children would collect and sell ladybirds to hop growers (55). However, it was the dramatic success of the Australian ladybird *R. cardinalis*, imported into California in 1889 to control the cottony cushion scale, *Icerya purchasi* Maskell (Homoptera: Margarodidae) (54, 55), that led to an explosion of interest in biological control in

the early part of the twentieth century. *R. cardinalis* is a stenophagous specialist on scale insects (coccidophagous) but also feeds on other coccids besides *I. purchasi* (e.g., 174). However, it was specialization that came to be seen as the key to success with biocontrol agents through most of the twentieth century. Theoretical developments too have, until recently, concentrated mainly on such specialists, perhaps because such systems are easier to parameterize. It has been suggested that an effective natural enemy must have a high degree of prey specificity, high searching efficiency, high reproductive capacity with respect to the prey, and be capable of surviving in the same range of environmental conditions as the prey (49, 97). Such qualities are clearly more relevant to specialist parasitoids, or highly stenophagous predators, than they are to generalist predators.

There is now a renewed interest in the long-recognized, but little exploited, background-level control exercised by assemblages of mainly generalist predators. This is manifest in the form of conservation biological control, which seeks to enhance natural enemy numbers and their ability to suppress pests using a range of habitat management and diversification techniques (14, 85, 171) (see "Manipulating Predator Populations to Enhance Pest Control"). Thus, biological control may be moving away from an era in which specialist biocontrol agents might, like magic bullets, be introduced to attack specific pests (with all the attendant risks of using such live ammunition) toward a period in which assemblages of native natural enemies are exploited as one of several natural regulatory mechanisms for controlling pests. The developing debate about the merits and demerits of specialists and generalists is central to current thinking.

Specialists Versus Generalists

GENERALISTS OR SPECIALISTS: WHERE AND WHEN IS ONE MORE APPROPRIATE THAN THE OTHER? Most successes in classical biological control appear to have been the result of introductions of specialist natural enemies to perennial crops (forestry, orchards) (4), with relatively little attention given to pests of annual crops in arable ecosystems (72, 227). The assumption has been made that the transitory nature of such habitats, periodically disrupted by cultivation, pesticides, and crop rotations, prevents the development of continuous predator-prey relationships and limits the number and diversity of natural enemies (87, 227). Hawkins et al. (99) analyzed the data in a different way and concluded that successful top-down control of exotic pests on exotic crops is most frequently effected by single species of specialist parasitoid, whereas control of native herbivores on native plants in more natural areas is more often brought about by communities of native generalist predators. Thus, effective control in simple species-poor ecosystems often associated with crops may require a specialist parasitoid operating in a simple food web, whereas in species-rich areas effective control of herbivores is usually the result of multiple links in more complex food webs. However, past successes using particular approaches should not be seen as a straitjacket constraining future strategies. Current attempts to improve the effectiveness of native natural enemies and enhance biodiversity, within both perennial and annual cropping ecosystems, by habitat

management and diversification (125, 171, 211), offer alternative strategies with considerable promise. Even exotic pest populations may be suppressed by assemblages of native natural enemies (60) and such effects can be enhanced, obviating the need to introduce exotic predators or parasitoids.

Although specialist, or at least stenophagous, natural enemies are usually selected for classical biological control introductions, the case for generalists to control pests in temporary agroecosystems has been made (60, 63, 72, 241). To be effective in such habitats the natural enemies should have (*a*) a rapid colonizing ability to keep pace with temporal and spatial disruptions; (*b*) temporal persistence that allows the predator to maintain its numbers when pest populations decline; and (*c*) opportunistic feeding habits that allow the predator to rapidly exploit a food resource, especially attacks by resurgent pests (60). The last two are inextricably connected and characteristic of generalists rather than specialists. Ehler & Miller (63) considered predators with a high reproductive and dispersal ability (previously designated as r-selected), with relatively low competitive capacity, were most successful in temporary agroecosystems.

TRADE-OFFS BETWEEN GENERALISTS AND SPECIALISTS Sabelis (190) identifies three main factors that distinguish predators (by implication generalists) from parasitoids: (*a*) Because predators produce fewer offspring per prey consumed, their numerical response to the prey is delayed and increases more slowly; (*b*) the functional responses of predators soon levels off as they become satiated, leading to relatively low-maximum predation rates for their time budget for searching and handling; and (*c*) the functional responses of predators may be modified further by the availability of alternative prey, resulting in a reduced response to increases in target prey density. In addition, predators with a wide prey range are unlikely to show either an aggregative or a numerical response to any single prey species, unless that prey constitutes a major component of the total available prey (216). The question is, do these apparently adverse properties of generalist predators prevent them from being effective control agents?

It is increasingly recognized that in practice there are trade-offs between the relative merits of specialists and generalists. The factors listed by Sabelis (190) can to a great extent be offset by the fact that polyphagy helps to sustain predators when pest density is low (50, 56, 59, 63, 112, 150). In temperate countries especially, specialists may take a long time to arrive in a crop and build up their numbers early in the season when pest densities are still low. The generalists, however, may be already present, subsisting on nonpest prey (197, 203). Suppression of the pests at this time may either delay or prevent the rapid growth phase that leads to a significant pest attack (33, 124, 241), or it may provide the time needed for the arrival of the specialists. Specialists, particularly parasitoids, have conventionally been considered to be dependent on a low stable equilibrium, with aggregation to host patches, to persist and be effective control agents (16, 94). Generalists may locally drive pests to extinction without necessarily leading to a decline in predator numbers. Thereafter, generalists may adopt a lying-in-wait strategy (50), maintaining their numbers on nonpest prey and preventing re-invasion by the pests.

For effective control, it may not even be necessary for the predators to choose to feed on, or show a density-dependent response to, the pests in preference to other prey if the pests constitute a substantial proportion of the total available prey (150, 216). Much depends on the quantity and quality of available nonpest prey. In practice, a high proportion of generalist predators collected from the field often appear to have empty guts (79, 206), and predators may normally be in a state of suboptimal nutrition (8, 19, 228). Communities of generalist predators, which are only loosely coupled to the densities of their prey, may maintain prey numbers at a low stable equilibrium (16). The more predators and prey interacting with each other within a system the more diffuse the interactions (112) and, by implication, the less likely that coupled relationships with distinct limit cycles will develop. Disruption of generalists, for example with pesticides, can, however, rapidly disrupt equilibrium point control, leading directly to resurgence of known pests and problems with new secondary pests (197).

The work of DeBach (47) and Ehler (59) provide good examples of where generalist predators were more effective than specialists at controlling pests (see also "Experimental Evidence from Manipulative Field Studies"). However, Chang & Kareiva (32) conducted a survey of over 600 papers dealing with biological control of pests from 5 leading journals and could find only 6 studies that actually compared control by specialists and generalists. In only 5 of these was there significant control. This small sample provided no evidence that specialists are more (or less) effective than generalists at controlling pests.

DEVELOPMENTS IN THE THEORY OF CONTROL BY GENERALIST PREDATORS

We make no attempt to detail the modeling literature on predator-prey interactions in the context of biological control, which has been widely discussed elsewhere (15, 17, 45, 94–97, 128, 149, 150, 242). There is space here merely to highlight briefly some of the issues most relevant to the question we pose. Gurr et al. (82) suggest that models in general have been of limited use to biological control in practice. The literature specifically on generalist predator-prey interactions has proved to be even less helpful in practice than models of host-parasitoid relationships, but a consideration of the problems involved can be illuminating.

Problems with Predation Models, Prey Choice, and Functional Responses in the Field

The predation models discussed to date have mainly been stable deterministic equations based on the Nicholson-Bailey model (16, 138, 154). These models assume that a low stable equilibrium must be achieved between the predators and the pests. For this to be achieved, the natural enemy should ideally be host specific, in synchrony with its prey, capable of reproducing rapidly when pest numbers

increase, and have a high searching efficiency. In addition it should need as few pests as possible to complete its life cycle. Such qualities admirably describe many parasitoids, but many more parameters are required to model interactions involving generalist predators, and estimating values for those parameters in the field is often impossible (16).

For example, where densities of two prey species are not reduced by predation, preference indices can be determined by dividing the ratio of the numbers of two prey species eaten by the ratio of the numbers of the two prey species available (37). However, in practice we are only really interested, from a biocontrol perspective, in situations where prey numbers are affected. Relative predation rates on a number of different prey species will be affected by functional responses to each prey, and preferences will change as the relative densities of the component prey species available change. Cock (37) proposed a model for measuring preferences under such circumstances, for which it was necessary to conduct functional response experiments between a predator and each potential prey separately. Even if we assumed that laboratory-measured functional responses were relevant under field conditions, which is doubtful (231), this approach is impractical. The shape of the functional response curves for each relationship will change in response to the quality (as well as density) of alternative prey (110). Even in simple arable ecosystems there may be tens or even hundreds of prey species available to generalist predators, the numbers and spectra of species changing rapidly over time. The absolute and relative densities of these prey will change constantly in response to both predation and other density-dependent and -independent biotic and abiotic factors. Handling times for each prey will vary considerably between microhabitats. The structure of the microhabitats will change as the crop grows, affecting the physical separation of predators and pests on the crop, changing the relative prey-capture efficiencies for prey at different levels within the crop and hence prey preferences. Many invertebrate prey contain toxins (221, 235) yet will sometimes still be eaten and provide nutritional benefits if consumed with other prey (220). The levels of toxins themselves often vary through different life stages of the prey or as toxins are sequestered from foodplants (104, 235). There is evidence that predators also choose to eat certain prey to balance their amino acid requirements (79), and therefore prey choice (and hence preference) may be affected by previous feeding history. The dynamic nature of preference, therefore, makes prediction based upon existing models unreliable other than in extremely simple systems involving small numbers of potential prey in relatively static environments.

An additional problem is that functional responses can be modified by intraspecific interactions between predators, which are affected by predator density, interference, and cannibalism (155). Where predators are both cannibalistic and interfere with one another, as cannibalism reduces predator number, interference decreases. At the same time per capita increases in functional response rates compensate for reduced predator number. Thus, from a biocontrol perspective, increasing the density of individual species of generalist predators may, beyond the point at which interference becomes significant, provide diminishing returns.

Similar processes must also occur during interspecific interactions within predator assemblages.

Switching Behavior

Switching behavior, where the proportion of target prey taken changes from less than to more than expected as the proportion of that prey increases (94, 147), is not easily predictable in multispecies systems. Under certain circumstances, switching may lead to stability of prey populations through feedback loops. Once the density of a prey (Species A) has been reduced to a level where the predator switches to feeding on another prey, Species B, Species A has the opportunity to recover. Such mechanisms mean in theory that switching and preference (e.g., feeding on the most abundant, often aggregated, prey) can enable communities of competing prey to coexist (250).

Effects of Keystone and Higher-Order Generalist Predators on Prey

Keystone species are those that, through their activities, determine community structure (164). Without such predators less competitive members of prey communities may become rare or be driven to extinction (165, 193, 245). This is not always the case. The presence of the fire ant *Solenopsis geminata* (F.) (Hymenoptera: Formicidae) decreased species richness in a tropical agroecosystem, but interestingly, by reducing numbers of other predators resulted in an increase in pest (aphid) numbers (182). Removal of a higher-order predator may, conversely, also allow other intermediate predators to increase in number, which in turn may have a negative impact on prey species at a lower trophic level (112). Effects of keystone predators are certainly important in conservation ecology where they help to maintain rare species and ecosystems (122). More relevantly here, the community instability brought about by removal of generalist predators (for instance by nonselective pesticides) may lead directly to a proliferation of secondary pests. In this instance it is only by removal of key predators that the presence of the most competitive (and therefore frequently most damaging) pests are revealed and their destructive potential realized.

Predator Strategies for Coping with Prey Scarcity

The discussion so far on prey preferences and switching implies that these processes are important. It is possible, however, that a choice is rarely available in the field where food may be scarce (228) and many generalist predators have to eat anything they can get to survive and reproduce (8, 19). Under these circumstances evolutionary processes might favor predators that can exploit a wider range of food resources than competing less polyphagous species. Den Boer (50) points out that to exploit a wide range of prey, generalist predators have evolved simple feeding strategies that, although possibly not always appearing to be optimal, provide

long-term survival advantages. Thus, most spiders catch and eat anything small enough for them to subdue that arrives in their webs, although they may reject prey that is toxic or whose cuticle is too hard to penetrate (153, 178). If the most numerous prey happen to be mildly toxic or nutritionally poor the result may be reduced predator fertility or longevity (220, 221). However, when spiders have an excess of prey, greater prey selectivity is exercised, and distasteful or toxic prey, which would be eaten when prey were scarce, may be rejected (178). Some carabids (like many other predators and parasitoids) may be adapted to searching for aggregated prey. Once they capture and consume a prey item, they conduct a restricted search of the immediate area for more of the same prey (145). It is possible that this behavior, combined with an unsophisticated measure of hunger (gut fullness) (145), can result in predators feeding on large numbers of nutritionally poor but aggregated prey (in years when these prey happen to be abundant), leading to reduced fecundity (50). If this is correct then highly generalist species such as these would be expected to aggregate to overall density of prey (within the range that the predator can subdue). There is good evidence that spiders do indeed locate their webs in areas of overall greatest prey density (93). The carabid *P. melanarius* has been shown to aggregate in areas of high slug (20, 217) and aphid (24, 243a) densities. These prey are so different that it suggests simple aggregation to the highest density of prey that, in arable ecosystems, are often pests. Such a strategy could, therefore, have advantages for biological control. The main restrictions on this strategy are imposed by microhabitat preferences, including suitable web sites for spiders and preferences for particular levels of moisture, light, and temperature exhibited by different species of carabid.

e Case in Favor of Generalists

The case for generalist predators as pest control agents has been argued by theoretical biologists, particularly in relation to ephemeral arable and horticultural crops where polyphagy helps to maintain predator numbers (59, 150). Aggregation to a pest by a generalist predator is likely if that pest represents a substantial food resource (20, 24, 93). Deterministic equations may be inappropriate where stochastic (irregular, nonincremental) events can lead to larger-scale persistence of the predator but local extinction of the prey rather than an equilibrium. In arable ecosystems, stochastic events include cultivation, harvesting, and application of agrochemicals. Species of generalist predator that are well adapted to the transient environments created by annual crops may be adversely affected, temporarily, on a local scale by such events but will persist on a larger scale and can re-invade from adjoining patches or fields. Without such stochastic events these predators would disappear entirely because the ephemeral environment to which they are adapted would change completely. It is clear that if the event happens to be detrimental to the prey but not to the predator (e.g., application of an aphicide), specialist predator numbers may decline too as total prey abundance declines.

Chang & Kareiva (32) describe a single-season theoretical model in which the trade-offs between specialist predators, which can exercise higher prey mortality per natural enemy (search and destroy), and generalists, which may be at greater density early in the season (lying-in-wait), could be evaluated. By running a number of simulations, they showed that increasing either parameter (predator killing efficiency or predator numbers early in the season) could result in a similar pattern of control. The model emphasized the importance of measuring killing efficiency and immigration rates in the field when evaluating natural enemies. They did not evaluate the effects of the availability of alternative prey or pest refugia.

Alternative Prey and Refugia

The question of alternative prey has been discussed by Holt & Lawton (112). In particular they describe the effects of apparent competition (111) between prey species that are attacked by a common predator. There are again trade-offs, associated with increased alternative prey, between promotion of higher predator numbers and diversion of predators from feeding on pests. In some instances this can be exploited in practical biological control by ensuring an abundance of such alternative prey early in the season, allowing predator numbers to increase, followed by a gradual decline in such alternative prey later in the year when pest attacks are expected (197). Practical means of increasing the abundance of alternative prey and hence predators are reviewed later.

Refugia have long been recognized as a critical element in host-parasitoid interactions (16, 100, 106, 148). A relationship may exist between the proportion of a host population that is parasitized and the ability of the parasitoid to reduce the density of the host (100). Thus, the smaller the refuge for the host, the more effective the biocontrol agent. Chang & Kareiva (32) note that if the refugia from a specialist parasitoid and a generalist predator were of equal size, the generalist would be more effective in the long term. This is because the specialist is more likely to go locally extinct than the generalist, which can subsist on alternative prey. However, specialists, because they are well adapted to their host and tend to have a higher searching efficiency (94), can effectively reduce the size of the host refuge. It then becomes a trade-off between the higher searching efficiency of the specialist and the persistence of the generalist. In practice there are likely to be many species of generalist natural enemy attacking any host or prey for every specialist, and the combined searching efficiency of many generalists, using different prey detection systems, may be as or more effective than those of the specialists. In addition, control is likely to be enhanced by complementary natural enemies attacking all life stages (avoiding invulnerable age classes) and different times of year (avoiding temporal refugia) (148).

Coupled Relationships Between Generalist Predators and Their Prey

The coupled relationships and population cycles that develop between specialist natural enemies and their prey are not usually associated with highly generalist

predators. Generalist populations are often assumed to be buffered from significant variation between years by polyphagy (132, 151, 202). In disturbed arable and horticultural systems, invertebrate populations are unlikely to be correlated between years because abiotic factors, such as the weather and agricultural interventions, are thought to have a greater effect than predation on between-year variation in predator and prey numbers (32). Neither scenario leaves much room for long-term coupled relationships. However, in the mammalian literature there are several examples of highly polyphagous predators in the subarctic demonstrating populations cycles with their prey (12, 225), where the prey form a substantial proportion of the total available food resources. Although it has been recognized that loosely coupled relationships can exist between generalist predators and their prey (94, 128), examples from the biological control literature are rare. Where they exist, density-dependent interactions usually involve stenophagous species of, for example, coccinellids or anthocorid bugs over a single season (103, 195, 246). Evidence of longer-term population cycles has been shown in relatively stenophagous species in perennial habitats such as apple orchards (73, 146). The only evidence of a long-term coupled relationship between a highly polyphagous predator and its prey in ephemeral crops within an arable ecosystem seems to be that between the carabid *P. melanarius* and its slug prey (216). In that five-year study one prey group (slugs) formed a sufficiently large proportion of the diet of the beetles to drive changes in the predator population between years, while predation affected slug numbers. There may well be other similar relationships awaiting detection, but they would be restricted to predator species that are resident within fields and have low diffusion rates through field boundaries. In most cases numerical responses will be dominated by immigration and emigration by the predators (and often the prey), making it difficult, if not impossible, to quantify the effects of within-field prey on predator reproduction between years. In the case of slugs and carabids, therefore, the first criterion identified by Ehler (60) for a successful generalist predator in a disturbed temporary ecosystem, namely a strong colonizing ability, does not apply.

EXPERIMENTAL EVIDENCE FROM MANIPULATIVE FIELD STUDIES

The guts of field-collected predators can be examined (by dissection, electrophoretic, immunological and molecular methods) to determine if the predators have eaten pests. On their own such post-mortem methods provide only an approximate indication of predation potential, and interpretation of such data requires care. Pests that have not been killed by the predator may be consumed, or the predator may kill pests yet contain no identifiable pest remains (207). Observations of predation in the field avoid these problems but are rarely adequate to fully quantify the impact that predators may be making on a pest population (80, 209). The most convincing test of predator impact is to manipulate predator density in the field and record any consequent changes in pest abundance, plant damage and crop yield. Evidence from studies that have taken this approach is reviewed below and summarized in Table 1.

TABLE 1 Percentage of manipulative field experiments (for which the design supported statistical testing) where pest abundance was reduced significantly by single species of generalist predators,[a] by assemblages of generalist predators, or by assemblages of natural enemies that included generalist predators[b]

	Percentage (no. studies)			
Pest group	**Single species of generalist predator**	**Assemblages of generalist predators**	**Assemblages of natural enemies, including generalist predators**	**Totals**
Mollusca	89(9)	100(1)	100(2)	92(12)
Acari	79(14)	75(4)	100(1)	79(19)
Coleoptera	89(9)	100(4)	100(1)	93(14)
Diptera	70(10)	43(7)	50(2)	58(19)
Hemiptera	68(31)	78(18)	86(14)	75(63)
Lepidoptera	71(17)	92(12)	100(7)	83(36)
Others[c]	67(12)	83(6)	—	72(18)
Totals	74(102)	79(52)	89(27)	77(181)

[a]For pragmatic purposes in selection of data for review, we arbitrarily defined generalists as species that prey on more than one Order of pest.

[b]Data are collated from published studies (1960–2001) pertaining to 22 countries (6 continents), 42 crops (protected, annual, perennial), at least 82 pest species, and at least 56 species of generalist predator.

[c]Thysanoptera, Orthoptera, and Diplopoda.

The Effectiveness of Individual Predator Species

In the majority of studies, individual species of generalist predator did reduce pest density significantly (Table 1). The predators involved were mites, spiders, earwigs, asilids, bugs, ants, mantids, lacewings, and beetles (carabids, staphylinids, and coccinellids). In general, the studies used controlled predator-prey combinations in field cages (pests reduced significantly in 70% of cases) or inundative releases of predators into open crop plots (pests reduced significantly in 82% of cases). Predators had a significant beneficial effect in reducing crop damage or increasing yield in 20 out of 21 cases (95%). Inundative releases of predatory mites (129) against spider mites and thrips were successful on citrus, grapevines, hops, and in lily propagation. In plot experiments in wheat in China, larvae of the robber fly *Promachus yesonicus* Bigot (Diptera: Asilidae) significantly reduced the density of white grubs *Anomala* spp. (Scarabaeidae) by 21–99% compared with controls and reduced damage to wheat significantly by 68–96% (239). Seven species of ants reduced pests significantly (mainly Hemiptera and Lepidoptera) (167, 232), and often damage, on annual and orchard crops. The ability of the carabid *Abax parallelepipedus* Piller & Mitterpacher to reduce slug numbers and crop damage was related to the growth stages of the lettuce crop into which they were released (212). Releases of lacewings were sometimes successful against aphids, leafhoppers, mites, and lepidopterans on top fruit, hops, grapevines, cotton, and cabbage, but

overall, the pest was reduced significantly in only 9 out of 15 cases (60%). Daane et al. (46) showed that release rate had only a weakly significant effect on success, and it was more effective to release lacewings as larvae rather than as eggs. Releases were often unsuccessful if the pest was already present at high density, emphasizing the need for early releases to obtain favorable predator-prey ratios.

The Effectiveness of Assemblages of Generalist Predators

The impact that assemblages of generalist predators may have on pest populations has been studied mainly with the use of exclusion cages, exclusion barriers, and by insecticidal reduction of predator populations (the insecticide check method). The authors of these studies (Table 1) reported that other natural enemies (specialist predators, parasitoids, and pathogens) were absent or at a low level of incidence during their studies. Pest abundance was reduced significantly by assemblages of generalist predators in 79% of cases (Table 1), and damage was reduced or yield increased significantly for 65% of the 26 cases where effects on plants were measured. There is a tentative suggestion from Table 1 that it may be more difficult for generalist predators to reduce Diptera than Lepidoptera and some of the other pest groups. Root flies and carrot flies in vegetables (175, 224) were not susceptible to significant levels of reduction by carabid and staphylinid beetles and by spiders, perhaps because a large proportion of the life cycle of these pests is spent in cryptic locations that are penetrated only by specialist natural enemies. The impact on hemipterous pests (aphids, leafhoppers, and bugs) by generalist predators (mainly beetles, spiders, and ants) was studied in cereals and other annual crops, and these pests were reduced significantly in 78% of cases and damage/yield affected significantly in 50% of cases (109, 124, 126, 200, 243).

Control failures can be due to predator populations being too sparse at an early stage of pest development or because predator (especially carabid, staphylinid, and spider) activity can be reduced, and pest reproduction increased during periods of hot dry weather at late crop development stages (109). Sucking pests are also influenced by crop fertilizer regimes, and there is evidence from other systems (grass-slug-carabid, apple-mite-mite) that generalist predators may not compensate sufficiently for the higher growth rate of the pest population under high fertilizer regimes (25, 236). Lepidopteran pests were reduced significantly, mainly on forest trees, graminaceous crops, soybeans, and cotton, by a diverse assemblage of predators, usually including ants (35, 59, 187, 240). Their populations were reduced significantly in 92% of cases and damage/yield was affected significantly in all seven cases where it was measured.

The Effectiveness of Assemblages of Natural Enemies that Include Generalist Predators

In some field studies involving exclusion cages, exclusion barriers, augmentative releases, and the insecticide check method, it was not possible to exclude parasitoids, specialist predators (such as syrphids, chamaemyiids, cecidomyiids, stenophagous ladybirds), and vertebrates (birds, snakes, rodents) from control

areas, which were also richly populated with generalist invertebrate predators. Therefore, the observed effects on pest populations may have been due to one of these natural enemy groups or any combination of groups, and the proportional contribution by generalist predators was not determined. Overall, in these studies, pest populations were reduced significantly in 89% of cases (Table 1), and damage was reduced or yield increased significantly in five out of seven cases. Aphids, coccids, and delphacids on top fruit, cereals, alfalfa, and lettuce were reduced significantly in 12 out of 14 cases, but yield was increased significantly in only half of the cases (102, 113, 157). Lepidoptera (on cabbage, cotton, maize, potato, soybean) were reduced significantly in all cases, and crop damage was reduced significantly in the few cases where it was measured (e.g., 28). Although the sample size (number of studies) is relatively small, the broad trends (of natural enemy impact in relation to target pest group) are similar to what was found for assemblages of generalist predators (see above).

Estimating the Potential for Conservation Biological Control

Natural enemies that are attracted to crops and kill pests while resident in the crop provide the raw material for conservation biological control (14). It is possible that these natural enemies (dominated numerically by generalist predators) sometimes make a significant impact on pest populations even before any enhancement measures [such as habitat diversification (211)] have been implemented. A subset of data from Table 1, excluding studies involving inundative releases, can be used to test this. To improve the realism and rigor of the test, it is also sensible to exclude studies that were carried out in sealed field cages (because densities of predator and pest may be abnormal, and foraging behavior is constrained by caging) and also studies using the insecticide check method. Exclusion of the latter is because some of the observed differences between treatments and controls might have been due to insecticides increasing the developmental and reproductive rates of pests, either directly (hormoligosis) or through modification of host plant physiology (trophobiosis). Evidence for such effects can be found in Luckey (131), Brandenburg & Kennedy (21), and Gerson & Cohen (71). After these fairly stringent conditions were met, pests were reduced significantly in 49 out of 67 cases (73%), and damage reduced or yield increased significantly in 22 out of 31 cases (71%), which is an encouraging baseline for conservation biological control.

Additional Negative and Positive Attributes of Generalist Predators Detected During Biocontrol Practice

NEGATIVE EFFECTS Endemic generalist predators may frustrate attempts to control weeds by the introduction of exotic herbivores (61, 75, 226). Generalist predators are also reported to reduce the efficiency of augmentative biocontrol programs by consuming a proportion of the biocontrol agents that are added to crops in inundative releases. For example, resident generalist Heteroptera, lacewings, ladybeetles, spiders, and ants ate larvae and adults of the ladybeetle *Delphastus catalinae* (Horn)

released into cotton and were considered to have impeded biological control of whitefly, *Bemisia argentifolii* Bellows & Perring (Homoptera: Aleyrodidae) (101). Spiders, harvestmen, carabids, ladybeetles, and gryllids ate eggs of *Perillus bioculatus* (F.) (Heteroptera: Pentatomidae) in the laboratory and inhibited control of Colorado potato beetle (*Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae) by inundative release of *P. bioculatus* in potato fields (114). Ants reduced the effectiveness of ladybeetle larvae [*Adalia bipunctata* (L.)] released to control aphids in organic apple orchards (248). Overall, however, ants are extremely useful as predators of a wide range of pests (238).

POSITIVE EFFECTS Generalist predators can wipe out invasion foci of exotic pests, thus helping to prevent establishment in new countries (61). Cook et al. (40) showed that the native generalist predator complex (especially ants and mice) rapidly destroyed pupae of gypsy moth [*Lymantria dispar* (L.)] (Lepidoptera: Lymantriidae) near the leading edge of its spread in the United States. Generalist predators can also reduce the rate of development of resistance breaking by pests on transgenic crops. Generalists were equally abundant on transgenic as on nontransgenic potato (176), and similar results were found for maize (161) and brassicas (181). Being polyphagous, they find alternative foods (including pollen) on crop plants. In contrast, specialist natural enemies, which behave in a density-dependent manner, were virtually absent from transgenic crops where the density of the target pest (their predominant food) was extremely low. Using experimental data and a mathematical model, Arpaia et al. (13) showed that the generalist ladybeetle *C. maculata* De Geer could decrease the rate at which *L. decemlineata* populations adapted to *Bt*-toxins in *Bt*-transgenic potatoes.

The movement of generalist predators can contribute significantly to the dissemination of pathogens of pests (166, 233), and foraging generalists can break up pest aggregations, cause them to drop from plants, and render them more susceptible to parasitism and desiccation (135, 139, 162, 226, 234). Generalists can sometimes maintain pests at a new low level once their numbers have been suppressed by introduced parasitoids (184). The challenge for ecologists and entomologists is to learn how to manage natural enemy communities in such a way that these positive interactions are maximized.

MANIPULATING PREDATOR POPULATIONS TO ENHANCE PEST CONTROL

Most of the literature on generalist predator manipulation is from high latitudes and involves a variety of taxonomic groups. The principal exceptions are rice and sugarcane, where the predators of interest are predominantly spiders and ants. The majority of studies involve enhancement of predator populations without regard to whether it leads to reduced pest populations or crop damage. It is striking, for example, that although carabids have been exhaustively studied and experimentally

shown to be capable of reducing pest populations (141, 212), there have been few attempts to determine whether enhancing carabid populations by field manipulations leads to pest population suppression (123). We emphasize studies that also look for evidence of efficacy.

Brute Force: Inundative Release

Most augmentative releases of polyphagous predators in the field have involved chrysopids, coccinellids, or pentatomids. Usually the animals are reared in mass culture, although coccinellids may be collected at estivation sites (160). Augmentation is sometimes effective in small-scale experiments (e.g., 18, 248), but large-scale successes are sporadic (46, 160). Causes of failure include emigration (57), cannibalism (160), and intraguild predation (101, 249). A promising approach to increasing success rates is behavioral manipulation of the predator (see Food Sprays and Semiochemicals below).

Even when inundative release does result in pest population suppression, it may be uneconomic (219); studies are underway to reduce the cost of rearing and release (120, 213). When augmentation is an integral part of a long-term IPM program, numbers needed, and hence cost, may decline as equilibrium predator populations are established (127). Also, where crops produced by organic or IPM methods command a higher price from consumers, the economics of augmentative release will improve (230). The history of successes and failures of augmentative release has engendered a salutary discussion of the quality control needs for what has become a significant pest control industry (74).

Hedgerow to Landscape: Manipulating the Habitat

The scale of potential habitat manipulations ranges from the microhabitat, including the soil and individual plant or local plant community, to the field, field border and adjacent communities, and the landscape in which fields are embedded (83, 125, 211). The structure of the vegetation may influence predator abundance and activity by a variety of mechanisms. At the level of individual plants and the local plant community, these include effects on predator mobility, adhesiveness and dispersal tendency, provision of alternate food sources and sites for lurking or web attachment, and prey accessibility (10, 41, 189).

STRAW MULCHES Straw mulch uniformly spread on the soil surface may dramatically increase predator numbers, with concomitant reductions in herbivore numbers and increased crop yields. The approach was pioneered in high-latitude vegetable plantings (22, 177), where populations of spiders, coccinellids, and chrysopids were increased. In a tropical rice system (1), spiders, carabids, staphylinids, and ants were increased. In temperate crops straw residues can, however, induce higher numbers of slug pests (217). Although the mechanisms increasing predator populations have been assumed to be providing shelter and buffering the abiotic environment at the soil surface, straw mulch may also support detritivore populations

that serve as alternative prey (244). Sustainability of the approach is increased when straw is produced on the farm.

LIVING MULCHES Plants, including weeds, may be sown, or allowed to invade, a primary crop to provide additional resources or environmental buffering for predator populations. The timing is critical to prevent plant competition from wiping out gains from predator enhancement. Ali & Reagan (7) found that annual broad-leaved weeds increased imported fire ant densities and pest population suppression but, unlike perennial weeds, died back following canopy closure and thus did not adversely affect sugarcane production; the system was more productive and profitable than a conventional weed-free system.

In orchards and vineyards, ground cover often increases overall predator abundance and diversity but seldom leads to enhanced control of pests (26, 42, 180). In a possible exception, by sowing weed strips along rows of an apple orchard, Wyss et al. (247) increased web spider densities on the trees, which may have contributed to a significant reduction in pest aphid numbers through interception of alates. Although traditional herbaceous ground covers have rarely been effective in orchards, adding native trees to tropical cashew plantations might increase ant populations sufficiently to have a significant impact on major cashew pests (168). It should be noted that even where undersowing increases predator numbers, and reduces pest numbers and crop damage, predation may not be a significant causal factor (69).

CONSERVATION TILLAGE There is a sizeable literature on the effects of tillage regimes on predator populations but little on the effects of tillage regimes on rates of predation on pests. *P. melanarius* aggregated in treatments with high slug density and had higher biomass of slug remains in their foreguts, under no-till compared with conventional tillage regimes in oilseed rape (217). Two studies in corn, one on an above-ground pest and the other on a subterranean one, are revealing. Densities of coccinellid and chrysopid species and rates of chewing and chrysopid predation on European corn borer egg masses were differentially and complexly affected by conventional and no-till regimes (9). Southern corn rootworm immatures suffered heavier depredations from acarid mites, centipedes, carabid and staphylinid larvae, and ants in no-till compared with conventionally tilled corn (23).

INTERCROPPING Whereas living mulches are noncrop plants sown within, or allowed to colonize, crop fields, intercrops are systems in which at least two crops are interspersed. Intercropping sometimes raises general predator densities, but few studies have evaluated the efficacy of the treatments at enhancing biological control; when efficacies have been evaluated the results are often disappointing or mixed (38, 58, 102, 169). Many unsuspected factors may determine the outcome. In a detailed study of a traditional intercropping system, Andow & Risch (11) found that it was not crop diversification per se, but rather the interaction of crops, predator dietary preferences, and specific plant resource and alternative prey densities and dispersions that determined the outcome.

DISCRETE SHELTERS AND WEB SITES A few predator taxa have been increased in number, with demonstrable biocontrol impact, by the provision of discrete shelters or foraging sites. Straw shelters show promise for attracting and retaining spiders, harvestmen, carabids, and staphylinids, with a concomitant reduction in plant damage nearby (88). Crates placed in soybean fields attracted web spiders, which consumed sufficient herbivores to decrease herbivory significantly on adjacent plants (31). Nesting boxes significantly increased the impact of vespid wasps on lepidopterous pests, but the tendency of wasps to seek alternative prey in other fields reduced their effectiveness (78). Overwintering boxes increased survival of lacewings, but this did not increase pest mortality significantly (196). In all such cases, the nature and number of shelters required poses logistical challenges. An advantage of straw shelters is that they might be constructed from material already on the farm, thereby enhancing sustainability of the method.

Providing artificial web sites by placing holes in the soil raises densities of wheat field linyphiid spiders by between one and two orders of magnitude, greatly increasing their already considerable aphid killing power (2, 191). This modification does not appear to work in the U.S. Great Plains (M.H. Greenstone, unpublished data), possibly because the most responsive species, *Lepthyphantes tenuis*, does not occur there (81).

FIELD BORDERS Borders are the interface between field level and landscape scales of vegetative diversification. Although they may simply consist of weedy strips or topographically differentiated zones surrounding fields, they may also be deliberately planted with noncrop plants to provide shelter or food for natural enemies. Field borders often contain diverse and abundant generalist predator assemblages, but relatively few studies have been performed to determine whether this actually contributes to biological control within fields.

Numerous plants have been investigated for border plantings as sources of nectar and pollen to provide alternate food for predators (3, 43). However, because they may also benefit pest populations, plants intended for planting must be selected with care (85, 125). *Ammi visnaga*, a Eurasian summer annual, harbors large populations of *Orius* and *Geocoris* spp. (Heteroptera: Anthocoridae; Lygaeidae), which may reduce pest populations on adjacent crop plants (27).

Irrigated rice in the Philippines is grown in small fields that are surrounded by raised bunds. These harbor diverse ant species assemblages that exert significant biological control on a variety of pest species (237).

THE LANDSCAPE Economic imperatives for farmers to diversify cropping systems (e.g., 52) offer an opportunity to manipulate predator populations, and their efficacy as biocontrol agents, by designing optimal landscape mosaics of crop fields and noncrop habitats. Investigations to date have consisted of descriptions of dispersions of predator populations across landscape elements and models whose goals are to maximize predator populations in the landscape (66, 89, 136, 222). Evaluation awaits future opportunities to perform large-scale agroecosystem landscape manipulations.

Food Sprays and Semiochemicals: Manipulating Individual Predator Behavior

One reason why habitat manipulations do not always work is that predators either arrive too late to arrest growing populations or depart before exerting effective control. Food sprays or semiochemicals may attract naturally occurring predators or retain released animals. Potentially useful semiochemicals include conspecific aggregation pheromones, pest kairomones, and synomones released from the prey-plant complex.

Simple sugar solutions or more complex concoctions may attract, arrest, and retain some general predators (29, 68, 86). The efficacy of this approach may depend on local predator densities and the availability of naturally occurring foods (29, 218). Commercial releases of green lacewings failed to control black bean aphid in California sugar beets, but application of a food spray containing yeast hydrolysate, sucrose, and molasses increased densities of *C. carnea* (Neuroptera: Chrysopidae) eggs and adults; the spray may effect control by recruitment of indigenous animals more effectively than mass release (62). The use of food sprays needs to be fine-tuned. For example, increased consumption of aphids by coccinellids may reduce natural honeydew production, which may in turn reduce naturally occurring parasitism (67). Sucrose sprays or granules may also attract or retain coccinellid, cantharid, and ant predators of some forest pests (144, 240). Investigations of the effect of commercially produced food sprays on the generalist predator complex attacking *Helicoverpa* spp. (Lepidoptera: Noctuidae) in Australian cotton fields showed that coccinellids, melyrids, nabids, and chrysopids, but not spiders, were increased in density (143); this highlights the need to understand which members of the generalist predator complex have the most impact on pest populations.

Kairomones are utilized for prey finding by many generalist predators (205); pest pheromones used for mating disruption may also have an indirect beneficial effect on generalist predators by reducing the use of broad-spectrum pesticides (e.g., 152). Synomones produced by the pest-plant complex may also be attractive to predators (188, 194).

Conspecific aggregation pheromones, which are best known from pentatomids and a few other heteropteran families (4, 6, 142), show great promise as adjuvants for mass release programs (5, 192). Furthermore, they may be exploited as host-finding cues by other natural enemies (4). Aggregation pheromones, such as that found by Peschke et al. (170) in a staphylinid beetle predator, may act synergistically with prey kairomones (188, 192).

Integrated Manipulation

Ant communities can be manipulated to some extent, to emphasize species of positive biocontrol value, by selective poisoning and supplemental feeding and by provision of nesting material. Some species can be easily moved (e.g., colonies of wood ants), which further improves the options for positive management (30, 34, 232). Ant communities can be extremely species rich in tropical crops, with

99–158 species in different crops. Studies aimed at a greater understanding of the functioning of ant communities are needed on which to base optimization of their management.

CONCLUSIONS AND FUTURE RESEARCH NEEDS

Both biocontrol theory and practice suggest that generalist predators can be effective control agents. Field studies show that individual species of generalist predator can reduce pest numbers by a significant degree, and in some cases reduce or prevent crop damage. This evidence is mainly from closed cage studies and inundative releases and shows the potential for pest control by individual predator species, providing that predator-prey ratios and the timing of introductions are optimized. There is also solid evidence from manipulative field studies that assemblages of generalist predators can reduce pests and yield loss to a significant degree. Most studies do not report whether complexes of generalist predators reduce pests below economic thresholds, but the results are encouraging and support the efforts to develop effective techniques of conservation biological control. Generalist predators also contribute to pest control successes achieved by an interacting community of different types of natural enemy. Few studies have disentangled the roles of each group of natural enemy in these interacting communities, but already it is becoming clear that interactions can have negative as well as positive implications for biological control and that the net effect of the interactions can vary with crop and season. Generalist predators have some unique biocontrol functions that are denied to specialists; they can impact immediately on immigration foci of exotic pests, and they can reduce the rate of resistance breaking by pests on transgenic crops. This positive evidence for the value of generalists supports the paradigm-shift that suggests that, on theoretical grounds, generalists can be at least as effective as specialists under many circumstances. We have also shown that there is scope for increasing the impact of generalists through habitat diversification at various scales and perhaps by behavioral manipulation with semiochemicals. We consider that detailed research into such enhancement techniques, coupled with strategic research aimed at gaining a full understanding of the functioning of natural enemy communities, will pay great dividends in the long run by improving the efficiency of biological control in practice.

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