The varying success of invaders[1]

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Introduction

Two questions are addressed in this paper. First, what statistical generalizations can be made about invaders? Second, how might we explain them? Answers to the first question are reasonably well established; those to the second are, as yet, vaguer and less satisfactory. We attempt to answer the second largely by looking at variation in the answers to the first.

During the SCOPE (Scientific Committee on Problems of the Environment) program on the ecology of biological invasions (Kornberg and Williamson 1987) a general consensus was that particular invasions are not predictable. Gilpin (1990), reviewing the SCOPE synthesis, said "we are never going to have a scheme to predict the success of invading species" and "the study of invasion should be... statistical... characterizing the probability of outcomes for classes of invasions." In agreement with Gilpin, we have adopted a statistical approach to study the proportion of imported species achieving different levels of invasion success—introduced, established, and pest (Williamson and Brown 1986, Williamson 1992, 1993). There is a regularity in these proportions, as indicated in the top line of Fig. 1, and a predictability about deviations. That is the thrust of this paper.

Statistical Rules

The tens rule

For a variety of British groups of animals and plants, the statistical rule holds that 1 in 10 of those imported appear in the wild (introduced or casual) (Williamson 1993), 1 in 10 of those introduced become established, and that 1 in 10 of those established become a pest (Holdgate 1986, Williamson and Brown 1986). This "tens" rule was originally the "ten-ten" rule, but there are now three tens. It needs to be interpreted with care, beginning with precise definitions of the terms "imported," "introduced," "established," and "pest" (Table 1). *Imported* covers species found in collections or accidentally brought into the country; *introduced* or casual means found outside control or captivity as a potentially self-sustaining population. In the terms used in the regulation of genetically engineered organisms (GEOs), introduced species are released, while imported but not introduced species are contained.

The three transitions between the four stages we call "escaping," "establishing," and "becoming a pest" (Table 1), and their probabilities constitute the tens rule. No statistical rule is exact; guidelines are needed for acceptable variation about the tens of the rule. Taking 10 to mean between 5 and 20 (Williamson 1992, 1993), close to the confidence limits of a binomial expectation of 0.1 in a sample of 100, encompasses almost all the possible, and perfectly reasonable, different views of which species to include in which category. These limits are shown in Fig. 1.
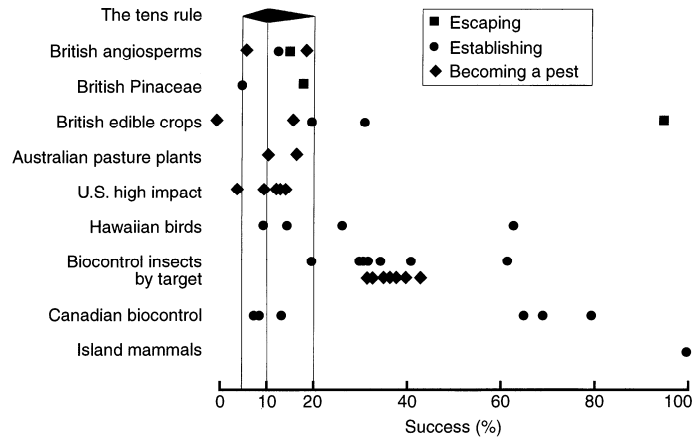

Fig. 1. The tens rule, showing ratios of the three invasion transition stages. The suggested range for the tens rule is shown by the black diamond at the top. For British angiosperms (from Williamson 1993) the two points for becoming a pest are for severe pests (left) and all pests. British Pinaceae data are from Williamson and Fitter (1996). For British edible crops see Table 2. Australian pasture plants are weedy species in Lonsdale (1994): legumes 10%, grasses 17%. United States "high impact" invaders are, left to right, fishes, plant pathogens, insects, mollusks, and terrestrial vertebrates (from OTA 1993: Fig. 2-2). Hawaiian birds are, left to right, all species in native forest, all species in native forest and open grassland, Columbiformes in all habitats, Passeriformes in all habitats (Table 3). Biocontrol insects by target are from Table 4, with the pest symbol used for those effecting control (see *Statistical rules: Exception three* . . .). Canadian biocontrol data are from Beirne (1975) (see *Statistical rules: Exception three* . . .). Island mammals are from Ireland and Newfoundland combined (see *Statistical rules: Exception four* . . .). For expanded definitions of symbols, see Table 1.

The tens rule is satisfactory for British angiosperms (Williamson 1993), the British Pinaceae (Williamson 1996), pasture plants in Australia's Northern Territory (Lonsdale 1994), and high-impact non-indigenous species in the United States, including terrestrial vertebrates, insects, fishes, mollusks, and plant pathogens (OTA 1993). These results are summarized in Fig 1.

Having established the general nature of the tens rule, it is instructive to consider exceptions—examples in which it does not hold (Fig. 1). Four good examples that we have found are British edible crop plants, Hawaiian birds, insects used in biological control, and mammals on two continental islands, Newfoundland and Ireland.

Exception one: crop plants

In Britain there are 71 out of 75 non-native crop plant species that are now casual or naturalized (Table 2), a most remarkable difference from the escaping 10. In other respects crops fit the rule rather well. The proportion of species establishing is only slightly higher than would be expected from the tens rule, namely between 20 and 31%, depending on the view taken of the intermediates (Table 2, Fig. 1). From the rule, one or two species should be a pest. None are in Britain, but three are in Canada, a reasonable fit (Crompton et al. 1988, Williamson 1994).

In discussions of risks from releases of GMOs, it is quite common to find statements that crop plants will not become pests because they cannot grow outside cultivation (e.g., Brill 1985). Such statements are largely not true. Crop plants are almost all strongly selected to grow well where they are cultivated. Consequently, in the same regions they normally grow well outside cultivation. The result is that almost all non-native crop species are either casual or naturalized. The tens rule does not apply when there has been selection to counteract it.

TABLE 1. Terminology used to distinguish among non-native species.

Term	Definition
Imported	Brought into the country
Introduced	Found in the wild; feral; casual
Established	With a self-sustaining population, naturalized
Pest	With a negative economic effect
Escaping	Transition from imported to introduced
Establishing	Transition from introduced to established
Becoming a pest	Transition from established to pest
The tens rule	Each transition has a probability of $\approx 10\%$ (between 5 and 20%)

TABLE 2. Fates of imported crop plant species grown commercially in Britain for human consumption. (Modified from Williamson 1994.)

Category	No. of species	Comments
A) Total no. of species imported into Britain	75	
B) Species found at least casually (introduced)	71	(95% of A)
C) Species possibly established (category D plus status of some doubt, e.g., very persistent)	22	(31% of B)
D) Species definitely established (naturalized)	14	(20% of B)
E) Pests in Canada (none are pest in Britain)	3	(17% of the average of C and D)

Exception two: Hawaiian birds

The second example is Hawaiian birds (Table 3). Oceanic islands are well known to be be vulnerable and invasible, so it is not surprising that >50% of birds introduced have become established. But Table 3 contains two other important points.

TABLE 3. Fates of introduced bird species in Hawaii.†

Type of species	Total no. introduced	No. established Any-where	In native forests‡	In open upland
Passeriformes	51	33	8	2
Columbiformes	19	5	1	1
Total	70	38	9	3

† Data sources: Moulton and Pimm (1986), Pratt et al. (1987), Simberloff and Boecklen (1991), Hawaii Audubon Society (1993), Moulton (1993).
‡ The names of the species we have taken as established in native forests are given in Rejmánek (1996).

The first is that the overall success rate is higher ($P < 0.01$) for Passeriformes (65%) than Columbiformes (26%), as noted by Moulton (1993). The second point is perhaps more important. There is scarcely any native habitat left over most of the lowland in Hawaii, where most of the introduced species live. However, there are some imported species in the native forests and a few in the high open habitats (Table 3). Both habitats have been much affected by other introductions (Stone and Stone 1989), but taking the figures at face value, 11— 17% (Fig. 1) have established in native habitats (depending on whether or not the open upland habitats are taken as native). Various figures from 5 to 20% can be found from subsets of the data in Table 3, but there are no significant differences between any of these subsets. So, surprisingly, invasion of

native habitats by birds on Hawaii conforms to the tens rule. The high invasibility of the lowland areas would seem to come from the extreme change of habitat there.

Exception three: biological-control insects

The third example is of insects used in biological control (Table 4). As these are all deliberately released, there can be nothing corresponding to the escaping ten here. For establishing and becoming a pest, instead of a tens rule, there is now something closer to a "threes" rule. About one third of the species introduced manage to establish, but there is significant heterogeneity between the different groups, arising from both the root and weed feeders, as can be seen in Fig. 1. Hawkins and Gross (1992) suggest that this difference has to do with refuges—that certain life styles give better protection against enemies. The proportion leading to control (Table 4) may perhaps be compared to the proportion of pests in the tens rule, as both involve an economic effect (Table 1). Note that there is little heterogeneity in the proportion controlled (Table 4, Fig. 1). If it is ease of discovery that is important as Hawkins and Gross (1992) surmise, it acts by determining whether a population can persist, not what its ultimate size will be.

TABLE 4.   Biological control success by insects, by target.†

| Control agent | Target | Insect species | | |
		Number of introductions	Established (%)	Effecting control, as % of established
Parasitoids	Root feeders	148	19.6	34.5
	Aboveground borers	610	28.5	30.5
	Mixed exo- and endophytic	196	30.6	40.0
	Leaf rollers/tiers	41	31.7	38.5
	External folivores	293	35.5	36.5
	Leaf miners	89	41.6	43.2
Herbivores	Weeds	1128	61.3	32.4
	Mean ± 1 SD		35.5 ± 13.2	36.5 ± 4.4
	Heterogeneity χ^2		$P < 0.01$	NS‡

† Data sources: Lawton 1990, Hawkins and Gross 1992.
‡ Not significant at $P = 0.05$.

Considering that control agents are selected to be successful, it may be surprising that only one third succeed, and not surprising that this fraction is much larger than one tenth. A major factor in the establishment success of biological-control insects is probably the size of the introduction (see Williamson [1989] and Lawton [1990]). From Beirne's (1975) survey, increasing the number released from <5000 to >30 000 improves success from 9% (about that expected from the tens rule) to 79% (well above any average in Table 4). Similarly increasing the number of individuals in a single release from below to above 800 changes the success rate from 15 to 65% (Beirne 1975). Using >10 releases rather than <10 gives 70% success compared with 10% (Beirne 1975).

Exception four: island mammals

Both Ireland and Newfoundland were cut off by rising sea level soon after the last glaciation, when they had only ice and tundra. The result is that both have strikingly impoverished boreal/temperate mammalian faunas. There are several species in both Britain and Canada that would be expected, from their distribution and general ecology, to thrive in Ireland and Newfoundland, respectively, if they could only get there. In historical times, there were no species of voles in Ireland, compared with three species in Britain. Bank voles *(Clethrionomys glareolus)* were introduced into southwest Ireland in the 1950s. They are well established and spreading steadily (Crichton 1974). For Newfoundland, snowshoe hares *(Lepus americanus)* were intro-

duced successfully in 1864, mink *(Mustela vison)* in 1938, masked shrews *(Sorex cinereus)* in 1958 (to control larch sawfly *[Pristiophora erichsonii]*, an accidental introduction from Europe in around 1900), and red squirrels *(Tamiasciurus hudsonicus)* in 1963 (Dodds 1983). With five examples from Ireland and Newfoundland we find 100% success. In this small sample, there is no record of failures on either island of species that would be expected on biogeographical grounds to succeed.

This fourth example of deviations from the tens rule shows that, with appropriate historical factors and a good ecological match, the probability of an invasive species establishing can be high (100% in this small data set) rather than 10%.

Discussion: Reasons for the Rules

What can explain the tens rule and deviations from it? In many studies of invasion three sets of factors seem to be important. The first is propagule pressure, the rate at which propagules, seeds, breeding individuals, and so on, are released. The second is the set of factors that allow species to survive, and increase, from low densities. The third is the set of factors that determine local abundance. Let us see how far these and other factors can explain both the tens rule and the deviations from it.

Escaping

The only evidence that we have presented on the first 10 of the tens rule is the contrast between all British angiosperms and Pinaceae, which fit the rule, and edible crop plants, which do not (Fig. 1).

What can explain this contrast? First, crop plants are selected to grow well in Britain, and are numerous. Many other species are imported in small numbers to places from which they cannot invade; plants in botanic gardens and with poor dispersal are obvious examples. Second, although a species thrives in cultivation, it may fail to produce or disperse propagules. The third is that the propagules die or are eaten before the species is recorded. The evidence of the Pinaceae and of crop plants is that the more widely a species is propagated, the more likely it is to be recorded as casual. Given the extraordinary variety, and variety of origins, of plant species that are imported, it is not surprising that only a few become casual. Explaining why "a few" is between 5 and 20% (the tens rule) will require more data on origins and performance.

Establishing

Perhaps the most interesting of the invasion transitions is that from introduced or casual to established or naturalized. Following the rule are angiosperms and Pinaceae in Britain, birds in native habitats in Hawaii, and Beirne's (1975) data on limited introductions of biological control insects. In contrast, there is significantly higher success in most groups of biological control insects, passeriform birds in Hawaii, and Beirne's large introductions. Introductions that would be expected to succeed on biogeographical grounds, mammals in Newfoundland and Ireland, have (on a small sample) 100% probability of establishing.

What do these examples tell us of the factors involved? First, propagule pressure is clearly important. That much is clear from Beirne's data and from many accounts in the literature where several introductions have often been needed even for species that eventually become abundant.

Second, the ability of a species to maintain itself until conditions are favorable, and to increase from rare, is probably an important differentiator. Data from the Ecological Flora Database (Fitter and Peat 1994) support this (Williamson and Fitter 1996). Possibly the difference between columbiform and passeriform birds in Hawaii relates to this, though the available habitat is probably more important.

However, neither propagule pressure nor persistence can explain the failure of many British edible crops to establish feral populations. More basic population dynamical effects must be involved. The two basic processes of population dynamics are reproduction and death; to establish a feral population the first rate must exceed the second. Observation of British casual species suggests that a failure of reproduction in adults is a common phenomenon, but a high death rate in young stages of the next generation can be important. The key factor is probably suitable habitat, a habitat favorable to all aspects of population dynamics. The data on biological control insects (Table 4) suggest that some broad classes of habitats, or resources, differ in a predictable way in their effects here.

Many have hoped that establishment can be predicted from the existence of empty niches, or climatic matching. When these correspond, as for mammals in Newfoundland and Ireland, prediction seems possible. Otherwise these factors are of little use in prediction (Williamson and Brown 1986, Lawton 1990).

Becoming a pest

The final "ten," that the probability of an established or naturalized species becoming a pest is 1 in 10, is supported by three of our examples—angiosperms in Britain, pasture plants in northern Australia, and imported pests in the United States. The only contrary case is the transition from failure-to-control to effective-control in insects used for biological control, for which the probability is about 1 in 3.

Pests are difficult to define (Holdgate 1986, Perrins et al. 1992) but nevertheless very important in the study of invasions. The cost they inflict is enormous (OTA 1993), and the probability of a genetically engineered organism becoming a pest is widely discussed (Williamson 1994). But all the indications are that they have no particular properties as species; each pest is a pest for its own reasons. This can be seen in the characters of British pest plants (Williamson 1994) and of pest vertebrates (Ehrlich 1989). A part of what makes most pests a pest is, of course, a high population density. So the 10% of established species that become pests, and the one third of established biocontrol insects that produce detectable control, may just represent the upper tail of the log-normal distribution commonly found (at least approximately so) in many communities. If so, studying why and how species establish may be a better path to understanding pest status than studying pests alone.

Conclusion

Although it is generally agreed that as yet we can hardly ever predict the success of individual invaders, there is no doubt that there are statistical regularities to invasions. The tens rule, although crude, encapsulates much of what is known, and the deviations from it are illuminating. The rule is, we hope, the first step to developing a more accurate and general algorithm. Propagule pressure and population dynamics are both involved, and both deserve better quantification. In particular, studies of the early stages of species establishment, of the causes of death and how these vary at different densities, and the real distribution of dispersive stages could lead to an improved algorithm. An interesting question is whether population dynamics contribute more to the understanding of invasions than invasions contribute to the understanding of population dynamics.