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THE CHARACTERS OF SUCCESSFUL INVADERS

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Abstract

The characteristics of invading species were explored using the Ecological Flora Database, and by using comparisons available in other studies. Invasion success has been related to both abundance and distribution in the native range, which are themselves related. Abundance is probably the key variable. In the British flora invading species are characterized more by their distribution and morphology than by their life history and reproductive behaviour. The size of the plant and characters related to propagule pressure created by humans come out as important correlates of success. For biological characters, genetic studies and the phenomenon of boom-and-bust both suggest that the critical interaction between species and habitat is often subtle. Nevertheless, studies on pines and squirrels show that such important biological characters can be determined. Copyright © 1996 Elsevier Science Limited

Keywords: invasion, Ecological Flora Database, propagule pressure, boom-and-bust, British plants.

INTRODUCTION

The first question in the SCOPE programme on the ecology of biological invasions (Drake *et al.*, 1989) was 'What are the factors that determine whether a species will be an invader or not ?' Those factors include both the species and the habitat. Here we concentrate on the characters of the species using primarily the Ecological Flora Database of plants growing in Britain (Fitter & Peat, 1994), but using also other data on both plants and animals.

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. ... we will need the raw data ... in computer databases'. This is the approach we have been pursuing in various ways, for ordinary invasions, for weeds and for releases of genetically modified organisms (Perrins *et al.*, 1992*a*,*b*, 1993; Williamson, 1993, 1994, 1996) for the last 10 years, and which we take forward here. The statistical characteri-

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zation of probabilities centres on the tens rule, discussed in Williamson and Fitter (1996), while the database is the Ecological Flora Database (Fitter & Peat, 1994), which has not been studied for the properties of invasive species before.

In the tens rule (Williamson & Fitter, 1996) three stages of invasion are distinguished (Table 1). Imported and introduced species, in our terminology, are distinct. *Imported* species are those brought into a country, while *introduced* are those found in the wild. Those forming self-sustaining populations we call *established*. The categories are nested: established are both introduced and imported, and introduced are also imported. Botanists have traditionally called species that are introduced, but not established, casuals; the established are called naturalized. The transition from imported to introduced, which can be called escaping, has a probability of around 10% in many cases, and the probability of establishing is also often about 10% (Williamson & Fitter, 1996). The reasons for these low proportions no doubt involve the characteristics of the species invading.

EXPLORATIONS WITH THE ECOLOGICAL FLORA DATABASE

The Ecological Flora Database (Fitter & Peat, 1994) contains information on 1777 native and naturalized British gymnosperms and angiosperms covering over 120 ecological characteristics. As yet it contains no information on species that have failed to establish, or on the remaining parts of the imported and introduced categories. So we have used this database to compare native and established species.

Abundance, distribution and invasiveness

Daehler and Strong (1993) suggest that success in invasion relates partly to the geographical amplitude of the native range of an invader, and quote an example from brome grasses. Moulton and Pimm (1986) found the same effect in Hawaiian passerines, and Ehrlich (1989) in a variety of vertebrates. Crawley (1987), using one of his databases, found that 'insect species which are widespread in their native lands are significantly more likely to become established than species with local or patchy distribution'. This may merely be a special case of a more general phenomenon. Species that typically

Table 1. Definitions (enlarged from Williamson and Fitter (1996))

Imported	Brought into the country, contained
Introduced	Found in the wild, feral, casual, released
Established	With a self-sustaining population, naturalized, feral and breeding successfully, released and breeding successfully
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 around 10% (between 5 and 20%)

form dominant populations and are abundant in their communities have much wider geographical distributions than those that occur as scattered or isolated individuals (Table 2). Established species are proportionately more likely to form dominant populations than natives: 23% of established species are dominant (26 of 112) compared with 14% of natives (137 of 974) (see Table 5).

In our view the relationship of invasiveness to distribution described in the literature is probably usually mediated by abundance and high local population densities. Scarce species tend to have small ranges and be less successful invaders. Ehrlich (1986) stated that 'successful colonists [invaders] do tend to be animals that are relatively abundant', a view supported by Crawley (1987). Several studies have found a significant relationship between abundance and distribution (Hanski *et al.*, 1993; Lawton, 1993; Sutherland & Baillie, 1993; Gibbons *et al.*, 1994). Rabinowitz (1981) distinguished three types of rarity: range, abundance and habitat specificity. Several studies have explained the relationship between the first two in terms of the third. We would caution that it is difficult to distinguish between habitat specificity and habitat scarcity. Abundant species may just be those that are specific to abundant habitats, rather than being habitat generalists. But whatever the causal relationships, it does seem statistically that abundant species make better invaders, scarce ones poor ones. A statistical rule implies that there are exceptions, and there are, of course, some well-known ones such as *Pinus radiata*, which has a restricted native distribution in California yet is a widespread invader in the Southern Hemisphere (Richardson *et al.*, 1994; Rejmánek, 1995) and *Vulpia fasciculata*, a rare annual grass of sand dunes in Britain

(Watkinson, 1978) and a major weed in Australia (McIntyre & Whalley, 1990).

Abundance may also be related to seed production (Williamson, 1989), and there is an indication in the Ecological Flora Database that invasiveness may be related to seed production, but unfortunately the data are too coarse and patchy for a satisfactory statistical study (Table 3).

Plant characters

We have examined the distribution of 26 quantitative and qualitative characters among native and established species in the British flora. Twelve of these showed a significant difference (Tables 4 and 5), but some types of characteristic are much more likely to be different between native and invasive species than others.

Of the eight characteristics that describe the distribution of morphology of species, seven differed significantly; of the 14 that described their life history or reproductive behaviour, only three differed, and for two of these the statistical significance was not great. The difference between these two sets is highly significant (corrected $\chi^2_1 = 8.56$, $p < 0.005$). This is a surprising result, since there is a common assumption in the literature (Drake *et al.*, 1989) that reproductive behaviour is an important determinant of invasiveness.

Of characteristics differing between native and established species, one group reflects the fact that established species are generally large: they are more often phanerophytes than expected, tend to be tall and taller than wide, and have large leaves as well as being dominant in the vegetation (Table 5). These characteristics may perhaps be viewed as biological predictors of

Table 2. Abundance vs distribution in British plants

Area, Britain is the number of '10-km square' records. Data from the Ecological Flora Database (Fitter & Peat, 1994).

Status	Mean area, Britain	Mean countries, Europe
Dominant	1556	23·0
Frequent	1410	23·0
Scattered	328	18·3

Table 3. Numbers of species with various numbers of seeds per plant

Data from the Ecological Flora Database (Fitter & Peat, 1994).

Plant status	Numbers of seeds		
	<1000	1000–10,000	> 10,000
Native	147	117	75
Established	12	12	11

$\chi^2 = 1.81$, NS.

Table 4. Significant and non-significant results from a simple comparison of native and invasive established species in the British flora for a range of ecological characteristics

Data from the Ecological Flora Database; see Fitter & Peat (1994) for a description of the characteristics.

	Significant ($p < 0.05$)	Non-significant
Habitat	Soil fertility Maximum altitude	Shade Soil pH
Distribution	South/north index East/west index Dominance	
Morphology	Life form Maximum height Spread (height/width) Leaf area	Leaf shape
Life history	Age at first flowering	Seedling growth rate Leaf longevity Flowering time Season of seed dispersal Season of germination
Reproductive behaviour	Pollen vector Dicliny	Method of fertilization Incompatibility system Monocarpy Dichogamy Mean seed weight No. seeds per plant

successful invaders. The other group reflects the fact that species establish better where people are active: established invaders tend to be found in the south and east of Britain (where population density is highest), at low altitudes, and to be on fertile soils. The characteristics that cannot be classified this way are the weak tendencies to be monoecious and to flower in the first year (for which the data are marginally satisfactory) and, strikingly, to be insect-pollinated. The latter probably reflects a human predilection for importing species with attractive flowers.

All these comparisons are between established invaders and natives. As the established are a subset of the introduced which are themselves a subset of the imported, the comparisons must to some extent be a mixture of the characters that distinguish each of these three sets from natives. The importance of morphology and of the characters associated with horticulture are consistent with the view that propagule pressure, the mix and quantities of species imported, is an important determinant of what invades. This is a view that has been urged by Simberloff (1989), and is consistent with some of the deviations from the tens rule discussed by Williamson and Fitter (1996).

Nevertheless the failure of life history and reproductive behaviour characters to be important is striking. It is matched by the failure of most characters (and in particular Baker characters) to relate to the weediness of a plant (Perrins *et al.*, 1992*a,b*; Williamson, 1993). Baker characters are those put forward as those of 'The Ideal (?) Weed' (Baker, 1965, 1974) and much used by

seed companies to argue that their genetically modified products will not become weeds. The strongest statistical relationship of weediness to Baker characters is a curvilinear one. Plants with an intermediate number of Baker characters are those most likely to be weedy (Williamson, 1993). There is no consistency of life history and reproductive behaviour across all weeds. In the same way that it can be said that each weed is a weed for its own reasons so it may be that each successful invader is a success for its own reasons.

It could be argued that the Database does not include the right characters, or that there are real biological distinctions within more closely defined groups that are obscured by the differences between groups. We return to that in the Discussion.

OTHER GENERALIZATIONS

Our explorations of the tens rule and the Ecological Flora Database have drawn our attention to other phenomena associated with successful invasion. Two of these are the role of genetics, and the boom-and-bust phenomenon.

Taxonomy, genetics and invasion

While we agree with Daehler and Strong (1993) and Lawton (1990) that previous success at invasion by a species is a good indicator that that species will establish, we disagree that it is true in general for invasions by related species. However, there seem to be no reliable statistics and we rely on examples known to us

Table 5. Ecological characteristics that differ significantly between native and established species in the British flora
Data from the Ecological Flora Database (Fitter & Peat, 1994). Numbers in tables are numbers of species, except for indices, altitude and height. Bold indicates values markedly exceeding expectations; those in italic are well below.

1. Habitat factors

| | Soil fertility | | | |
	Very fertile	Fertile	Infertile	Very infertile
Native	252	636	750	493
Established	36	**91**	79	*37*

$\chi^2 = 12\cdot29$ $\quad$ $p < 0\cdot01$
Species may count in more than one category.

| | Mean maximum altitude | |
	m	95% confidence interval
Native	578	21
Established	407	23

2. Distribution

| | South/north index | |
	0–10 scale (10 = northern)	95% confidence interval
Native	3·34	0·11
Established	2·80	0·22

| | East/west index | |
	0–10 scale (10 = western)	95% confidence interval
Native	4·52	0·09
Established	4·24	0·24

| | Dominance | | |
	Dominant	Frequent	Scattered
Native	137	413	424
Established	**26**	38	48

$\chi^2 = 7\cdot35$ $\quad$ $p < 0\cdot05$

3. Morphology

| | Life form | | | | | |
	Phanero	Chamae	Hemicrypto	Geo	Helo/Hydro	Thero
Native	131	150	670	119	235	359
Established	**41**	20	88	22	*17*	57

$\chi^2 = 29\cdot4$ $\quad$ $p < 0\cdot001$

Table 5. *contd*

3. Morphology–*contd*

	Spread		
	Height>width	Height=width	Height<width
Native	588	667	200
Established	**113**	*68*	22
$\chi^2 = 17 \cdot 1$ $\quad p <0\cdot001$			

	Leaf area (cm²)				
	<0·1	0·1–1	1–10	10–100	>100
Native	50	249	474	374	*44*
Established	2	27	52	76	**22**
$\chi^2 = 40 \cdot 9$ $\quad p <0\cdot001$					

	Maximum height	
	cm	95% confidence interval
Native	136	20·5
Established	248	68·3

4. Life history

	Age at first flowering	
	<1 year	>1 year
Native	66	153
Established	**8**	7
$\chi^2 = 3 \cdot 49$ $\quad p = 0 \cdot 06$		

5. Reproductive behaviour

	Pollen vector		
	Insect	Wind	None/selfed
Native	889	392	190
Established	**156**	*23*	*14*
$\chi^2 = 30 \cdot 6$ $\quad p <0\cdot001$			

	Dicliny				
	Dioecious	Androecious	Gynoecious	Monoecious	Hermaphrodite
Native	58	51	223	**144**	1057
Established	12	5	*22*	*11*	166
$\chi^2 = 10 \cdot 3$ $\quad p <0\cdot05$					

and in the literature. One such example is *Impatiens capensis*, a North American species and a successful invader in south-east England, but its allospecies *I. noli-tangere* (Hultén & Fries, 1986) is a rare and declining native species centred on north-west England (Perrins *et al.*, 1993); the characters distinguishing the two would normally be called trivial. Ehrlich (1989) gives several cases of differential success in closely related vertebrates, and National Research Council (1989) similarly for plants, indicating that small genetic differences can have large effects on invasion potential.

Indeed, different genetic demes of a species may differ in their success at invasion. Some well-attested cases are quoted by National Research Council (1989) and Williamson (1992). There are many speculative such cases in the literature, such as rosebay willowherb (fireweed in North America) *Epilobium* (or *Chamerion* or *Chamaenerion*) *angustifolium*. This plant changed from a rare British native to an aggressive and widespread species early this century. Maybe new genes were introduced from garden or North American stocks (Salisbury, 1961), but the evidence, as in most such examples, is lacking. Another possible example is *Phragmites australis* in the eastern US.

Boom-and-bust

In Britain cases in which invading species go to a peak of population density and then decline are known but unusual. They include the little owl *Athene noctua*, Canadian pondweed *Elodea canadensis* and the rhododendron lace bug *Stephanites rhododendri* (Hemiptera, Tingidae), American speedwell (in Britain) or neckweed (in America) *Veronica peregrina* (Williamson & Brown, 1986; Williamson, 1994), but none that we know of have led to the complete extinction of the invader, though some became locally extinct. Extinction has occurred fairly frequently in rabbits *Oryctolagus cuniculus* on islands and also in the cats *Felis catus* introduced to control them (Thompson & King, 1994). Reindeer on three islands in the Bering Sea show the same pattern, though only on one, St Matthew, would the population have become extinct, being reduced to 41 females and one sterile male (Williamson, 1981).

Yet in Hawaiian passeriform birds extinction seems to have followed this pattern frequently, as judged by the time to extinction. Moulton (1993) gives introduction and extinction dates for passerines on Oahu. Time to extinction varies from one year to 40, with a median of 12.5. Even successful introductions such as the myna *Acridotheres tristis* (Stone, 1989) and the red-billed leiothrix *Leiothrix lutea* (Pratt *et al.*, 1987) follow the pattern.

It would seem that species of simple and anthropogenic habitats are particularly prone to show this pattern. It is most likely ascribed either to interactions between the invader and its prey species or resources, or to a build-up of enemies (predators or pathogens). Competition, despite strong advocacy (Moulton, 1993), seems a less likely general explanation.

DISCUSSION

The reasons for the general failure of species to invade —the reasons that lead to the tens rule—are still obscure, yet are important for conservation. When looking at the success of those that do establish, it is important to factor out the effects of propagule pressure, which acts both through the range of species imported and the rate at which each species is imported.

Many of the relationships that we find significant can be ascribed to propagule pressure. The exceptions are dominance and size characteristics and, dubiously as it is not statistically significant, the number of seeds per plant. The number of seeds is propagule pressure of a biological rather than a human kind, and the distinction is worth making. Because of gardeners' preference for large and showy plants even dominance and size may to some extent reflect human propagule pressure.

These generalizations can be compared to similar generalizations that have been published elsewhere. Pyšek *et al.* (1995) find height, hemicryptophyte form, C-strategy, moist soil and frequent planting important correlates of invasive success. It would seem that they, like us, have found the importance of propagule pressure from human imports.

In pines *Pinus* (Rejmánek, 1995; Rejmánek & Richardson, 1996), a discriminant function was found based on seed weight, interval between large seed crops, and minimum juvenile period. These results show the value of studying invasiveness in a group of well-known closely related species. In British plants, seed weight was not significant, but age at first flowering was (Table 4). The interval between large crops is not a variable that applies to most groups, and is not available in our Database. Pines with smaller seeds are more invasive, suggesting that pines with more seeds would be too, but that variable was not studied. We remain sceptical of the importance of r, the intrinsic rate of increase, in general, though it may well be associated with invasion of disturbed habitats (Williamson & Brown, 1986). Biological propagule pressure is distinct from r, and may well be more important. Even in *Pinus* the lack of invasiveness of *P. sylvestris* in South Africa may be from a lack of propagule pressure (Richardson *et al.*, 1994).

The success of species abundant (and so with a large range) in their native habitats may point to their superior ability to find a suitable habitat when introduced. Suitable habitat means one favourable to all aspects of population dynamics. 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. Climatic matching, in as far as it is important (Williamson & Brown,

1986; Lawton, 1990), probably most commonly acts in this way rather than by affecting the general health of adults.

However, a sustainable state requires sustainable resources and not too many enemies. The boom-and-bust phenomenon suggests that sustainable resources are frequently lacking. The study of British squirrels, the native *Sciurus vulgaris* and the invasive *S. carolinensis*, shows that even when the population effect is obvious (Okubo *et al.*, 1989) the resource involved may be subtle (Kenward & Holm, 1993). Cornell and Hawkins (1993) show that invaders generally suffer a lower rate of attack from parasitoids than natives. A lack of enemies, whether predators, parasites or diseases, has often been suggested as a major reason for differential success.

The interactions between population dynamics and human and habitat factors are starting to emerge from the myths that sometimes cover the analysis of invasions. Better databases will be vital in fostering this emergence.

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