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The Population Biology of Invaders [and Discussion]

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The population biology of invaders

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It is shown that invading species are most likely to establish where levels of competition among the resident species are lowest. Thus, of the higher trophic levels, herbivores are more likely to establish than carnivores or detritivores. Invading plants are most likely to establish in communities where the average level of cover is low. Competition is certainly not the only important process involved in establishment, however. Analysis of invasions by insects released as biocontrol agents against weeds, where exploitation and interference are likely to be negligible, show that the probability of successful establishment is closely related to the insect's intrinsic rate of increase. The main biological causes of failure are generalist predators, with parasites and diseases rather less important. For herbivorous insects, host–plant incompatibility is a major cause of failure in establishment.

A general model for the dynamics of an invading species is proposed, which stresses: (*a*), the importance of distinguishing explicitly between exploitation and interference competition; (*b*), the potential importance of generalist natural enemies; (*c*), the role of mutualists; (*d*), the importance of refuges of various kinds in affecting the probability of establishment. Examples are provided to emphasize how far we still are from real, predictive ability in relation to the likely success of proposed or anticipated invasions.

Introduction

Charles Elton's (1958) classic book, *The ecology of invasions*, catalogued the spread of exotic species through habitats into which they had been introduced (intentionally or accidentally) by man. To his long list of case histories we can now add many others. The aim of this paper is to survey the demographic attributes of successful and unsuccessful invaders, in the hope that the patterns that emerge will throw some light on the structure and dynamics of ecological communities in general. These introductions of animals and plants into new habitats are some of the most important field experiments ever carried out in ecology. They are somewhat flawed by want of replication and randomization, but they represent an unparalleled source of information from which we should be able to learn a great deal.

The population biology of invading species can be described by a limited number of so-called 'demographic parameters', which quantify the schedules of birth, death and rate of development that are typically exhibited by the species. I shall be concerned with fecundity (the average number of females produced by females surviving to reproductive age), survivorship (the average proportion of individuals surviving from birth to reproductive age), development rate (the time from birth to reproduction), and the intrinsic rate of increase, r, a single parameter that integrates the other three measures:

$$r = (\ln R_0)/T,$$

Where R_0 is the expected number of female offspring produced by the average female in her lifetime, and T is the average generation time. In addition, it will be necessary to consider how these parameters are related to the population density of the invading species, to the age structure of its population, and to the ecological conditions in the community into which it is introduced (e.g. food resources, habitat requirements, natural enemies, competitors and so forth).

I shall begin by considering broad patterns across trophic levels, to establish whether different kinds of organisms (plants, herbivores, carnivores or decomposers) are more or less likely to make successful invaders. I shall then consider how particular combinations of demographic attributes, and particular configurations of community structure, influence the probability of successful invasion.

TROPHIC PATTERNS

One of the most resilient (some would say unfortunate) hypotheses in community ecology is embodied in the argument proposed by Hairston *et al.* (1960), that, because the world is green, herbivores cannot be food-limited, with the corollary that, because everything has to be limited by something, herbivores must be limited by enemies. This means that the other trophic levels (plants, carnivores and decomposers) must, so the argument goes, be resource-limited. I have described the weaknesses of the assumptions underlying this hypothesis, and its shortcomings as a descriptive model of trophic structure, elsewhere (Crawley 1983). Nevertheless, if we take the hypothesis at face value, we can see that it implies that there are likely to be differences in the importance of competition at the different trophic levels. Competition will be intense for plants, carnivores and decomposers because they are resource-limited, but relatively unimportant for herbivores, since these are kept scarce in relation to their resources by the action of natural enemies. Following the Darwinian (but currently unfashionable) line that competition is the prime determinant of community structure, we predict that invasion ought to be difficult into plant, carnivore and decomposer communities, but relatively easy into herbivore communities.

We can evaluate these predictions in relation to the patterns of invasion exhibited by various groups of alien organisms in Britain, always bearing in mind the possibility that we might observe the right pattern for the wrong reasons.

(*a*) *Herbivores versus carnivores*

British birds and mammals represent two of the best known faunas in the world, and we have very accurate data on the distribution and abundance of recently established herbivore and carnivore species (table 1). The data include species deliberately introduced by man, as well as species that have invaded under their own steam. Both for birds and for mammals there are significantly more herbivores than carnivores among the invaders when compared to the abundance of these groups in the native fauna.

Of course, we cannot make a direct test of the success rates of invasion, based on the relative likelihood of establishing a herbivorous or carnivorous bird or mammal, because we do not know: (1) the number of species that arrived (or were released) but failed to establish; (2), the number of arrivals (or releases) of each species; or (3), the size of the initial immigration (or release). None the less, the pattern is consistent with expectation: alien carnivores are less common than alien herbivores.

TABLE 1. INTRODUCED BIRDS AND MAMMALS IN GREAT BRITAIN, CATEGORIZED AS HERBIVORES AND CARNIVORES

(Note that a great many herbivorous birds are carnivorous as young. We do not have sufficiently detailed information to calculate the rate of establishment directly, and must resort to a comparison between the percentage makeup of the successful invaders and the resident community. From information in Sharrock (1976) and Corbet & Southern (1977).)

(*a*) *Mammals established in Great Britain*

	herbivores	carnivores
	red-necked wallaby	mink
	rabbit	feral cat
	grey squirrel	
	Orkney vole	
	musk rat (extinct)	
	house mouse	
	ship rat	
	common rat	
	fat dormouse	
	coypu	
	Sika deer	
	fallow deer	
	muntjac deer	
	chinese water deer	
	feral goat	
	feral sheep	
percentage established	88	12
percentage native	29 (42)*	71 (58)

* Bats excluded

(*b*) *Breeding birds established in Great Britain*

	herbivores	carnivores
	mandarin duck	little owl
	wood duck	night heron (zoo)
	ruddy duck	little ringed plover
	gadwall	Slavonian grebe
	wigeon	goosander
	pintail	black-tailed godwit
	Egyptian goose	Cetti's warbler
	Canada goose	firecrest
	red-legged partridge	black redstart (urban)
	pheasant	
	golden pheasant	
	Lady Amherst's pheasant	
	collared dove	
	red-crested pochard	
	bob-white quail	
	serin	
	ring-necked parakeet	
	budgerigar	
	Muscovy duck	
	Chinese goose	
	Barbary dove	
	barnacle goose	
	canary	
	Java sparrow	
	pintailed wydah	
percentage established	74	26
percentage native	23	77

For other animal groups, the comparisons are difficult or impossible to carry out. For example, all introduced fish species, and the great majority of native species, are carnivorous. For important groups of smaller animals, such as the insects, the taxonomic 'difficulty' of the carnivorous species (e.g. the parasitic Hymenoptera) precludes meaningful comparisons.

(*b*) *Plants*

According to the trophic-level argument, alien plants should be scarce, since competition between plant species is supposed to be intense. The British flora, however, is rich in alien plants (Crawley 1987). None the less, different plant communities do contain radically different numbers of introduced species (figure 1), and these differences do appear to be related to interspecific competition. Relatively stable communities, such as natural woodlands and grasslands, contain rather few aliens, whereas ephemeral communities, especially those created and maintained by man, support a great many alien plant species. The best correlate of high invasibility in plant communities is the average degree of plant cover; low cover is associated with high invasibility. In natural communities, low plant cover occurs on unstable substrates, or on soils with low nutrient levels, intense below-ground competition for water, or heavy grazing by domestic livestock (Crawley 1986). The communities richest in aliens (e.g. urban waste ground) combine severe disturbance, low soil nutrient levels, high soil toxin levels, and rather small seed banks (Crawley 1987).

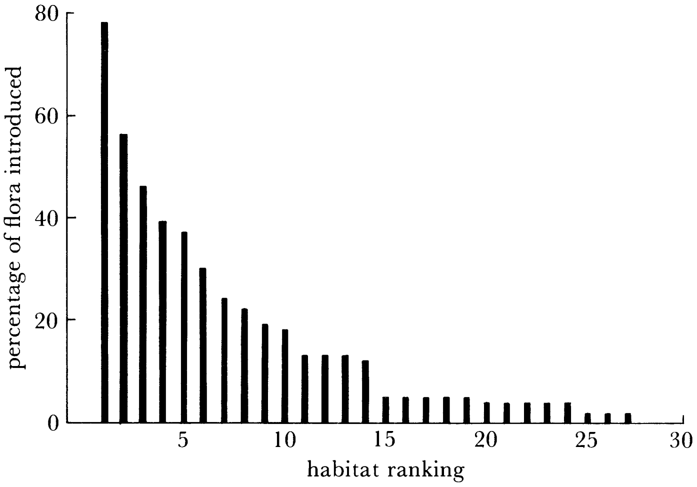

FIGURE 1. Introduced plant species in different terrestrial habitats, ranked by the percentage of their total flora made up by alien species (ties are given median rank). For details of the method of calculation, see Crawley (1987). Rank numbers indicate: (1) waste ground, 78%; (2) coniferous plantations, 56%; (3) walls, 46%; (4) river shingle, 39%; (5) weeds of arable fields, 37%; (6) shady banks of streams, 30%; (7) open banks of streams, 24%; (8) hedgerows, 22%; (9) parkland, 19%; (10) sea cliffs, embankments and walls, 18%; (12) lowland damp grasslands, 13%; (12) sand dunes, 13%; (12) beaches, 13%; (14) fast upland streams, 12%; (17) deciduous woodlands, 5%; (17) bog, 5%; (17) peatlands, 5%; (17) lowland dry grasslands, 5%; (17) seaside shingle, 5%; (22) marsh, 4%; (22) upland springs, 4%; (22) limestone pavements, 4%; (22) shady rocks, 4%; (22) saltmarsh, 4%; (26) fen, 2%; (26) heaths and heather moorland, 2%; (26) upland grasslands, 2%; (30) native pine forest, 0%; (30) mountain summits, 0%; (30) rock ledges on inland cliffs, 0%; (30) upland screes, 0%. The main correlates of high alien richness are proximity to sources of alien seed (as, for example, in docks, gardens, railways etc.), average area of bare ground within the community, and degree of substrate disturbance. Note that some disturbed systems (e.g. upland screes) are extremely poor in aliens; these systems are both unproductive and isolated from sources of seed.

Disturbance itself, however, is rather poorly correlated with alien species richness. In the famous Broadbalk experiment at Rothamsted, England, winter wheat has been grown every year since the 1840s (Brenchley & Warrington 1930; Thurston 1969). There has been regular disturbance every year for the past 140 years, since the soil is ploughed up each autumn. Despite this, only 10% of the 50 or so weed species growing in the field are aliens (table 2); three of the species are relatively important weeds (*Avena ludoviciana*, *A. fatua* and *Veronica persica*) and two are unimportant (*Galium tricorne* and *Agrostemma githago*). Of course, disturbance is not associated with low cover or low interspecific competition in the Broadbalk experiment. Wheat is the dominant species, but even without the crop, sufficient numbers of annual weeds germinate (from current seed production or from the bank of dormant seeds in the soil) to ensure both high cover and intense competition. (The maintenance of high species-richness and the determinants of relative abundance in this unique community of annual plants will be the subject of a forthcoming paper.)

In general, species-richness of plants tends to peak at intermediate levels of disturbance (Grime 1979; Connell 1979; Crawley 1986), but our data are too poor to test this hypothesis for the British flora as a whole. It does appear, however, that the more intense the interspecific competition, the lower the likelihood of invasion, consistent with the trophic-levels hypothesis.

(*c*) *Decomposers*

Of all the groups, decomposers are the most obviously resource-limited (as evidenced by the fact that the earth is not covered by an ever-increasing layer of excrement and dead remains). They are also the group about which the least is known. It is exceptionally difficult, for example, to determine whether or not a new species of fungus is an alien, because the mycelium could have been with us for centuries without ever producing a recognisable fruiting body. There are a great many alien fungus species associated with imported timber trees (e.g. the larch bolete, *Suillus grevillei*), but most of these species are mycorrhizal, introduced on the roots of imported plants, rather than decomposers. The macrofungi of decomposing hardwood timber exhibit a rather high degree of substrate-specificity, and among native forest trees, for example, oak, ash, elm, beech, alder and willow all have their characteristic fungal decomposers. An apparent minority of hardwood-decomposing fungi (e.g. *Stereum hirsutum*) are generalists. With coniferous timbers, the decomposer fungus flora appears to be much more cosmopolitan, but recent research suggests that there are species-specific strains of such widespread and taxonomically generalist fungi as *Heterobasidium anosum* (J. Gibbs, personal communication), so their catholicism may be more apparent than real. Introduction of novel substrates would seem likely, therefore, to open the way for the invasion of specialist decomposing fungi, but the British quarantine regulations on the importation of timber seem to have succeeded in excluding such species.

Similar kinds of substrate-specificity are found among carrion-feeding vertebrates. Perhaps the best (and certainly the most gory) example comes from the guild of vultures feeding on the carcasses of dead ungulates on the plains of east Africa. There are typically three species of vulture in any one area: the largest (usually a species of *Gyps*) has a featherless neck and rips out the soft intestines and other inner organs; a medium-sized species eats the skin and muscles; and a small, bone-picking species feeds on the left-overs. Although there is very little overlap in resource use between the different vultures, their guilds are strongly structured by interference competition, with the larger species driving off the smaller species when they attend the same carcass (Konig 1983).

Table 2. Native and introduced plant species in the Broadbalk experiment at Rothamsted, England

('Seed bank' gives the number of viable seeds in the top 10 cm of 2 m^2 sample areas of soil; Blanks indicate that no seeds of that species were discovered, even though mature plants were recorded. Germination time relates to the time of peak germination: A, autumn; S, spring; W, winter; SU, summer; all, year round. Dormancy: short, less than 2 years; moderate, 2–4 years; long, over 4 years. Competitiveness: low, markedly suppressed by the crop; high, markedly suppresses the crop. Seed bank data from Brenchley & Warrington (1930).)

native species	seed bank	germination time	dormancy	competitiveness	habit
Papaver rhoeas	2000–30000	S + A	long	low	erect
Scandix pecten-veneris	46–260	A	short	—	erect
Torilis arvensis	1–2250	A	long	—	erect
Galium aparine	44–2100	A	—	—	scrambling
Polygonum aviculare	5–726	S	moderate	low	prostrate
Veronica arvensis	1000–7000	A	long	—	prostrate
Myosotis arvensis	187–788	A	—	—	erect
Capsella bursa-pastoris	290–660	all	—	—	erect
Tripleurospermum inodorum	20–130	all	long	low	spreading
Vicia sativa	—	—	—	—	scrambling
Medicago lupulina	126–1200	S(+A)	short	—	prostrate
Ranunculus arvensis	—	A + W	—	—	erect
Legousia hybrida	700–1100	A	long	—	erect
Alopecurus myosuroides	5000–12000	A	short	high	erect
Aphanes arvensis	4500–9500	A + W	long	—	prostrate
Arenaria serpyllifolia	300–1100	W	long	—	prostrate
Lithospermum arvense	—	—	—	—	erect
Stellaria media	182–1200	A + S	short	—	prostrate
Odontites verna	200–400	S	long	—	erect
Veronica hederifolia	540–840	A + W	long	—	prostrate
Poa annua	50–300	all	short	—	prostrate
Lathyrus pratensis	—	—	long	—	scrambling
Knautia arvensis	—	—	—	—	erect
Valerianella locusta	—	—	—	—	erect
Anagallis arvensis	0–4	W	long	—	prostrate
Chaenorrhinum minus	—	W + S	short	—	erect
Euphorbia exigua	11–118	W	long	low	erect
Aethusa cynapium	13–141	all	long	—	erect
Atriplex patula	6–317	W + S	?	—	erect
Viola arvensis	—	S + A	moderate	—	erect
Cerastium vulgatum	—	A	short	—	erect
Senecio vulgaris	10–231	all	short	—	erect
Taraxacum officinale	—	—	short	—	rosette
Plantago major	—	Su	—	—	rosette
Polygonum convolvulus	0–15	W + S	—	—	scrambling
Fumaria officinalis	—	all	—	—	scrambling
Sinapis arvensis	—	S + Su	short	—	erect
Allium vineale	—	—	—	—	erect
Chenopodium album	—	all	short	—	erect
Epilobium montanum	—	—	short	—	erect
Lamium purpureum	—	—	short	—	erect
Lapsana communis	—	—	—	—	erect
Thlaspi arvense	—	all	short	—	erect
Sonchus arvensis	1–28	W + S	short	—	erect
introduced species					
Agrostemma githago	—	—	—	—	erect
Avena ludoviciana	—	A + W	long	high	erect
Avena fatua	—	S	long	—	erect
Galium tricorne	2–46	A	—	—	scrambling
Veronica persica	22–1900	all	—	—	prostrate

There are some examples of extremely successful invasions by decomposer animal species. Perhaps the best known is the establishment of the earthworm, *Lumbricus terrestris*, in New Zealand, and the spectacular improvements in soil fertility which this brought about. In the United States, earthworms were introduced as fishing baits, where a few escaped to swim ashore and invade the country adjacent to the river bank. In Britain, soil amphipods have reached the mainland from New Zealand via the Scilly Isles; these animals feed on much the same kinds of dead organic matter as do isopods, but unlike these animals they form soil burrows and create a markedly more friable soil structure (J. Anderson, personal communication). Presumably, the paucity of alien soil animals is due in no small part to the low rates of immigration resulting from the limited international trade in soil.

The combination of resource-limitation with highly structured feeding guilds makes decomposer organisms intriguing subjects for the study of invasions, but as yet we know rather little about the numbers of alien decomposer species in most natural habitats. The possibility exists that, as organic matter decomposes and becomes more amorphous as the chemical heterogeneity of the different substrates decreases, so micro-spatial resolution becomes progressively more important in the coexistence of decomposer species (Swift 1976; J. Anderson, personal communication). Thus, although macro-decomposers may show patterns of resource-specificity and niche differentiation, micro-decomposers may be much more catholic in their use of resources, but more specialized in their microhabitat selection.

Thus, over the four trophic levels, the generalizations emerging from the Hairston, Smith & Slobodkin hypothesis (Hairston *et al.* 1960) appear to be broadly correct, and we do find more alien species where we imagine interspecific competition to be less intense. We must now address the possibility that the patterns are right for the wrong reasons. To do this, I shall present a new model for the population dynamics of an invading species, and draw on data from the biological control of weeds to test its predictions.

Population dynamics

A comparison of the demographic attributes of successful and unsuccessful invaders may allow us to form a clearer picture of how the patterns exhibited between different trophic levels come about. To do this, I shall draw chiefly on data relating to the intentional release of insect species to control (mainly exotic) weed species. The advantage of this approach is that we have information, albeit limited, on the failures of establishment, data which, quite naturally, are unavailable for most undisturbed systems. The body of data was drawn together in a collaborative project between Imperial College at Silwood Park, CIBC, CSIRO, and many of the biocontrol practitioners, worldwide, who have been directly involved in biological weed control. The project is described in more detail elsewhere (Crawley 1987).

Rather than deliver lots of minor caveats throughout this section, I shall issue one big caveat here. The data are neither replicated nor random samples; there are very many internal correlations between the different variables, and no clear means of isolating cause and effect. None the less, these are some of the best data we have, on some of the largest-scale field experiments in all ecology, and we owe it to ourselves to make the most of them. The nature of the data, however, does make statistical testing something of a nonsense.

To investigate the demographic attributes of successful invaders, I shall present a new model for the population dynamics of the invading species. Previous models of invasion (see, for example, Turelli 1981) have tended to assume in advance that either competition or natural enemies are the main force opposing establishment. Where competition is assumed, no distinction is usually made between exploitation and interference competition (but see Vance 1985), and within exploitation, contest and scramble are not normally distinguished. Models involved with natural enemies often do not simulate the dynamics of generalist predators, assuming their numbers to be determined by other factors (e.g. the abundance of other, preferred prey species (Hassell & May 1986)). Mutualisms are rarely considered in the context of invasions, and, when they are modelled, they are treated as being both symmetrical and constant over all densities (Addicott 1981). Finally, most models of invasions assume the environment to be both spatially and temporally uniform. Non-equilibrium conditions are explicitly excluded, and refuges caused by spatial heterogeneity, slight niche differences or the aggregative behaviour of the constituent species are typically ignored.

A model of invasion

Consider an invading species, i, with N_i individuals. Under absolutely ideal conditions, this species exhibits a rate of increase per head, r_i, which we call its intrinsic rate of increase. Thus the minimal condition for invasion is that $r_i > 0$ under the climatic and other abiotic conditions that occur in the habitat to which the species has been introduced. The remainder of the model takes account of various processes that tend to reduce the actual rate of change per head below r_i:

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = r_i\,N_i - f_1(\psi, N_i) - f_2\left[\sum_{j=1}^{i-1} N_j,\ N_i\right] - f_3\left[\sum_{k=1}^{i-1} N_k,\ N_i,\ P\right] - f_4(M,\ N_i) + X$$

where f_1 is a function describing the effects of exploitation competition, acting through the resource supply rate, ψ; f_2 is a function describing the effects of interference competition, acting through the number of individuals of all species (j) that are more 'fierce' than the invading species (the N_j are ranked from the most fierce (1) to the last species that is fiercer than the invader ($i-1$); f_3 is a function describing the influence of natural enemies (P) and is related to their preference for alternative prey and to the abundance of prey species preferred to the invader (N_k); f_4 describes the effect of a lack of mutualists (M) on the ability of the invader to increase when rare. The final factor is the 'mystery ingredient', X. This is essentially an immigration rate; it may represent immigration from outside, or it may represent recruitment from members of the invading species that are protected in refuges of various kinds. The details of these functions, and the bearing of the weed data on them, are now considered separately.

(*a*) *Intrinsic rate of increase*

The components of r_i are fecundity, survivorship and developmental rate. In addition, the number of generations per year (the invader's 'voltinism') influences the actual rate of increase, at least when the invader is scarce. Table 3 shows the components of rate of increase of the control agents for three classes of weed; it is clear that for establishment, and for successful depletion of weed abundance, agents with higher intrinsic rates of increase are more likely to succeed. Because intrinsic rate of increase shows a close negative correlation with body size across different taxa (Southwood 1976), it is not surprising to find that small insects are more likely to become established than large ones.

Species with low rates of increase do not appear to make good invaders, and it is difficult

TABLE 3. THE DEMOGRAPHY OF WEED BIOCONTROL AGENTS. (*a*) FACTORS INCREASING THE PROBABILITY OF SUCCESSFUL ESTABLISHMENT; (*b*) FACTORS INCREASING THE DEGREE OF WEED CONTROL

(Table entries represent the response to an *increase* in the row factor; thus an increase in insect size led to lower probability of establishment on *Lantana*; n.d., indicates that a factor makes no difference to establishment probability or degree of control. From the Silwood Project on Weed Biocontrol.)

(*a*) *Demography and probability of establishment*
(attributes associated with an increased probability of establishment: v51 = 1)

demographic parameter	*Opuntia*	*Lantana*	other weeds
fecundity	n.d.	n.d.	higher
egg aggregation	lower	n.d.	lower
voltinism	n.d.	higher	higher
size	n.d.	lower	lower
damage per head	too few data	lower	lower
development rate	n.d.	higher	n.d.
adult longevity	higher	higher	higher
diapause	n.d.	lower	n.d.

(*b*) *Demography and degree of control*
(attributes associated with a high degree of control; v57 > 2)

demographic parameter	*Opuntia*	*Lantana*	other weeds
fecundity	higher	higher	higher
egg aggregation	higher	n.d.	higher
voltinism	higher	n.d.	higher
size	lower	n.d.	lower?
damage per head	lower	n.d.	lower
development rate	higher	n.d.	higher?
adult longevity	lower	lower?	lower
diapause	n.d.	n.d.	n.d.

to find examples where a successful invader had a markedly low intrinsic rate of increase for its particular body size (although some plants, once established, can persist for protracted periods, only spreading very slowly, if at all (Crawley 1987)). This conforms with the model's most elementary prediction; the lower the value of r_i, the lower the probability that dN_i/dt will exceed zero.

(*b*) *Exploitation competition*

In exploitation competition, the rate of resource supply determines the invader's rate of population change. When all individuals suffer equally under resource shortage, the process is called 'scramble'; when some individuals get their fill and the others pick up the scraps, the process is called 'contest'. Both have quite different effects on population dynamics (Hassell 1978). The rate of resource supply to the invader depends on the standing crop of resources (which is itself a function of the previous feeding behaviour of the resident competitor species), their productivity, and the rates of resource removal by the resident competitor species. The important point in relation to invasibility, is whether the available rate of resource supply, ψ, is great enough, or the numbers of competitors low enough, that $r_i N_i > f_1(\psi, N_i)$.

Unfortunately, our weed control data are of little use here, because resources (weeds) are virtually limitless when the biocontrol agent is first introduced. For successfully established agents, competition may become important later, once weed abundance has been reduced to very low levels (table 4).

Table 4. Demography of the invading insect: the pattern of population dynamics after introduction

(Each of the 627 cases was allocated to one of the eight categories below. Note that the much-vaunted 'genetic adjustment period' (several years at low density after release) does not usually appear to lead to important time-lags. Data from the Silwood Project on Weed Biocontrol.)

explosive increase	28 %
gradual increase	16 %
rapid increase after several years at low density	4 %
gradual increase after several years at low density	3 %
persists at low density	13 %
declines to low densities	1 %
extinction after one or more generations	8 %
extinction without completing a single generation	27 %

(c) *Interference competition*

Interference competition occurs when individuals of one species reduce the fitness of individuals of another species through some kind of behavioural interaction that is not directly related to resource abundance. Thus plants interfere when they produce allelochemicals that are more toxic to members of other species than to their own. Many animal species interfere with members of their own species through display, threats or fighting, and some animals interfere with individuals of other species by similar means. Interspecific interference normally involves a larger species excluding a smaller one, though, in general, it would involve 'fiercer' species excluding 'less fierce' ones. Most interference interactions are hierarchical, so that if A is fiercer than B and B is fiercer than C, then A will be fiercer than C.

To model this, it is necessary to know the total number of individuals belonging to all species that are fiercer than our invader. Thus, if the invader is larger than all the residents, interference is likely to be negligible, whereas if there are several, abundant resident species larger than the invader, interference might be important. Unless a similar invasion has been observed elsewhere on a previous occasion, however, there is no way of knowing in advance what kind of behavioural interactions, if any, will occur between the invader and the residents. A predictive model would have to assume the nature of likely behavioural interactions, based on relative body size of members of the guild of residents.

As with exploitation, native herbivores are likely to be scarce on exotic weeds targeted for biological control, so our data can throw little light on this process. However, other well-studied systems do allow some conclusions to be drawn. Perhaps the best-known example involves the *Anolis* lizards of the West Indies, which have been studied by Roughgarden and his colleagues (Rummel & Roughgarden 1983, 1985; Roughgarden *et al.* 1984). On most islands in the Lesser Antilles, it appears that a larger species can invade and displace a smaller one, but not vice versa. This effect appears to be due to interference rather than to exploitation, as I shall discuss later. Other cases where a successful invader has excluded a resident through interference are anecdotal. In some cases where the spatial distributions of the invader and the resident species are suggestive of interference, detailed study provides no evidence of interaction at all (e.g. the fish-eating birds, goosander and red-breasted merganser, in Britain; (N. Carter, personal communication).

Another important topic is related to the kind of competition that occurs in guilds structured by body-size differences. The question arises as to whether a guild can be invaded 'from above' by a larger species, or 'from below' by a smaller species. Since body-size is positively correlated with competitive ability through interference (Grant 1971), we would expect guilds structured by interference to be most readily invaded by larger species (as in Roughgarden's lizards). On the other hand, guilds structured by exploitation competition should be most readily invaded 'from below', by smaller species, since populations of smaller individuals can reduce the resource supply rate to levels so low that larger species cannot be supported. Guilds of *Daphnia* and rotifers exhibit just this pattern with smaller species found at lower rates of resource supply (Tillman & Lampert 1984; Stemberger & Gilbert 1985). Thus along a gradient from low to high productivity, one would predict increasing body size, and a shift from exploitation towards interference as the most important kind of competition.

(*d*) *Natural enemies*

Natural enemies can prevent invasion or reduce the rate of spread of invading species (Goeden & Louda 1976; Moran & Zimmermann 1984; Lawton 1986). In some cases, an invading species brings its specialist natural enemies with it (particularly its diseases and microparasites). The resident natural enemy species only represent a threat to the extent that they are capable of expanding their diets to include the invader. Thus, the depressive effects of native natural enemies on the invader depend on the number of enemy species, their population densities, their feeding preferences, and the total number of resident prey species that are of higher preference than the invader (Crawley, 1983). The invader is unlikely to suffer severe attack when it invades a community rich in prey species more preferred than it is. On the other hand, when the invader is attractive and accessible to natural enemies, through lack of protective coloration, or for want of skulking behaviour, it may easily be excluded by them.

In the 'weeds' data, natural enemies figure prominently among the factors known to be important cases of failure (table 5). Predators appear to be about twice as important as parasitoids, and parasitoids rather more important than diseases in preventing establishment or reducing the degree of weed control. It is likely that the role of disease is underestimated, since it is notoriously difficult to carry out post mortems on insects. Also, the turnover rate of most diseases is so rapid that the percentage of the hosts exhibiting symptoms at any one time can be very low (Anderson & May 1981). It is clear from this and from other studies (reviewed by Lawton 1986) that the presence of high densities of resident, generalist natural enemies can be just as potent a force in resisting invasion as the presence of competitors. This raises the

Table 5. Factors limiting the impact of the introduced insect

(The number and percentage of cases in which certain factors were recorded as being known to be important causes of reduced impact in weed biocontrol. 'Unknown' causes of failure have been omitted. In addition to these categories, over 50 % of cases involved unspecified 'other factors'. From the Silwood Project on Weed Biocontrol.)

	unimportant	important	percentage of cases
climate	188	148	44
predators	218	61	22
parasitoids	283	34	11
disease	243	21	8
incompatibility	353	173	33
competition	475	67	12

extremely important, but unresolved, question as to whether natural enemy populations drive prey dynamics (as most models assume (Hassell & May 1986)), or are driven by them (as field studies sometimes suggest: lions and wildebeest (Schaller 1972); parasites of larch budmoth (Varley & Gradwell 1970). Clearly, only enemies of the first kind are likely to play an important role in hindering invasion, although driven enemies may be important when the invader is scarce if they exhibit switching and feed disproportionately heavily on the invader.

(*e*) *Mutualists*

I have included mutualists in the model as a negative term. The purpose of this unconventional device is to avoid what May (1976) has so graphically described as the 'orgy of mutual benefaction', which tends to result when models include mutualisms as beneficial to both species at all densities. To counter these exponential trends, most models of mutualism have to include intense intraspecific competition to constrain population growth (i.e. they become explicitly competition models (Addicott 1981)). A more realistic approach (see, for example, Tonkyn, 1986) is to assume that the full capacity for increase, r_i, can only be exhibited when the individual has its full complement of obligate mutualists (mycorrhizae, pollinators and root nodulators for plants, or gut microflora for animals). Only when these mutualists are in limited supply is the actual rate of increase reduced.

The model can also cater for indirect mutualisms. For example, the trophic structure of the resident community may mean that some of the resident species benefit the invader, either by making its potential competitors less abundant, for example by interference (Davidson 1985) or selective predation (Crawley 1983), or by reducing the abundance or searching efficiency of the invader's natural enemies (e.g. enemies of the enemies, or plants that mask host-finding cues (Root 1973)). Thus, indirect mutualisms are modelled by the competition, or natural enemy, functions (f_1, f_2 and f_3).

The 'weeds' database tells us nothing about the importance of mutualisms in promoting or hindering invasion. Lack of obligate mutualists must be a very common, but rarely recorded, reason for the failure of invasions in other systems, however. A great many plant invasions probably fail for want of specialized pollinators or mycorrhizae. In Puerto Rica, for example, it was impossible to establish pine plantations on upland, sandy soils until the mycorrhizal fungus *Pisolethes littoralis* was intentionally introduced (R. Watling, personal communication). A great many introduced plants fail to set seed in gardens, and failure of pollination must be at least one of the causes (e.g. in the failure of *Viola odorata* and *Primula* spp to spread in New Zealand (Good 1964)). Orchid species will not establish from seed without the fungal species that is parasitized by the plant during early growth, and orchids are uncommon in many apparently suitable habitats, despite the wide dissemination of their tiny seeds (Summerhayes 1956; but see Bradshaw & McNeilly (1981) for exceptional establishment of orchids on industrial waste tips). Among animals, most of the mutualisms affecting invasion will be indirect (e.g. ants to protect Homoptera, enemies to attack the invader's competitors, and so on). Nevertheless, the omission of mutualisms from invasion models will tend to reinforce the notion that they are of trivial importance compared with competition and natural enemy attack (see Boucher 1985), and mean that a great many failures of establishment are either unexplained, or wrongly attributed to other causes.

(*f*) *Refuges*

Just as in the standard Lotka–Volterra models, the first five terms of the model describe a world that is spatially and temporally uniform. Through these five terms the invader is exposed to the full rigours of competition and natural enemy attack. These homogeneous models therefore define the set of conditions that is *most difficult* to invade. The 'mystery ingredient', X, in the model helps rectify this shortcoming. It is intended to represent two different processes: (1) immigration of individuals of the invading species from outside (which allows that initial reverses suffered by the invader are not necessarily terminal); and (2) the existence of various kinds of refuge, which protect the invader from the full weight of competitor and enemy attack.

Immigration over a protracted period will certainly increase the likelihood of successful invasion, simply because the experiment of invasion is repeated many times, under what are likely to be different conditions of weather, competitor density and natural enemy abundance. The 'weeds' data demonstrate this effect clearly. The probability of establishment increases with the size of the individual release, but also with the number of releases. Furthermore, species whose adults are long-lived are more likely to establish than species with short-lived adults. High adult longevity ensures that eggs are laid over a protracted period, and the probability of encountering suitable conditions for establishment is increased. It is interesting to note, however, that there is no indication in the data base for a threshold minimum population size for successful invasion. Some successful biocontrol attempts have been initiated by the release of a single gravid female (Moran & Zimmermann 1984). We do not know enough about the biology of most of the species, however, to say that 'Allee effects' do not occur, and, clearly, in species that did suffer deleterious low density effects, protracted immigration might be vital for establishment.

Refuges of various kinds permit recruitment to the invading population despite intense natural enemy attack and despite the attentions of fierce competitors (table 6). The description and analysis of new and different kinds of refuges has become something of a growth industry in recent years (Hassell & May 1974; Atkinson & Shorrocks 1981; Hanski 1981, 1983). Refuges provide either 'enemy-free space' or 'competitor-free space' for the invader, by specifying either spatial or temporal heterogeneity in the rates of encounter between individuals of the invader and resident species. Various physical refuges may also provide protection from extremes of the abiotic environment.

Among the most interesting developments in the study of refuges concern the spacing behaviour of the species. When, for one reason or another, species exhibit aggregated spatial distributions, and the correlations between different species distributions are less than perfect (i.e. they are not all aggregated in the same places), then the invader is provided with a refuge in those parts of the environment where it happens to co-occur with low numbers of enemies and/or competitors. This kind of behaviourally based heterogeneity may be sufficient to explain a great deal of the variability in guild structure between one community and another (for example, in *Drosophila* guilds; B. Shorrocks, personal communication). In any event, adding heterogeneity to simple models can dramatically increase the likelihood of successful invasion.

It is interesting, in this context, to note that, for the 'weeds' data, aggregation by the herbivores has different effects on establishment and on the level of control achieved. Compared with species that lay their eggs singly, insects laying their eggs in batches are more likely to fail to establish, but, once established, batch-laying species bring about better weed control.

Table 6. Refuges of various kinds in which the invader might obtain partial protection from natural enemies or from competitors

(For details of the species involved, see References.)

	example	references
refuges from enemies		
hiding places	*Tribolium* in glass tubes	Crombie 1945; Gause 1934
inaccessible micro-habitat	ovipositor length in gall parasitoids	Askew 1961; Arthur 1962
habitat selection	incomplete spatial overlap	Vinson 1981; Huffaker & Kennet 1959
microhabitat selection	differential use of host plant parts	Gardner & Dixon 1985
enemy behaviour	aggregation at high prey densities	Hassell & May 1974
enemy selectivity	switching or search image for other species	Crawley 1983
prey behaviour	predator avoidance	Hamilton 1971
prey morphology	crypsis	Hassell 1978
prey polymorphism	*Cepaea*	Jones *et al.* 1977
multilayered egg batches	central eggs inaccessible, e.g. *Spodoptera*	Braune 1982
parental care	limited number of eggs protectable	Callan 1944
inaccessible reserves	underground organs of plants	Noy Meir 1975
phenology	differential susceptibility	Crawley 1983
mobility	migratory prey, sedentary enemies	Sinclair 1979
mutualists	enemies of enemies	Davidson *et al.* 1985
host plant effects (i)	lack of enemy attractants	Weseloh 1976
host plant effects (ii)	presence of enemy deterrents	Woets & van Lenteren 1976
lack of other similar prey	low enemy density	Messenger 1975
refuges from competitors		
resource partitioning	incomplete resource overlap	Boag & Grant 1984
spatial behaviour	incomplete habitat overlap	Hanski 1983
aggregation	imperfect spatial overlap	Atkinson & Shorrocks 1981
phenology	incomplete temporal overlap	Brenchley & Warrington 1930
selective enemies	potential competitors kept scarce	Crawley 1983
mutualists	interference excludes competitors	Davidson 1985
fragmentation of resources	smaller pieces allow coexistence	Hanski 1987
tolerance of extremes	plants of poor or toxic soils	Gurevitch 1986

The most obvious ecological explanations of these effects are that generalist predators are exceptionally adept at eliminating whole clutches of eggs (Moran & Zimmermann 1984), but batch-laying species do more damage to the plants than do individual layers (Crawley 1983). There is no evidence to suggest that this is an artefact of biocontrol release strategy (e.g. more species of batch-layers are released as eggs, because batched eggs are easier to handle, and releases of eggs are more likely to fail than are releases of other life stages); releases of eggs were only slightly more likely to fail (46% compared to 40% failure from larval or adult releases).

Discussion

The most pronounced patterns to emerge from this analysis of weed control agents relate to the insects' intrinsic rate of increase. Species with higher values of r are more likely to establish after introduction, and more likely to depress weed abundance to low levels. For the large group of plants classified as 'other weeds' in table 3 (i.e. all cases except those involving *Lantana* or *Opuntia*), the insects with the greatest probability of establishing exhibit higher fecundity and smaller body size and pass through more generations per year. The insects most likely to depress weed abundance to low levels show precisely the same combination of traits. For both establishment and control, it is also clear that species with lower damage rates per head (small insects, each taking a small amount from each plant) are likely to make better control agents than big insects, where each individual is highly damaging. For the two weed groups we have analysed separately, the patterns are less clear. Successful invaders amongst the *Lantana* insects were smaller, and had higher development rates and higher voltinism, but they were not significantly more fecund than the inferior invaders. The data for *Opuntia* are coloured by the fact that one of only two agents (a moth, *Cactoblastis cactorum*, or cochineal insects, *Dactylopius* spp) has been employed in most releases, and these differ so widely in their biologies that the variance associated with average demographic parameter values is far too high to detect significant differences.

The most common causes of failure during introductions were abiotic factors (usually bad weather). Among the biotic factors, generalist predators are the most important (often predatory ants), with parasitoids and diseases less important. Host plant incompatibility was a frequent cause of failure, often stemming from taxonomic confusion about the precise identity of the weed or the insect (or both). Recent successes with carefully selected insect strains from the heart of the weed's native range (see, for example, Room *et al.* 1985) throw further doubt on Pimentel's (1963; Hokkanen & Pimentel 1984) suggestion that good control is more likely with agents and weeds that have not shared a close evolutionary history (M. J. Crawley, in preparation).

The simple, traditional models of invasion greatly overestimate the difficulty of invasion. In most communities there will be times or places where a combination of available resources, scarce competitors and low densities of natural enemies, provide conditions where invaders can establish. The existence of these refuges greatly enhances the probability of invasion. Given a sufficient immigration rate, establishment will then depend upon the relative abilities of the invader and the residents to occupy and preempt these sites.

The model presented here distinguishes explicitly between interference and exploitation competition, so that it can account for occasions when an invader, kept rare by natural enemies (and hence not likely to suffer exploitation competition), is still further depressed by the presence of fierce competitors through interspecific interference. Again, the model can allow for the invasion of a large, fierce species into a community structured by exploitation competition, when the longevity of the invaders is sufficient to allow the standing crop of resources to recover from the low level to which it had been depressed by the resident species. Thus the model is sufficiently flexible to allow invasion either by larger or by smaller species, depending upon the circumstances. Models that fail to distinguish between the different kinds of competition would always predict the success of either smaller species (if they assumed exploitation) or larger species (if they assumed interference). It is notable that, even among the writings of the foremost practitioners, confusion still exists over the distinction between exploitation and interference. In several publications, for example, Roughgarden (e.g. in Rummel & Roughgarden 1983; Roughgarden *et al.* 1984) suggests that the fact that the smaller of two lizard species has fewer flies in its stomach when it is enclosed with a larger lizard than when it is on its own is evidence for exploitation competition. It is certainly evidence for competition, but it cannot be used to distinguish the two kinds of competition. Interference, by driving the smaller lizards into marginal microhabitats where the rate of resource supply was lower, would produce precisely the same result.

It is also apparent that models that fail to include details about both lower and higher trophic levels, and which do not account explicitly for the dynamics of resources and natural enemies, are unlikely to be valuable in predicting the outcome of invasion. The model presented here may prove to be of value in more general discussions concerning the determination of species richness in different communities. For example it is traditional to distinguish between the pool-exhaustion, niche-preemption (competition) and enemy-regulation hypotheses of species accumulation (Lawton 1986), but there will certainly be circumstances when immigration rates, competition and natural enemy attack are all important. For instance, in structuring a guild of species, the order in which the species arrive may make a difference. Although the present model does allow for the inclusion of demographic subtleties such as these, it does not address the more long-term questions of species replacement, or the evolution of niche-shifts after the successful establishment of an invader (see, Roughgarden 1976; Case 1982; Loeschcke 1985).

I shall end with two cautionary tales, both of which emphasize that, for all our ability to categorize likely causes of success or failure of invasions, we are still a long way from any real predictive ability.

(*a*) *The rate of spread of weed biocontrol agents*

During analysis of the successful cases of weed biocontrol (where complete or substantial weed control was eventually obtained) the results were divided into two classes, based on whether the introduced agent spread rapidly or slowly after release. I had anticipated correlating the rate of spread of the agent with such dispersal attributes as its means of spread (e.g. wings versus silken threads), dispersal stage (larval or adult), and its potential range and speed of movement. It became clear, however, that there was virtually no overlap between the two categories in the species of *host plant* involved; all the insects on some weeds tended to spread slowly, whereas all the insects on other weeds tended to spread rapidly (table 7). The point is that attributes of the host plant can play a vital role in the dispersal dynamics of the introduced herbivores. The plants on which the herbivores spread slowly were long-lived species with substantial powers of re-growth and vegetative reproduction; those on which they spread rapidly were rather short-lived herbaceous species, reproducing mainly by seed. This is not to say that the dispersal attributes of the insects are unimportant; far from it. Certain insect dispersal syndromes certainly are associated with certain kinds of host plant (Dingle 1984). However, at least part of the explanation for behaviour at one trophic level (in this case the herbivorous insects) requires an understanding of the details of the biology of the components of the lower trophic level (in this case, the resources). A model which treated all plants simply as 'a resource' could not hope to mimic behaviour at this level of resolution.

(*b*) *The invasion of the knopper gall*

The cynipid wasp *Andricus quercuscalicis* forms the characteristic 'knopper galls' that have recently become such a common sight on acorns in autumn. The wasp is a native of southern and central Europe, where it passes through two generations each year, alternating between host-plant species. In the spring, the sexual generation emerges from galls on the male flowers of the turkey oak, *Quercus cerris*, and in summer, the agamic generation develops in galls on the female flowers of the English oak, *Q. robur*. In common with other gall-forming cynipids on oaks, both generations of the insect are attacked by a variety of hymenopterous parasitoids, which are polyphagous on all or part of the guild of gall-formers.

In Britain, almost all of these European parasitoids are already common members of the

Table 7. Rate of spread of insect agents after successful establishment

(Weed control was eventually scored as 'complete' or 'marked'. Note that there is little overlap of weed species between the category where the insects spread slowly and the category where they spread rapidly. The first number in parentheses following the weed's name is the number of releases against that weed (where there was more than one); the second number shows how many different insect species were released. Thus, for *Lantana*, 21 releases involving 7 insect species led to marked or complete control, after slow spread of the agents. The lower part of the table summarizes the biological attributes of the plant species on which insect species spread slowly rapidly. From the Silwood Project on Weed Biocontrol.)

rate of spread of the insect agent	
slow	rapid
Alternathera philoxeroides (3:2)	*Argeratina riparia* (2:2)
Eichhornia crassipes (7:3)	*Carduus nutans* (2:1)
Eriocereus martinii	*Centaurea diffusa* (4:1)
Hakea sericea (2:2)	*Chondrilla juncea*
Lantana camara (21:7)	*Cirsium vulgare*
Opuntia dillenii	*Clidemia hirta*
Opuntia elatior	*Cordia macrostycha* (3:2)
Opuntia ficus-indica (3:2)	*Eichhornia crassipes*
Opuntia imbricata (2:1)	*Emex australis*
Opuntia inermis (2:2)	*Emex spinosa*
Opuntia stricta (2:2)	*Eupatorium adenophurum*
Opuntia tardospina	*Hypericum perforatum* (6:3)
Opuntia tomentosa	*Linaria vulgaris* (3:2)
Opuntia vulgaris (6:1)	*Salvia aethiopis*
Opuntia sp.	*Salvinia molesta*
Salvinia molesta (2:1)	*Senecio jacobaea*
Senecio jacobaea	*Tribulus cistoides* (2:1)
	Tribulus terrestris

attributes of the plants in the two categories

life span	long	short
maximum sixe	large	small
regrowth potential	high	low
food quality	lower	higher
spreads by	vegetative*	seed
biogeography	hot, arid	temperate

* Note that *Lantana* is an exception, spreading by seed alone.

established fauna, where they attack our native guild of gall-formers on oak. If a list of enemies resident in Britain before invasion had been drawn up, it would have been concluded that 'enemy-free space' might well be limiting to any invasion by the knopper gall insect. As it turns out, of course, the insect proved to be an exceptionally able invader. Not only that, but the resident natural enemies failed dismally to conform with predictions. Although the sexual generation did pick up three of the common parasitoids that attack it on the Continent, their combined attack rate is less than 25% per year. In contrast, the agamic generation suffers no parasitism at all in most parts of Britain (Collins *et al.* 1983; R. Hails, in preparation). Our best efforts at prediction would have been a failure. As it turned out, the entire guild of resident parasitoids either failed (for reasons we do not yet understand) to recognise the knopper galls as potential hosts, or was unable to attack them successfully (perhaps because of differences in seasonal phenology).

There are two morals to be drawn from these cautionary tales. First, the models that have traditionally been used to describe the population dynamics of invasions have been too simple to encompass the kinds of interaction that allow or prevent establishment in real communities.

I regard the model presented in this paper as representing the minimum level of complexity consistent with this aim. Second, the data make forcibly clear that, no matter how protracted the modelling effort, we are still a very long way from possessing the kind of ecological sophistication that might allow us to make predictions about the probable success of a particular proposed introduction. We can show that there are broad patterns of demographic behaviour that are correlated with success in establishment, but it is impossible to go beyond this. We are still unable to recognise a vacant niche except by carrying out the tautological experiment of introducing a species and seeing if it becomes established.

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Discussion

Sir Hans Kornberg F.R.S. (*Department of Biochemistry, University of Cambridge, U.K.*). Why is the knopper gall not parasitized?

M. J. Crawley. I can only speculate, but perhaps British parasitoids have been separated from the knopper gall for so long that it is not 'recognized' as a potential host. It may be a case of 'race memory' combined with phenology.

Sir Hans Kornberg, F.R.S. This could be tested experimentally. Has it been?

M. J. Crawley. No.

J. H. Lawton (*Department of Biology, University of York, U.K.*). Some of R. D. Holt's models on enemy-free space look at patchiness, in adaptations of Lotka–Volterra models. The more an invader overlaps ecologically with a resident species, the more it is likely to be controlled. Patchiness can be accommodated in the model.

M. B. Usher (*Department of Biology, University of York, U.K.*). In the introduction to his paper, Dr Crawley showed that 88% of the mammals that have been introduced into Great Britain are herbivores. Can any of his conclusions about herbivorous insects be applied to these herbivorous mammals?

M. J. Crawley. I do not have enough information on the demography of introduced mammalian herbivores. There are no birth rate:death rate ratio measurements.

Sir Hans Kornberg, F.R.S. Is it really true that budgerigars and canaries are naturalized in Britain?

M. J. Crawley. According to Sharrock's book, yes, in restricted areas.

Sir Richard Southwood, F.R.S. (*Department of Zoology, South Parks Road, Oxford, U.K.*). The completeness and complexity of the analysis are both interesting. Dr Crawley selected *Opuntia* and *Lantana*, he said, because they were extremes; yet in every table they appeared to be the same!

M. J. Crawley. There were real differences. The situation in *Opuntia* is confused by the dominance of *Cactoblastis* and *Dactylopius* over other species. I did not leave these two in with the other weeds because the *Opuntia* data are dominated by two main control agents, whereas with *Lantana* there is a rich variety of control agents, different species succeeding in different microhabitats.

R. J. O'Connor (*British Trust for Ornithology, Beech Grove, Station Road, Tring, Herts. U.K.*). The list of birds includes escapes from captivity, such as canaries. There is a risk that these will weight the balance towards herbivores, because the latter are much easier to keep in captivity.

M. J. Crawley. I agree. We really need the rates of failure in the data so that we can contrast successes and failures.

J. H. Lawton. I do not believe there is any difference in the probability of establishment of carnivores and herbivores.

A. Gibbs (*Research School of Biological Sciences, Australian National University, Box 475 PO, Canberra, A.C.T., Australia*). Can some of the differences between *Opuntia* and *Lantana* reflect in genetic diversity differences? *Opuntia* was introduced a small number of times and hence the population was genetically narrow, whereas *Lantana* was introduced many times and was genetically diverse; might not this affect ease of colonization by control species?

M. J. Crawley. If you look at the 'other weeds' category, it suggests that there can be good control both where plants grow at different rates and where insects also spread slowly or rapidly. Control in each case appears to have more to do with the plant than with the insect. Fast-growing plants need rapidly spreading insects as control agents.