Biological Invasions: a Global Perspective
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CHAPTER 3

Which Insect Introductions Succeed and Which Fail?

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3.1 INTRODUCTION

Why some insect introductions succeed (survive) and others fail to survive has been a central question since the first systematic studies of introduced insects (e.g. Elton, 1958; Baker and Stebbins, 1965) but no satisfactory answer has emerged for several reasons.

Firstly, the question has been asked at several levels. For example, some studies have focussed at a very high level: why insects from one biogeographic region tend to be more successful at invading another region than vice versa, or why insects of certain kinds of habitats seem to be more successful at invading new regions than insects of other habitats. Other studies have looked more proximately at the causes of success and failure: for example, what life history traits affect success? The nexus between the levels has not been established. For example, if it were true that mainland species are more likely to be successful when they invade islands than vice versa, is the reason that island and mainland species differ in characteristic ways with respect to life history?

Secondly, attempts to understand success or failure of invasions have not always controlled for opportunity. For example, it is well known (e.g. Greathead, 1976) that European insects have successfully invaded many other regions more frequently than species from those regions have invaded Europe. This imbalance is part of a larger pattern—European plants, vertebrates, even disease organisms seem to have been more successful at invading a number of other regions than vice versa (Crosby, 1986). However, before seeking to explain this disparity by invoking superiority of European species on one grounds or another, one must ask if some fraction of the pattern simply results from more European species being transported to other regions than vice versa. Many ships sailing from Europe to North America loaded soil as ballast in southwestern England (Lindroth, 1957). In North America, the soil was unloaded and exchanged for cargo. Small wonder that 90% of the insects known to have been introduced into North America before 1820 were beetles, many of them soil-dwellers found in southwestern England (Sailer, 1983). A similar transport of ballast from South

America to North America about a century later brought, among other species, the imported fire ant, *Solenopsis invicta* (Sailer, 1983). In both cases, because the transport was one-way, one does not try to explain the greater establishment in one site as a consequence of competitive or other superiority of one biota's species over the other's. However, these cases happen to be ones for which we know about the differential opportunity for successful invasion because of differential transport. Usually there are no firm data on rates of transport by humans from one site to another.

This gap is part of a larger problem that besets attempts to explain success or failure: we know about a much larger fraction of successes than of failures. Without knowledge of the failures, it is impossible to answer questions at any of the levels listed above simply by observing numbers of successful invasions in different habitats or regions, or numbers of successful invasions by species with particular suites of life history traits. Of course it is possible to say which source area or which habitat or which sort of life history typifies the most survivors but one cannot determine anything about probabilities: whether invaders of disturbed habitats are more likely to succeed, for example, as opposed simply to being more numerous. For insects, the only data that begin to approach equal coverage of successes and failures are those on biological control.

Thirdly, even without equal data on successes and failures, it would be possible to seek generalities in the proximate reasons why particular species succeed or fail if the trajectories of enough species were studied carefully, particularly trajectories of failures. The best way to do this would usually be experimentally because controlled experiments are best at implicating or eliminating potential factors as reasons for failure. If one suspects predation by ants prevents establishment, one precludes ants. Experiments are costly and difficult, however, and one would not expect strong experimental evidence on most cases. Thus, perhaps the best one could hope for would be detailed observations, especially on naturally occurring mortality in recently initiated populations. But detailed observations are exceptional. Usually the reports, if they suggest any reason at all for a failure, base the suggestion on rather casual observation: ants appeared to be eating the invader, the weather seemed too cold, etc.

Fourthly, often the only information available on an insect is that it reached some site and either succeeded or failed. We lack information on how many propagules were involved and how large those propagules were. Yet in many biological control projects, of several apparently replicated introductions, some succeed and others fail. For example, the parasitic wasp *Hungariella peregrina* was released in five southern California locations to control *Pseudococcus longispinus*, but only one release resulted in establishment (Clausen, 1978). This apparent lack of replicability is an outstanding problem in the ecology of introductions (Simberloff, 1985). There is probably a stochastic component to success, analogous to the stochastic aspects of flour beetle competition in Park's classic experiments (Park, 1962). By 'stochastic,' I do not mean there are no good reasons why one propagule persists and another disappears. Rather, I mean that all the forces that contribute to this difference cannot be specified and measured but the result can be viewed as a random draw from a specified distribution.

A fraction of what passes for stochasticity in introductions may result simply from different propagule sizes. The concept of the 'minimum viable population size' (Shaffer, 1981) is relevant here. An accruing literature in conservation biology (e.g. Soulé and Simberloff, 1986) indicates that, for a variety of reasons, the probability of persistence is characteristically less for small than for large propagules, even if there is no precise threshold population size above which establishment in an appropriate habitat is assured and below which it is precluded. Biological control records sometimes contain accounts of number of attempts for particular species and information on the numbers of individuals released. Greathead (1971), observing that some very small propagules have succeeded and some very large ones have failed in African biological control projects, downplays the importance of propagule size. He suggests that, if a few modest releases fail, this usually means the habitat is unsuitable and larger propagules will not help. However, there are counterexamples. The chrysomelid *Chrysolina hyperici* was introduced as a propagule of 120 adult beetles in Victoria in 1930 to control St John's wort and failed, while an inoculum of 1, 340 adults in 1934 succeeded (Clausen, 1978). One cannot prove that the sizes of these propagules were responsible for the different outcomes, but there are enough similar examples that one suspects large propagule size aids establishment. Williamson (this volume) tabulates data on 159 introductions for biocontrol in Canada and finds that increasing numbers of individuals released and increasing numbers of releases both increase the probability that a species will be successfully established.

In spite of these problems with the available data base, there are a number of interesting syntheses, at one level or another, on which insect introductions succeed and which ones fail. In the remainder of this contribution I will summarize many of these and examine the prospects that they offer for accurate predictions on the fates of introduced insects. Much of the literature on insect introductions treats biological control projects and most of these are conducted in more or less modified habitats such as those of agriculture and silviculture. The degree of modification has not been systematically recorded. Other papers, both theoretical and data-based, treat pristine and modified habitats indiscriminately. One can imagine that conclusions drawn about introductions into pristine habitats may differ from those about introductions into modified habitats, so I will indicate when an author's comments are meant to be restricted to biocontrol introductions.

3.2 OPPORTUNITY FOR COLONIZATION

For North America north of Mexico there is a continually updated list of all insects known to be introduced into any habitat whatever, compiled by the United States. Department of Agriculture (1986) (Sailer, 1983). Of the 1554 species, two-thirds are from the western palearctic region. Only 14% are from South and Central America and the West Indies, which surely have many more insects than the western palearctic and would seem by geographic proximity to be at least as likely to provide introductions into North America (Simberloff, 1986). Sailer argues convincingly that the vast majority of introduced insects reached North America not under their own steam but through anthropogenous transport, either deliberate or inadvertent. The main means have been ship ballast, introduced plants, and deliberate introduction of beneficial insects for biological control (Sailer, 1983). The latter category alone encompasses 227 species (as opposed to only two of 177 successful insect introductions into the British Isles, indicated by data from Brown (1985)). Further, most traffic that would have provided the opportunity for invasion, especially by the first two means, was from the western palearctic.

Greathead (1976) observes that Europe, especially Britain, has played a disproportionate role as source for natural enemies in biological control projects in North America, Australia, and New Zealand. For example, about half of the species brought into the United States for this purpose up to 1950 came from Europe (Clausen, 1956). On the other hand, very few came from Africa (Greathead, 1971). Early classical biological control was mainly an Anglo-American enterprise. It is thus unsurprising that a large fraction of the deliberate introductions (and therefore a large fraction of the successes) were European, especially British. In fact, as Greathead (1976) notes, this is in spite of the fact that Britain would not, on objective grounds, have seemed a promising source for predators and parasites.

The preponderance of European species among successful insect introductions of all sorts in North America cannot automatically be taken to indicate inherent qualities that make European insects better colonists than those of other regions. Yet this hypothesis is tempting. Matthew (1915) argued that Palearctic animal species are stronger than others, having been honed in the 'more efficient workshops of the north,' and that the biogeographic history of the earth was the progressive replacement of species in other regions by occasional immigrants from the Palearctic. Crosby (1986) constructs a similar scenario for the success of animals, plants, and pathogens introduced from Europe to other temperate regions and relative failure of species that moved in the opposite direction. One would like comprehensive data on the number of introduced nearctic species in Europe (and preferably some data on failures as well as successes) in order to assess whether it is true that there is a higher probability of success for a European colonist in the nearctic than vice versa. The opportunity for European species to reach other areas was greater, so the same success rate may simply have produced a larger number of successes. The dearth of African insects introduced into the United States (and, in fact, into most other regions) probably results at least partly from lack of opportunity. There has historically been less traffic from Africa to North America, for example, than from Europe.

3.3 SUITABLE HABITAT

Wilson (1960) detected a correlation between the climate of source areas of insects successfully introduced for biological control into Australia and the climate of the part of Australia where the introduction occurred. The similarity of habitat between much of Europe and much of North America may partially account for the fact that such a large fraction of the successful introductions into North America came from Europe, though it is impossible with available data to separate this factor from opportunity. In addition to climatic similarity between the palearctic and the nearctic, there is broad vegetational similarity in both growth form and taxonomic composition (far more plant taxa held in common than, for example, between Africa and South America). The arguments about the reasons for the taxonomic similarity (e.g. Sailer, 1983) need not concern us, but the fact remains that the vegetation is similar. Lattin and Oman (1983) suggest that vegetational similarity between source and target for a potential introduction is at least as important as climatic similarity for insects that use plants as food or habitat.

Several biological control workers have argued that successful invasions are more likely between sites within one region than between different regions. Few of these reports examine both failures and successes systematically so it is impossible to say whether intra- or inter-region introductions are more likely to succeed, but the impression is that it is the former. For example, Wilson (1960) reports several successful introductions from eastern to western Australia and from one part of New Guinea to another, while Clausen (1956) describes successful transfer of species within the United States. A higher fraction of transfers of insects within Canada resulted in successful establishment than did introduction of insects into Canada from other regions (Commonwealth Institute of Biological Control, 1971). A preliminary hypothesis for the apparently greater success rate of intra-region introductions is that the climatic and vegetational similarity is greater.

Holdgate (1986) argues that invasion depends more on species–habitat interactions once dispersal has occurred than on dispersal itself. For insects it is difficult to see on what basis such a claim can currently be made, especially without much more information on failed invasions. It is, of course, true that those introduced species surviving at any site have found a suitable habitat, and one possible reason for the failure of those that have landed but not survived is that the habitat is unsuitable. On the other hand, all those species that survived at a site also had to reach it, and to assess the importance of dispersal we would have to know how many species dispersed there but failed to survive, and how many have not dispersed there, by their own means or with human help, but could have survived if they had gotten there. No entomological data fill these needs.

3.4 THE BIOTIC RESISTANCE HYPOTHESIS

Several hypotheses about why some introductions succeed and some fail rest on the argument that biotic resistance to an invader is the key (Simberloff, 1986). For example, it is often argued, for insects as for other taxa, that mainland species typically invade island communities more readily than island species invade mainlands (e.g. Elton, 1958; Carlquist, 1965). The underlying reason is often thought to be superior competitive ability of the mainland species. Carlquist (1965) views continental species as 'steeled by competition.' One could also imagine that, since continents have more predator, pathogen, and parasite species than islands do, mainland species would deal more successfully with all sorts of interactions. Greathead (1971) says that, because there are fewer species per unit area on islands, island species occupy broader niches and a wider array of habitats. Thus they are likely to be less well adapted to any particular food or habitat than is a potential competitor from a continent.

However, in spite of the many well-known examples, for insects as for other species, of the devastation of island communities by mainland invaders (e.g. Elton, 1958), it is far from clear that mainland species are really more likely to invade successfully. For one beetle and five wasp genera widely used in biological control efforts around the world, Simberloff (1986) classified the 281 introductions (Clausen, 1978) into four categories: mainland to island, mainland to mainland, island to island, and island to mainland. A multiway contingency test was performed with three dimensions of two levels each: source (mainland or island), target (mainland or island), and outcome (success or failure). The null hypothesis, that success or failure of an introduction does not depend on whether source or target is island or mainland, could not be rejected. Of course almost all these introductions were into agricultural communities that are typically both highly modified and more similar from site to site than other communities. It might be that a different result would be obtained for introductions into pristine habitats, but no comparable data exist for such introductions. As to why the view has arisen that island communities are more easily invaded or that mainland species are better colonists, it may be that mainland species simply have more opportunities to invade islands than vice versa, both because there are more mainland species and because they are more likely to be transported deliberately or by accident. For example, of the 281 biocontrol introductions just discussed, 71 were from mainland to island but only 15 were from island to mainland. The source for 247 of these introductions was mainland, while only 34 originated on islands.

Because many early successes of biological control were on islands, the view arose (e.g. Imms, 1931) that only the simplified communities of islands would allow successful invasion and propagation. However, Doutt and DeBach (1964), DeBach (1965), Huffaker *et al.* (1976), and Laing and Hamai (1976) all present data on mainland successes that contradict the 'island theory.' None of these studies closely examines success rate on islands versus mainland. Greathead (1971) compared 73 projects in Africa to 53 on islands and found the African success rate to be 23% as opposed to 45% on the islands. However, 'success' here means economic success of the project, not survival of the introduction as throughout the rest of this paper. Greathead (1971) gives examples of species that have survived on both Africa and islands but that provide effective control only on islands; he implies such situations are common.

Another pattern often detected, for plants as for insects, is that 'disturbed habitats' are much more readily invaded than 'undisturbed habitats.' Elton (1958) and Sharples (1983) attribute this pattern to biotic resistance, the competitors, predators, parasites, and diseases that an invader encounters in pristine habitat. These authors assume that disturbance decreases numbers of species in all categories. Neither author tabulates success and failure rates in the two kinds of habitats, so it is difficult to know whether this pattern is real or simply an impression. Two possible tendencies may make it appear that invasions are more likely to be successful in disturbed habitats (Simberloff, 1986). First, the disturbed habitats studied are almost all modified habitats associated with humans—primarily agricultural, and secondarily associated with dwellings. These habitats are most important to us and so are studied more carefully than pristine habitats. We are thus more likely to detect successes. Secondly, the opportunity was almost certainly greater for introduction into this kind of disturbed habitat. Biological control agents were imported into these habitats, as were agricultural and ornamental plants and the insects they might have carried. There must have been far fewer deliberate or inadvertent introductions into pristine habitat.

So a tentative hypothesis would be that disturbed habitats *seem* to be more easily invaded because there have been more introductions into some of them (because of greater opportunity) and successes are more likely to be detected. It would be interesting to study systematically and exhaustively naturally rather than anthropogenously disturbed habitats (e.g. fire disclimaxes) to see if disturbance *per se*, rather than a particular kind of disturbance, makes invasion easier. Even if it should turn out that generic disturbance did increase the ease of invasion, one would still have to demonstrate that reduced biotic resistance is the reason. Even the assumption that disturbance leads to a reduced number of species may not be correct. For some sorts of communities, intermediate levels of disturbance are associated with highest species richness (Connell, 1978), so it is not automatically clear why biotic resistance should be lessened as disturbance increases. Furthermore, Howarth (1985) even argues that increasing the number of species in a site *increases*, rather than decreases, the probability that a future propagule will establish, because creation of new niches is facilitated.

Yet another example of the biotic resistance hypothesis is the contention by Tallamy (1983) that, for parasitic insects introduced to control gypsy moth (*Lymantria dispar*) in the United States, later species were competitively precluded by earlier ones. Washburn (1984) concedes that later introductions had a lower success rate but argues that the earlier ones were exactly those species that were *a priori* more likely to succeed. Hall and Ehler (1979) and Ehler and Hall (1982) similarly found, for a veriety of insects introduced for biological control, that species introduced simultaneously with or after other introductions were less likely to succeed than those introduced early and alone. Although Ehler and Hall (1984) were loath to draw strong conclusions about why this pattern was obtained, Keller (1984) was quick to argue that it need *not* imply competitive exclusion of later invaders by earlier ones. He suggested a number of biases in typical control procedures (such as the tendency for early, single releases to be of species *a priori* most likely to succeed) as well as statistical reasons why the biological control literature would make it *appear* that some introductions would exclude others even if this were not happening.

Lawton and Brown (1986) emphasize predators, parasitoids, and diseases rather than competitors as likely determinants of success or failure of all kinds of insect introductions. Though they provide several interesting examples this proposition has yet to be sufficiently closely studied. Many discussions of deliberate release of biological control agents cite predators as frequently preventing establishment (e.g. Commonwealth Institute of Biological Control, 1971; Goeden and Louda, 1976; Crawley, 1986a, 1986b) but much of the evidence consists of casual observation. Crawley (1986b) finds that predators were reported to cause reduced impact of insects introduced for weed control in 22% of cases, parasitoids in 11%, and diseases in 8%. Climate, by contrast, was reported to be important in 44% of cases.

3.5 BIOLOGICAL TRAITS FAVORING SUCCESSFUL INTRODUCTION

There is a long tradition of trying to predict success or failure of an introduced species from its characteristics, particularly its life history traits such as birth rate, death rate, etc. This approach is epitomized by several papers in *The Genetics of Colonizing Species* (Baker and Stebbins, 1965) in which lists of traits that should conduce to successful invasion are proposed. Though such lists invariably make good sense and may, on average, be borne out when comprehensive data become available on opportunities, successes, and failures for given taxa, there is widespread doubt that this approach will be very useful in predicting the outcome of a particular introduction (e.g. Crawley, 1986b). Thompson (1939) believed that introduction of insects for biological control would always be a trial and error process because of the number and complexity of factors acting on an introduction in nature. Sharples (1983) cites many other authors, writing on a variety of taxa, who made the same claim.

Lawton and Brown (1986) point out that the problem is that extinction in population dynamic models based more or less on the models of MacArthur and Wilson (1967) is generated by demographic stochasticity, whereas environmental stochasticity is likely to be a far more important force in the field. This argument may well be true, although much of the conservation literature, focussing on the relation between demographic and genetic stochasticity, emphasizes the importance of demographic stochasticity (National Research Council, 1986). As the conservation modelers realize, environmental stochasticity is extremely difficult to model. There are two components—rare catastrophes that occur randomly in time (such as hurricanes or catastrophic fires) and the average, day-to-day fluctuations that are the composite of many forces that are themselves continually varying and all of which affect a population. By 'random' and 'stochastic,' I do not mean that there are not deterministic reasons why a catastrophe occurs or why a particular force fluctuates from day to day. All that is meant is that, with respect to the forces included in the model, these components are not completely predictable, and their occurrence can at best be drawn from a specified statistical distribution.

It is difficult to imagine how to incorporate catastrophes into a predictive model, but Leigh (1981) suggests that the effects of day-to-day fluctuations can be captured by looking at the coefficient of variation of a population's fluctuations in size among generations. His conclusion is that, the higher the coefficient of variation, the lower the likelihood of persistence (or of initial establishment for an introduction). For most insect species, the coefficients of variation of their population fluctuations are no better known than their intrinsic rates of increase, birth and death rates, and carrying capacities.

Lawton and Brown (1986) find a nearly perfect inverse correlation between mean body length and probability of successful establishment for six insect orders whose successful and failed introductions into England have been recorded, but the reason for the correlation is obscure. The relationship between mean body size for these orders and mean coefficient of variation of population fluctuation or other population parameters is unknown. The importance of size would be more strongly implicated if probabilities of establishment for the individual species within the orders were shown, for different size ranges. Without this information, it seems just as reasonable to say that some traits of the natural history of, say, Hemiptera predispose them to successful invasion while traits of Lepidoptera predispose them to fail. In any event, as interesting as this correlation among the six points is, it is still far from allowing us to predict the fate of an individual invader. For insects introduced to control weeds, Crawley (1986a, 1986b) detected positive correlations between intrinsic rate of increase and probability of success for insects on plants other than *Opuntia*, even within orders. He attributes an inverse correlation between size and probability of success to an inverse relationship between size and intrinsic rate of increase. However, for neither intrinsic rate of increase nor size is the correlation so strong as to allow sound prediction of the fate of a particular introduction.

'Niche breadth' often surfaces as an important feature in discussions of reasons for success or failure of introductions. There have been exactly opposite predictions about how niche breadth should affect invasion success. On the one hand, Mayr (1965), discussing birds, Howarth (1985), discussing invertebrates, and Holdgate (1986), summarizing reports on many taxa, suggest that a broad range of possible foods and/or habitats should facilitate invasion. The underlying reasoning seems to be that the such species are more 'versatile' ecologically, thus more likely to carve out a niche they can persist in. Wilson's 'taxon cycle' (Wilson, 1961), in which generalized ant species from the mainland or large islands continually invade smaller islands and replace their more specialized inhabitants, rests on such reasoning. Dritschilo *et al.* (1985) examined several hundred insects introduced by a variety of means into California and found that typically they could survive in a variety of habitats and on a variety of foodstuffs. On the other hand, Greathead (1971) argues that mainland species are more likely to drive out island species exactly because the island species have broader niches, and so are less suited to any particular habitat and/or food than are the more specialized mainland species. DeBach (1965) finds that, among entomophagous insects introduced for biological control, most successes are very specialized for their hosts, rather than having a broad food niche (though he did not analyze *probability* of success for narrow- versus broad-niched species). Phytophagous insects deliberately introduced for weed-control are chosen to be very host-specific and are often rigorously tested for this trait before release. Thus the fact that most of the successful species in this realm of biological control have a narrow range of host plants tells us little about whether host range is an important predictor of success.

Part of the confusion about how niche breadth bears on invasion success rests on the fact that consistent, measurable, and meaningful measures of 'niche breadth' and 'specialization' have not been used. Another part of the problem is that failures have not been examined as thoroughly as successes, so, even if one *could* measure niche breadth, one would need more data in order to say how it is associated with probability of invasion success, if at all. If consistent definitions and comprehensive data are available, it would be interesting to see what correlations arise, but I doubt if the single compound trait 'niche breadth' will ever be a very strong predictor of invasion success for insects.

The method of sex determination may predispose certain insects to succeed upon introduction of small propagules. Howarth (1985) found that a large fraction of invertebrates successfully introduced into Hawaii are either hermaphroditic or parthenogenetic and argued that such species are favored because the problem early in the invasion process of finding a mate is lessened or eliminated. Simberloff (1986) noted that haplo-diploidy, spanandry, and intense inbreeding might be expected to favor parasitic Hymenoptera by lowering the threat of inbreeding depression, often cited (e.g. Shaffer, 1981) as a threat to very small populations. As a preliminary test of this idea, I checked Clausen (1978) for all biocontrol introductions in which the propagule size was given and did not exceed 1000. I counted only field releases, not projects in which a small propagule was used for mass rearing and subsequent large-scale release. Multiple releases in one region as part of one project were counted only once. Results are given in Table 3.1. The results are generally consistent with the hypothesis, although Hymenoptera, Coleoptera, and Diptera differ in so many other ways that one could hypothesize other reasons for these results. It is interesting that, in total and in the categories '1–20' and '101–1000' the order of probability of success, Hymenoptera > Coleoptera > Diptera, is exactly the opposite of that determined by Lawton and Brown (1986) for all insects introduced, by any means, into the British Isles.

I did not count projects in which a single small propagule was used for mass rearing and subsequent large-scale release, on the grounds that such a procedure can rapidly lessen inbreeding depression (Senner, 1980; Soulé, 1980). However, there are several such examples, most involving parasitic wasps. Simberloff (1986) discusses the braconid *Aphidius smithi*. Here may be added the encyrtid *Hambletonia pseudococcina*. Two females of a unisexual race were used in Puerto Rico to rear about 7000 individuals, which established and spread rapidly upon release. Also the encyrtid *Pauridia peregrina*: stocks were propagated from a single female, and release resulted in permanent establishment in California. And the encyrtid *Anarhopus sydneyensis*. For this wasp, stocks were reared from eight individuals, and several subsequent releases in California were successful. In Hawaii, the chalcidid *Brachymeria agonoxenae* was propagated from one female and several males, after which three males and eight females were released and established. The eulophid *Tetrastichus incertus*, imported into the United States from France, was mass reared and successfully released from eight adults. *T. giffardianus* in Fiji was mass reared from ten individuals and successfully established. The only such non-hymenopteran cited by Clausen (1978) is the coccinellid beetle *Scymnus smithianus*. From Sumatra, 27 living adults reached Cuba, but the stock declined to a single female. However, it then built up sufficiently to allow a successful release.

Table 3.1. Intentional small field releases of biological control agents in three insect orders. Multiple releases as parts of single projects counted only once. S = survival; E = extinction. Data from Clausen (1978)

	Propagule size					
	1–20		21–100		101–1000	
	S	E	S	E	S	E
Hymenoptera	10	11	17	37	43	72
Coleoptera	3	10	9	27	18	52
Diptera	1	4	3	7	3	26

3.6 CONCLUSIONS

Predicting which insect introductions succeed is still not a very precise business and there may be an inherent stochasticity to the process so that predictions will never be better than statements of probability of success given a certain number of propagules of certain sizes. Even the broad generalizations about which sorts of introductions historically have tended to succeed at the highest rate are beclouded by deficiencies in the data base, particularly regarding failed introductions. The reasons for such venerable patterns as the predominance of European successes, the frequency of invasion of islands, and the frequency with which disturbed habitats are invaded cannot be definitively given without much more information on opportunities for various sorts of invasions. There is absolutely no doubt that the habitat in the target area is always important to the potential invader, and there are some instances where other species already there seem to be crucial, but there is no basis for saying that patterns of observed introduction are more a reflection of species–habitat or species–species interaction than of the historical distribution of dispersal opportunities.

Continuing efforts to make more precise predictions about successful introductions based on such gross inherent biological traits of the potential invaders as size or intrinsic rate of increase do not seem to be very promising. There may be interesting patterns relating life history, population dynamic, genetic, and other traits to probability of success, but there will always be exceptions, perhaps partly owing to inherent stochasticity in the invasion process, certainly partly owing to interactions between a potential invader and the habitat and/or species it encounters. It is depressing to be unable to draw striking generalizations about introduced insects but it would serve no worthwhile purpose to generalize prematurely.

However, very detailed study of the natural history of an organism, including its phenology and life history, may allow more precise prediction. For example, DeBach (1974) describes the results of the accidental introduction into Fiji of *Pediculoides ventricosus*, a mite that attacks larvae and pupae (but not eggs and adults) of the coconut leaf-mining beetle *Promecotheca reichei*. The mite destroyed all the larvae and pupae during the dry season in some sites. The adult beetles then oviposited and died, converting the beetle population into one with synchronous, non-overlapping generations. The consequent absence during certain periods of larvae and pupae caused the mite population to crash. Similarly, two native parasitoids that had controlled the beetle were almost eliminated because they did not live long enough to persist during the intervals between occurrences of the host stages that they require for oviposition. The beetle population greatly increased. However, a parasitoid was sought that was not so restricted in the host stages it requires for oviposition and with sufficient longevity that it could survive periods when hosts are rare or absent. The chalcid wasp *Pleurotropis parvulus* in Java satisfied these criteria and controlled the beetle remarkably well after it was imported into Fiji.

There is every reason to think that careful consideration of the biotic and physical habitat into which a species is to be introduced, plus insightful study of its natural history, will yield sounder prediction than the sorts of general models that have been attempted to date. Crawley (1986a) says that ecological theory has contributed little or nothing to the practice of choosing insects for weed control and is quite pessimistic that it ever will. Part of the problem may well be that the models deployed to date are mostly too general and idealized, but that models tailored to particular cases will be more successful in predicting the outcomes not only of biocontrol introductions but of other types as well.

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