

## CHAPTER 15

# *Theories of Predicting Success and Impact of Introduced Species*

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### 15.1 INTRODUCTION

The purpose of this paper is to review some theoretical ideas relating to two questions: can we predict whether an introduced species will successfully invade a community and, if it does, can we predict whether that species will have a disruptive effect on the community? I shall use empirical studies to examine whether the theoretical ideas are reasonable. This demonstration is strictly limited in its scope, as I shall rely heavily on sources which deal with introduced vertebrates. For these taxa, the theories do seem reasonable, but this is not necessarily true of other groups of organisms. I shall try to indicate where the theories will prove to be inadequate for these other organisms.

This paper is in three sections. In the first section, I shall address the problems a species must overcome when it first arrives in a new community—essentially a species-oriented view of the problem of invasion. In the second section, I shall address the resistance to invasion a community may possess, which is the community-oriented view of the problem of invasion. I am not convinced that we can totally separate the prediction of invasion into species and community components, rather it is more likely that we must look to the interaction of species and communities. None the less, the division I shall use is a reasonable way of getting across many of the major ideas. In the third section of the paper, I shall consider the effects of introduced species.

### 15.2 THE PROBLEMS OF SMALL POPULATIONS

There are many cases of successfully introduced species which started with tiny founder populations. The lower limit in population size for a successful invasion is demonstrated by one pregnant female in the anecdote about the colonization of the Aland archipelago (in the Baltic) by the red squirrel (Jarvinen, personal communication). Some introductions have been made with such large numbers that the problems besetting small populations are irrelevant. But many introductions, particularly accidental ones, have been made with small numbers

of individuals. For these, success will not be certain: many more than one pregnant female may be required for success. Small populations are prone to extinction and I shall argue that some species are much more likely to become extinct at a given small population size than others. Clearly, such extinction-prone species are less likely to be successful invaders.

### 15.2.1 Theory

The theory of extinctions for small populations has usually been presented in the context of extinctions—not introductions. The results, as I have argued, seem readily applicable. Diamond (1984) and Pimm *et al.*, (1988) provide a review of several ideas.

The chance of extinction rapidly increases as population sizes decrease. Even in a perfectly constant environment, small populations face risk of extinction from demographic accidents—the chance fluctuations of deaths and births, and consequent changes in numbers and sex ratios. There are three other factors:

1. Populations are more likely to become extinct if their numbers fluctuate considerably.
2. Populations of long-lived species will have a lower risk of extinction, per year (but not per generation) than short-lived species.
3. Populations with a low intrinsic rate of increase should have an increased risk of extinction because they recover more slowly from reductions in numbers.

These expectations are based on a number of mathematical models: the case of constant environments was considered by MacArthur and Wilson (1967), and Richter-Dyn and Goel (1982); both constant and fluctuating environments were considered by Leigh (1975, 1981). The exact formulations of the models seem less important to me than their general implications, which seem reasonably independent of the exact equations used.

The three factors mentioned above are not independent of each other. Theoretically, there is likely to be a relation between the intrinsic rate of increase,  $r$  and a population's long-term variability in density. A high  $r$  means a fast recovery from low numbers. Of course, too high an  $r$  can mean the population repeatedly overshoots its equilibrium density. So, the sign of the correlation between  $r$  and variability is not obvious. For some bird populations the sign is negative; high  $r$  does confer some population stability, but the relationship is a relatively weak one (Pimm, 1984). Still, the basic result is that high  $r$  and low variability are both advantageous and that the former helps to impose the latter.

There is a much stronger, *negative* correlation between how long organisms live and their  $r$ . From protozoa to elephants, and animals in between, there is an order-of-magnitude reduction in  $r$  for every order-of-magnitude increase in longevity. Both  $r$  and longevity are closely correlated with body size (Peters, 1983).

Thus, we can ask in a given period, is a small, short-lived species with high  $r$  more or less likely to become extinct than a large, long-lived species with correspondingly lower  $r$ , given that both have the same population size? Sample calculations, using Leigh's equations, show that the combination of small body size and high  $r$  is nearly always advantageous. The exception occurs at very low population densities of about half a dozen pairs or less. At these low densities, the extinction rate of large, long-lived species is lower.

### 15.2.2 Empirical tests 1: island birds

Diamond (1984) has assembled a large number of studies that document the rapidly increased chance of extinction as a population becomes small. But how should we test the additional predictions of the theory? We would need a data base that includes many observations of extinctions under 'natural conditions,' in which species have not been inexorably driven to extinction by man-made changes. Pimm *et al.* (1988) used the data on the repeated, annual, breeding censuses of 16 British islands. These have already been analyzed by several previous studies of species turnover (Lack, 1969; Diamond and May, 1977; Williamson, 1982; Diamond 1984). For each of these islands, the number of breeding pairs of land birds has been determined in consecutive years, for several decades. Some populations became extinct, others were founded, while others underwent successive extinctions and recolonizations. The islands are of different sizes, and the populations exhibit a range of long-term variations in numbers.

These data, too, show the overwhelming effect of population size on extinction rate. The risk of extinction drops steeply with increasing population size. There is, however, a considerable amount of scatter about this relationship. Pimm *et al.* were able to relate this to the three theoretical factors by first partially correcting the data for the dominant effects of population size. They divided the species into two groups: 'large' species were non-passerines plus the Corvidae (crows, jays, etc.) whereas 'small' species were the passerines minus the Corvidae. Large species were expected to have lower  $r$ 's and longer generation times than small species. The critical results were:

1. Small, short-lived species were less prone to extinction at densities above seven pairs per island, than large, long-lived species.
2. Below seven pairs per island, large, long-lived species were less likely to become extinct than the small, short-lived species.
3. In both large and small species, and at all population densities, species with highly variable numbers were more likely to become extinct than species with relatively constant numbers. Wrens (*Troglodytes troglodytes*), for example, are small insectivores whose numbers are greatly decreased by occasional cold winters. Their numbers are particularly variable, and, for their population sizes, they are particularly prone to extinction.

### 15.2.3 Empirical tests 2: island insects

Lawton and Brown (1986) have examined the predictors of success among the various animal taxa introduced to Britain. Comparisons of nematodes, spiders, molluscs, insects, flatworms and various vertebrates, show there is a weak, positive correlation between body size and the chance of successful invasion. There is, therefore, an implied negative correlation between invasion success and  $r$ . Lawton and Brown argue that the smaller species may fail more often because their small size may make them more vulnerable to the vagaries of the British climate, or because small size often correlates across taxa with the magnitude of population fluctuations. Within the insects, there is a strong, negative correlation of invasion success with body size, implying a positive correlation of invasion success with  $r$ . Lawton and Brown write: 'by concentrating on one group of organisms, we may have reduced the range of variation encountered in the amplitude of population fluctuations, making...[intrinsic growth rate and equilibrium density]...rather than...variation in population size the most important determination of population establishment.' There are obvious difficulties with studies as broad ranging as this one, but it tentatively supports the importance of intrinsic growth rate as a predictor of invasion success. Williamson (this volume) also discusses the relationship between  $r$  and the chance that a species will successfully invade.

### 15.2.4 Empirical tests 3: Hawaiian vertebrates

For their size, the Hawaiian Islands have received more vertebrate introductions than anywhere else on earth. These introductions have been the subject of a number of studies by Moulton (Moulton, 1985; Moulton and Pimm, 1983, 1986a, 1986b, 1987). These introductions afford unusual opportunities to test various ideas on species invasions, independent of the ideas on intrinsic growth rate and population variability that I have been discussing.

Moulton and Pimm (1986a) first considered the area of origin of the bird introductions to see if different faunal regions (palearctic, ethiopian, etc.) were more likely to be sources for successful introductions. They were not. Surprisingly, even if it was known whether the bird introductions came from the tropics or temperate regions, invasion success could not be predicted. Of the species that could be strictly attributed to either temperate or tropical areas, 13 to 23 temperate species were successful, but only 14 of 28 tropical species were successful. The Hawaiian Islands, of course, are tropical and the introduced species are largely confined to the lowlands, rather than the more temperate montane areas of the islands.

I take this result to mean that species possess broad, physiological tolerances. We would certainly expect that many introductions will fail because they involve a total mismatch between the introduced species and its environment. None the less, the abundance of temperature forest birds in tropical, wet, lowland forest on

Hawaii is graphic evidence that such 'physiological mismatches' are not the only, or even likely, the most important factor, in determining which species introductions succeed.

Moulton and Pimm did find that the size of a species range predicted invasion success. Species with larger ranges were more likely to be successful than species with smaller ranges. Of course, this might be because species with larger ranges may have been introduced earlier. Species with larger ranges are more likely to be subject to man's attempts at moving them than species with geographically restricted ranges. Date of introduction is an important predictor of success, as species introduced earlier faced fewer competitors (see below).

Finally, Moulton and Pimm examined differences between taxa. Bird introductions were more likely to fail than mammal or reptile introductions, for reasons that are not obvious.

Many introductions will succeed only if their numbers can increase quickly, beyond the small population size where extinction is likely. Individual species characteristics, especially the intrinsic growth rate and the propensity for densities to vary, are important predictors of extinction of small populations. These characteristics should also be important predictors of invasion success and some empirical studies suggest that they are. These are not the only population-oriented characteristics that may be useful in predicting success. There are also differences between taxa that do not readily fit into this theoretical framework. For at least some species, the match between the habitats from where the species originated to where it is introduced, does not predict whether the species will succeed.

### **15.3 COMMUNITY STRUCTURE AND CHANCE OF INVASION**

Community characteristics are also likely to modify whether an introduction succeeds. There are many starting points for this discussion. There has been a prolonged debate over community structure and competitive exclusion, which dates from at least 1944 (Ano., 1944) and continues today in the arguments between Florida and California schools (Lewin, 1983a, 1983b). Elton (1946) argued that community patterns could be interpreted to mean that communities were excluding species—i.e. they were probably hard to invade. Others, taking Williams' (1964) lead, have argued that the data imply that many species are absent from a community because they cannot reach that community.

#### **15.3.1 Models of community assembly**

I shall take a rather different starting point, and consider models of community assembly (Post and Pimm, 1983). These models use differential-equation systems to model the sequential addition of species to communities. The essential features are illustrated by Figure 15.1. The models start with a given number of plant

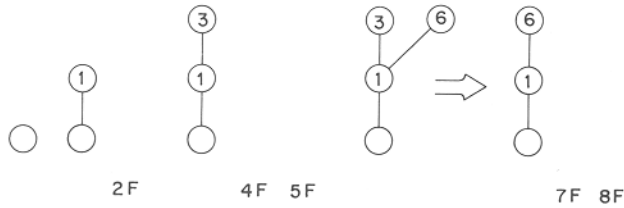


Figure 15.1. Diagram of community assembly process discussed in the text. Circles represent species, lines represent feeding interactions between species. The model starts out with a plant, and then adds successive animal species. Species 1, 3, and 6 succeed, species 2, 4, 5, 7, and 8 fail. Species 6 causes the extinction of species 3

species, then attempt to add animals (and, in some unpublished simulations, both animals and plants). Some attempts fail because the species cannot increase when rare. Other introductions succeed and add to the existing community. Yet other introductions succeed and replace species, or cause widespread extinctions. The principal results (Figure 15.2) involve the number of species in the model communities and the number of attempted introductions it takes before an introduction succeeds. Both these variables are plotted in terms of the total number of attempted invasions. The exact details of the simulations vary slightly with different assumptions. The major results, however, are robust.

Species numbers increase rapidly at first, but then rise to an asymptote. The final level of species numbers depends on the *connectance* of the community. Connectance is the number of actual inter-species interactions divided by the possible number of inter-species interactions. (In an  $n$ -species system there are  $n(n-1)/2$  possible interactions). Connectance enters as a parameter in the models, by choosing how many species of predator and of prey with which the introduced species is likely to interact. Communities with high connectance have few species compared to those with low connectance. (This is a result well-known from analyses of food web models (Pimm, 1982).)

The difficulty of invasion continuously increases with the accumulated number of attempted invasions. Communities with high connectance are much harder to invade than those with low connectance. In simple terms, high connectance means that the invading species suffers from many competitors and predators.

I interpret these results to show two effects on the difficulty of invading a community. First, a community with relatively few species is likely to be easier to invade than community with many species. This is a familiar result, as it is the same as that suggested first by Elton: the presence of lots of competitors and predators confers on a community a 'biotic resistance' (Simberloff, 1986). Second, once the community has reached its equilibrium number of species, the process of community assembly itself makes the community harder to invade. Simply, each successive, successful invasion makes the community less likely to be invaded.

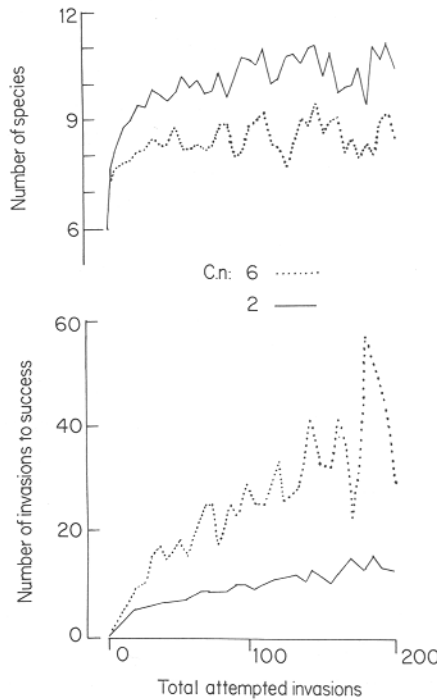


Figure 15.2. Typical results of community assembly models, simplified from Post and Pimm (1983). As assembly proceeds (measured by the total number of attempted invasions), the number of species increases ( $n$ ) then asymptotes. The number of attempted invasions, before one successfully invades the community, increases continuously, even after the number of species has levelled off. The details of the simulations depend on connectance ( $C$ ; defined in the text) and  $n$

Ecologists are well aware that 'disturbed' communities seem easy to invade. I suggest that ecologists often use 'disturb' in three separate ways. The first meaning describes communities which are clearly short of individuals. For example, there may be an abundance of bare ground in which plants can germinate. The significance of this is not apparent in the assembly models, because they only consider communities where the individuals have had time to reach their equilibrium densities. The second meaning describes communities that are short of species, i.e. they are 'unsaturated.' The third meaning is more elusive. Communities, whose species compositions are of only recent origins, in the sense that they are not the end point of a long process of community assembly,

might also have been considered to be 'disturbed.' A community of recent origin may be easy to invade, even though its species richness is high. Simply, the 'age' of a community may be a very important predictor of ease of invasion.

There is a final and obvious point. These community models assume an infinite supply of species. The supply of species that can reach a real community may be strictly limited, and the number of species that can actually survive there may be even smaller. Just because the number of species in a community is limited, does not mean that the community is resistant to invasion. The community may not be resisting species, simply because none are attempting to invade.

### **15.3.2 Details of community resistance**

So far, I have considered only species number, connectance, and the history, of the community's assembly as predictors of successful invasion. What are the details of community organization that might be expected to predict, more closely, the difficulties an invading species encounters?

#### *15.3.2.1 Competitors*

There is a large amount of literature on the effects of competition in structuring animal and plant communities. Irrespective of the debate about whether competition shapes communities and how we might go about demonstrating the existence of competition, the literature does suggest some interesting ideas.

First, there is the effect of morphological similarity. Lack (1947) and later Hutchinson (1959) suggested that morphologically similar species might be unable to coexist. Second, there is the effect of taxonomic similarity. Elton (1946) suggested that there might be limits to the number of species per genus that could coexist.

Both morphology and taxonomy are merely surrogates for ecology. We might use any one of a large number of ecological measurements of similarity and predict that the more similar the invading species to a species already present, the less likely is the success of the invader.

#### *15.3.2.2 Predators*

The more predation a species suffers, the less likely it is to successfully invade. But how should we measure this? A rather surprising result about predation is incorporated in the discussions of 'enemy free space,' whose significance has been discussed by Jeffries and Lawton (1984, 1985) and Holt (1977, 1984). Recall an empirical observation: the numbers of species of predator and the number of species of prey are closely correlated over communities that contain various numbers of species (Cohen, 1977; Briand and Cohen, 1984; Jeffries and Lawton,



1984). Jeffries and Lawton argue that we cannot expect such a good correlation on the basis of the number of predatory species being determined solely by the number of prey species. For such a good correlation, the numbers of species of predators may, in addition determine the number of species of prey. For communities where predators exercise a controlling influence on their prey species, one would expect a community with a single predator to be harder to invade than one with several predator species. This leads to the superficially surprising prediction that, for a given number of prey species, communities with the most species of predator may be the easiest for prey species to invade.

### 15.3.3 Empirical studies 1: the role of competition

#### 15.3.3.1 Hawaiian birds

Many studies of introduced species deal with relatively small numbers of introductions, so they cannot be expected to test the ideas suggested above. The Hawaiian Islands provide an obvious system on which to test ideas of community resistance, because they have received so many introductions. Moreover, the fate of the introductions is relatively well known.

There are virtually no native land birds below 1000 m on the Hawaiian Islands, and the islands are too remote to receive anything other than very infrequent avian visitors from the mainland. There are predators, on the islands: the mongoose (*Herpestes auropunctatus*), the native Hawaiian hawk (*Buteo solitarius*), and two species of owls (the barn owl, *Tyto alba*, is introduced, whereas the shorteared owl, *Asio flammeus*, is native). But, with the exception of the mongoose's absence from Kauai, and the hawks' presence only on Hawaii, each island has the same set of predators. The lowland communities are thus isolated and form close-to-ideal, experimental systems to test ideas on community assembly.

Is there any evidence of community-wide effects in determining the success of introduced species? The conclusions of several of Moulton's studies (1985; Moulton and Pimm, 1983; Moulton and Pimm, 1986a, b) are, in brief:

1. Species introductions were generally successful when there were less than 10 introduced species per island. When there were more introduced species, a substantial proportion of the introductions failed.
2. The chance that a species will succeed decreases significantly as the morphological similarity increases between it (the invader) and the nearest congeneric species already present.
3. The surviving species are morphologically more dissimilar than one would expect by chance. Morphologically similar species cannot coexist.
4. The abundances of species present across all the islands are lower on islands

where there are more introduced species, and hence, more potential competitions.

5. Species were *not* less likely to succeed if there were congeners present, than if congeners were absent.

Result 5 rejects Elton's (1946) idea about a limit on species-to-genus ratios imposed by competition. But with this exception, the results demonstrate the dominant effect of competition from existing species is determining which species succeeded on the islands.

#### 15.3.3.2 *The application to other taxa*

The studies of Hawaiian birds provide large-scale, essentially experimental evidence for the role of community structure in general, and competition in particular, in determining which species can invade a community. The results are almost exactly what one might expect for bird communities shaped by competition. But how applicable are the results to other studies?

To test ideas on how difficult it is for species to invade a community, one needs large numbers of introductions and a knowledge of which species have failed. The successes, of course, are obvious. Not many studies meet these criteria, so it is difficult to evaluate the generality of the Hawaiian results. One comparable study involves insects introduced for biological control.

Early analyses of these data suggested that the patterns were consistent with the dominant role of competition determining which species succeeded (Ehler and Hall, 1982, 1984). Simultaneous introductions of several species at once seemed more likely to fail than when one species was introduced. Simberloff (1986) has argued forcefully that such a result is probably a consequence of the ways in which the introductions were undertaken. Multiple introductions are often undertaken with less care than single species introductions. Moreover, when an introduction is successful, further introductions are not necessary. I agree with Simberloff that the role of competition in determining invasion success for these insects seems minimal.

#### 15.3.4 **Empirical studies 2: the role of predation**

The role of predation in determining invasion success is difficult to demonstrate. Certainly, introduced species suffer predation, but to what extent do community patterns predict the probability of an invasion failing because of predation?

An intriguing suggestion, based on the ideas of 'enemy free space' discussed earlier, is that communities rich in predatory species might be easier to invade than those with few predatory species. There is some evidence for this seemingly counterintuitive result. Rainbow smelt (*Osmerus mordax*) have been introduced

widely into lakes in Canada as a source of food for predatory fish. Evans (1986) has shown that smelt are more likely to be found in lakes with greater numbers of predatory fish species. Initially, I thought that this result might be due to a coincidental correlation with some other variable. That is, predators are found in certain kinds of lakes (large rather than small, for example), and smelt also favor the same feature. But unpublished analyses that I have performed on Evans' data using log-linear models show that irrespective of whether the lakes are large or small, deep or shallow, acid or alkali, clear or turbid, the result still holds. Smelt apparently invade more readily when there are more predatory species.

This result is tantalizing because there is one other explanation. That is, that fisherman introduce smelt differentially to predator-rich lakes, irrespective of the lakes' physical and chemical characteristics. This explanation cannot be ruled out because we do not know in which lakes smelt introductions failed.

### 15.3.5 Empirical studies 3: community assembly

The final pattern to be discussed involves the difference in ease of invasion between communities with similar numbers of species, but which differ in how long the communities have been accumulating species. Some communities are clearly ancient, while others, such as those defaunated by volcanic eruptions or ice sheets, may be relatively recent. Yet others, like the man-made communities in lowland Hawaii and elsewhere, are only decades old. According to the theory, these age differences should play a major role in determining ease of invasion. Testing this idea is extremely difficult, because communities that differ in age, also differ in many other characteristics.

There is one observation, however, which though non-quantitative and anecdotal, I find interesting. Many introduced species are clearly in man-made and, therefore, only recently assembled communities. Much older, native communities, typically have many fewer introduced species. The upland, Hawaiian forests are good examples of this phenomenon. Of all the introduced bird species, only the Japanese white-eye (*Zosterops japonicus*) occurs in substantial numbers in the upland forests. What is striking is the distribution of habitats and the bird species in them.

The upland forests are cool, often temperature forests. On the leeward sides of the islands, the lowland forests consist of dry woodlands dominated by introduced legumes, for example kiawe (*Prosopis pallidus*). These dry woodlands merge into savanna-like habitats as rainfall decreases. In the lowlands on the windward sides of the islands, wet rain forests of introduced species predominate. In these lowland tropical habitats, the introduced species are temperate-forest bird species, but they do not occur in upland temperature habitats, which seems strange. This observation may be an example of a species-poor, native and thus, relatively old community, being unusually resistant to species invasions.

#### 15.4 WHAT DETERMINES THE IMPACT OF AND INTRODUCED SPECIES?

There are really two aspects to this question: which species are the most damaging, and which communities are the most vulnerable? The data to answer these questions are many, scattered, and of very uneven quality. Their interpretation is often difficult. One of the earliest summaries, by Simberloff (1981), has recently been criticized by Herbold and Moyle (1986) and by a compendium of bird and mammal introductions, assembled by Ebenhard (1988).

Simberloff reviewed 10 papers covering 850 plant and animal introductions. The basic results were:

1. Less than 10% of the introductions caused species extinctions (there were only 71 extinctions). Of the 10 studies, Greenway's book (1967), which was devoted to avian extinction, reported the highest percentage of extinctions (i.e. 30%, which accounted for 55 of the 71 extinctions in Simberloff's analysis). Introductions apparently tend to add species to a community, rather than to cause extinctions.
2. Of Greenway's 55 extinctions, over 90% were on islands.
3. Over all the 10 studies, and within Greenway's study, predation was the principal cause of extinction; this accounted for 51 of the 71 extinctions in Simberloff's analysis, and 42 of the 55 in Greenway's study. Habitat change, which accounted for 11 of 71 extinctions, whereas competition caused only 3 extinctions and so was a distant third.

Simberloff's summary might be interpreted to mean that introductions rarely have much of an impact. But Herbold and Moyle show how difficult it is to interpret his results in this way. Examination of the three papers from which Simberloff tallied 525 of his 854 cases, shows that his determination of 'no' generally conflicts with conclusions of the original papers.

From Elton (1958), Simberloff extracted 241 instances of species introductions and reported only four of them as showing 'any effect at all.' But Elton's accounts included chestnut blight, spruce budworm, gypsy moth, argentine fire ant, Norway rat, black rat, house mouse, starling and house sparrow. Elton, however, found only four species that had no apparent effect and which had 'been able to edge in without producing any noticeable disturbances or making... species extinct.' Atkinson (1985), for example, provides a detailed discussion of the effects of rat introductions world wide, which shows that serious effects and extinctions are legion.

Herbold and Moyle also point out that many of the apparently benign introductions are into highly man-modified habitats, where species have already been lost for other reasons. Using California fishes as examples, they find that 48 of the 137 species of freshwater fishes come from outside the state. Analysis of the habitat of these introduced species shows that 21 occur mainly in such highly modified habitats as reservoir and farm ponds, whereas another 21 occur mainly

in moderately modified habitats, such as streams with altered temperature and flow regimes and six occur in near-pristine habitats. The latter include four species of trout and salmon introduced into lakes without fish, where the introduced fish altered invertebrate and amphibian populations. In all, 24 of 48 introductions have been documented as having a negative impact on the native fauna. The effects of the remaining 22 species occur in limited, artificial habitats of farm ponds and sewage treatment plants.

I have discussed these results with Dr Simberloff. He agrees that his study was a cursory one which probably overlooked effects. But he and I also agree that the impression that there is likely to be an effect of an introduced species is not proven. It might be true, but the data are inadequate.

### 15.5 CAN WE ANTICIPATE THE EFFECT OF AN INTRODUCED SPECIES?

Some useful insights to this question can be obtained from studies of the effect of removing species from communities. This may seem a perverse way of tackling the question. However, an introduction may be a success because its predators or competitors are few or absent in its new surroundings. A successful introduction may then cause extinctions whose effects will cascade through the community. One vehicle for generating insights about introduced species are differential-equation models of food webs (Pimm, 1982). Though the details are complex and tedious, the models' main features are simple and obvious (Figure 15.3).

Removing a plant species from the base of a simple food chain destroys the entire system (Figure 15.3; top left). But the loss of one of the several plant species utilized by a generalized herbivore, in the more complex, system, would have much less of an effect, because the herbivore is not so dependent on one species (Figure 15.3; middle). These effects are obvious and well known. Less obvious are the effects of removing species from the top of food chains. Removing a predator from a monophagous herbivore probably leaves the plant at a lower density, but it is likely to survive (Figure 15.3; top right). Special conditions are required for a predator to eliminate its sole prey, before it, too, becomes extinct. In the more complex system, the predator's absence may lead to the herbivore exterminating all but the one resistant plant species, which then regulates the herbivores' numbers (Figure 15.3; bottom).

There are three 'don'ts' for species introductions. Impacts will likely be severe when:

1. Species are introduced into places where predators are absent: this is equivalent to removing predators from communities. Examples would include the introduction of large herbivores to islands, or predators that feed high in a good chain and which lack predators as a consequence. In a similar way, we might expect introductions to have more severe impacts when competitors are also absent.

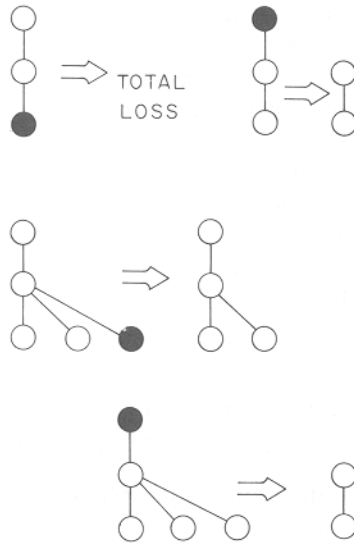


Figure 15.3. Effects of removing species from food webs, simplified from Pimm (1982). Circles represent species, lines represent feeding interactions between species. Removing the plant species at the base of a simple food chain results in the total loss of all the species. Removing a predator from the top of a simple food chain probably leaves the remaining species extant, even if at different densities. These results are reversed in the more complex system. Removing a plant from the base of the more complex system may cause no extinctions. Removing a predator from a polyphagous herbivore may be disastrous, as the herbivore eliminates all but one of the plant species

2. Polyphagous species are introduced: predator removals are likely to be more severe when the herbivores are polyphagous.
3. Species are introduced into relatively simple communities where the removal of a few plant species will cause the collapse of entire food chains.

Ebenhard (1988) provides dramatic evidence of the first effect, suggestive evidence for the second, and there are some compelling case histories to support the third.

By researching over 800 introductions, Ebenhard has classified those species that have an effect in changing abundance, species composition or in causing extinctions. Overall, I suspect effects are likely to be missed (compare Simberloff's and Atkinson's comparisons of the effects of rats). Yet the comparisons of the incomplete data are interesting. Herbivorous mammals introduced to continents were recorded as having effects in 28% of 89 cases. Yet on oceanic islands, which likely lack predators, 50% of 363 introductions show effects.

Almost all of the herbivorous mammals have generalized diets, but among five introductions of specialized herbivores, none were recorded as having an effect.

For the last feature, we can compare the fate of island and continental birds following the destruction of various plant species. In North America, there appear to be no extinctions of vertebrates and few insect extinctions attributable to the loss of chestnut trees following the introduction of chestnut blight (Opler, 1978). Chestnuts were locally one of the commonest trees. Contrast this with Hawaii. Some of the larger nectarivorous birds seem to have been differentially sensitive to extinction, perhaps when a few, important, nectar-producing plants were exterminated by goats and pigs (Pimm and Pimm, 1982). Similarly, the threatened palila depends on the immature seeds of one species of tree, the mamane (*Sophoa chaysophylla*), which does not regenerate when large herbivores are present (van Riper III, 1980), and the akiapolaau, (*Hemignathus munsoi*) an insectivore, depends on the presence of large koa trees (*Acacia koa*) (Ralph and van Riper III, 1985), which are a popular source of wood for objects d'art.

Not surprisingly, the introduction of generalized herbivores to islands is often devastating, because all three 'don'ts' operate. But, equally, some introductions should have little effect on the community to which they are introduced. Ebenhard finds that bird introductions rarely seem to have an effect.

## 15.6 CONCLUSIONS

There is an inevitable tendency to consider species introductions as isolated events. When one does this, which species succeed or fail and which species, when successful, are benign or damaging, may not be readily appreciated. There do appear to be some general rules about introductions. Some species are much more likely to survive at low population densities than others. Communities with high numbers of species are likely to be resistant to species because the introduction is more likely to encounter a strong competitor. Under some circumstances, communities with large numbers of predatory species might be relatively easy to invade. The age of a community—how long its species have been assembling may be a very important determinant of invasion. Species introduced without their predators are likely to be damaging, especially if the species are polyphagous. Communities with simple food chains are likely to be very vulnerable to the introduction of herbivores.

Details of the ecology of species, and the communities into which they are being introduced are bound to be extremely important in determining whether a particular invasion will succeed. Yet, considering introductions in total, it is clear that there are some simple theoretical expectations and there are some equally simple general patterns.

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