

LETTER

A null model of temporal trends in biological invasion records

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Abstract

Biological invasions are a growing aspect of global biodiversity change. In many regions, introduced species richness increases supralinearly over time. This does not, however, necessarily indicate increasing introduction rates or invasion success. We develop a simple null model to identify the expected trend in invasion records over time. For constant introduction rates and success, the expected trend is exponentially increasing. Model extensions with varying introduction rate and success can also generate exponential distributions. We then analyse temporal trends in aquatic, marine and terrestrial invasion records. Most data sets support an exponential distribution (15/16) and the null invasion model (12/16). Thus, our model shows that no change in introduction rate or success need be invoked to explain the majority of observed trends. Further, an exponential trend does not necessarily indicate increasing invasion success or ‘invasional meltdown’, and a saturating trend does not necessarily indicate decreasing success or biotic resistance.

Keywords Cumulative invasions, introduction rate, invasibility, invasion rate, invasion success, null model, biotic resistance, invasional meltdown.

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INTRODUCTION

Biological invasions are a major and increasing element of global change (Mack *et al.* 2002; Rahel 2002; Olden & Poff 2003; Mooney *et al.* 2005). The growth and magnitude of the non-native component of biodiversity is well illustrated by detailed historical reviews of invasion records from a variety of ecosystems. In many of these regions, the total number of recorded invasions appears to be increasing supralinearly, which has been taken to indicate that invasion success or introduction rates may be increasing or even accelerating (e.g. Pickard 1984; Cohen & Carlton 1998; Cowie 1998; Leppäkoski & Olenin 2000; Ruiz *et al.* 2000; Ricciardi 2001; Wonham & Carlton 2005). It is not, however, straightforward to infer the processes underlying these observed trends.

A primary challenge stems from the inherently probabilistic nature of invasions, where a species must be introduced, must survive, and – to appear in a database – must also be detected and reported (Johnstone 1986; Crawley 1989; Carlton 1996; Levine & D’Antonio 1999; Ruiz *et al.* 2000; Costello & Solow 2003; Solow & Costello 2004). Since the data records are the outcome of the preceding stages of introduction, survival, and detection, it is important to ask what these observations can tell us about the underlying prior dynamics.

We address this question in three steps. First, we develop a simple probabilistic model of the invasion process to clarify our null expectations for temporal records. Our model focuses on the first two stages of species introduction rates and subsequent survival; the effects of the detection process combined with the introduction rate are elegantly treated by Costello & Solow (2003) and Solow & Costello (2004). Second, we ask how variation in species introduction rates and invasion success alter our null expectations. We examine increasing and decreasing invasion success, increasing and decreasing introduction rate, and saturating survival probability for individual species. Third, we analyse the temporal trends in 16 marine, aquatic and terrestrial data sets of invasion records. We use maximum likelihood analysis to compare the fit of four descriptive statistical distributions to the data (constant, linear, exponential and parabolic). We then compare the fit of the null invasion model and its extensions.

A NULL MODEL FOR INVASION RATES

Interpreting exponential distributions

As our model is to be compared with empirical data, we begin by considering what these data represent. In the cartoon example in Fig. 1a–d, a certain number of species

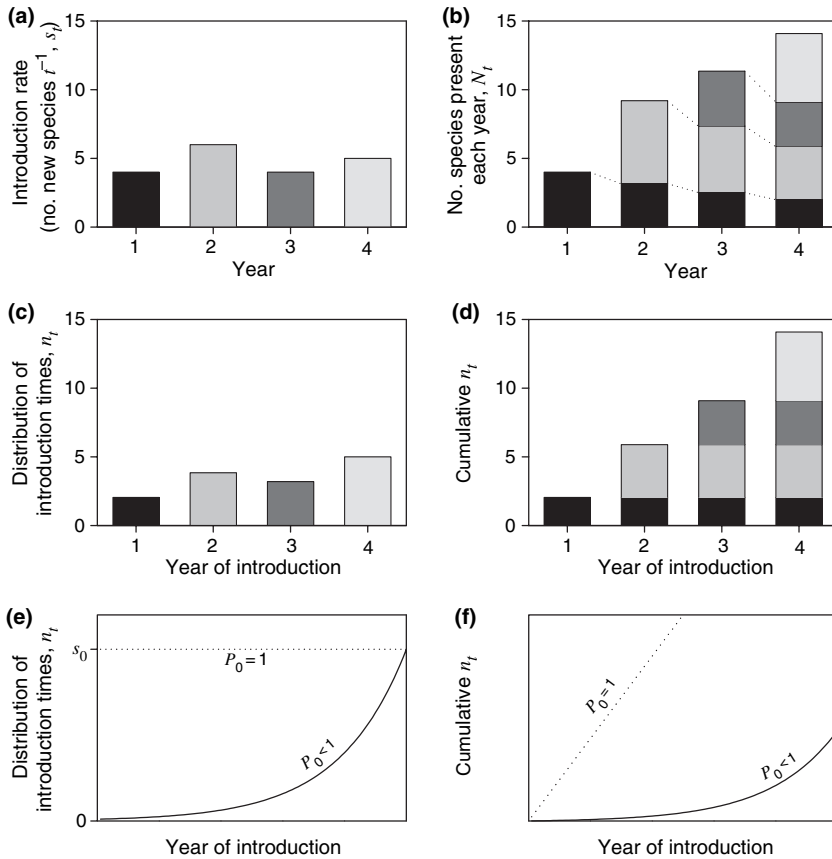


Figure 1 Illustration of temporal trends in species invasion records. The cartoon depiction in panels (a–d) shows the number of new species arriving in each year 1–4 (a), the number of species present in each year, N_t , given that some introductions fail (b), the resulting distribution of introduction times, n_t , of all invaders that survive to the fourth year (c), and the cumulative distribution of n_t (d). Panels (e,f) show more generally that n_t is constant only when the species annual survival probability $p_0 = 1$, and is otherwise exponentially increasing (e). This leads to the linear and exponential distributions of cumulative n_t in (f).

are introduced to a region each year (Fig. 1a), with some probability of survival from year to year (Fig. 1b). Imagine we are present in year 4 to collect and identify the surviving species, and we have sufficient literature records to determine when they were introduced. The fourth bar in Fig. 1b then represents our hard-won data, from which we can generate the distribution of introduction times shown in Fig. 1c. These data are often presented in the literature as the cumulative distribution shown in Fig. 1d. Thus, although the processes illustrated in Fig. 1a,b are typically unknown to us, we would like to infer as much as possible about them from the data distributions shown in Fig. 1c,d.

It is important to note that the distributions of N_t in Fig. 1b and cumulative n_t in Fig. 1d differ. Only when the survival probability for every species is equal to one are these distributions identical, but as a rule this is not the case. Indeed, sampling data indicate that the number of reported established invaders is far lower than the number of species that have been introduced (Carlton & Geller 1993; Smith *et al.* 1999; Wonham *et al.* 2000; Lester 2005; Ruesink 2005), and that in many cases recorded invaders have subsequently failed (Simberloff 1981; Frank & McCoy 1993; Carlton 1996; Williamson 1996; Kolar & Lodge 2001; Duncan *et al.* 2003; Forsyth *et al.* 2004; Marchetti *et al.* 2004).

For our analysis, we will focus on the non-cumulative distribution of introduction times, n_t , for two reasons. First, its shape is more informative than that of the cumulative distribution: for example, an exponential cumulative distribution can arise from underlying linear, exponential or increasing-parabolic non-cumulative distributions. Second, we wish to compare the model to empirical data. As the non-cumulative data are less temporally autocorrelated than the cumulative data, they are more amenable to classical statistical analysis.

For well-documented intentional invasions, the underlying introduction rate, species survival probability, and sampling effort may be known, but for most inadvertent invasions they are not. It has been clearly shown that a delay in invasion detection, given a presumed exponential population growth, can generate an exponential data distribution (Costello & Solow 2003; Solow & Costello 2004). Here, however, we focus only on the invasion process itself, prior to any detection delays, to identify the trends generated by the underlying biological dynamics. The null model thus uses species introduction rates and invasion success to determine the number of species present in each year, N_t (as in Fig. 1b) and the distribution of introduction times, n_t (as in Fig. 1c).

Table 1 Null invasion model and simple extensions for species invasions over time

Number of surviving invaders N_t	Distribution of introduction times n_t	Cumulative n_t	Parameter scaling	Parameter expression	Model	Figure
Simplest case $s_0 \sum_{i=0}^t p_0^{t-i} = s_0 \frac{p_0^{t+1}-1}{p_0-1}, p_0 \neq 1$ Variable invasion success p_t (constant $s_t = s_0$)	$s_0 p_0^{T-t}$	$s_0 \sum_{i=0}^t p_0^{T-i}$	s_t and p_t constant	$s_t = s_0$ $p_t = p_0$	Null	Fig. 1c,f
Variable introduction rate s_t (constant $p_t = p_0$)	$s_0 p_t^{T-t}$	$s_0 \sum_{i=0}^t p_i^{T-i}$	p_t linear with time p_t exponential with time p_t linear with N_t p_t exponential with N_t	$p_t = p_0 + \epsilon_1 t$ $p_t = p_0 e^{\epsilon_2 t}$ $p_t = p_0 + \epsilon_3 N_t$ $p_t = p_0 e^{\epsilon_4 N_t}$	P1 P2 P3 P4	Fig. 2a,b Fig. 2a,b - -
Increasing survival probability of individual species p_t (constant $s_t = s_0$)	$s_t p_0^{T-t}$	$\sum_{i=0}^t s_i p_0^{T-i}$	s_t linear with time s_t exponential with time	$s_t = (s_0 + \epsilon_5 t)$ $s_t = s_0 e^{\epsilon_6 t}$	S1 S2	Fig. 2c,d Fig. 2c,d
$s_0 \sum_{i=0}^t \prod_{j=0}^{i-1} p_j$	$\prod_{i=0}^{T-t-1} p_i$	$s_0 \sum_{i=0}^t \prod_{j=0}^{T-i-1} p_j$	p_t logistic with τ , time since introduction, given per capita growth rate r	$p_t = \left[1 + e^{-r\tau} \left(\frac{1}{s_0} - 1 \right) \right]^{-1}$	P5	Fig. 2e,f

Number of surviving invaders N_t , distribution of introduction times n_t for species surviving to time T , and cumulative n_t shown for constant and changing species invasion success p_t and introduction rate s_t over time t , and increasing survival probability of individual species, p_t , over time since introduction τ .

Null model

We define the introduction rate as the number of species arriving per unit time (e.g. 1 year). Invasion success is determined by a survival probability assigned to each species in each time step. Invaders are thus allowed to fail and go locally extinct. The focus is on species presence or absence; density and population growth are not explicitly modelled, and we assume each species is introduced only once. We introduce the model by building up from the simplest case to more complex scenarios (Table 1). Derivation of the general formulation is given in Appendix S1 in Supplementary Material.

The model consists of a simple probability statement linking species introduction and success to determine the number of surviving species. We represent the number of introduced species present this year as the number of species that were introduced this year, plus the number introduced last year that survived 1 year, plus the number introduced the previous year that survived 2 years, etc. (Table 1).

In the null case, we consider constant and equal invasion success for each species ($p_t = p_0$), and a constant introduction rate ($s_t = s_0$). When the invasion success and the introduction rate are constant, the number of species present at time t (as in Fig. 1b) is given by

$$N_t = s_0 \sum_{i=0}^t p_0^{t-i},$$

where p_0 is the species survival probability per time step and s_0 is the number of new non-native species added per time step (Table 1). When $p_0 < 1$, N_t is a saturating function. Only when every introduced species is successful ($p_0 = 1$) does N_t not saturate.

Next, we examine all the species surviving to time T and the time when they were introduced (as in Fig. 1c). The probability that a species introduced at time $t = 0$ survives until time T is $s_0 p_0^T$; for a species introduced at $t = 1$ it is $s_0 p_0^{T-1}$, and so on. For constant s_0 and p_0 , the distribution of introduction times for all species surviving until year T is thus $n_t = s_0 p_0^{T-t}$ (Table 1). This gives the distribution of cumulative n_t (as in Fig. 1d) as $s_0 \sum_{i=0}^t p_0^{T-i}$ (Table 1). When $p_0 < 1$, both n_t and cumulative n_t are exponentially increasing functions of time (Fig. 1e,f). Only when $p_0 = 1$ are these distributions not exponential (Fig. 1e,f).

In biological terms, this null model illustrates a key result: when the introduced species' survival probability is less than one, the distribution of n_t and of cumulative n_t increase exponentially even when both the introduction rate and the survival probability are constant (Fig. 1e,f). This arises because the probability of a given species surviving for an ever-longer time period declines exponentially, so the species most likely to have survived to time T are those that were introduced most recently. In other words, the

exponential distribution results from the attrition of invaders over time: the longer an invader has been in the system, the more time it has had to go extinct.

MODEL EXTENSIONS

Our null model with constant invasion success and constant introduction rate predicts an exponential distribution of introduction times n_t (Fig. 1e,f). It is reasonable, however, to expect both the underlying processes to vary through time.

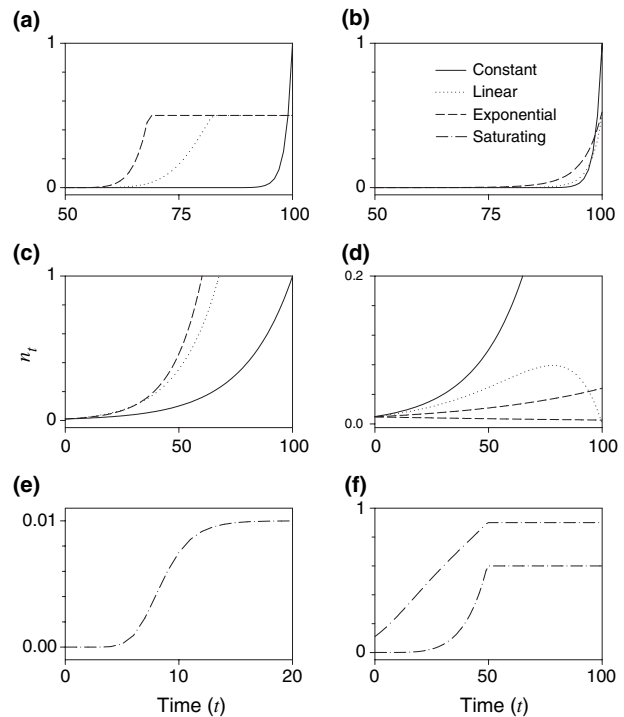


Figure 2 Distribution of introduction times n_t for constant and variable invasion success (a,b), introduction rates (c,d), and species survival probability (e,f). For ease of comparison, n_t in all cases is rescaled to a proportion of n_T for the constant case (with $T = 100$). The survival probability in (a) is constant ($p_0 = 0.955$), linearly increasing ($c_1 = 0.006$), and exponentially increasing ($c_2 = 0.01$); in (b) it is constant ($p_0 = 0.5$), linearly decreasing ($c_1 = -0.003$), and exponentially decreasing ($c_2 = -0.002$); in both panels, the constant introduction rate $s_0 = 100$. Introduction rate in (c) is constant ($s_0 = 5$), linearly increasing ($c_3 = 0.25$), and exponentially increasing ($c_6 = 0.03$); in (d) it is constant ($s_0 = 100$), linearly decreasing ($c_5 = -0.99$), and exponentially decreasing (upper dashed line, $c_6 = -0.03$; lower dashed line, $c_6 = -0.052$); in both panels, the constant survival probability $p_0 = 0.955$. Individual species survival probability p_t in (e) is saturating quickly ($r = 0.6$, $p_0 = 0.01$) and in (f) is saturating slowly with two different initial values (lower line $p_0 = 0.6$; upper line, $p_0 = 0.9$; $r = 0.05$ for both); in both panels the constant introduction rate $s_0 = 100$. Parameter values chosen to allow curves to be shown on same plots. Note different x- and y-axis scales.

As we are interested in exploring how such variation influences the predicted distribution of introduction times, we model this variation by changing survival probability and introduction rate directly, without explicitly representing the mechanisms that may drive them.

We treat the following five scenarios: increasing and decreasing invasion success, increasing and decreasing introduction rate, and saturating survival probability for each individual species (see explanations below). To compare the predictions of these different model variations, we show the analytical expressions for N_t , n_t and cumulative n_t (Table 1) and illustrate n_t graphically (Fig. 2). We note that in all cases where n_t is monotonically increasing, the cumulative distribution of n_t is necessarily supralinear.

Variable invasion success

We consider species invasion success to have two biological interpretations: the probability of survival for a given invader, and an index of community invasibility. We might expect success to vary both with the number of resident species, and over time. As a first approximation, we allow the survival probability of each introduced species, p_t , to depend on the time step t in which it is introduced (Table 1, Fig. 2a,b). Once a species is introduced, its survival probability remains constant. We allow p_t to scale both linearly and exponentially as a function of time while the introduction rate remains constant, $s_t = s_0$.

When survival probability increases, the distribution of introduction times n_t increases supralinearly, and saturates when $p_t = 1$ (Fig. 2a). When p_t decreases, n_t remains exponential, although it is flatter than with constant p_t (Fig. 2b). Biologically, these results illustrate that our null expectation for an exponential distribution of introduction times is not altered by systematically increasing or decreasing invasion success over time. The predictions generated by allowing p_t to scale with N_t are qualitatively similar to those reported for p_t scaling with t (Table 1).

Variable introduction rate

To explore the effects of variable introduction rate, we allow the number of new introductions s_t to change as a function of time while the survival probability remains constant and equal for all species, $p_t = p_0$ (Table 1, Fig. 2c,d). With increasing s_t , n_t rises faster than with constant s_t (Fig. 2c). For linearly declining s_t , n_t is unimodal (Fig. 2d). For exponentially declining s_t , n_t increases exponentially unless the introduction rate declines fast enough, i.e. $[a_0 + (T - t) \ln(p_0)] > 0$, in which case it decreases exponentially (Fig. 2d).

Biologically, these results show that both increasing and decreasing introduction rates can generate an exponential distribution of species introduction times. Thus, systematic

variation in introduction rate can still be consistent with our null expectation of an exponential distribution. Decreasing introduction rates can also generate unimodal and monotonically decreasing n_t distributions.

Variable survival probability in individual species

Thus far, our model has used a constant invasion success for all species. We now focus more closely on how a species' survival probability may vary over time. For this simple illustration, we imagine that survival probability scales with population size, which we assume grows logistically. As population growth is not treated explicitly in our model, we assign an initial survival probability to each species, which determines its immediate success. Thereafter, its survival probability p_t grows as a sigmoid function of τ , the time since introduction (Table 1, Fig. 2e,f). An introduced species can still go extinct in this model, but the longer it persists the lower its chance of doing so. We assign all species the same initial survival probability and the same saturating function for p_t .

The resulting distributions of introduction times all increase monotonically up to the saturation point at which $p_t = 1$ (Fig. 2e,f). Thus, the biologically reasonable assumption of sigmoid behaviour in p_t for individual species can generate initially exponential and ultimately saturating distributions of n_t even when the introduction rate is constant and the survival probability is equal for all species.

In summary, the null model and its extensions can all generate exponential distributions of n_t ; the model extensions can also generate other distributions. We now analyse a series of empirical data sets to determine the observed distribution of invasion records, and to compare the fits of the null model and its extensions to these data.

EMPIRICAL INVASION RECORD ANALYSIS

Methods

We used maximum likelihood to compare the fit of four statistical distributions and eight versions of our invasion model to invasion record data from 16 marine, freshwater and terrestrial systems (Table 2). These represent a range of ecosystems and locations for which a sizeable published list of introduced species and their first collection dates are readily available. None of the data sets has previously been analysed using maximum likelihood to compare the fits of alternate distributions.

From each study, we used first-record dates for established invaders, and omitted records that were indicated by the original authors to be of uncertain date (< 10% of records). Except in the case of deliberate releases, historical records typically provide only collection dates, which may follow considerably after a species' arrival (Carlton 1996;

Table 2 Comparison of four statistical distributions and eight probabilistic models fit to the introduction dates of non-native species for 16 data sets of Y years and S species

System	Y	S	Statistical distribution				Invasion model								
			Con	Lin	Exp	Par	Null	P1	P2	P3	P4	P5	S1	S2	
BA	155	59	29.52	4.62	0.00	7.65	40.70	0.00	42.69	42.69	42.69	42.69	42.69	42.69	42.70
BL	156	61	81.52	33.82	0.00	35.90	0.00	1.25	1.25	1.25	1.25	1.21	2.00	2.09	
CS	75	35	0.08	0.00	0.25	8.08	0.44	2.44	1.82	2.44	2.44	2.37	0.00	0.50	
MS	187	98	146.06	66.27	0.00	72.03	0.00	0.19	0.18	0.19	0.18	0.56	2.00	1.35	
NS	197	71	33.68	2.00	0.00	4.77	0.00	0.61	0.61	0.61	0.61	0.41	1.34	1.18	
FR	160	66	39.40	7.54	0.00	10.15	0.00	1.93	1.93	1.93	1.93	1.94	1.73	2.36	
UK	189	46	21.18	1.22	0.00	4.10	1.25	0.18	0.17	0.18	0.17	0.95	0.00	3.25	
SF	142	145	49.17	4.15	0.00	12.11	0.00	0.69	0.69	0.69	0.69	0.66	2.00	2.00	
NP	96	92	24.36	1.96	0.00	8.88	0.00	2.08	2.08	2.08	2.08	2.08	2.13	2.13	
HM	131	69	41.78	5.34	0.00	6.96	0.00	1.29	1.30	1.29	1.30	0.91	1.86	2.44	
PP	119	90	21.52	10.30	0.00	59.12	39.95	0.57	0.00	0.57	0.00	23.96	41.95	41.95	
GL	165	132	32.30	0.00	1.88	4.13	0.00	1.13	1.13	1.13	1.13	0.81	1.40	2.00	
HS	149	27	0.00	1.14	1.28	11.33	0.00	1.25	0.18	1.25	0.18	1.44	1.20	2.00	
FL	120	36	25.32	8.17	0.00	10.84	0.00	1.46	1.46	1.46	1.46	1.53	2.00	2.00	
CR	223	167	7.08	0.25	4.64	0.00	52.81	0.03	0.00	0.03	0.00	59.18	28.35	54.42	
LH	129	153	49.20	10.85	0.00	37.29	4.36	0.00	0.00	0.00	0.00	0.52	6.36	6.36	

Distributions are Con, constant, Lin, linear, Exp, exponential and Par, parabolic. Invasion models are as in Table 1. Maximum likelihood Δ AIC values shown for each case: value of Δ AIC = 0 indicates the highest support; values of Δ AIC < 2 indicate indistinguishably strong model support (shown in bold). All significant models were increasing over time; parabolic model was convex-up. Likelihood and parameter values are given in Appendix S2. Systems: BA, Baltic Sea marine taxa since 1844 (Leppäkoski & Olenin 2000); BL, Black Sea marine taxa since 1844 (Gomoiu *et al.* 2002); CS, Caspian Sea marine taxa since the 1920s (Aladin *et al.* 2002); MS, Mediterranean marine plants and algae since 1813 (Ribera-Siguan 2002); NS, North Sea aquatic and marine taxa since 1800 (Reise *et al.* 1999); FR, North Atlantic marine taxa on the French coast since 1840 (Gouletquer *et al.* 2002); UK, North Atlantic marine taxa on the UK coast since 1808 (Eno *et al.* 1997); SF, San Francisco Bay marine taxa since 1850 (Cohen & Carlton 1998, original data provided by authors); HM, Hawai'ian marine taxa since 1866 (Coles *et al.* 1998); PP, marine taxa from Port Philip Bay, Australia since 1879 (Hewitt *et al.* 2004); NP, northeast Pacific marine taxa since 1876 (Wonham & Carlton 2005); GL, Laurentian Great Lakes aquatic taxa since the 1830s (Mills *et al.* 1993; Ricciardi 2001); FL, Florida amphibians and reptiles since 1875 (Butter *et al.* 1997); HS, aquatic and terrestrial snails in Hawai'i since 1846 (Cowie 1998); LH, terrestrial plants from Lord Howe Island since 1853 (Pickard 1984); CR, terrestrial plants from the Czech Republic since 1750 (Pyšek *et al.* 2002).

Costello & Solow 2003; Solow & Costello 2004). For simplicity, we assumed that this effect was equal across all data sets, and took the collection dates as equivalent to first record dates. For the San Francisco Bay data set from Cohen & Carlton (1998), we used the original data from their Fig. 1b, provided courtesy of the authors; all other data sets were available in table or text form. Dates listed as a decade were entered as the middle of the decade (e.g. 1920s entered as 1925). Dates listed as prior to a given year were entered as that year (e.g. < 1950 entered as 1950). For easier comparison, all data sets were scaled to start in year $t = 1$.

The distributions and the models were fit to these non-cumulative invasion records using maximum likelihood, and assuming an underlying Poisson error distribution. In other words, we assumed that at each time point new invaders arrived from a large species pool with a small probability of success.

For the four statistical distributions, we compared the fit of constant, linear (i.e. straight line with slope significantly different from zero), exponential and parabolic curves.

These correspond to linear, quadratic, exponential, and sigmoid distributions, respectively, in cumulative n_t . The distributions were formulated as: constant $n_t = k_1$, linear $n_t = k_2t + k_3$, exponential $n_t = k_4e^{k_5t}$ and parabolic $n_t = k_6t(k_7 - t)$, where n_t is the number of species introduced in year t and surviving to the last year of the data set, T , and k_i are constants. Parabolic distribution fits were constrained such that $k_6 > 0$ and $k_7 > 0.5T$, to ensure a positive, convex-up parabola. For the invasion models, we used the same methods to compare the fit of the null model and its seven extensions (Table 1).

We compared the distribution fits and model fits using Akaike Information Criterion (AIC), and interpreted all distributions and models with Δ AIC < 2 to have indistinguishably strong support (Burnham & Anderson 2002). As the three non-constant statistical distributions and the seven model extensions all have two parameters, it is their shape rather than number of parameters that affects their goodness-of-fit to the data. The Δ AIC values are given in Table 2 for both statistical distributions and invasion

models. The Appendix S2 gives negative log likelihood and parameter values for all data sets, as well as results for taxonomic, regional and invasion pathway subsets of marine invader records in the northeast Pacific.

Results

Best-fit distributions and models are shown for four sample data sets in Fig. 3. Among the statistical distributions, 15 of 16 data sets supported an exponential model (Table 2). Ten

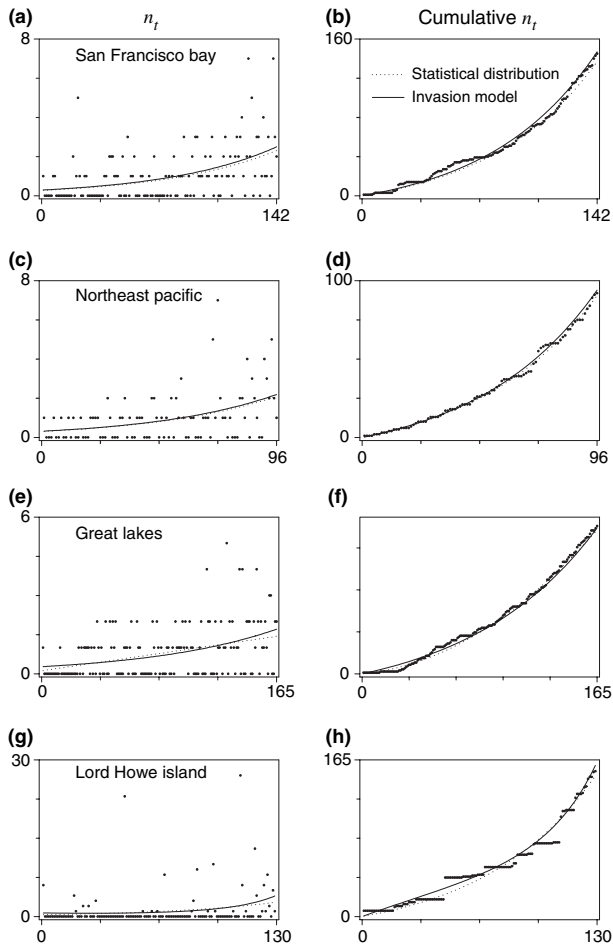


Figure 3 Statistical distributions and invasion models fit to four example data sets. Filled circles show n_t , the distribution of introduction times, in left-hand panels and cumulative n_t in right-hand panels. Solid line is the best-fit model and dotted line is the best-fit statistical distribution for each case. Data for marine invaders in San Francisco Bay are fit with the null model and an exponential distribution (a,b), data for marine invaders in the northeast Pacific are fit with the null model and an exponential distribution (c,d), data for aquatic invaders in the Laurentian Great Lakes are fit with the null model and a linear distribution (e,f), and data for terrestrial plants on Lord Howe Island are fit with model P1 (as an example) and an exponential distribution (g,h).

supported this model alone, and five supported the linear and/or constant models as well (Table 2). The remaining data set, terrestrial plants in the Czech Republic, supported the parabolic and linear models. For the latter, the parabolic maximum was predicted to occur far in the future (Appendix S2), so the shape of the curve appears linear within the timeframe of the data. All distributions but one (marine invaders in the Caspian Sea) were increasing over time (Appendix S2).

For the invasion models, 12 of 16 data sets supported the null model (Table 2). One data set supported the null model exclusively (marine invaders in the northeast Pacific), and one supported an increasing survival probability model exclusively (model P1, aquatic and marine invaders in the Baltic Sea). One data set, aquatic and marine invaders in the North Sea, failed to distinguish among any of the models. In general, the data tended to support models of changing invasion success (15/16) over models of changing introduction rates (8/16). Both increasing and decreasing models of invasion success and introduction rates were supported (see parameter values in Appendix S2).

Several of the original studies also listed first record dates for cryptogenic species. As these species may or may not be non-native, we tested the effects of their inclusion in the analyses. We repeated our analysis, adding in established cryptogenic species for Hawai'ian marine invaders (26 additional species or 27% of the combined data set), Hawai'ian snail invaders (four species or 13%), and marine invaders in Port Phillip Bay, Australia (54 species or 33%). The best-fit distributions and models remained the same in all cases except for the Hawai'ian snails. Here, the best-fit model switched from the null model to P5, a model that was also supported in the first analysis.

An analysis of taxonomic, invasion pathway and regional subsets of the northeast Pacific data illustrate that data subsets generally, but do not always, support the same distributions and models as the overall data set (Appendix S2). Although the total species list supported an exponential distribution and the null model, invasions by molluscs best supported a constant distribution and model P5. Invasions via ballast water showed the same trend as the overall data set, but those via commercial oysters supported a constant distribution with the null model, and those via ship fouling best supported a constant distribution with model P5.

There was no particular correspondence evident across the data sets between the best-fit statistical distributions and invasion models. Parameter values for the best-fit distributions and models are given in Appendix S2.

DISCUSSION

We have combined empirical data analysis and simple mathematical models to investigate the observed and

expected temporal patterns in invasion records. Our analysis of empirical records from 16 regions showed that most data sets were best fit with an exponential distribution, and with the null invasion model of constant species survival and constant introduction rate. As the null model generates an exponential distribution, no particular mechanisms need be invoked to explain the empirical observations.

Null model extensions treated varying invasion success, introduction rate and individual species survival probability. Invasion success has been predicted to vary both as a function of the number of resident species, and as a function of time. Decreasing invasion success (or invasibility) has been associated with increasing resident species richness in theoretical, microcosm, and field studies of biotic resistance (see reviews by Levine & D'Antonio 1999; Davis *et al.* 2000; Richardson *et al.* 2000; Mack *et al.* 2002; Byers & Noonburg 2003; Fridley *et al.* 2004; Herben *et al.* 2004). At the same time, increasing invasion success has been associated with the establishment of additional facilitative invaders, in the invasional meltdown hypothesis (Simberloff & Von Holle 1999; Ricciardi 2001). It has also been suggested that invaders' success may decrease over time if the weaker invaders in a given source pool remain behind (MacArthur & Wilson 1967), or may increase if aggressive invaders continue to establish widely and constitute an ever larger proportion of invasion source pools.

Our model shows that both increasing and decreasing invasion success, as a function of time or of the number of resident species, can generate exponential distributions of introduction times. A pattern of increasing success or invasional meltdown, predicts an exponential increase in n_t that saturates if and when the invaders' survival probability reaches 1. A pattern of decreasing success or biotic resistance, predicts only an exponentially increasing distribution in n_t . An exponential distribution of n_t cannot, therefore, be taken as evidence of invasional meltdown, as it is consistent both with the decreasing invasion success of biotic resistance and with the more parsimonious scenario of constant invasion success.

Species introduction rates are generally considered to be increasing with increasing global trade, transport pathways, and source populations (e.g. Carlton 1996; Levine & D'Antonio 2003). On the other hand, with increasing regulation of invasion pathways (e.g. IMO 2004), introduction rates in certain areas may be expected to decline. More generally, we can imagine that in some instances global homogenization and species loss may reduce the richness of invasion source pools and therefore reduce the rate at which new species are introduced. Our null model shows that both increasing and decreasing introduction rates can generate exponentially increasing distributions and therefore may not be distinguishable from the null model. Only when linear decline continues long enough or when the exponential

decline is sufficiently rapid, are qualitatively different distributions generated.

A number of important considerations arise in interpreting these results. First, empirical invasion records are difficult to pin down, as species in general are likely to have arrived some time prior to their discovery and transient invaders may never be detected. This uncertainty in species records necessarily propagates into errors in the data and therefore errors in the choice of best-fit distributions and models. Second, a trend that appears constant or linear today may be the initiation of a future exponential, parabolic or other curve. Thus, the distribution selected by the data may differ from the best fit that would emerge from a longer temporal data set of the same process. Third, although some data sets were unable to distinguish statistically between linear and exponential or linear and parabolic distributions, the long-term predictions of these different distributions would clearly differ substantially.

Our null invasion model is a simple caricature designed to isolate the two fundamental elements of a region's biotic invasions: the rate of species introduction and the success of those introduced species. The model shows that constant introduction and success are sufficient to explain the observed exponential distributions of introduction times. A third process, the rate at which invaders are detected, can also generate exponential trends (Costello & Solow 2003; Solow & Costello 2004). As all three of these processes operate in concert to determine the data that we observe, specific models for any particular region should incorporate them all together.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online from: <http://www.Blackwell-Synergy.com>

Appendix S1 Formulation of the general model for the number of introduced species over time.

Appendix S2 Maximum likelihood and parameter values for statistical distributions and invasion models fitted to the empirical data sets shown in Table 2.

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