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The effect of propagule size on the invasion of an alien insect

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Summary

1. The movement of species from their native ranges to alien environments is a serious threat to biological diversity. The number of individuals involved in an invasion provides a strong theoretical basis for determining the likelihood of establishment of an alien species.

2. Here a field experiment was used to manipulate the critical first stages of the invasion of an alien insect, a psyllid weed biocontrol agent, *Arytainilla spartiophila* Förster, in New Zealand and to observe the progress of the invasion over the following 6 years.

3. Fifty-five releases were made along a linear transect 135 km long: 10 releases of two, four, 10, 30 and 90 psyllids and five releases of 270 psyllids. Six years after their original release, psyllids were present in 22 of the 55 release sites. Analysis by logistic regression showed that the probability of establishment was significantly and positively related to initial release size, but that this effect was important only during the psyllids' first year in the field.

4. Although less likely to establish, some of the releases of two and four psyllids did survive 5 years in the field. Overall, releases that survived their first year had a 96% chance of surviving thereafter, providing the release site remained secure. The probability of colony loss due to site destruction remained the same throughout the experiment, whereas the probability of natural extinction reduced steeply over time.

5. During the first year colonies were undergoing a process of establishment and, in most cases, population size decreased. After this first year, a period of exponential growth ensued.

6. A lag period was observed before the populations increased dramatically in size. This was thought to be due to inherent lags caused by the nature of population growth, which causes the smaller releases to appear to have a longer lag period.

Key-words: alien, biocontrol, establishment, invasion, lag period, release size.

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Introduction

The deliberate or inadvertent translocation of species from their native ranges to alien environments is a major threat to biological diversity (Schmitz & Simberloff 1997; Sala *et al.* 2000; Blackburn & Duncan 2001). Introduced species can cause serious damage to the environment in addition to the high economic costs

incurred through introduction of new agricultural pests. However, while the introduction of some species leads to them becoming serious pests others fail to establish, and while some species that establish go on to become serious pests, others do little or no apparent harm to their new communities. Without an understanding of the processes underlying the variation in invasion success, invasion ecology is almost certainly destined to remain a descriptive science.

Each biological invasion goes through the four main stages of arrival, establishment, dispersal and range expansion. These stages have not been studied in an

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equitable fashion. Thus while there are excellent data on the dispersal of many alien species and good data on their eventual range, there is a paucity of information on the arrival and establishment phase. Moreover, the data that do exist are almost certainly biased towards reporting successful establishment, and particularly of those species that have a significant impact on native species or ecosystems. The real proportion of introductions actually succeeding among those initiated is probably very low; Williamson & Brown (1986) suggest that just 1% of introduced species establish in the field.

The number of individuals involved in an invasion, the 'propagule size', has a particularly strong theoretical basis for determining its likelihood of establishment. Moreover, both theory (Richter-Dyn & Goel 1972; Pimm *et al.* 1988; Pimm 1989; Grevstad 1999a; Shea & Possingham 2000) and retrospective analysis (Hall & Ehler 1979; Cameron *et al.* 1993; Hopper & Roush 1993; Wolf *et al.* 1996; Green 1997; Blackburn & Duncan 2001; Forsyth & Duncan 2001) demonstrate the same general effect: the larger the initial release size, the higher the chance of establishment success. While the effect of propagule size upon establishment is well studied, very little is known of the impact of propagule size upon population growth rate or upon population persistence, both of which are important factors in the invasion process, and both of which could interact with propagule size.

During the early stages of an invasion, the rates of population growth and range expansion of an alien species can vary markedly. Some invasive species, for example Africanized bees (Winston 1992) and zebra mussels (Crooks 1996), have rapid rates of local population growth and range expansion. However, many other species, for example the collared dove (Hengeveld 1993) and Oxford ragwort (Harris 2002), appear to have a long lag time between their initial introduction and a later population explosion. The presence of lag times in some species raises the significant question of whether alien species that are currently rare are going to stay rare, or whether they are merely sitting out a lag phase before becoming a serious pest. In spite of there being considerable differences in the colonizing patterns exhibited by different invasive species, the underlying ecological factors operating during the early stages of an invasion remain poorly understood (Crooks & Soule 1996) and the outcome of a species introduction is usually impossible to predict.

One explanation for the failure of invasion biology as a predictive science is the absence of manipulative experiments in the tradition of modern community ecology (Kareiva 1996). The development of experiments studying replicated introductions could reveal the underlying ecological processes and yet experiments manipulating the factors implicated in invasion success, for example propagule size, remain rare (Hee *et al.* 2000). We are aware of only eight published studies in which propagule size has been manipulated: Berggren

(2001) with crickets, Hee *et al.* (2000) with ants, Memmott *et al.* (1998) with thrips, Grevstad (1999b) with beetles, Ebenhard (1987) and Crowell (1973) with rodents, Schoener & Schoener (1983) with lizards, and Campbell (1976) with parasitoids. In only three of these studies, however, (Schoener & Schoener 1983; Grevstad 1999b; Berggren 2001), were the populations followed for more than their first year in the field. Three of these eight studies, Campbell (1976), Memmott *et al.* (1998) and Grevstad (1999b), used a biocontrol agent as their experimental alien organism. Biocontrol programmes offer unparalleled opportunities to study the invasion process (Memmott *et al.* 1998) and the work presented here comprises a 6-year, large-scale, field experiment based around a weed biological programme in New Zealand.

A biological control programme for broom (*Cytisus scoparius* (L.) Link) began in New Zealand in 1981. Broom is a weedy legume that has been introduced deliberately to many countries and, like many alien plants, has become a serious weed of pasture, forest and conservation areas (Williams 1981; Parsons & Cuthbertson 1992; Bossard & Rejmanek 1994). The weed biological control agent, *Arytainilla spartiophila* (Hemiptera: Psyllidae), was given high priority for introduction because large populations build up on broom in the United Kingdom causing substantial damage (Waloff 1968), and the psyllid is highly host plant-specific (Hodkinson & Hollis 1987; Syrett *et al.* in prep). The aim of our research was to use a field experiment to manipulate the critical first stages of the invasion of the psyllid, *A. spartiophila*, in New Zealand and to observe the progress of the invasion over the following 6 years. The objectives of the study were to determine the effect of propagule size on: (1) the probability of establishment; (2) the probability of persistence; and (3) medium-term population growth, particularly the presence/absence of a lag period.

Methods

PSYLLID BIOLOGY

Psyllids (Hemiptera) feed on plant phloem in both nymph and adult stages. *A. spartiophila* is a European psyllid that feeds exclusively on broom. Its natural history is explained in detail in Waloff (1968) and is summarized briefly here. This psyllid species is univoltine with a diapause in the first instar nymph stage (Fowler, personal observation). In Great Britain overwintering eggs of *A. spartiophila* are inserted into the stems of broom from June to August. Up to 200 eggs are laid per female. After a prolonged diapause, young nymphs hatch the following March or April, developing through to adult during spring. *A. spartiophila* was subjected to host-range tests as a part of the biological control programme and was exposed to 59 plant species from 28 families according to biocontrol safety practices at that time (Wapshere 1974). No nymphs survived on

plants other than *C. scoparius*, although there was slight feeding on *Robinia pseudoacacia* (Syrett *et al.* in preparation).

REARING AND IMPORTATION

Psyllid nymphs were collected from sites in the south of England and flown to New Zealand in seven shipments between 1992 and 1994. All collections were made in the locality of Silwood Park in the South of England. Only one shipment had the collection site identified and these were from Chobham Common, Berkshire (grid ref: SU950650). Field collected adult psyllids were reared on potted plants in England. The resulting nymphs were flown to New Zealand on cut shoots of broom and maintained in quarantine until adult. Adults from each shipment were released from quarantine following verification of identification and confirmation of disease clearance. Permission to release *A. spartiophila* in New Zealand was given in July 1991 by the Ministry of Agriculture and Fisheries. As the seasons in New Zealand are the opposite of those in Europe, the psyllid's life cycle was rephased by manipulating temperature and daylength under artificial conditions. Once rephased to emerge in October/November (New Zealand spring), adult psyllids were released onto potted broom bushes growing in insectaries. No attempts were made to keep the different shipments separate, and mixed colonies reared from progeny of several shipments were used for all releases.

THE FIELD SITE

The releases were made along a linear transect, 135 km in length, stretching East to West from coastal Otago to Central Otago. No psyllids had been released previously in this part of New Zealand. Release sites were a minimum of 1 km apart as the psyllid flies (mean = 2 km, range = 1 km to 4.5 km). A linear release strategy was chosen to minimize potential migration between sites. Each release site consisted of a discrete patch of healthy broom or, more rarely, the corner of a larger stand. Sites were selected in areas where broom was not likely to be removed in the short term and landowners were asked not to remove the broom for at least 5 years following release.

RELEASE PROTOCOL

Psyllids were released on 14 and 15 December 1994. Adult psyllids were collected from insectaries at Lincoln, Canterbury on 13 December 1994, by beating broom over a tray and then aspirating the psyllids from the tray into a plastic vial. The insects were transported in brown paper bags, which acted as paper boxes and kept condensation to a minimum. Each bag contained a bouquet of broom cuttings, approximately 20 cm long, with the base of the stems wrapped in wet cotton wool and sealed with plastic film. The bags were stored

Table 1. Planned and actual release sizes used in the experiment

Planned release size	Mean release size	Range
2	1.9	1–2
4	3.8	3–4
10	8.7	7–10
30	25.7	10–30
90	79.2	69–90
270	205.2	152–258

in cooled, insulated boxes for transport to the field site, 370 km south in Otago.

Six different propagule sizes were used: two, four, 10, 30, 90 and 270 psyllids. An upper limit of 270 was chosen as preliminary data suggested that this size of release was likely to establish. For the releases of two, four and 10 psyllids, equal numbers of males and females were collected. For the larger releases psyllids were collected, unsexed, from the colony. Pilot counts showed no evidence that the sex ratio of the colony was skewed. Ten replicate collections were made of release sizes two, four, 10, 30 and 90, and five replicate collections of release size 270. Overall, a total of 2710 insects were released into 55 release sites.

Twenty-two releases were made on the first day and 23 releases on the second day, starting at the east end of the transect and moving westwards, site by site. The release size at each site was allocated randomly on each day. To make a release, broom bouquets were tied to a broom bush marked with a waterproof paper tag. Live insects left in the bags were transferred using a camel-hair paintbrush. Some mortality took place between psyllid collection and release. This mortality was particularly noticeable for the largest release size and was caused by psyllids being squashed as the bag moved in transit. The live psyllids appeared healthy. The number of dead psyllids in each bag was recorded, and spare psyllids were used to top up the releases to their original sizes. For the smaller releases, care was taken to ensure that additional psyllids were of the required sex. Given that there was a limited number of spare psyllids, the actual numbers released at each site varied slightly from the planned releases (Table 1). In the one case where a single psyllid was released (Table 1), this was female.

SAMPLING PROTOCOL

The release sites were sampled for psyllids once a year for 5 years following release. Thus five generations of psyllids were sampled. All release sites were checked for the first 3 years. In year 4, only sites where psyllids were known to be present were checked. In year 5, sites where psyllids were known to be present were sampled, and some of the sites recorded as psyllid-free were also checked. The rest of the psyllid-free sites were sampled

in year 6. These psyllid-free sites were sampled to check for false extinctions, i.e. sites that were initially scored as extinct, but later shown to be successfully colonized.

To sample for psyllids, two people searched each release site for 15 min by beating branches of broom onto a tray and collecting psyllids from the tray by aspirator. This method is known to collect broom herbivores efficiently (Memmott *et al.* 2000). Fresh green growth was targeted, as this is the psyllids' preferred feeding site. The sampling dates were chosen to coincide with the peak emergence of adult psyllids in the overall area, and progressed from East to West along the transect. At each site, searching started at the release bush and worked outwards until no further psyllids were found, at which point the samplers turned back towards the centre of the colony. All psyllids collected in 15 min were retained, counted and then released back onto the broom patch. Occasionally, when a site was recorded as psyllid-free one year but then psyllids were found in a subsequent year (i.e. a false extinction), it was assumed that sampling had failed to locate psyllids in the year that they were recorded missing.

In this study system colonization success is highly unlikely to be a result of immigration of individuals from neighbouring sites, as the sites are spatially separated by at least 1 km and most biocontrol agents tend not to move this far during the early stages of a release programme. To check this assumption, for the first 3 years of the experiment we sampled broom patches equidistant between sites where 270 psyllids were released (the largest release size) and the adjacent release sites along the transect. It was assumed that if psyllids from these largest releases had not reached the halfway point, then psyllids from the other releases are unlikely to have reached an adjacent release site.

Sampling efficiency was measured by releasing 10 psyllids onto each of 10 isolated bushes, leaving them for 8 h to disperse throughout the bush and then sampling the bushes for psyllids. The bushes were located in an area where psyllids had not been released and were therefore psyllid-free. Psyllids were found on nine of the 10 bushes with a mean of three psyllids per bush (range = 1–6), giving a sampling efficiency of 30%. Consequently the number of psyllids collected from the bushes was multiplied by 100/30 to give an estimate of population size.

SITE LOSS

At some sites, burning, herbicide application, cutting or bulldozing destroyed the broom, and hence the psyllids colony. These sites were noted, along with the date of destruction and its cause.

STATISTICAL ANALYSIS

The data allow us to estimate parameters associated with the three key processes identified by Shea and

Possingham (Shea & Possingham 2000). They are: colonization, transition from insecure to established colonies and local extinction. Statistical analysis was carried out using SPSS release 9.0.0, GENSTAT 5.3.2 and R 1.5.1 (Ihaka & Gentleman 1996). The population growth analysis used an individual growth curve approach, which was extended through fitting a hierarchical linear model using the HLM 5.04 package (Raudenbush *et al.* 2000).

There were four stages to the analysis: the calculation of (1) colonization probability; (2) the probability of transition from insecure to secure colony; (3) extinction probability; and (4) the prediction of medium-term population growth. Those colonies that were lost through site destruction were removed from the data set and played no further part in subsequent analysis. For example, data from a colony destroyed in year 3 were used in analyses concerned with the first 2 years but not thereafter. The statistics of the four analysis stages are described below.

Colonization probability

We first investigated whether or not the probability of reaching the status of an insecure colony was related to the colony release size. We did this in two stages. In the first we carried out a logistic regression analysis of the field data. In the second we used two different methods to compare the field data with current theory as represented by the Shea–Possingham model of colony establishment (Shea & Possingham 2000). In this model, the probability of establishment to insecure colonies is related to release size by the following equation:

$$p(x_i) = p_m(1 - e^{-ax_i^2})^2 \quad \text{eqn 1}$$

where $p(x_i)$ is the probability of establishment for release size x associated with colony i ; p_m is the maximum probability of establishment and a is a constant.

To fit this model, it is necessary to estimate the parameter a . We have performed this in two ways. In the first, we calculated the predicted probabilities of establishment using the coefficients derived from the logistic regression and then estimated a using a non-linear least-squares regression algorithm. In the second, we derived an expression for the likelihood from the Shea–Possingham equation as a function of the observed outcomes for the colonies (i.e. established or not). We then derived the maximum likelihood estimate of a by applying a non-linear minimization algorithm to the expression for the deviance. The relative goodness of fit of the three methods (direct logistic regression, Shea–Possingham using logistic probabilities and Shea–Possingham using the maximum likelihood fit to the actual outcomes) was compared using Akaike's information criterion (AIC: Akaike 1973), as this allows comparison of models of different kinds with different numbers of estimated parameters. Results

were also displayed graphically as a plot of the actual data along with the curves predicted from the three methods. The location of the asymptote differs between models and is a further useful way to compare them. We have defined the asymptote arbitrarily as the point at which the probability of establishment first exceeded 0.999.

Transition from insecure to secure colonies

The next stage of colonization involves the probability of an insecure colony growing to be a secure colony (given the symbol g by Shea & Possingham (2000)). This implies that unambiguous definitions exist for the state of colonies. For the purposes of the model exact definitions have been made, but in practice there are often difficulties with these. A colony may be defined as established if it survives in the long term, but even established colonies have a non-zero probability of going extinct and colonies may remain in an insecure state for some time. Consequently long-term survival is not a sufficient definition of establishment. An alternative approach is to adopt a population size above which a colony is defined as established. This is likely to be more accurate, but can only be applied with extensive knowledge of the natural history of the system studied. The first definition is more practical for studies where such information is lacking. In this study, we defined any colony that survives past the first year as established. There is a complication associated with this definition, however. In the model (Shea & Possingham 2000), g is defined in terms of a given time interval which, as with $p(x)$, is generally taken to be 1 year. In reality, some colonies may remain in an insecure state for several years before either becoming established or going extinct. However, our definition forces us to assume that all transitions from insecure to established colonies occur between year 1 and year 2. The estimate of g given here is therefore likely to be an overestimate.

Extinction probability

Shea & Possingham (2000) distinguish two extinction probabilities: e_s , the probability of an established colony becoming extinct and e_i , the probability of an insecure colony becoming extinct, both defined for a given time interval. The assumption that all transitions to the established state occur between the first and second years means that only one estimate of e_s can be made here. Because it is not possible to know how many 2-year-old colonies are, in reality, insecure or established, it cannot be said whether this estimate is an over- or an underestimate.

Three estimates can be made of e_s : between years 2 and 3, years 3 and 4 and years 4 and 5. Because some of these extinctions are of insecure rather than established colonies, and insecure colonies have a higher extinction probability than established colonies (Shea & Possingham 2000), these estimates are likely to be

overestimates. In Shea and Possingham's (2000) model, no distinction is made between extinction due to demographic processes (referred to here as natural extinctions) and extinction due to site destruction. As we show later, the probability of site destruction is constant over time and so can simply be added as a constant to any probability functions generated in the analysis.

Prediction of medium term population growth

We have assumed that colonies undergo a process of establishment during the first year so have examined population growth characteristics only from the end of year 1. This assumption appears to be justified by the data (see Results). As described earlier, sampling efficiency was assumed to be 30% so the recorded number of recaptures was multiplied by 100/30 in order to estimate actual population size. Using these corrected data, the colonies tend to show roughly exponential population growth over time. As it was both biologically reasonable and apparently justified by the data, we assumed that colony growth was exponential and so data were transformed in order to fit the following equation:

$$\ln(y_t) = \beta_0 + \beta_1(t) + \epsilon_t \quad \text{eqn 2}$$

where y_t is the population size at time t , β_0 is the intercept equal to the natural logarithm of the population size at the end of year 1, β_1 is the exponential growth constant and ϵ_t is an error term. The coefficients of this model were first estimated for each colony individually by linear regression and then this individual growth curve analysis was extended using a hierarchical linear design (Raudenbush & Bryk 2002). Specifically, we examined the effect of release size on the values of the coefficients in eqn 2 by fitting the following models to the data:

$$\beta_0 = \gamma_{00} + \gamma_{01}(x) \quad \text{eqn 3}$$

$$\beta_1 = \gamma_{10} + \gamma_{11}(x) \quad \text{eqn 4}$$

where β_0 and β_1 are the coefficients of eqn 2; γ_{00} and γ_{10} are the values of β_0 and β_1 averaged over all colonies, while γ_{01} and γ_{11} are, respectively, the average changes in β_0 and β_1 associated with a unit increase in the release size x . In effect, we have viewed the individual growth curves as being nested within the higher level structure imposed by the intended release size. Fitting a hierarchical linear model allows actual release size to be used directly in eqns 3 and 4 while retaining a nested structure based on intended release size. We can therefore determine if the release size has any effect on the size of the colony at the start of the growth phase (i.e. at the end of year 1 of the experiment) through an influence on β_0 , and/or the rate of growth of the colony through an influence on β_1 . This method has the advantage over

Table 2. Number and percentage of colonies surviving to various stages of the study; also number and percentage of sites lost during the same time

Intended release size	No. of sites	No. of colonies (%) extant after year					No. of sites (%) destroyed after year				
		1	2	3	4	5	1	2	3	4	5
2	10	2 (20)	2 (20)	2 (20)	2 (20)	2 (20)	2 (20)	2 (20)	3 (30)	3 (30)	4 (40)
4	10	3 (30)	3 (30)	3 (30)	2 (20)	2 (20)	1 (10)	2 (20)	2 (20)	2 (20)	2 (20)
10	10	4 (40)	3 (30)	3 (30)	3 (30)	3 (30)	0 (0)	3 (30)	4 (40)	4 (40)	4 (40)
30	10	6 (60)	5 (50)	4 (40)	3 (30)	3 (30)	1 (10)	1 (10)	3 (30)	4 (40)	4 (40)
90	10	8 (80)	8 (80)	8 (80)	8 (80)	7 (70)	1 (10)	1 (10)	1 (10)	1 (10)	2 (20)
270	5	5 (100)	5 (100)	5 (100)	5 (100)	5 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)

Table 3. Estimated parameters and goodness of fit of models fitted to field data. As with deviance, the smaller the AIC the better the fit. The asymptote is defined arbitrarily as the release at which the predicted probability of establishment first exceeds 0.999

Method	Regression coefficients	Estimate of <i>a</i>	AIC	Asymptote
Logistic regression	Constant = 0.98 coefficient of <i>x</i> = 0.0629		51.2	83
Non-linear regression		0.003024	127.0	41
Maximum likelihood		0.006194	114.7	29

a repeated-measures ANCOVA design as it is able to use incomplete data; an extremely useful feature for individual growth-curve analysis. The ANCOVA method is restricted to colonies for which we have data for all years with no gaps and is therefore a less powerful test.

Results

At the end of the experiment broom psyllids were present in 22 of the 55 release sites (Table 2). No psyllids were found at sites equidistant between the large releases and their two adjoining neighbouring release sites so it can be assumed that there was no migration between release sites.

COLONIZATION PROBABILITY

Analysis by logistic regression showed that the probability of establishment to the status of at least an insecure colony was significantly and positively related to initial release size (deviance ratio_{1,47} = 19.71; approx. *P* < 0.001) giving the following regression equation:

$$\log\left(\frac{\hat{p}(x_i)}{1 - \hat{p}(x_i)}\right) = 0.0629(x_i) - 0.980$$

One colony, a severe outlier on all diagnostic measures used, was removed from this and subsequent analyses. There was no significant difference between years in the relationship between probability of establishment and release size, suggesting that the first year was the most critical and that the assumption that an individual release either becomes an insecure colony or goes extinct during the first year was probably justified (results not shown).

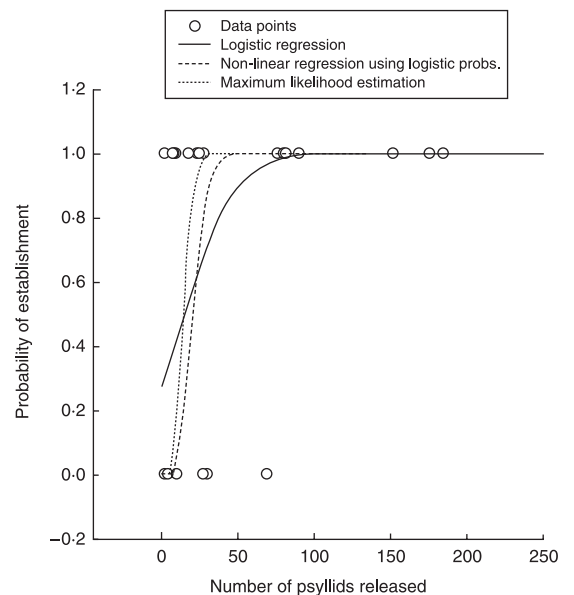


Fig. 1. Release size vs. the binary outcome (population extant or extinct). The raw data are shown along with the three models: direct logistic regression, non-linear least-squares fit to the Shea–Possingham equation using predicted probabilities from the logistic regression and maximum likelihood estimation of the Shea–Possingham equation using the raw data.

We went on to examine the fit between data and theory by estimating the coefficient *a* of the Shea–Possingham equation as described in the Methods. The values of the estimates and their associated AIC scores are given in Table 3. For each method we calculated fitted values for the probability of establishment and these are plotted with the field data in Fig. 1.

Table 4. Yearly estimates of probability of extinction due to natural extinction and site destruction. Binomial CIs were calculated using SC (Dusoir 1997). When estimating probability of extinction due to site loss, the total number of sites was the number at the start of the given time period. To estimate natural extinction, the appropriate total number of sites is the number that were still extant at the start of the time period, less the number that were lost due to site destruction during that time period. Note also that a given site may be counted twice if it first suffers natural extinction and is then subsequently lost due to site destruction

To end of year:	Probability of natural extinction	95% binomial CI	Probability of site loss	95% binomial CI
1	0.44	0.30–0.59	0.09	0.09–0.20
2	0.04	0.00–0.19	0.08	0.02–0.19
3	0.04	0.00–0.20	0.09	0.02–0.21
4	0.00	0.00–0.12	0.05	0.01–0.16
5	0.00	0.00–0.12	0.05	0.01–0.17

Fitting the Shea–Possingham equation direct to the data produced a better fit than going through the preliminary stage of estimating establishment probabilities by logistic regression. However, neither method employing the Shea–Possingham equation fitted the data as well as the simple logistic regression. An examination of Fig. 1 suggests that much of the lack of fit of the Shea–Possingham-based methods is due to an underestimation of the probability of establishment of small colonies. However, while the logistic regression model fits best overall, it yields an unrealistically high asymptote.

TRANSITION FROM INSECURE TO SECURE COLONIES

The probability of moving from the status of an insecure colony to a secure colony is the probability of surviving from the end of the first year to the second year. There were 28 colonies extant at the end of the first year with one being lost (it was sprayed with herbicide by the landowner) during the second year. The assumption is made that the probability of moving from an insecure to a secure colony was the same for the colony that was lost as for the ones that were not lost. Of the 27 remaining colonies, 26 were still extant at the end of the second year. Therefore, the estimate of the probability of moving from the status of an insecure colony to a secure colony (g) is $(26 \div 27) = 0.96$.

EXTINCTION PROBABILITY

The probability of colony loss due to site destruction remained the same throughout the experiment, whereas the probability of natural extinction reduced steeply over time (Table 4).

Only in the first year was there a significant difference between the probability of extinction due to natural processes and extinction due to site loss as seen by the non-overlapping 95% CIs. After the first year, extinctions tended to be due to site loss rather than natural processes. Furthermore, probability of extinction due to natural processes over the 5 years of the experiment was related negatively to release size (logistic regression $P = 0.04$; $n = 55$; goodness of fit =

49.2) while site loss was random with respect to release size (logistic regression $P = 0.18$; $n = 55$; goodness of fit = 52.5). We therefore suggest that the probability of extinction due to site loss can be treated as a constant, at least over the time-span of this experiment. Its value (0.06) is the mean of the estimates for the individual years of the study, precision-weighted to take advantage of the greater accuracy of those estimates based on larger samples.

By definition, the transition from an insecure to an established colony occurs between years 1 and 2 (see Methods); so the single estimate of e_n gave a value of 0.04, which shows that providing the colony survives the first year, the risk of extinction is very low. The subsequent 3 years gave estimates of e_s , with the unweighted mean equal to 0.01. As discussed in the Methods, this will be an overestimate. Extinction of an established colony is more likely to be observed the longer the experiment runs, simply because more insecure colonies will either have gone extinct or become secure. It is nevertheless very clear that the probability of an established colony going extinct was much less than that for an insecure colony: thus, the probability of natural extinction is 0.44 by the end of year 1, but 0.04 or less thereafter (Table 4).

PREDICTION OF MEDIUM-TERM POPULATION GROWTH

During the first year, colonies were undergoing a process of establishment and, in most cases, population size decreased (Fig. 2). This is a genuine decrease in abundance as we corrected for sampling efficiency. If, however, a colony survived to the end of the first year, population size then tended to increase over time (Fig. 2). As these two stages have both a different theoretical treatment (Shea & Possingham 2000) and appear different empirically (this study), we analysed data on population growth only from the end of the first year onwards. Plotting the natural log of the population size against time showed a roughly linear relationship for most colonies after the first year, suggesting that the assumption of exponential growth was probably justified as a first approximation (Fig. 2). Results of fitting exponential models to the individual

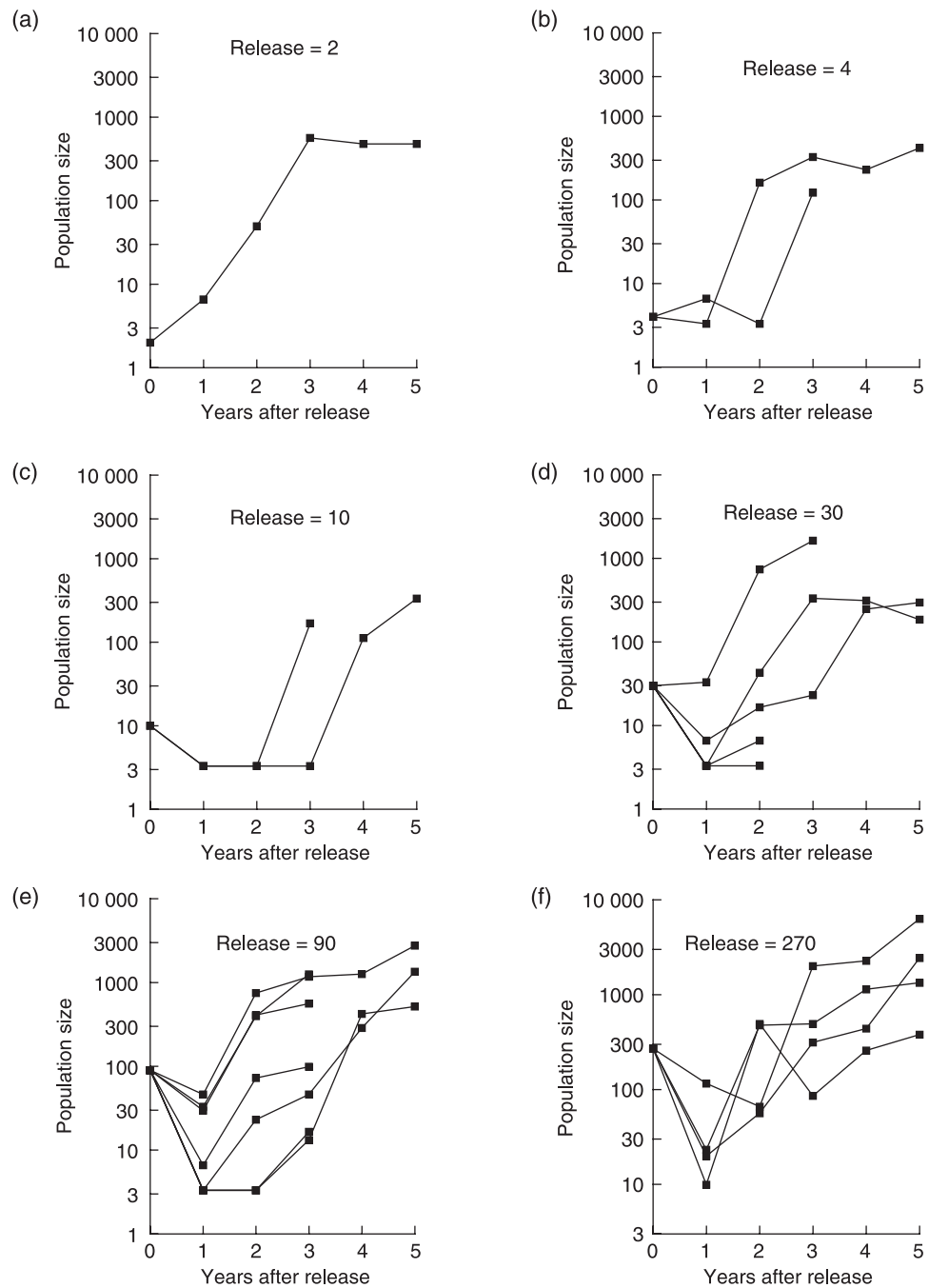


Fig. 2. Population growth of each release size over time. Only releases for which there are uninterrupted data are shown.

colonies are given in Table 5. The lack of statistical significance in many cases is due almost certainly to the small sample sizes as well as the presence of significant residual variation (see below). While residual variation was large, patterns of residuals suggested the assumption of an underlying exponential relationship appeared justified and alternative models provided a noticeably poorer fit.

The next level of analysis in the hierarchical design adopted here involved examining the possible effect of release size on the coefficients of the exponential models fitted in the first level of the analysis (Table 6). Both γ_{01} and γ_{11} were not significantly different from zero,

indicating that there was no significant effect of release size on the demographic behaviour of colonies either in terms of the intercept (that is, the size of the colony after one year) or the slope of the fitted exponential model (that is, the rate of growth of the colony). Rather, the analysis indicates an average behaviour of colonies unrelated to release size such that:

$$\ln(\hat{y}) = 3.292 + 0.432(t) \quad \text{eqn 5}$$

Examination of the table of variance components showed that there was significant variation between colonies in the location of the intercept (β_0), but not in

Table 5. Coefficients of exponential growth models fitted to each colony individually and grouped by intended release size. Regression was carried out in SPSS and is identical to that in the first level of analysis in HLM (Raudenbush *et al.* 2000). The regression was conducted in two packages as HLM does not give significance probabilities

Intended release size	β_0	β_1	F	P	R^2 (%)
2	2.74	1.09	9.7	0.05	69
4	4.98	0.25	3.1	0.22	41
	1.18	1.46	1.4	0.45	16
10	0.48	1.22	6.5	0.13	65
	4.92	0.21	0.04	0.66	NA
30	1.75	1.03	33.6	0.01	89
	4.06	0.43	1.0	0.42	1
	3.90	1.95	8.5	0.21	79
	1.20	0.70	NA	NA	NA
90	-0.46	1.84	2.9	0.34	49
	1.30	1.46	203.3	<0.01	98
	4.79	0.87	9.8	0.05	69
	3.83	-0.51	NA	NA	NA
	5.19	-0.06	<0.1	0.94	NA
	3.78	1.47	4.9	0.27	66
	2.25	1.36	5.0	0.27	67
270	4.45	1.01	9.26	0.06	67
	3.00	1.17	105.7	<0.01	96
	4.16	0.90	9.2	0.06	67
	3.57	0.66	2.3	0.23	24

Table 6. Results of fitting a hierarchical linear model based on a structure of colonies nested in intended release size; relationships between the coefficients are given in eqns 2, 3 and 4 in the Methods

Fixed effect	Coefficient	Standard error	t	Approx. d.f.	P
For β_0					
γ_{00}	3.292	0.457	7.21	18	0.000
γ_{01}	0.002	0.003	0.60	18	0.553
For β_1					
γ_{01}	0.432	0.139	3.11	18	0.007
γ_{11}	0.002	0.001	1.60	18	0.126

Table 7. Variance components indicating the relative degree of variation explained by the stated effects between colonies. Rows 1 and 2 show the influence of variation in the coefficients of the exponential models fitted to the data while row 3 indicates the extent of residual variation remaining in the population growth data after the models were fitted

Effect of variation in	Variance component	d.f.	χ^2	P
β_0	1.248	18	36.5	0.006
β_1	0.156	18	20.68	0.295
Residual	1.094			

the rate of exponential growth (β_1) (Table 7). Colonies therefore varied significantly in size after 1 year but this could not be predicted from release size. The non-significant variation in rate of exponential growth suggests that all colonies have similar average rate of

population growth. Once the full model (composed of the average behaviour of a colony plus individual variation in the size of β_0 and β_1) was fitted to the population growth data there was still a relatively large, residual component of the variation left unexplained (Table 7). This indicates the degree to which an exponential model of population growth did not fit the data and suggests that there was significant unexplained fluctuation in individual colony size from year to year, which is unlikely to be explained by any simple model.

Discussion

Our experiment provides four important pieces of information regarding the invasion behaviour of broom psyllids. First, release size was related positively to the probability of establishment, but only during the first year in the field. While the vast majority of natural extinctions occurred during the first year, a colony that survived the first year was highly likely to survive throughout the experiment, providing its site was not destroyed. Secondly, population size decreased the year after release and increased thereafter. Thirdly, population growth was not related to original release size. Finally, the data indicate that one year of monitoring of field sites might suffice for this species. In this section we discuss the main findings of the study with respect to the establishment, persistence and population dynamics of the broom psyllid in the field, and we end by considering the implications of our results for invasion ecology.

COLONIZATION PROBABILITY

While there are records of biocontrol agents establishing from very small numbers, for example Cameron *et al.* (1993), Grevstad (1999b) and Memmott *et al.* (1998), these have usually been considered rare events. Here, however, 20% of the releases of two, and 40% of the releases of four psyllids established and 20% of each persisted until the end of the experiment (Table 2). This suggests that small releases may have a higher probability of establishment than is usually assumed. However, while these initially seem very small release sizes, the female broom psyllid has an average fecundity of 93 eggs (Waloff 1968). Thus, providing she is mated and lives long enough to oviposit, each female psyllid may be viewed more realistically as 93 potential insects. A single female was the founder of one of the successful establishments (Fig. 2a, Table 1), a phenomenon also reported by Grevstad (1999b).

There are at least two explanations for why the small releases were more likely to fail, these not being mutually exclusive. Predation by natural and introduced enemies may be an important factor. A second possible explanation is that the reproductive rate was less than unity during the first year for most of the releases (Fig. 2). Small populations are less able to buffer a decrease in their numbers during this period and may

simply go extinct. Predation and population size may interact, further complicating the picture.

At least three explanations can account for the low reproductive rate in the psyllids during their first year. First, the reproductive rate could be low in the first generation and high thereafter. This could occur, for example, if the insects are affected by handling during the release process. While there were handling effects in our releases, in that some psyllids died in transit by becoming caught in the folds of the transport container, those that did not die appeared healthy. However, the possibility remains that they laid eggs in the bouquet prior to release, thereby depleting their egg reserves. Secondly r could be low in the first generation and increase slowly thereafter. Many reciprocal transplant experiments show that the individual host plant from which the herbivore was taken, provides the best environment for that insect (Edmunds & Alstad 1978; Karban 1989). Given that broom lives for an average of 10–15 years (Waloff 1968) there is an average of 10–15 generations of psyllids on the same plant, which may provide time for local adaptation, assuming they stay on the same bush. Finally, r could vary with the initial size of release due to Allee effects and other demographic and stochastic effects on small populations. In contrast to our results with broom psyllids, different-sized releases of crickets (Berggren 2001) failed to show lowered reproductive rate during their first year in the field, possibly because the sexes can communicate acoustically over relatively large distances, thereby reducing the size of an Allee effect.

Richter-Dyn & Goel (1972) suggest that there is likely to be a crucial propagule size that greatly increases colonization success. This critical propagule size is likely to differ from species to species. For example, for psyllids, a release of 90 insects has a probability of establishment of 80% (Table 2) whereas for gorse thrips (*Sericothrips staphylinus*, also released in New Zealand), 270 insects were needed to approach this level of establishment (Mommott *et al.* 1998). The parameter a in eqn 1 (from Shea & Possingham (2000) specifies the probability of establishment and a good estimate of a is important for cross-species or cross-environment comparisons.

TRANSITION FROM INSECURE TO SECURE COLONIES AND EXTINCTION PROBABILITY

If the psyllids survive the first year, the probability of surviving thereafter is 96% regardless of release size (Table 4). While extinction for demographic reasons was very low after the first year, extinction due to site loss remained constant. Overall, site loss was a surprisingly high source of psyllid extinction during the experiment, especially as we specifically asked landowners (mostly farmers) not to destroy the sites. This level of site loss may not be a common occurrence outside biological control programmes working on relatively transient populations of agricultural weeds. For

example, conservation releases of captive bred or translocated endangered species will only be made into protected habitats where site destruction is hopefully a rare occurrence. Similarly, biocontrol agents released against environmental weeds should not face a large site destruction problem either. The problem of site loss is particularly problematic for broom psyllids and other insects that are confined to their host plant for an extended period. Psyllids remain inside broom stems for about 10 months and while protected from natural predators during this period, they have no defence against a farmer armed with a chainsaw, herbicide or a bulldozer. During the first year, particularly, the entire colony is effectively trapped inside, and dependent upon, a small number of broom bushes.

EXTINCTION PROBABILITY

The probability of natural extinction reduced steeply over the five psyllid generations, a similar result to that seen by Grevstad (1999b) working with three generations of beetles in Central New York State, USA. In contrast to Grevstad's results, however, we found some evidence for a minimum viable size above which the psyllid colonies were highly likely to establish. All the largest release size ($n = 270$) survived the duration of the experiment, provided that their site was not destroyed. However, even this release size is unlikely to guarantee establishment given the variation present in population sizes between the different sites. Interestingly, while it survived the experiment, one of our large releases does appear to be struggling (Fig. 2f) and ended the experiment with a much smaller population size than some of the smaller releases (e.g. Fig. 2e). Thus, it is not possible to state that a large colony will have a large population after 1 year or have a fast population growth rate, even though it is more likely to survive the first year.

PREDICTION OF MEDIUM TERM POPULATION GROWTH

There is considerable anecdotal evidence from biocontrol practitioners and invasion ecologists that both deliberately and accidentally introduced alien organisms have a long lag time before they 'suddenly' become very abundant. The data sets presented here provide some of the most rigorously quantified lag times to date. Although the raw data (Fig. 3) appear to show that small releases are simply surviving with no obvious sign of becoming abundant, it is clear from the log data (Fig. 2) and our analysis that they are increasing in numbers at the same rate as the larger releases. Obviously these small releases will take longer to reach a given population size because they are starting from a much lower level. However, the important point is that considering population size *per se* is not that useful; rather it is the annual rate of change that provides the information on an alien's potential to become an

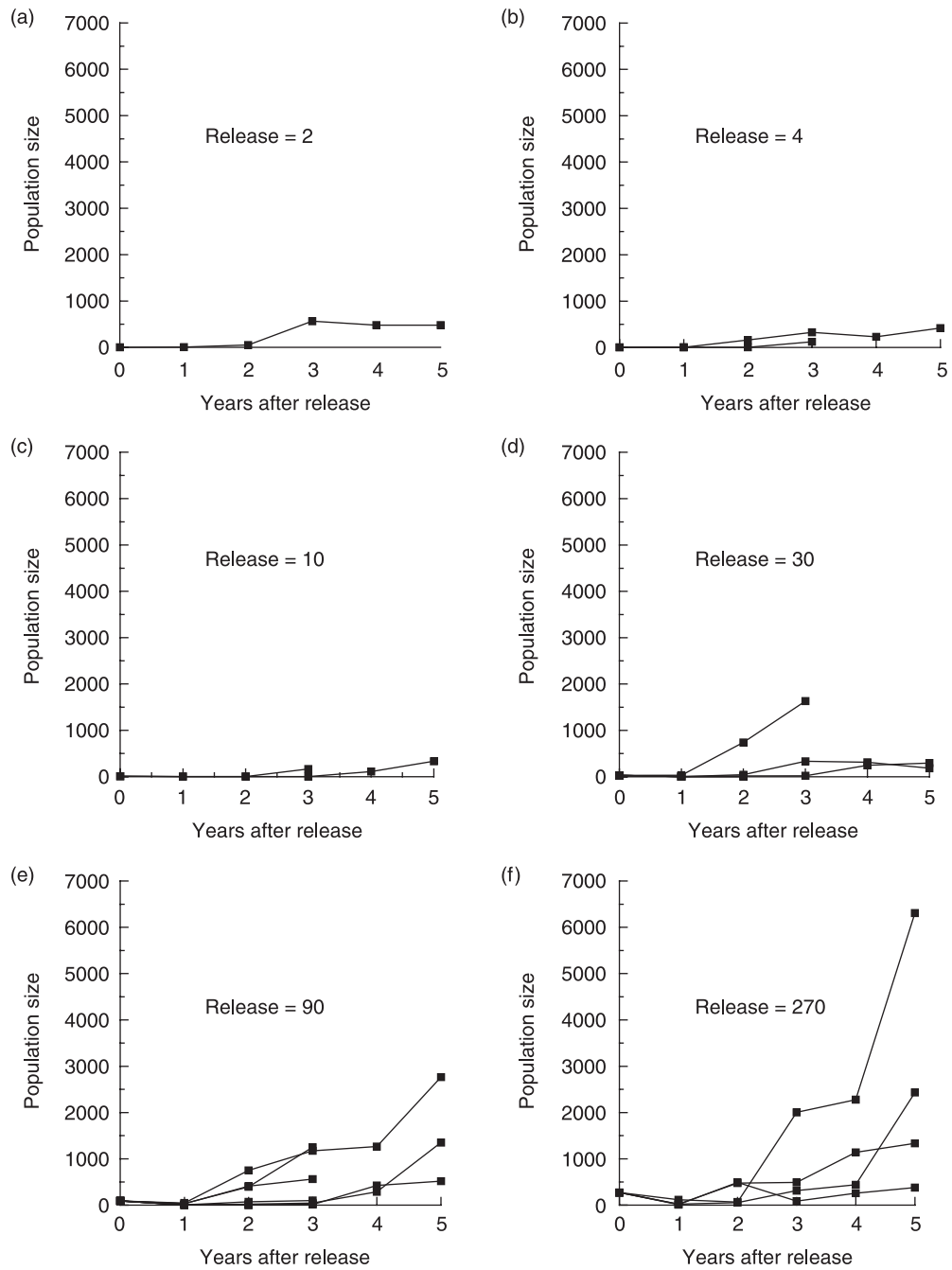


Fig. 3. Number of psyllids recaptured each year of the experiment for the different release sizes.

abundant species. An increase from two, to six, to 45 psyllids (Fig. 2a) would be difficult to spot in the field, let alone use as an indicator of population persistence. In population dynamic terms, however, the fourfold increase (Fig. 2a) hidden in the lag phase (Fig. 3a) suggests that in a further 4 years, more than 8000 psyllids may be present at the site.

Crooks & Soule (1996) describe three categories of lag: (1) inherent lags caused by the nature of population growth *per se*; (2) environmental lags caused by changes (i.e. improvements) in ecological conditions that favour the alien; and (3) genetic lags caused by a relative lack of fitness of the alien in the novel environment. These three types of lag each come with different

predicted patterns of population dynamics: inherent lags will be seen as a population simply taking time to build up to a visible size; environmental lags will be apparent, as the alien will show a sudden increase in abundance as the environment becomes more suitable; and genetic lags should be influenced by population size, as there is a positive feedback between population size and rates of genetic adaptation (Crooks & Soule 1996). It is possible that conditions for the psyllids did improve during the second year in the field, as a sudden increase in abundance was seen. However, this improvement in conditions must have been over a large scale as psyllids 200 km apart showed the same response and it is not obvious what accounted for this

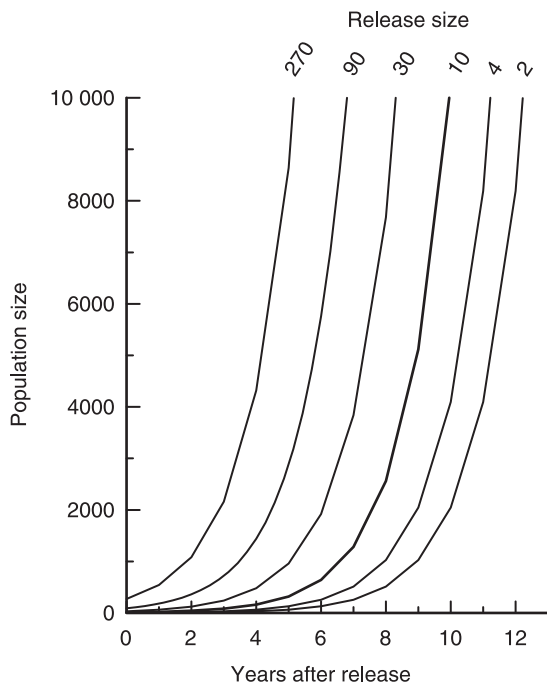


Fig. 4. Simple model showing that different sized colonies (at year 0) will have different lag rates, despite having the same reproductive rate.

improvement in conditions. A genetic lag is not likely either as, if anything, there was a slight negative feedback between population size and growth rate. This leaves inherent lags caused by the nature of population growth as a probable explanation for our data. A simple model using the same growth rate and a range of propagule sizes shows that a small population will reach the same size (upper limit), but will take longer to get there, making small populations appear to be in a lag phase (Fig. 4).

In all except three of the successful introductions, there was a decrease in abundance during their first year in the field. Both Grevstad (1999b) and Memmott *et al.* (1998) also report this effect for beetles and thrips. Moreover, there is considerable anecdotal evidence that biocontrol introductions decline in abundance before increasing slowly in numbers. As discussed earlier, this decrease in numbers makes it more likely that the smaller releases will go extinct.

Conclusion and implications for invasion ecology

Under natural conditions, repeated small invasions are probably far more likely to occur than single large invasions. For example, the repeated invasion of one or two individual psyllids on imported plants in the horticultural trade is far more likely both to occur, and to escape notice, than a single invasion of a thousand psyllids. The fact that these very small releases can have a surprisingly high probability of establishment means that biologists and biosecurity officers cannot be sanguine about small invasions. If they survive the first

year, their chance of persistence is exactly the same as for large releases, and experience shows that it is 'virtually impossible to extirpate an exotic once it has achieved its explosive growth phase' (Crooks & Soule 1996).

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References

- Akaike, H. (1973) Information theory and an extension of the maximum likelihood principle. In: *International Symposium on Information Theory* (eds B.N. Petran & F. Csáki), pp. 267–281. Akadémiai Kiadó, Budapest.
- Berggren, A. (2001) Colonisation success in Roesel's bush-cricket *Metrioptera roeseli*: the effects of propagule size. *Ecology*, **82**, 274–280.
- Blackburn, T.M. & Duncan, R.P. (2001) Determinants of establishment success in introduced birds. *Nature*, **414**, 195–197.
- Bossard, C.C. & Rejmanek, M. (1994) Herbivory, growth, seed production, and resprouting of an exotic invasive shrub *Cytisus scoparius*. *Biological Conservation*, **67**, 193–200.
- Cameron, P.J., Hill, R.L., Bain, J. & Thomas, W.P. (1993) Analysis of importations for biological control of insect pests and weeds in New Zealand. *Biocontrol Science and Technology*, **3**, 387–404.
- Campbell, M.M. (1976) Colonisation of *Aphytis melinus* Debach (Hymenoptera, Aphelinidae) in *Aonidiella aurantii* (Mask.) (Hemiptera, Coccidae) on citrus in South Australia. *Bulletin of Entomological Research*, **65**, 659–668.
- Crooks, J.A. (1996) The population ecology of an exotic mussel, *Musculista senhousia*, in a Southern California bay. *Estuaries*, **19**, 42–50.
- Crooks, J.A. & Soule, M.E. (1996) Lag times in population explosions of invasive species: causes and implications. In: *Norway/UN Conference on Alien Species* (eds O.T. Sandlund, P.J. Schei & A. Viken), pp. 39–46. Directorate for Nature Management and Norwegian institute for Nature Research, Trondheim, Norway.
- Crowell, K.L. (1973) Experimental zoogeography: introductions of mice to small islands. *American Naturalist*, **107**, 535–558.
- Dusoir, A.E. (1997) *SC – Statistical Calculator*, V1 52. Mole Software, Belfast.
- Ebenhard, T. (1987) An experimental test of the island colonisation survival model – bank vole (*Clethrionomys glareolus*) populations with different demographic parameter values. *Journal of Biogeography*, **14**, 213–223.
- Edmunds, G.F. Jr & Alstad, D.N. (1978) Coevolution in insect herbivores and conifers. *Science*, **199**, 941–945.
- Forsyth, D.M. & Duncan, R.P. (2001) Propagule size and the relative success of exotic ungulate and bird introductions to New Zealand. *American Naturalist*, **157**, 583–595.
- Green, R.E. (1997) The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand. *Journal of Animal Ecology*, **66**, 25–35.

- Grevstad, F.S. (1999a) Factors influencing the chance of population establishment: implications for release strategies in biocontrol. *Ecological Applications*, **9**, 1439–1447.
- Grevstad, F.S. (1999b) Experimental invasions using biological control introductions: the influence of release size on the chance of population establishment. *Biological Invasions*, **1**, 313–323.
- Hall, R.W. & Ehler, L.E. (1979) Rate of establishment of natural enemies in classical biological control. *ESA Bulletin*, **25**, 280–282.
- Harris, S.A. (2002) Introduction of Oxford ragwort, *Senecio squalidus* L. (Asteraceae) to the United Kingdom. *Watsonia*, **24**, 31–43.
- Hee, J.J., Holway, D.A., Suarez, A.V. & Case, T.J. (2000) Role of propagule size in the success of incipient colonies of the invasive Argentine ant. *Conservation Biology*, **14**, 559–563.
- Hengeveld, R. (1993) What to do about the North American invasion by the collared dove. *Journal of Field Ornithology*, **64**, 477–489.
- Hodkinson, I.D. & Hollis, D. (1987) The legume-feeding psyllids (Homoptera) of the west Palaearctic Region. *Bulletin of the British Museum of Natural History (Entomology)*, **56**, 1–86.
- Hopper, K.R. & Roush, R.T. (1993) Mate finding, dispersal, number released, and the success of biological-control introductions. *Ecological Entomology*, **18**, 321–331.
- Ihaka, R. & Gentleman, R. (1996) R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics*, **5**, 299–314.
- Karban, R. (1989) Fine-scale adaptation of herbivorous thrips to individual host plants. *Nature*, **340**, 60–61.
- Kareiva, P. (1996) Contributions of ecology to biological control. *Ecology*, **77**, 1963–1964.
- Memmott, J., Fowler, S.V. & Hill, R.L. (1998) The effect of release size on the probability of establishment of biological control agents: gorse thrips (*Sericothrips staphylinus*) released against gorse (*Ulex europaeus*) in New Zealand. *Biocontrol Science and Technology*, **8**, 103–115.
- Memmott, J., Fowler, S.V., Paynter, Q., Sheppard, A.W. & Syrett, P. (2000) The invertebrate fauna on broom, *Cytisus scoparius*, in two native and two exotic habitats. *Acta Oecologica – International Journal of Ecology*, **21**, 213–222.
- Parsons, W.T. & Cuthbertson, E.G. (1992) *Noxious Weeds of Australia*. Inka Press, Melbourne.
- Pimm, S.L. (1989) Theories of predicting success and impact of introduced species. In: *Biological Invasions: a Global Perspective* (eds J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmanek & M. Williamson), pp. 351–367. John Wiley & Sons Ltd, New York.
- Pimm, S.L., Jones, H.L. & Diamond, J. (1988) On the risk of extinction. *American Naturalist*, **132**, 757–785.
- Raudenbush, S.W. & Bryk, A.S. (2002) *Hierarchical Linear Models: Applications and Data Analysis Methods*, 2nd edn. Sage Publications, Thousand Oaks, CA.
- Raudenbush, S.W., Bryk, A.S., Cheong, Y. & Congdon, R.T. (2000) *HLM 5: Hierarchical Linear and Non-Linear Modeling*. Scientific Software International, Chicago.
- Richter-Dyn, N. & Goel, N.S. (1972) On the extinction of a colonizing species. *Theoretical Population Biology*, **3**, 406–433.
- Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. & Wall, D.H. (2000) Biodiversity – global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.
- Schmitz, D.C. & Simberloff, D. (1997) Biological invasions: a growing threat. *Issues in Science and Technology*, **13**, 33–40.
- Schoener, T.W. & Schoener, A. (1983) The time to extinction of a colonizing propagule of lizards increases with island area. *Nature*, **302**, 332–334.
- Shea, K. & Possingham, H.P. (2000) Optimal release strategies for biological control agents: an application of stochastic dynamic programming to population management. *Journal of Applied Ecology*, **37**, 77–86.
- Syrett, P., Fowler, S., Harman, H.M., Hayes, L.M., Memmott, J. & Sheat, J.J. (2004) Establishment of *Arytainilla spartiophila* Forster (Hemiptera: Psyllidae), a new biocontrol agent for broom, *Cytisus scoparius*, in New Zealand, in press.
- Waloff, N. (1968) Studies on the insect fauna on Scotch broom *Sarothamnus scoparius* (L.) Wimmer. *Advances in Ecological Research*, **5**, 87–208.
- Wapshere, A.J. (1974) A strategy for evaluating the safety of organisms for biological weed control. *Annals of Applied Biology*, **77**, 201–211.
- Williams, P.A. (1981) Aspects of the ecology of broom (*Cytisus scoparius*) in Canterbury, New Zealand. *New Zealand Journal of Botany*, **19**, 31–43.
- Williamson, M.H. & Brown, K.C. (1986) The analysis and modeling of British invasions. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, **314**, 505–522.
- Winston, M.L. (1992) *Killer Bees: The Africanized Honey Bee in the Americas*. Harvard University Press, Cambridge, MA.
- Wolf, C.M., Griffith, B., Reed, C. & Temple, S.A. (1996) Avian and mammalian translocations: update and reanalysis of 1987 survey data. *Conservation Biology*, **10**, 1142–1154.

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