Modeling the relationship between propagule pressure and invasion risk to inform policy and management

Marjorie J. Wonham,[1,5] James E. Byers,[2] Edwin D. Grosholz,[3] and Brian Leung[4]

[1]*Quest University Canada, 3200 University Boulevard, Squamish, British Columbia V8B 0N8 Canada*
[2]*Odum School of Ecology, 140 East Green Street, University of Georgia, Athens, Georgia 30602 USA*
[3]*Department of Environmental Science and Policy, University of California, One Shields Avenue, Davis, California 95616 USA*
[4]*Department of Biology, McGill University, 1205 ave Dr. Penfield, Montreal, Quebec H3A 1B1 Canada*

Abstract. Predicting population establishment based on initial population size is a theoretically and empirically challenging problem whose resolution informs a multitude of applications. Indeed, it is a central problem in the management of introduced, endangered, harvested, and pathogenic organisms. We focus here on introduced species. We synthesize the current state of modeling in this predictive enterprise and outline future directions in the application of these models to developing regulations intended to prevent the establishment of invaders. Descriptive and mechanistic models of single-population introductions are fairly well developed and have provided insight into invasion risk in laboratory and field conditions. However, many invasions stem from large-scale and repeated releases of a multitude of species from relatively indiscriminate invasion vectors associated with international trade and travel. Vector-scale models of invasion risk are less well developed and are characterized largely by the use of untested proxy variables for propagule pressure. We illustrate the problems associated with proxy variables and introduce a more mechanistic theoretical formulation characterizing vector-scale invasion pressure in terms of propagule pressure (number of introduced individuals) and colonization pressure (number of introduced species). We outline key questions to be addressed in applying both single-population and vector-scale models to the development of threshold-based invasion regulations. We illustrate these ecological and applied questions using examples from terrestrial, aquatic, and marine systems. We develop in detail examples from ballast-water transport that, as one of the best-characterized global invasion vectors and one that is subject to emerging international threshold-based biosecurity regulations, provides a rich case study.

Key words: Allee effects; ballast water; biological invasions; biosecurity; conservation; introduced species; invasion vectors; population establishment; population modeling; population viability analysis; propagule pressure; risk–release relationships.

Introduction

The risk–release problem

Understanding how the risks of population establishment and extinction vary with the size of the initial population has long been a central pursuit of ecology (e.g., Mason 1977, Lande 1993, Lawton and May 1995, Courchamp et al. 2009). This relationship is at the core of a wide array of applied ecological problems including stock–recruitment analysis in fisheries management, recovery planning for endangered species, intentional introductions for restoration and biological control, and the prediction and prevention of biological invasions.

Our theoretical understanding of this relationship is relatively well developed (Allee 1931, Lande 1993, Middleton and Nisbet 1997, Drake 2004, Courchamp et al. 2009), but exceeds our ability to predict the

outcome of particular cases in the real world where environmental and demographic heterogeneity and stochasticity can readily frustrate specific predictions of small-population dynamics (Gause 1932, Huffaker 1958, Gurney and Nisbet 1998, Taylor and Hastings 2005). Nevertheless, it has served as the basis for a wide range of applied efforts to facilitate or to discourage species establishment (Lockwood et al. 2009, Simberloff 2009, Ricciardi et al. 2011). Although the relationship applies broadly to questions of population establishment and persistence, we focus on its application to biological invasions and examine how the number of organisms and species initially released determines the risk of a successful invasion.

Invasions are a dominant agent of global change with widespread ecological, epidemiological, and economic implications. The pathways of invasion are many, and are subject to increasing regulation (Carlton and Ruiz 2005, Lodge et al. 2006, Costello et al. 2007, Reaser et al. 2008, Hulme 2009, Blackburn et al. 2011, Albert et al. 2013, Frazier et al. 2013, Lee et al. 2013). Hulme et al. (2008) distinguish between the major pathways of

intentional and unintentional introduction; among unintentional invasions associated with trade and travel, they distinguish contaminants on commodities from stowaways on transport vectors. Contaminants include the pathogens, parasites, and commensals on imported plants, animals, and soil. Stowaways include seeds on shoes, clothing, and tires, and plants and animals in shipping containers, on recreational boats and gear, and on and in commercial vessels (Hulme et al. 2008).

The temporal, geographic, taxonomic, numeric, and economic scales of introduced contaminants and stow-aways are staggering (Carlton and Ruiz 2005). By way of example, the U.S. Department of Agriculture recorded over 770 000 pest interceptions at ports of entry from 1984–2000 (McCullough et al. 2006), and 232 species of ants alone arriving in shipping containers from 1927–1985 (Suarez et al. 2005). An estimated 69% of the 82 highest impact nonnative forest pests in the United States likely arrived in shipments of live plants (Liebhold et al. 2012). Commercial shipping itself leads to the release of hundreds of millions of metric tons (Mg) of ballast water and its resident organisms annually in U.S. ports alone (Miller et al. 2011, NRC 2011). The costs of species control, commercial damage, and lost ecosystem services are difficult to estimate, but clearly run to billions of U.S. dollars annually (Pejchar and Mooney 2009, Aukema et al. 2011, Oreska and Aldridge 2011).

The extensive consequences of biological invasions have driven a proliferation of preventive regulations at state, national, and international levels that attempt to interrupt incipient invasions at the point between transport and release (Lodge et al. 2006, Hulme et al. 2008, Reaser et al. 2008, Blackburn et al. 2011, NRC 2011). Many of these are taxon-specific regulations focused more on commodities and contaminants than on stowaways (Hulme et al. 2008, Reaser et al. 2008). A major exception is the emerging international and U.S. federal regulation of ballast water, one of the world's largest and best-documented invasion vectors. With a global fleet of over 100 000 commercial vessels, the pending adoption of abundance-based organism release thresholds constitutes an enormous experiment in applied population management (IMO 2004, Miller et al. 2011, NRC 2011, Albert et al. 2013, EPA 2013, Frazier et al. 2013, Lee et al. 2013).

Setting scientifically based regulations for an invasion vector clearly requires understanding the risk–release relationship at both population and vector scales. However, the mechanics of applying single-population models to vector-scale assemblages poses significant challenges. Our understanding of single-population invasion dynamics is derived primarily from intentional introductions where a known initial number of individuals are released into the wild or into controlled experimental conditions. In contrast, our understanding of vector-scale invasion processes—the simultaneous and repeated release of multiple species—is based primarily on vector records of contaminants and stowaways, and field records of successful invaders in recipient habitats. The complexity of the dynamics and the resolution of the available data are thus very different between these two scales.

Our goals are (1) to review and synthesize current modeling approaches to predicting population establishment in relation to propagule pressure, (2) to expand on single-population models to outline a preliminary mathematical framework for characterizing vector-scale invasions, and (3) to identify opportunities, challenges, and next steps in using both scales of model to inform invasion-prevention policies. At the single-species scale we offer terrestrial, aquatic, and marine examples of invasion models. At the vector scale we take advantage of the relatively well-characterized vector of ballast-water transport to illustrate the complex dynamics of repeated releases of multiple species.

The risk–release relationship

We use the term *risk–release relationship* to refer to the relationship between invasion risk and the size of the initially released population (also described as a "dose–response relationship"; Ruiz and Carlton 2003). In the case of a single introduction, we think of risk as an introduced population's probability of establishment. In the case of an invasion vector, we think of risk variously as the number, rate, or probability of successful introductions in a region.

We equate release with propagule pressure. In its broadest sense, propagule pressure encompasses the combined frequency, timing, viability, diversity, and abundance of released individuals (Colautti et al. 2006, Lockwood et al. 2009, Simberloff 2009, Ricciardi et al. 2011, Briski et al. 2012). For single invasions we will think simply in terms of the number or density of released individuals, also known as "population-level propagule supply." For an entire invasion vector we will consider both the abundance and number of species, or the combination of propagule pressure and colonization pressure (Colautti et al. 2006, Chiron et al. 2009, Lockwood et al. 2009, Ricciardi et al. 2011, Briski et al. 2012).

The realized invasion risk in a region clearly depends not only on propagule and colonization pressure, but also on the life history of the species in question, their survival and dispersal in the local abiotic environment, and their facilitation or inhibition by resident biota: the roles of these factors are dominant themes in the invasion literature (e.g., Elton 1958, Byers and Pringle 2006, Simberloff 2009, Blackburn et al. 2011, Gurevitch et al. 2011, Seastedt and Pyšek 2011, Wells et al. 2011). To focus our scope, however, we restrict our attention to invasion risk as a function of propagule and colonization pressure alone. We use the terms *invasion* and *establishment* interchangeably, and *risk* and *probability* likewise, appreciating that biological invasions are only one

example of the general topic of population establishment and persistence in ecology and management.

The shape and the strength of the risk–release relationship have important implications for understanding and managing invasion risk (Ruiz and Carlton 2003, Carlton and Ruiz 2005, Lockwood et al. 2005, Reaser et al. 2008). It is well established that this relationship is generally positive, and that increased propagule pressure (variously defined) contributes significantly to the success of many invasions (reviewed recently by a large number of authors, including Colautti et al. 2006, Clark et al. 2007, Blackburn et al. 2008, 2011, Lambdon et al. 2008, Chiron et al. 2009, Lockwood et al. 2009, Simberloff 2009, van Wilgen and Richardson 2012), although perhaps not in all cases (Haydar and Wolff 2011, Moulton et al. 2011, 2012, Yeates et al. 2012). However, most empirical tests of the effect of propagule pressure have been limited to just a few abundances (often only two levels of abundance per species, or analyses combining multiple species with only one level each) and many have lacked appropriate control treatments or null hypotheses, making it difficult to assess with confidence the shape and strength of the relationship (Clark et al. 2007, Lockwood et al. 2009, Simberloff 2009).

A priori, a number of standard shapes could describe the risk–release relationship (Ruiz and Carlton 2003, Lockwood et al. 2005; Fig. 1a). If the relationship were linear, a given reduction in release would always lead to a proportional reduction in invasion risk. If the relationship were nonlinear, however, interesting patterns and thresholds would emerge. With a hyperbolic relationship, a given reduction in release would be most effective at lower release sizes; along a sigmoid curve, it would be at intermediate release sizes around the inflection point (Fig. 1a).

For the establishment probability of a single population in a suitable environment, only the hyperbolic and sigmoid curves have a clear theoretical justification (Allee 1931, Leung et al. 2004). Assuming each individual has the same chance of establishment, each additional individual increases the population establishment probability toward a limit of 1; discounting the probability that establishment has already occurred results in a hyperbolic curve (Fig. 1b). If individuals interact positively (e.g., Allee effects), an accelerating phase may occur, resulting in a sigmoid curve (Fig. 1b). For vector-scale analyses, the risk–release relationship is often analyzed in terms of the number of successfully established species vs. propagule pressure. Here the expected shape of the relationship is less clear, and both linear and nonlinear models have been applied to empirical data (e.g., Lonsdale 1999, Levine and D'Antonio 2003, Taylor and Irwin 2004, Ricciardi 2006, Reusser et al. 2013). It is the unknown shape of this relationship in particular that has the potential to inform vector-scale management of contaminant and stowaway invaders.

We review the structure and fit of candidate models to empirical risk-relationship data at two scales: isolated releases of single populations, and multiple releases over space and time of multiple species at the vector scale. Vector-scale models have received less theoretical attention, and pose greater empirical challenges in parameterizing. However, because this is the scale at which growing invasion management and policy apply; it is also the area that presents the greatest potential for progress.

Risk–Release Models

Population-scale release

It is informative to examine the risk–release relationship at the scale of a single release of a single species, for three main reasons. First, this approach allows examination of certain model species, which could be used to obtain upper bounds for general release levels (e.g., Liebhold and Bascompte 2003, Tobin et al. 2011). Good candidate species would be fast-growing, high-impact, or commonly released invaders. Second, it allows for clarification of model structures and assumptions before extending to vector-scale models. Third, from a pragmatic perspective it is easier to obtain data to parameterize a model for one population and location than for many.

For ease of discussion, we distinguish three general modeling approaches with increasing degrees of biological specificity. We will use *descriptive statistical models* to refer to splines and regressions that describe the population's establishment probability P_E as a function of the initial population size N without explicitly considering the individual establishment probabilities or the population dynamics that connect these two variables. We will use *biological probability models* to refer to those that describe establishment probability P_E as a function of a baseline probability p of each of N individuals establishing, and their potential to interact with one another (e.g., through Allee effects, Leung et al. 2004). In these two categories, models are typically fit directly to empirical data of P_E vs. N. We will use *dynamic demographic models* to refer to models that explicitly consider population dynamics. This may be achieved using systems of difference or differential equations, and through numerical simulations and more complex individual-based models that express the change in population size over time as a function of demographic parameters (e.g., birth, death, maturation). Through multiple stochastic simulations, these dynamic models can be used to generate a relationship between P_E and N to which a statistical or a probabilistic model can then be fit (e.g., Gertzen et al. 2011).

These three approaches are by no means mutually exclusive (e.g., Jerde and Lewis 2007, Leung and Mandrak 2007, Drake and Jerde 2009, Jerde et al. 2009), but they are helpful in organizing the universe of risk–release models at both single-species and vector scales. Since we are interested in exploring the shape of
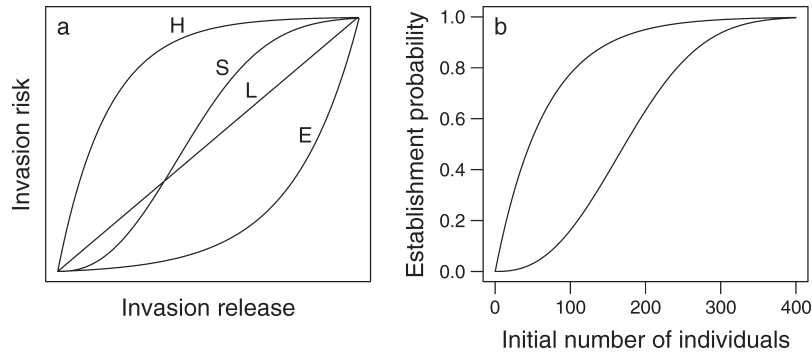
Fig. 1.   The risk–release relationship for biological invasions. For a single population, risk is generally the probability of species establishment, and release is the number of individuals introduced. For vectors, risk is often characterized as the number of successfully established species, and release as the number of individuals, species, or some proxy variable for propagule pressure. (a) Simple candidate shapes for the risk–release relationship: H, hyperbolic; S, sigmoid; L, linear; E, exponential (both axes linear); adapted from Ruiz and Carlton (2003) and Lockwood et al. (2005). (b) Predicted risk–release relationship for a single population as a function of propagule pressure, or number of individuals, based on a simple probabilistic model, where p is the baseline probability of a single individual establishing, and c is a shape parameter that for values $c > 1$ generates the sigmoid shape characteristic of an Allee effect (Eq. 1; modified from Leung et al. [2004]). In the absence of density dependence, the relationship is necessarily hyperbolic (upper curve, $p = 0.010$, $c = 1$); for a population exhibiting Allee effects, it is expected to be sigmoid (lower curve, $p = 0.005$, $c = 3$).

the risk–release relationship, we draw illustrative examples primarily from case studies that used five or more initial organism densities, where both the original data and the model fit were readily available for visualization.

Descriptive statistical models.—These models characterize the risk–release relationship with a regression, spline, or similar model. Their chief advantage is that they can be formulated and parameterized without having to understand or specify much of the underlying biological mechanism by which release leads to risk. Their key disadvantage, as a result, is that they offer little mechanistic insight, and must be extrapolated with care (Drake and Jerde 2009): unless carefully specified, for example, they can predict a nonzero population establishment probability even with zero individuals. More-complex statistical models can describe invasion risk and release over a spatial domain using species distribution models (also known as "environmental niche models"; e.g., Guisan and Thuiler 2005, Herborg et al. 2007, Dullinger et al. 2009). However, these models generally make predictions more closely related to equilibrium densities and distributions, rather than to early invasion dynamics, and are less immediately relevant to invasion-prevention regulations.

A variety of general and generalized linear models have been used to estimate the impact of propagule pressure on establishment. Most of these have used only a very few initial abundance levels and therefore can provide little insight into the shape of the risk–release relationship (reviewed by Clark et al. 2007, Chiron et al. 2009, and Simberloff 2009). Some that have been fit to a broader range of levels include the flowering probability of scentless chamomile as a function of the number of seeds planted (Drake and Jerde 2009), the six-year survival of European thistle as a function of seeds

produced by founder plants (Jongejans et al. 2007), the six-year survival of a biocontrol psyllid as a function of the number of insects released (Memmott et al. 2005), and the establishment of biocontrol insects as a function of four indices of propagule pressure (Yeates et al. 2012) (Fig. 2a, b).

Where propagule pressure is not known directly, proxy variables have been used instead, particularly for modeling the regional spread of a species once it has been introduced (e.g., recreational boat traffic for aquatic species in lake systems; Potapov et al. [2011], Compton et al. [2012]; nearby population abundance for apple snails, Yamanishi et al. [2012]; number of introductions and proximity to introduction site for biocontrol insects, Yeates et al. [2012]). We highlight opportunities and pitfalls in the use of such proxy variables below in *Promise and perils of proxy variables.*

Biological probability models.—These models represent the probability of population establishment P_E as the product of independent Bernoulli trials such that $P_E = 1 - (1 - p)^N$ for each of N individuals, and p is the probability that a given individual establishes (Leung et al. 2004). In its simplest form, this model predicts a hyperbolic risk–release relationship; modifications allow it to represent Allee effects both descriptively and mechanistically (Leung et al. 2004, Jerde and Lewis 2007, Leung and Mandrak 2007, Jerde et al. 2009) (Fig. 1b). The key advantages of this probabilistic approach are that it is built from a logical and biological foundation, and is relatively straightforward to parameterize from empirical data.

This simple probability statement has served as a basis for a variety of empirical and theoretical analyses of risk and release. These include the probability of persistence after 100 days for cladoceran populations in mesocosms
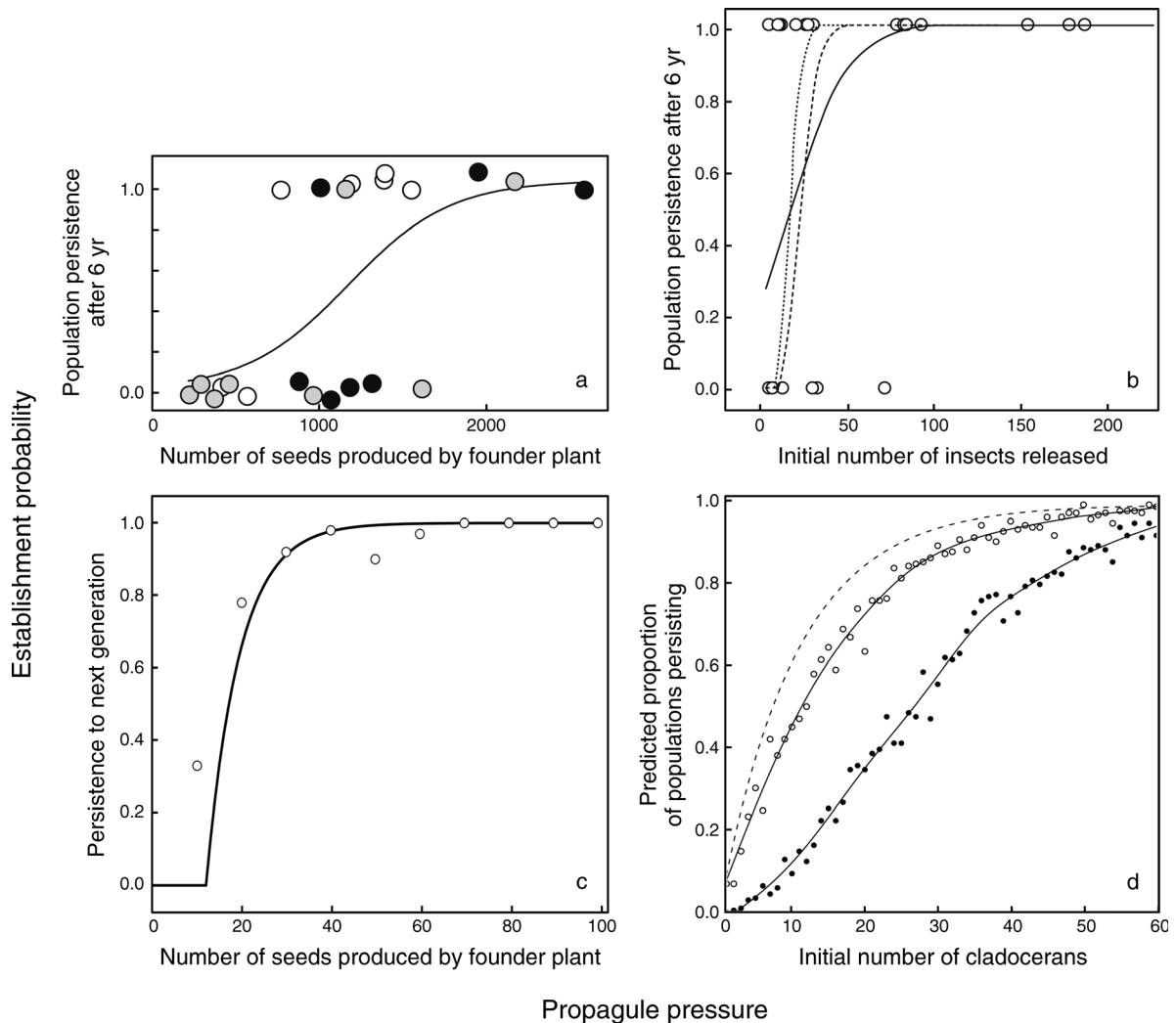
FIG. 2. Single-species risk–release relationships from statistical models (top panels), and probabilistic models (bottom panels). (a) Logistic regression fit to experimental outcome (success or failure) for European thistle *Carduus acanthoides* when surrounding native plants were clipped or not: no clipping (black); clipped once (open); clipped twice (gray). Panel (a) is modified from Jongejans et al. (2007: Fig. 1). (b) Two models fit to the outcome (success or failure) of experimental releases of the biocontrol psyllid *Arytainilla spartiophila* (solid line, logistic regression; dashed and dotted lines, two fits of the Shea and Possingham (2000) functional form model of population establishment). Panel (b) is modified from Memmott et al. (2005: Fig. 1). (c) Observed and predicted persistence from seed to flowering of scentless chamomile *Matricaria perforata* as a function of the initial number of seeds planted in experimental plots. Panel (c) is modified from Drake and Jerde (2009: Figs. 1 and 4). (d) Dynamic demographic model of the proportion of cladoceran (*Daphnia magna*) populations extant after 40 time steps as a function of initial population size (dashed line, type I functional response; solid lines, splines fit to outcome of stochastic simulations of demographic model under low (open circles) and high (solid circles) predation treatments (figure created by J. Drake using data in Kramer and Drake [2012]).

(using a diffusion approximation to exponential growth; Bailey et al. 2009), the proportion of laboratory cladoceran populations persisting after 40 time steps (incorporating demographic and environmental stochasticity; Drake et al. 2006), the probability of persistence to the next generation for scentless chamomile planted in experimental plots (Drake and Jerde 2009), and the probability of persistence to the next generation for Chinese mitten crab and apple snail invasions in the wild (incorporating mate-driven Allee effects; Jerde et al. 2009) (Fig. 2c). In all these examples the basic

probability structure has been extended to incorporate elements of a dynamic demographic approach. Probabilistic models have also been extended to represent population establishment across a spatial landscape using gravity models (e.g., Leung et al. 2004, Potapov et al. 2011) or the temporal accumulation of species in a location (Wonham and Pachepsky 2005, Costello et al. 2007).

Dynamic demographic models.—Whereas the models treated thus far are written in terms of establishment probability, dynamic demographic models are written in

terms of the underlying birth, death, and maturation rates, where the solution is the population size at a given time, N_t. The shape of the risk–release relationship in terms of P_E vs. N_0 can in some cases be derived analytically; more generally, however, it may be characterized by fitting a second model (either descriptive or probabilistic) to the outcome of multiple stochastic simulations of the demographic model. These dynamic models have the advantage of using independently estimated demographic parameters to generate the risk–release relationship from a more biologically mechanistic framework, but require a tremendous investment of time and effort in empirical parameter estimation.

Dynamic demographic models have served as the basis for the population viability analysis (PVA) of threatened and endangered species (Morris and Doak 2002). They have been applied more recently to analyze the threshold invader density needed to establish a population (Bartell and Nair 2004, Andersen 2005), and have been proposed for use in evaluating ballast-water discharge standards (USCG 2012). It is useful to recall that the goals and outcomes of population viability analysis are not the exclusive domain of demographic models: although the term "PVA" typically refers to the analysis of these models, any modeled population may be subjected to an analysis of its viability. Indeed, such analysis is inherent in the construction of a probabilistic establishment model.

Several recent examples apply dynamic demographic models to predicting species-establishment probability, using age-, stage-, or sex-structured populations (Scotch broom, Parker 2000; a copepod, Barry and Levings 2002; spiny water flea, Kramer and Drake 2010, Gertzen et al. 2011) (Fig. 2d). Once a group of organisms are released, they move through advection and locomotion, leading to net aggregation or dispersal. The effects of dispersal on population establishment have been explored in considerable detail by expanding demographic models to a reaction–diffusion framework and its extensions (e.g., Skellam 1951, Grosholz 1996, Shigesada and Kawasaki 1997, Hastings et al. 2005, Wells et al. 2011), but for the most part these models have not been used to predict risk–release relationships (cf. Drake et al. 2005).

Single-invasion models are a comparatively tractable and well-developed approach to investigating the establishment dynamics of one introduced population at a time. Of the first two approaches, probabilistic models can offer a more mechanistic representation than descriptive models of the same empirical data, and are therefore preferable. Where sufficient data are available, models with additional demographic parameters will offer a more nuanced understanding of the underlying dynamics. Regardless of the model type, if establishment is assumed to increase monotonically with propagule pressure, the final relationship must adopt a sigmoid or hyperbolic shape, with establishment probabilities in the range 0 to 1, and specific thresholds determined by the biology of the individual species. Because the parameterization of demographic single-species models demands considerable empirical effort, these have been developed for only a handful of species and under only a few conditions, and therefore do not capture the full range of spatial, temporal, and taxonomic heterogeneity inherent to the multitude of introductions associated with major invasion vectors.

Vector-scale release

Most introductions occur not in isolation, but as mass releases of multiple contaminant and stowaway species (Carlton and Ruiz 2005, Hulme et al. 2008, Tatem 2009). Understanding and managing these unintentional invasions is hampered by not knowing the abundance, diversity, and identity of the assemblages associated with each repeated arrival of an invasion vector. However, this is the scale at which many preventive regulations are developing (IMO 2004, Lodge et al. 2006, Hulme et al. 2008, Reaser et al. 2008, NRC 2011, Albert et al. 2013, Frazier et al. 2013, Lee et al. 2013).

The risk variable at this scale is often the number or rate of successful invasions. The release variable necessarily includes both the abundance and number of species, i.e., both propagule and colonization pressure (Lockwood et al. 2009, Ricciardi et al. 2011, Briski et al. 2012). When risk is characterized as a probability (e.g., of at least one population establishing), it must saturate toward 1; when it is characterized as the number of established species, it must saturate toward the number of species in the source pool(s). The predicted shapes of these relationships clearly have the potential to inform vector-scale management. They have been investigated thus far primarily using linear and non-linear descriptive models fit to empirical data. We illustrate examples of this approach, and take the first steps toward introducing a theoretical probabilistic formulation to help refine vector-scale invasion modeling.

Descriptive statistical models.—Some descriptive models of vector-scale risk–release relationships have addressed propagule pressure alone (e.g., Levine and D'Antonio 2003, Taylor and Irwin 2004, Ricciardi 2006, Costello et al. 2007), whereas others have used multivariate analyses to tease out the relative importance of propagule pressure among other factors contributing to invasion success (Lonsdale 1999, Drake and Lodge 2004, Jeschke and Strayer 2006, Dehnen-Schmutz et al. 2007, Blackburn et al. 2008, Castro and Jaksic 2008, Cameron and Bayne 2009, Chiron et al. 2009, Dawson et al. 2009, 2011, Copp et al. 2010). The latter approach emphasizes, and can account for, correlations among potential explanatory variables such as the combined propagule-delivery and environmental-disturbance effects of human activity (e.g., Lonsdale 1999).

For unintentional introductions of contaminant and stowaway species, detailed introduction records are
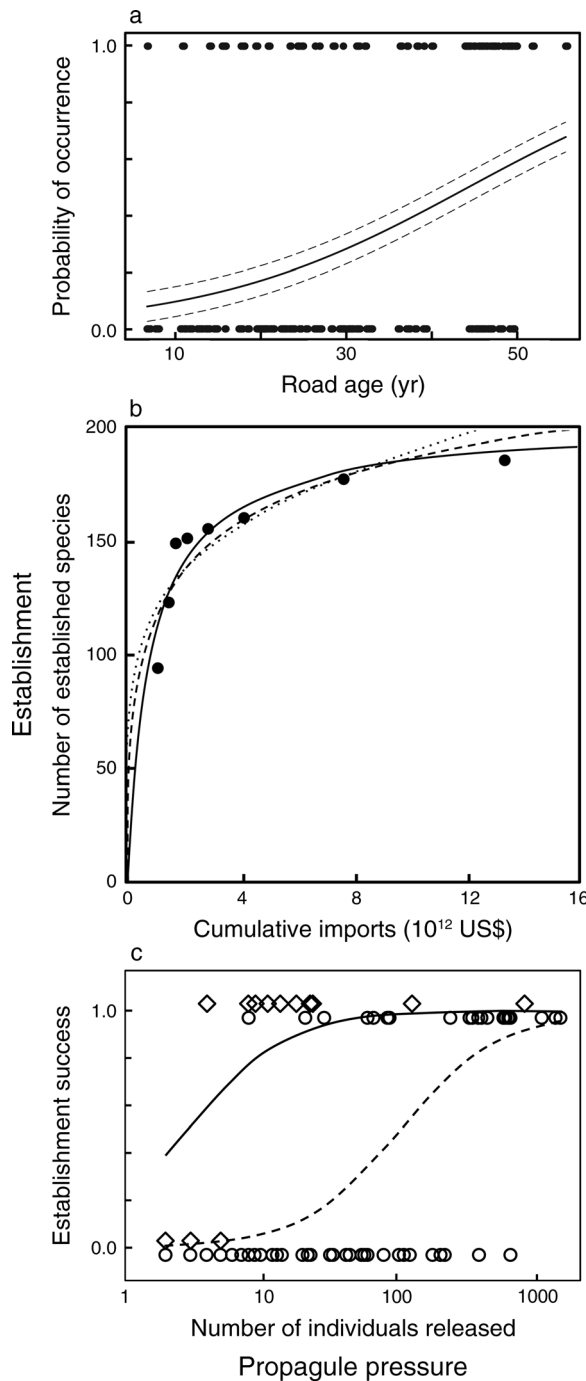
FIG. 3. Vector-scale risk–release relationships represented by statistical models. (a) Probability of nonnative roadside earthworm occurrence as a function of the road age in western Canada, fit with a generalized estimating equation (solid line) with 95% confidence intervals (dashed lines). Panel (a) is modified from Cameron and Bayne (2009: Fig. 2). (b) Number of established nonnative plant pathogens vs. cumulative imports over time in the United States, fit with log–log (dotted line), log–linear (dashed line), and Michaelis-Menten (solid line) equations. Panel (b) is modified from Levine and D'Antonio (2003: Fig. 1). (c) Establishment success of individual species and logistic regressions for 76 bird species together (circles, dashed line) and 14 ungulate species together (diamonds, solid line) as a function of the minimum known number of individuals introduced, in New Zealand. Panel (c) is modified from Forsyth and Duncan (2001: Fig. 3).

rarely available and propagule pressure is typically unknown. As a result, the accumulation of species has been analyzed with respect to less direct proxy variables. Some proxies are measures of trade and transport, such as road age for earthworm invasions (Cameron and Bayne 2009) (Fig. 3a), or shipping activity for aquatic and marine invasions (Grigorovich et al. 2003, Drake and Lodge 2004, Ricciardi 2006, Costello et al. 2007, Rup et al. 2010, Lo et al. 2011, Chan et al. 2012, Reusser et al. 2013). Others are measures of human visitation and population density, particularly for terrestrial plants (e.g., Lonsdale 1999, Vilà and Pujadas 2001, Castro and Jaksic 2008, Pyšek et al. 2010) but also for other taxa (e.g., Leprieur et al. 2008, Potapov et al. 2011, Huang et al. 2012). The least direct proxies are metrics of economic activity (e.g., Vilà and Pujadas 2001, Levine and D'Antonio 2003, Taylor and Irwin 2004, Leprieur et al. 2008, Hulme 2009, Pyšek et al. 2010, Huang et al. 2012) (Fig. 3b). Below, in *Promise and perils of proxy variables*, we examine in more detail the important question of how well such proxies reflect propagule pressure.

More-direct approaches are available for modeling intentional releases of multiple related species recorded in historical time. Where records of the species, numbers, locations, and release frequencies are available, they have been used to characterize the risk–release relationship for groups of taxonomically related species: for example, for birds and for ungulates introduced to New Zealand (Forsyth and Duncan 2001; see also Blackburn et al. 2011, Moulton et al. 2011, 2012), and for squirrels released worldwide (Bertolino 2009) (Fig. 3c). Colonization pressure has similarly been modeled for groups of related species, with number of species introduced used as the predictor for number of species established (e.g., Blackburn et al. 2008, Chiron et al. 2009). In other cases, a fairly direct proxy variable for propagule pressure has been used: for example, the number of introduction events (Colautti 2005, Jeschke and Strayer 2006, Křivánek et al. 2006, Lambdon et al. 2008, Dawson et al. 2009, van Wilgen and Richardson 2012) or the imported number or commercial availability of ornamental and pet species (Semmens et al. 2004, Duggan et al. 2006, Dehnen-Schmutz et al. 2007, Gravuer et al. 2008, Copp et al. 2010). The distinction between number of events and number of individuals has been explored in detail for bird introductions to New Zealand (Blackburn et al. 2011, Moulton et al. 2011, 2012). These models have focused more on the taxon than on the vector per se, and make the implicit assumption that all species share an identical individual

establishment probability, or at least that the establishment probability of those species can reasonably be represented by an average value. They thus represent intermediate scenarios between single-population and vector-scale models of risk and release.

Biological probability models.—To characterize the vector-scale invasion risk, we extend the single-population probability model described above to outline a framework characterizing the invasion risk associated with the release of multiple species at multiple locations and times. We distinguish between colonization pressure (number of species) and propagule pressure (number of organisms per species, which itself can be separated into number and frequency of organisms released; e.g., Lockwood et al. 2009, Briski et al. 2012, USCG 2012), and demonstrate that propagule pressure and colonization pressure together determine the vector-scale risk of establishment. From these joint probabilities, we can obtain metrics such as the expected probability of at least one species establishing and the expected number of established species.

We begin with the equation for the probability of establishment of a single species and single release event as a function of the initial number of individuals (see Leung et al. 2004, for more details):

$$P_E = 1 - (1 - p)^{N^c}. \tag{1}$$

Here, P_E is the probability of population establishment due to the release event, p is the baseline probability of a single individual establishing, and N is the number of individuals released. We include a shape parameter c, to generate the sigmoid shape characteristic of an Allee effect (in the special case of $c = 1$, p represents the independent probability of an individual propagule establishing; Leung et al. 2004). In the absence of density dependence, the relationship is necessarily hyperbolic (Fig. 1b). This is because even if the individual establishment probability p is low, the total probability P_E increases inexorably toward 1 as ever more individuals are released into a suitable environment. If the population exhibited depensatory density dependence, P_E would be reduced at low values of N (Allee 1931, Leung et al. 2004, Jerde et al. 2009). The resulting sigmoid shape can be produced by increasing the value of the shape coefficient $c > 1$ (Fig. 1b). The combination of p and c describes the behavior of the system, and for a given empirical data set the two parameters must be fit simultaneously.

Eq. 1 can be extended to include repeated releases of multiple species (i.e., colonization pressure). To allow first for repeated releases of the same species, we define establishment probability as the complement of all release events failing to establish:

$$P_E = 1 - \prod_{r=1}^{R}(1 - P_r)^{N_r^{c_r}} \tag{2}$$

where R is the number of release events (propagule frequency) into a region of interest, and r is a given release event. The subscript r in N_r, p_r, and c_r denotes that parameter values can differ among release events, because of spatiotemporal variation in environmental conditions and propagule number. We specifically focus on variation related to propagule pressure, but more-complex environmental models are also possible (e.g., making use of invasibility estimates or species-distribution models; Leung and Mandrak 2007). We note that there is some complexity with respect to the timing of release events, in that if the timings are very close, multiple small releases may behave as a single larger release. In Eq. 2, for simplicity, we treat release events as independent (cf. David et al. 2013).

To extend the model to include colonization pressure, or multiple species, we take the complement of all species failing to establish. The full model thus characterizes risk of establishment at the vector level when a total of S species are released. The establishment probability of species s is then

$$P_{E,s} = 1 - \prod_{r=1}^{R}(1 - p_{r,s})^{N_{r,s}^{c_{r,s}}} \tag{3}$$

and the probability of at least one species establishing, P_S, is

$$P_S = 1 - \prod_{s=1}^{S}\prod_{r=1}^{R}(1 - p_{r,s})^{N_{r,s}^{c_{r,s}}} \tag{4.1}$$

or

$$P_S = 1 - \prod_{s=1}^{S}(1 - p_{E,s}). \tag{4.2}$$

Subscripts r and s have been added to $N_{r,s}$, $p_{r,s}$, and $c_{r,s}$ to allow their values to differ among release events and among species. This is useful, as we would expect different species to have different per capita establishment probabilities, and different Allee effect strengths, and to be released at different initial abundances.

From Eq. 3 we can obtain a second metric of invasion risk, the *expected number* of species establishing in a region of interest, which is simply the sum of individual probabilities across all species:

$$E_S = \sum_{s=1}^{S} P_{E,s} \tag{5}$$

where E_S is the expected number of species establishing, given R release events (and therefore within a given time frame), and other notation is as for Eqs. 3 and 4.

This formulation of vector-scale invasion risk (Eqs. 3 and 4) represents propagule pressure as both abundance and frequency of organisms released, and colonization pressure as the number of species (S) with nonzero propagule pressure. If no individuals of species s are introduced in release r, then $N_{r,s}$ is 0. If there are no releases at all of species s, then $P_{E,s}$ is zero. If there are

no releases of any species, $P_{E,s}$ is 0 for all s, and P_S is 0. Since propagule pressure and colonization pressure are not necessarily well correlated (Briski et al. 2012), it is essential that both be represented in the model of vector-scale invasion risk.

The central challenge posed in applying this model is the extensive parameterization required, namely, estimating the distribution of establishment probabilities over a range of propagule pressures and abiotic variables, for all the species of interest. Since the number of species that could be introduced by a single invasion vector runs easily into the hundreds (e.g., Carlton and Ruiz 2005, Suarez et al. 2005, McCullough et al. 2006, Miller et al. 2011), simplifying options may be needed. These could include treating individuals across all species as equal in the absence of better information (i.e., identical p and c values across species), and estimating the probability of each species establishing based on its relative propagule pressure (e.g., Bradie et al. 2013). With better information, for instance on species traits, it may be possible to estimate variation in p and c values between species and more fully parameterize our model. The preliminary framework introduced provides a logical basis from which to explore both the theoretical and empirical behavior of vector-scale introductions, and warrants further analysis of its assumptions, biases, behavior, and data requirements.

Dynamic demographic models.—In principle, demographic models for individual species could be summed to model the total invasion risk presented by the release of multiple species on multiple occasions. This approach has not yet been applied to predicting the success of multiple species introduced simultaneously, and again would clearly require a great deal of empirical data for parameterization. However, a related approach using a reaction–diffusion model (Skellam 1951, Okubo et al. 1989) offers interesting insights. The classical version of these models returns the invasion's rate of spread, rather than the probability of establishment, but a recent application connecting the two using some simplifying assumptions (Drake et al. 2005) warrants validation.

In addition to the examples above, probabilistic and demographic models of species assemblages have been developed in the context of island biogeography (MacArthur and Wilson 1967), local–regional species richness patterns (e.g., Shurin et al. 2000, Lee and Bruno 2009), community assembly (e.g., Case 1995), and metacommunities (Holyoak et al. 2005). All of these approaches explore the risk–release relationship in its broadest sense; however, since they are less immediately relevant to the practicalities of managing invasion risk directly, we do not consider them further here. Neither probabilistic nor demographic approaches have yet been used to incorporate interactions among the introduced species released together as an assemblage.

PROMISE AND PERILS OF PROXY VARIABLES

Since the propagule pressure associated with an invasion vector can be logistically difficult to measure, proxy variables are appealing for analysis in both ecological and policy realms. However, their use is premised on the largely untested assumption of a tight relationship between the proxy and propagule pressure, which may not always hold (Lockwood et al. 2009, Simberloff 2009, Haydar and Wolff 2011). In employing proxy variables, the two main challenges are to identify variables that influence propagule pressure alone and to determine the strength of the relationship (Lonsdale 1999, Chiron et al. 2009, Simberloff 2009, Haydar and Wolff 2011). We illustrate some of the motivations for and difficulties with proxies using the example of ballast water in North America, one of the best-documented global invasion vectors and one for which proxy variables have been extensively used but remain thus far generally untested.

To determine empirically the shape and strength of the risk–release relationship for ballast-mediated invasions would require, at a minimum, ballasted-organism records and invasion records from the same times and places. Ballast has been discharged into North American ports for over a century, but surveys of ballasted organisms have been conducted only since the 1980s and primarily in the last two decades. Surveys of successful invasions and of ballasted organisms have been conducted in some, but not all, of the same ports (NRC 2011). By their very nature, ballast surveys have generally targeted small planktonic and benthic organisms, including larval or encysted stages, as well as protists and bacteria (numerous surveys since Carlton 1985; recent North American examples include Carlton and Geller 1993, Sun et al. 2010, Briski et al. 2012, DiBacco et al. 2012). In contrast, invasion records from field surveys typically capture the establishment of larger metazoans and macroalgae that are more readily identifiable to species (Cohen and Carlton 1998, Ruiz et al. 2000, Wonham and Carlton 2005, Ricciardi 2006, Fofonoff et al. 2009). Even when taxonomic data are matched, the remaining temporal and spatial mismatches make it difficult to know how well recent propagule-pressure data should be expected to predict the historical accumulation of invaders.

In contrast to direct measures of organism abundance in ballast, historic records of vessel traffic, tonnage, and ballast volume are substantially easier to determine, and have therefore been used widely as proxies for propagule pressure (Grigorovich et al. 2003, Drake and Lodge 2004, Ricciardi 2006, Costello et al. 2007, Rup et al. 2010, Lo et al. 2011, Chan et al. 2012, Reusser et al. 2013). The wealth of available data for this vector allows us to examine more closely the validity of these proxies. Logic, theory, and empirical evidence all lead us to expect a positive relationship between propagule pressure and the number of successful invasions, and therefore a similar one with a proxy variable. Two

examples, one from temporal and one from spatial snapshot data, reveal that this is not always the case.

First, in the Great Lakes, analyses of temporal data have demonstrated different risk–release relationships using similar taxa and proxies. Ricciardi (2006) found a significant positive relationship between the number of successful invasions and net shipping tonnage (Fig. 4a), whereas those from Grigorovich et al. (2003) appear to show no clear relationship (Fig. 4b). Data from Grigorovich et al. (2003) and from Costello et al. (2007) suggest no clear relationship between the number of invasions and the number of vessels (Fig. 4c, d). Second, Reusser (2010) assembled invasion and shipping records for 17 ports across North America that show no clear relationship between the number of invaders and either the number of ships or the annual volume of discharged ballast water (Fig. 4e, f).

Some of these discrepancies among studies may result from the use of different subsets of taxa, vessels, and time windows. Regardless, it is not clear that the risk and release variables are well matched in space, time, and taxonomic resolution. Even if they were, the use of vessel characteristics for propagule pressure would be premised on the critical assumption that organism density and diversity is homogeneous across tanks and vessels—an assumption that is well known not to hold (e.g., Smith et al. 1999, Murphy et al. 2002, Minton et al. 2005, Verling et al. 2005, Lawrence and Cordell 2010, Sun et al. 2010, Casas-Monroy et al. 2011, Villac and Kaczmarska 2011). Thus, it is not clear a priori that either propagule pressure or colonization pressure should necessarily be expected to correlate strongly with currently available measures of vessel traffic.

As a result, the meaning of relationships (or lack thereof) with these proxy variables is difficult to interpret. It is not clear whether the absence of a significant relationship between invasion risk and a proxy reflects post-release processes that overwhelm the underlying risk–release relationship, or whether the proxy variable is simply not a good measure of propagule pressure. Similarly, when a significant relationship is obtained (e.g., Figs. 3a, b, and 4a), it is unclear to what degree it reflects simple correlation between measures of human activity, or to what degree it may be causative. Proxy variables are potentially very useful in informing invasion management, but clearly must be tested rigorously before being used to develop a scientifically based management of any invasion vector (e.g., Haydar and Wolff 2011).

Informing Invasion Management

Models are generally useful in exploring ecological theory and informing environmental management because they provide a transparent framework, force an explicit statement of assumptions, allow us to predict and compare future projections under different scenarios, and can be updated in their structure and parameter estimates as new information emerges. Different mod-

eling approaches provide different kinds of insight into the risk–release relationship, but they share similar challenges in their direct application to managing invasion risk. Here, we summarize the future approaches we consider most promising, and highlight key questions to address in applying those models to developing and implementing invasion-management policy.

Modeling approaches

Single-population models are appealing in their relative simplicity. Since theory predicts that the risk–release relationship for a growing population is hyperbolic or sigmoid, interesting management implications arise. These models are particularly relevant to managing individual intentional invasions, but may also prove illustrative at a larger scale in modeling particular species thought to be representative invaders, or aggressive, worst-case scenario invaders. In this way, single-species models could be used to provide bounds on the establishment probabilities of a much larger set of species for which gathering comprehensive data would be prohibitively time consuming. It then becomes particularly interesting to ask how establishment probability varies across genotypes, life stages, and environmental conditions, to better understand the nuances of propagule pressure interactions with the abiotic and biotic environment. Probabilistic models afford a more explicitly mechanistic representation of invasion establishment than descriptive models, and can be easier to parameterize than dynamic demographic models.

At the vector scale, the risk–release relationship has primarily been characterized using descriptive statistical analysis of empirical data. Because invasions have accumulated over an historical timeframe whereas vectors are being quantified only in the present day, substantial mismatches may arise in the temporal, spatial, and taxonomic scales of the risk and release variables. The advantage of using proxy variables is that they may be quantified over a more relevant spatial and temporal scale, with the possibility of obtaining historical data. However, variables that initially seem to be logical proxies may, in fact, not correlate well with propagule pressure, making it difficult to interpret the resulting patterns or to predict management outcomes based on regulating the proxy. Proxies clearly represent a reasonable approach to representing propagule pressure—when their validity is independently tested and confirmed.

Approaching the vector-scale risk–release problem from a theoretical perspective, we have introduced a probabilistic model incorporating both propagule (population) and colonization (species) pressure in a framework allowing multiple repeated introductions. Future steps include exploring the theoretical behavior of this model, and examining how it may best be parameterized and tested. The latter step is conceptually straightforward, but is currently hampered by insufficient empirical
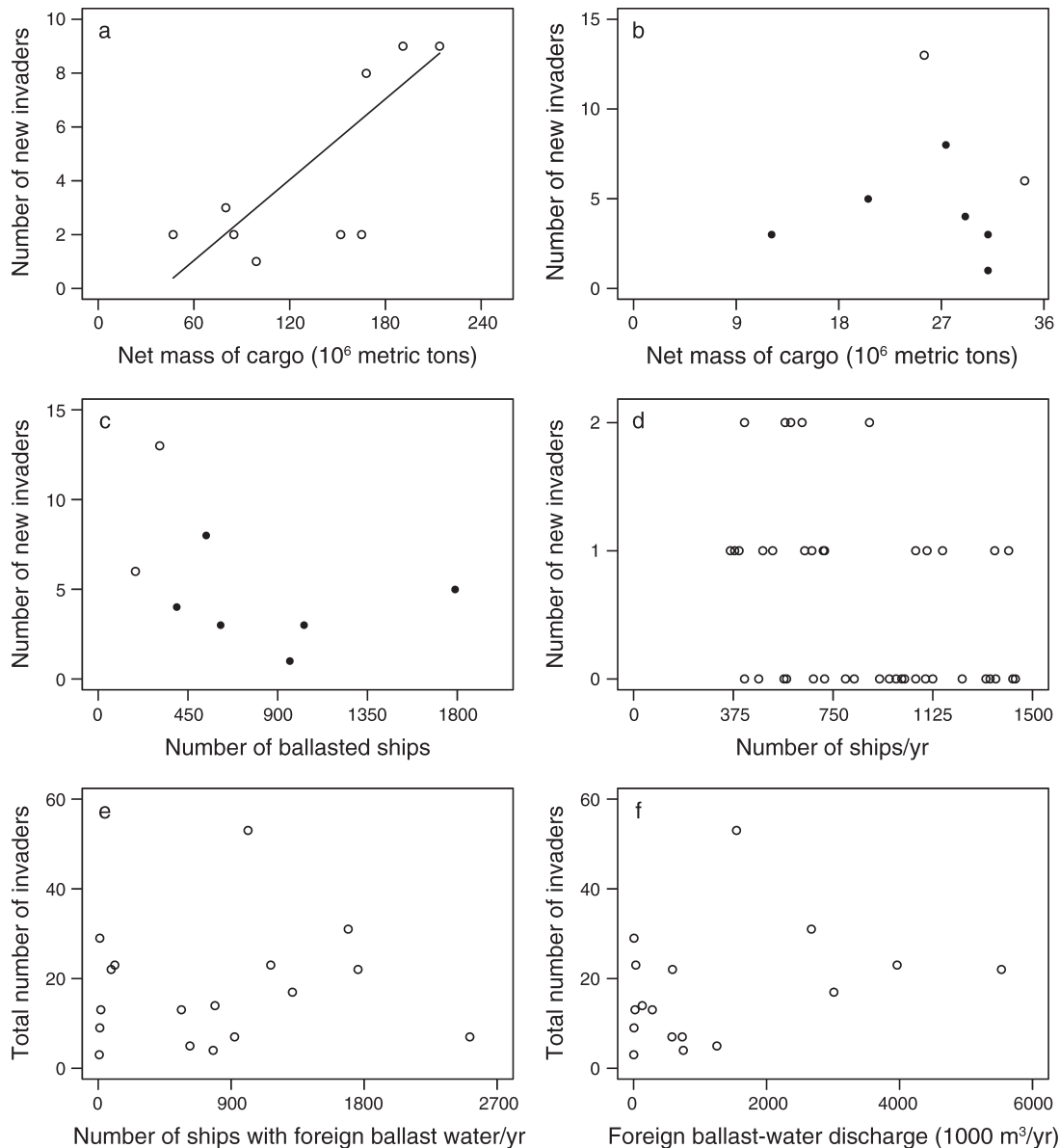
FIG. 4. Vector-scale risk–release relationships for (a–d) ballast-mediated invasions using proxy variables for invasion pressure in the Laurentian Great Lakes and (e, f) 17 U.S. coastal ports. (a) Number of new ship-mediated invaders (plants, algae, invertebrates, fishes) established vs. net cargo tonnage in millions of metric tons (1 metric ton = 1 Mg), by decade, 1900–1999. The panel is replotted from Ricciardi (2006: Fig. 3), with recalculated least-squares linear regression, $y = 0.05x - 1.95$, adjusted $r^2 = 0.45$, $P < 0.02$. (b) Number of new invaders (metazoans and protozoans) established vs. net cargo tonnage in millions of metric tons, by five-year intervals, 1959–1999 (before [solid circles] and after [open circles] ballast-exchange regulations; these time periods should be considered separately). The panel is replotted from Grigorovich et al. (2003: Figs. 3 and 6). (c) Data as for panel (b), vs. number of ballasted ships. (d) Number of new invaders (animals) established vs. number of ships arriving annually, 1959–2000. The panel is replotted from Costello et al. (2007: Fig. 1a, b). (e) Total number of invaders (invertebrates and macroalgae) reported 1981–2006 vs. number of foreign ballast-water ships arriving annually, 2005–2007. The panel is replotted from data in Reusser (2010). (f) Data as for panel (e) vs. volume of ballast water discharged 2005–2007, in thousands of m³/yr.

data: a typical invasion vector may deliver tens to hundreds of unidentified taxa, whereas population growth and establishment parameters are available only for a handful of species in a given system. To characterize invasion risk for all the species delivered through nationwide ballast-water discharge would require an extraordinary amount of empirical work; nevertheless, analytical exploration and simulation analysis based on representative species will help refine our expectation of the shape of the vector-scale risk–release relationship, and inform our use of simpler and more tractable descriptive models.

Developing organism-release standards

It is appealing to imagine that with a robust risk–release model we could predictably reduce the risk of invasion by reducing the number of organisms released by a vector, and could optimize our approach based on the shape of the relationship. However, to translate such a model into effective management, additional essential questions need to be addressed. Here we briefly outline some of the key future steps in applying risk–release models to refining release management. For illustration, we again use the example of ballast-water management. This is a particularly germane area, in that the International Maritime Organization (IMO) and the U.S. Environmental Protection Agency (EPA) have developed ballast-water discharge standards intended to manage invasion risk by specifying a maximum threshold density of organisms that a vessel may release into a port (IMO 2004, NRC 2011, Albert et al. 2013, EPA 2013, Frazier et al. 2013, Lee et al. 2013). The EPA standards will come into effect at the end of 2013, and the IMO standards will apply internationally when sufficient Member States have ratified the Ballast-Water Management Convention (IMO 2004).

For single-population models, the primary challenge is to convert laboratory and mesocosm results into vessel-scale management thresholds. We can imagine that laboratory and mesocosm studies of a target species could determine that a release of a certain number of organisms corresponded to a particular level of invasion risk that was deemed acceptable. Connecting results from such controlled studies to real-world probabilities and ultimately to a vessel-scale discharge threshold is obviously an exercise in compounded uncertainties, but we can bound the possibilities as follows. The laboratory-derived acceptable-release number could serve as the discharge limit for each species on board, or for all taxa combined; to apply the former would require knowing how many species were on each ship. The number could serve as the limit for each ship, or for all ships combined in a time period or a given location. For sampling and enforcement, the absolute discharge threshold of organisms would need to be converted to a density or organisms per unit volume of ballast water; this conversion could be based on the smallest or largest ship classes, or could be tailored to individual vessels. The threshold number could be taken as a constant, or could be modified to accommodate changes in invasion risk with the source port, season, tidal cycle, or local hydrodynamic conditions. To be an enforceable threshold, it would of course have to fall above the detection limits of the available sampling methods (Frazier et al. 2013). Ultimately, applying this approach requires determining how much the realized invasion risk from many species in many ships across many locations differs from the predicted risk of one species in controlled conditions.

For vector-scale models, the challenges depend greatly on whether proxy or direct measures of propagule pressure are used. In the former case, the primary challenge is to establish the causal reliability of the proxy variable before implementing management thresholds. Again, we could find that a certain level of vessel traffic corresponded to a certain level of invasion risk that was deemed acceptable—but how confident would we be that a given reduction in vessel traffic would lead to the predicted reduction in invasion rate? With a more directly mechanistic model we could instead find a relationship between invasion risk and total invasion pressure (abundance and richness of species combined). Here the challenge would be determining relative contributions of organism abundance (propagule pressure) and species richness (colonization pressure) (Lockwood et al. 2009), and assessing the effectiveness of a single discharge standard across various permutations of both. Emerging genetic-sampling methods (e.g., Blanchet 2012) may prove useful in rapidly identifying ballasted assemblages, which could allow some customization of discharge thresholds.

On a daily basis, an unknown number of unidentified species are released by myriad invasion vectors around the world at largely unknown abundance, density, and frequency. For all vectors, simple logic suggests that reducing the level of release must reduce the risk of successful invasion. However, understanding more clearly the shape of this risk–release relationship and the mechanisms underlying it will allow managers to better identify the circumstances where an additional marginal investment in reducing propagule pressure will result in marginal reduction in risk. The challenges in then developing biologically based release standards are those of moving from the dynamics of an individual population to those of multiple releases of multiple species, and moving from the variables of empirical study (number of organisms or species, and proxies thereof) to the variables of a useful discharge standard (i.e., density of organisms). In summarizing the state of applicable modeling approaches and evaluating their pros, cons, and data requirements, we have identified the major gaps in our understanding and also promising ways forward in this enterprise. The modeling approach we have introduced here applies not only to propagule pressure from ballast water, but to the management of populations generally, and allows for future theoretical and empirical analysis of a rich ecological and applied question.

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