Proceedings of the Eighth International Symposium on Biological Control of Weeds
2-7 February 1992, Lincoln University, Canterbury, New Zealand.
Delfosse, E. S. and R. R. Scott (eds.). DSIR/CSIRO, Melbourne, pp. 83-91 (1995).

Evolutionary History of Pest-Enemy Associations

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In an evolutionary context, there are at least 4 categories of pest-enemy associations, as opposed to just new versus old. "New" associations exist when the pest and enemy have no coevolutionary history; however, such associations should be considered "recent" after the pest and enemy have had the opportunity to coevolve for some period of time. In "quasi-old" associations, a formerly coevolved pest-enemy system is reunited, but only after the pest has had the opportunity to evolve free of its natural enemy for a considerable amount of time. "Old" associations exist where pest and enemy have a long and continuous coevolutionary history. This classification can also be applied to multi-species assemblages of enemies (e.g., "new exploiter" associations). It is suggested that the type of pest-enemy association can have implications for introduction strategy in classical biological control of both insect pests and weeds, and that such strategies should be evaluated whenever possible. The introduction of *Encarsia aurantii* into California for biological control of obscure scale (*Melanaspis obscura*) is described and used to illustrate the concept of "target-specific" introduction strategy, in which a blend of induction, deduction, experience, intuition, and inspiration is employed to derive an introduction strategy to suit the particular needs of a given pest problem.

Introduction

Biological control of weeds through introduction of stenophagous phytophagous insects and biological control of phytophagous insects through introduction of predaceous and parasitic arthropods are based on the same set of ecological principles and thus have many scientific and practical issues in common. One such issue is the evolutionary history of the target pest and the enemies chosen for introduction. Pimentel (1963) noted that enemies which had no coevolutionary history with the pest had been successfully employed in classical biological control, and further suggested that the lack of co-evolutionary history was instrumental to their success. Hokkanen and Pimentel (1984) further elucidated this concept, and even suggested that such "new" exploiter-victim associations should be the preferred method in selecting biological-control agents. Hokkanen (1985) also extended the argument to include plant pathogens utilized in weed control. Goeden and Kok (1986) criticized Hokkanen and Pimentel's thesis as it related to biological control of weeds, whereas Waage (1990) was unable to verify the hypothesis with respect to biological control of insect pests. In the latter case, old associations showed a higher success rate, although new associations were successful also. In contrast, Dennill and Moran (1989) analyzed herbivore-crop associations in South Africa (considered analogous to insect-weed associations), and concluded that new associations between herbivore species and host plants may have potential in biological control of weeds.

My purpose here is to argue that the conventional dichotomy of new *vs.* old is insufficient to characterize the nature of pest-enemy associations which arise in classical biological control. I suggest that there are at least 4 types of associations, rather than 2. First, there are of course "new" associations, in which an exotic enemy is introduced against a target pest, and the 2 have no coevolutionary history. (New associations also result when native agents exploit an introduced pest species.) Many of these introductions have resulted in establishment, followed by sustained pest-enemy interaction for a relatively long period of time. For these associations, which are no longer very "new," I suggest the term "recent." In "quasi-old" associations, a previously co-evolved pest-enemy association is reunited in a new location, but only after the target pest has been established for a long period and thus has had sufficient time to undergo evolutionary change in the new environment. Finally, there are "old" associations, in which a coevolved natural enemy and target pest are reunited relatively soon after the latter is introduced into a new environment. New and recent associations represent 2 points on the same continuum, as do quasi-old and old. It is important that we reconsider the controversy over old *vs.* new associations in light of these categories, not only because we stand to gain a better understanding of pest-enemy interactions, but also because of the relevance to database analysis and introduction strategy in classical biological control.

New Associations

There is little doubt that enemies having no coevolutionary history with the target pest have been successful in classical biological control of both insect pests and weeds. However, I am not sure that this should be the "preferred" strategy, as suggested by Hokkanen and Pimentel (1984). I am also uncomfortable with the putative explanation for the success of new associations–*viz.*, that new associations are successful because of the absence of coevolved "homeostasis" between pest and enemy. In this context, it is important to consider alternative hypotheses, for just because a new association results in success, this does not necessarily mean that the postulated mechanism is empirically verified.

In those cases where new associations have resulted in some degree of success, it is also important to assess the control potential of the introduced agent in its native home. We may find that the insect simply has the attributes of a successful natural enemy, such that it would provide control of a number of taxonomically-related target pests, regardless of previous coevolutionary history. The introduction of the gall midge, *Rhopalomyia californica* Felt (Diptera: Cecidomyiidae), into Australia for biological control of *Baccharis halimifolia* L. (Asteraceae) may be a case in point. The target weed is native to coastal areas of the eastern and southeastern United States, whereas *R. californica* occurs only in central and northern California where its larvae develop in terminal galls on a related species, *B. pilularis* De Candolle. In 1982, *R. californica* was introduced into Queensland; the midge established and has shown considerable promise for biological control of *B. halimifolia* (McFadyen 1985). This is not surprising because my own investigations indicated that *R. californica*, when freed from its natural enemies, would also be an effective natural enemy of *B. pilularis* in California (i.e., no coevolved "homeostasis"). During 1981-2, portions of the San Francisco Bay Area were sprayed repeatedly with malathion-bait mixture as part of the eradication campaign against Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae). In a heavily sprayed area where *B. pilularis* was plentiful, the midge population exploded (after 24 applications) and ultimately reached levels 90 times greater than those observed in an adjacent unsprayed area (Ehler *et al.* 1984). This outbreak was attributed to wholesale destruction of natural enemies of the midge, chiefly predators of eggs and neonate larvae, and parasites of endophagous larvae. *Baccharis* plants in the spray zone were so devastated by the gall midge and other insects that the study had to be terminated prematurely. Measurements taken several years later revealed that the midge population had returned to normal (Ehler and Kinsey 1991). At the height of the outbreak, a large proportion of the *Baccharis* terminals were galled by the midge, a clear indication of the potential of this biological control agent when freed from the restraint of its natural enemies. Similar situations exist in other disturbed environments in northern California, including urban areas, where the midge has temporarily escaped from its natural enemies. If the introduction of *R. californica* is eventually rated as a success in Queensland, the fact that it is a new association with *B. halimifolia* may be largely irrelevant. A similar situation may also exist in the case of other successful "new" associations, and this possibility should certainly be investigated.

Recent Associations

After a new pest-enemy association has existed for a relatively long period of time, it is difficult to still consider it as new, because both pest and enemy may have undergone coevolutionary adjustment. The amount of time required for this change in status will of course vary with rate of evolution in the particular organisms. Classical biological control of insects has been practiced on an organized basis for just over 100 yrs, so there are a number of new associations which might now be considered as recent. Those associations which originated fortuitously prior to 1889 might be even better examples. The number of generations/yr is of course more relevant than the total number of years, so this effect can be expected to be more pronounced in those cases where both pest and enemy are multivoltine. Classical biological control of weeds has been practiced on an organized basis for just under 100 yrs (Goeden 1988), and presumably there are new pest-enemy associations which might now be classified as recent. An obvious candidate would be *Cactoblastis cactorum* (Berg) (Lepidoptera: Phycitidae) *vs. Opuntia inermis* De Candolle and *O. stricta* Haworth (Cactaceae) in Australia. This introduction occurred over 60 yrs ago and is certainly one of the most successful cases in classical biological control of weeds (Moran and Zimmerman 1984). In their database analysis, Hokkanen and Pimentel (1984) were correct to score this success as a new association, for in 1925 it clearly fit the category. However, as their basic hypothesis suggests a gradual lessening of an enemy's ecological impact over time, recent associations such as this present a new opportunity to assess this controversial hypothesis. This aspect of the controversy should definitely be explored whenever possible, both for pertinent insect pests and weeds. In doing so, we must also keep in mind that reduced severity on the part of the biological control agent can be due to other factors; e.g., incumbent enemies that respond (or perhaps adapt) to this new resource and thereby reduce the agent's effectiveness.

For some target pests, we may have the choice between a new *vs.* recent association involving the same enemy. For example, *B. halimifolia* is a target weed both in its native home (e.g., Texas) and in transcaucasian Georgia. The gall midge *R. californica* is available from either *B. pilularis* in California (new association) or from *B. halimifolia* in Queensland where it has been associated with its new host for about 10 yrs. (Note: in Queensland, *R. californica* is clearly in the early stages of the new-to-recent continuum.) Such options should be considered when devising introduction strategies, particularly in cases where our ability to establish a new association is perceived to be relatively reduced. In such cases, a more recent association might be more appropriate.

Quasi-old Associations

There are many examples in classical biological control where the eventual introduction and establishment of an enemy from the native range of the target pest is not achieved for 50-100 yrs or more after the pest first established. Because of founder effects (including genetic drift), the surviving population may be considerably different from the source population. Furthermore, it is reasonable to assume that the target pest has had the opportunity to undergo evolutionary change as a result of the (1) absence of selective forces found in its native range and (2) presence of new selective forces in the exotic range. Unfortunately, empirical data to support this prediction are scant (Baker and Stebbins 1965, Murray 1985), and although there is considerable theoretical work on this question, it is concerned primarily with genetic changes in founding populations which might eventually lead to speciation (e.g., Carson and Templeton 1984, Barton and Charlesworth 1984). Nevertheless, there is good reason to expect that many introduced pests undergo considerable genetic change in the new environment (see also Myers 1978). For example, numerous insect pests and weeds have developed resistance to pesticides in a relatively short time (Gould 1991, Warwick 1991), a clear indication of their evolutionary potential. Introduced pests, particularly insects, are often under considerable pesticide pressure, more so perhaps than in their native home where they may be kept at relatively low levels by their natural enemies. In addition, some weeds may hybridize with either closely related species or conspecific races in the new environment, further altering the genetic structure of the population (Mulligan 1965, Sands and Harley 1980, Warwick 1991). Recent studies indicate that populations of herbivores and the structure of herbivore guilds can be altered in zones of hybridization (Whitham 1989, Whitham *et al.* 1991). Finally, some weeds were originally introduced as ornamentals and may have undergone considerable artificial selection. In view of these considerations, it is important to consider the amount of time the target pest has already existed in the exotic range before the arrival of one of its coevolved enemies. This is especially true for annual and biennial weeds, compared to long-lived species, such as woody perennial weeds. As the interval between pest introduction and natural enemy establishment lengthens, the justification for classifying these as old associations decreases, hence the term "quasi-old." In fact, many of these so-called old associations may be "more new than old!"

Quasi-old associations raise some new issues in applied biological control. For example, associations previously considered to be old for the purpose of database analysis should be reassessed, and a new analysis performed if warranted. We should also explore the possibility that rates of establishment and success can be influenced by the length of time that the target pest has existed in the exotic range prior to introduction of a natural enemy. There is some evidence to suggest that the rate of establishment of natural enemies of insects and arachnids worldwide has actually declined since the early days (Hall and Ehler 1979). Similarly, both Crawley (1989) and Julien (1989) suggest a downward trend in rate of success for biological control of weeds. If these trends are real, rather than artifacts of the empirical record, it would be instructive to determine the contribution of quasi-old associations, particularly for recent introductions against target pests that established over 100 yrs ago. On the other hand, it is possible that an introduced weed, free of its coevolved herbivores for a considerable amount of time, could gradually lose its herbivore defenses, such that a natural enemy from the native home might then be more effective in the new environment compared to the native one (see also Wapshere 1973).

Genetic variability in target pests has not received its share of attention compared to similar variability in natural enemies. It is evident that host incompatibility has been a common problem in classical biological control of weeds (Sands and Harley 1980, Ehler and Andres 1983), and may have contributed to the lack of success noted above. Both Burdon *et al.* (1981) and Crawley (1989) suggest that biological control has been more successful against weeds displaying greater genetic homogeneity, compared to more genetically variable species. The latter species would seem more likely to undergo post-colonization change, thereby perhaps increasing the chance of host incompatibility for an imported enemy from the native range of the pest. If this is indeed the case, there would be good justification for a quick response when such a newly introduced pest is first discovered–i.e., assuming we wish to re-establish an old association. This will, of course, be easier in biological control of insect pests compared to weeds, because candidate enemies can be cleared for release in a relatively short period of time.

Old Associations

We should continue to employ old associations in classical biological control (as advocated by Dennill and Moran 1989), but at the same time we should strive to explore the implications of the Hokkanen/Pimentel hypothesis. Where such associations have been reunited in an exotic region and resulted in successful biological control, they should be monitored for any signs of decreased severity in enemy intensity over time. While this may seem scientifically trivial to some, it is important to remember that both policymakers and the general public are rightly concerned about the degree of permanence in classical biological control.

An appropriate example from biological control of insect pests is cottony-cushion scale, *Icerya purchasi* Maskell (Homoptera: Margarodidae), which has been under virtual complete control in California for just over 100 yrs. In this case, natural enemies were introduced from Australia and New Zealand *ca.* 20 yrs after the scale was first observed in the state; of these, vedalia beetle, *Rodolia cardinalis* (Mulsant) (Coleoptera: Coccinellidae), and a parasitic fly, *Cryptochaetum iceryae* (Williston) (Diptera: Cryptochaetidae), were successful in bringing cottony-cushion scale under control. This level of control has evidently been maintained since then, and investigations by Quezada and DeBach (1973) and Thorarinsson (1990) reveal no evidence for a lessening in the severity of these 2 natural enemies. Nevertheless, this pest-enemy association should be continually monitored. In biological control of weeds, an appropriate example would appear to be *Dactylopius ceylonicus* (Green) (Homoptera: Dactylopiidae) *vs. Opuntia vulgaris* Miller (Cactaceae) in northern India (Moran and Zimmerman 1984, Goeden 1988). This pest-enemy association was reunited almost 200 yrs ago, shortly after the pest was first noted. Thus, it would seem appropriate to assess the severity of the enemy at this time, in addition to continuous monitoring of the pest-enemy association for evidence of reduced intensity of exploitation by the cochineal scale.

Unfortunately, long-term data on ecological impact of successful natural enemies are seldom, if ever, available. In view of this, perhaps the best we can do at this point in time is to determine whether or not the level of biological control today could actually be any better. My observations for cottony-cushion scale in northern California suggest that both imported natural enemies are about as effective as they could possibly be.

It is also important to investigate old pest-enemy associations in their native range, particularly in cases where enemies are clearly ineffective or not very abundant. In this context, Wapshere (1973) and Myers *et al.* (1989*b*) suggested that insects that are rare in their native environment may in fact be successful as biological-control agents against weeds because the target plant may not have evolved compensatory responses to the type of damage they cause. This hypothesis certainly warrants testing, but at the same time we must not ignore the underlying reasons for the rareness or ineffectiveness of a natural enemy (Myers *et al.* 1989*a*). For example, in the parasite guild associated with *R. californica*, 2 of the 4 obligate primary parasites are relatively rare and ineffective, but apparently for different reasons (Ehler 1986). One species, *Torymus baccharidis* (Huber) (Hymenoptera: Torymidae), has a relatively low reproductive rate and does not appear capable of controlling its host even when free of the hyperparasites and interspecific competitors in the guild (Force 1970, 1974). In contrast, an undescribed species of *Tetrastichus* (Hymenoptera: Eulophidae) has a relatively high reproductive capacity, but it also appears to be an inferior competitor. However, when freed from its competitors and hyperparasites, this species is one of the most effective members of the parasite guild (Force 1970, 1972, 1974). This suggests that natural enemies which are ineffective in their native homes may be of great value in classical biological control whenever such ineffectiveness (or rareness) is due to interspecific interactions, rather than an intrinsic limitation (e.g., low reproductive capacity) or some kind of "ecological homeostasis."

Enemy Assemblages

Our view of the evolutionary history of pest-enemy associations need not be restricted to single-species systems, for the attendant issues may be relevant to enemy assemblages as well. Here, I am particularly concerned with guilds of enemies, where "guild" is defined as a group of species that exploit the same class of resources in a similar way (Root 1967). In an evolutionary context, there are at least 3 kinds of guilds: natural, restructured, and synthetic or anthropogenic (Ehler 1992).

A natural guild would consist of those species which exploit a developmental stage or plant structure of a particular host species in its native home and have a long coevolutionary history with both each other and their host. Natural guilds can be "restructured" by the addition of 1 or more exotic species; this can occur fortuitously, or through classical biological control (e.g., of a native pest). Synthetic guilds are derived strictly through human activity; e.g., introduction and establishment of enemies for control of exotic pests (classical biological control) or release of commercially available species (augmentative biological control). In many cases, members of synthetic guilds have little or no coevolutionary history. Restructured guilds, and those synthetic ones containing non-coevolved species, both qualify as "new-exploiter" associations (or recent, as the case may be). Of the 51 successful projects in insect control which Hokkanen and Pimentel (1984) rated as "new associations," 26 involved 2 or more enemy species, representing various kinds of new-exploiter associations (Ehler 1990). Thus, both old and new exploiter associations have been successful in classical biological control of insect pests, and there appear to be similar examples among weeds as well. The next question to be addressed, in data-base analysis and applied biological control, is the relative merit of such exploiter associations. We should also compare the guild structure of new exploiter associations with that of natural or coevolved guilds. As a large part of current ecological theory is derived from natural systems, such comparisons would seem critical to making biological control a more predictive science.

Practical Application

The manner in which the evolutionary history of a given pest-enemy association might be exploited in applied biological control will vary with the nature of the particular pest problem. In the space that remains, I will describe a relevant example from my research in California.

Obscure scale, *Melanaspis obscura* (Comstock) (Homoptera: Diaspididae), is a native scale which is distributed throughout the eastern USA where it is associated primarily with oaks, *Quercus* spp. (Fagaceae) and pecan, *Carya illinoensis* (Wangenheim) K. Koch (Juglandaceae). As expected, this scale is exploited by a complex of enemies in its native home, including a guild of parasites, several predators, and at least 1 pathogen (Baker 1933, Stoetzel and Davidson 1971, Potter *et al.* 1989). The parasite guild consists of at least 12 species in 8 genera, and was apparently "restructured" by the introduction of *Encarsia aurantii* (Howard) (Hymenoptera: Aphelinidae) over 100 yrs ago. This is a cosmopolitan species which has been reared from a number of diaspidid scales. My working hypothesis is that *E. aurantii* is of Oriental origin, and that it was fortuitously introduced into the United States in diaspidid hosts such as yellow scale, *Aonidiella citrina* (Coquillett), and Florida red scale, *Chrysomphalus aonidum* (L.). Because of its broad host range, it was sufficiently preadapted to exploit obscure scale, thereby restructuring the attendant parasite guild. The introduction of *E. aurantii* resulted in (1) a new association with obscure scale and (2) a new-exploiter association with other members of the parasite guild. However, at this point in time, these associations should probably be regarded as recent.

Obscure scale has been imported into California at least 3 times during this century (Ehler 1992). Two of these infestations were eradicated, whereas the third (in Sacramento) resisted eradicative efforts. It became a target for classical biological control in 1981. Because the scale infestation in Sacramento was limited in scope and spreading very slowly, there was time for a more experimental approach to classical biological control, based in large part on preintroductory investigations. Exploration for candidate enemies was conducted between 1983-8, and concentrated on parasites associated with obscure scale on pecan in southern Texas. Scale-infested pecan twigs were collected in Texas, transported to Davis, California, and held in quarantine for parasite emergence. Four species in the family Aphelinidae consistently made up over 75% of the individuals which emerged; *viz.*, *Ablerus clisiocampae* (Ashmead), *Physcus varicornis* (Howard), *Coccophagoides fuscipennis* (Girault), and *E. aurantii* (Ehler 1992). One of these (*A. clisiocampae*) is believed to be a secondary parasite.

Given at least 3 dominant primary parasites in the guild, there were a number of introduction strategies possible. However, I chose a single-species release of *E. aurantii*, for the following reasons. This species has a relatively short generation time (*ca.* 45 d under laboratory conditions) whereas the host is univoltine. The culture which cleared quarantine was thelyotokous, a clear advantage for a colonizing species and biological-control agent. Finally, its lack of host-specificity and presumed invasion (and restructuring) of a diverse, natural parasite guild suggested that *E. aurantii* is an opportunist. Therefore, I decided to release this opportunist free of its hyperparasites and competitors. Clearly, the evolutionary history of this pest-enemy association played a major role in my decision.

In 1987, *E. aurantii* was cleared for release. In the fall of that year, *ca.* 50 females were released followed by >11,000 females during the late summer and fall of 1988. Immediate establishment was obtained. Evaluation of the ecological impact of *E. aurantii* is now underway. Preliminary results are very encouraging.

Introductions of biological control agents are indeed "grandiose field experiments" (Myers 1978). However, these "experiments" are usually planned to suppress the target pest, rather than to test one of several introduction strategies. This is certainly understandable, especially in situations where there is an urgent need to secure and release effective agents for suppression of a serious pest. At the same time, however, there is a critical need for experiments of the sort described for obscure scale. There will of course be problems of experimental design; e.g., the obscure-scale experiment is "pseudoreplicated" (only 1 infestation available) and it is not possible to simultaneously assess 2 or more introduction strategies. Nevertheless, experimental introductions such as this should be attempted whenever feasible, and I would urge weed control workers to seek the appropriate settings and pursue similar approaches when possible.

Concluding Remarks

The evolutionary history of pest-enemy associations is but one part of the central problem of introduction strategy in biological control. By introduction strategy, I simply mean the choice of a species or combination of species to introduce for suppression of a target pest in a given environment. There are 2 broad approaches to the problem: (1) the empirical approach, in which one simply releases all suitable enemies that are available with the hope that the best species or combination of species will be sorted out in the field; and (2) the predictive approach, in which extensive pre-introductory investigations are conducted in order to determine the best species or combination of species to release (Ehler 1990). These are clearly 2 points on a continuum and it is possible to adopt elements of both. The predictive (or analytical) approach can be carried out in either a: (1) reductionist manner, with emphasis on key attributes of a species, such as searching capacity, host-specificity, etc.; or in a (2) holistic manner, with emphasis on ecological interactions at the community level, such as guild structure, species packing, etc. (Waage 1990). In the context of introduction strategy, we may have read too much into the inductive search for general patterns, such as the attributes of some ideal natural enemy that would be suitable for most any control program. This is not to say that the inductive method should be ignored, for the patterns derived (as in database analysis) can be useful in generating and testing hypotheses, etc. We should be equally skeptical of deductive derivation of practical guidelines, particularly those based on simplistic mathematical models of predator-prey systems.

There is a growing concern that introduction strategy should be developed on a case-by-case basis, rather than relying on generalizations. With this in mind, I suggest that whenever the option exists, each target pest problem should be viewed as sufficiently different–at least until there is good reason to think otherwise–to justify a "target-specific" introduction strategy.

Such strategies would take into account the attributes of the target pest, the type of suppression desired, the ecological structure of the target environment, and the natural-enemy pool which is available. Modifications in the strategy would likely be required in cases where exotic enemy species are established sequentially. This was in fact the kind of approach I used in the introduction of *E. aurantii* for control of obscure scale in California, and it should also apply to biological control of weeds where so often the ecological structure of the target system is critical to the success of the introduction (*cf.* Harris 1991).

Target-specific introduction strategies are neither strictly reductionist or holistic nor deductive or inductive. Instead, they represent a blend of induction, deduction, experience, intuition, and inspiration. Some good fortune along the way will also be helpful.

Acknowledgments

I thank L.A. Andres, V.C. Moran, J.H. Myers, J. Rosenheim, and R.T. Roush for critical review of an earlier version of the manuscript.

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