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RESEARCH ARTICLE

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Incorporation of colonization pressure into the propagule pressure-based global ballast water standard

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Abstract

Aim: In 2024, cargo vessels must meet the International Maritime Organization's global ballast water discharge standards (IMO D-2) that limit the concentration of living organisms. D-2 focuses on reducing invasion risk by reducing 'community propagule pressure (CPP)', though it does not consider colonization pressure (CP).

Location: Global.

Methods: We modelled risk differences in IMO D-2-compliant discharges (10 ind. m^{-3}) for communities that had inverse patterns of CP and species' individual propagule pressures (IPP). Secondly, we determined the effect on risk of varying CPP and CP. As part of this, we tested whether the IMO D-2 standard for zooplankton-sized organisms of <10 individuals m^{-3} was an optimal choice. Risk was defined as probability of at least one species invading using four risk–release models.

Results: Risk differed strongly at the D-2 limit based on community composition. At low CPP (<25 ind. m^{-3}), risk was strongly affected by CP for hyperbolic and linear risk–release models and weakly for exponential and logistic models, while CPP affected only the former two model types. Across a much wider range of CPP values, risk was affected by CP, CPP and by their interaction for all models.

Main Conclusion: The IMO D-2 standard for zooplankton-sized organisms requires very low CPP and even lower IPPs in mixed-species releases, which will impede successful colonization. Species-abundance theory predicts that discharges meeting the D-2 standard (low CPP) will also have low CP. Much more empirical data are required to determine whether vessels can consistently reduce CP as it lowers CPP in order to meet these requirements.

KEYWORDS

ballast water, biological invasions, colonization pressure, community propagule pressure, individual propagule pressure, invasive species, propagule pressure

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1 | INTRODUCTION

Vessel-mediated transport has been a principal pathway of aquatic non-indigenous species (NIS) introduction globally, with strong contributions by both ballast water and sediments (e.g. Boltovskoy et al., 2011; Carlton et al., 1995; Gollasch et al., 2019; Ruiz et al., 2000) and by hull biofouling (e.g. Chan et al., 2015; Floerl et al., 2005; Gollasch, 2002; Meloni et al., 2021). Global ballast water discharges of ~3.1 billion tonnes per year provide ample opportunity for transfer and introductions of NIS (David et al., 2015). Owing to its importance and to the relative ease of access to tanks for quantitative sampling, ballast water is one of the best-quantified invasion pathways, especially relative to vessel hull fouling (e.g. Bailey, 2015; Briski et al., 2012; Chan et al., 2013; Ricciardi & MacIsaac, 2022; Seebens et al., 2019).

Global management guidelines for ballast water were first instituted in 1989 for vessels inbound to the Saint Lawrence River and Laurentian Great Lakes, with a recommendation that filled tanks be exchanged in the deep ocean far from the coast (Bailey, 2015). This voluntary guideline became effectively mandatory in 1993. The International Maritime Organization (IMO) in 2004 developed the Convention for the Control and Management of Ships' Ballast Water and Sediments (IMO, 2004). This Convention included regulation D-1 that requires mid-ocean ballast water exchange with an efficiency of at least 95% volumetric exchange or three times the ballast volume. While IMO D-1 appears to have reduced the number of new NIS discovered in the Great Lakes (e.g. 87%; Ricciardi & MacIsaac, 2022), the procedure appears less effective for marine:marine source:destination port pairs than for strictly freshwater pairs that involve ocean crossings (Briski et al., 2015; Gollasch et al., 2019; Molina & Drake, 2016; Simard et al., 2011). In many other cases, route limitations preclude or sharply reduce effectiveness of ballast water exchange (Miller et al., 2011). For example, phytoplankton species number and individual species abundances may increase following ballast water exchange under some circumstances (McCollin et al., 2007; Villac et al., 2013).

The IMO developed regulation IMO D-2 that was intended to supplant D-1. This set of performance standards for ballast water discharges limit abundance to: (i) <10 viable organisms m^{-3} that are ≥50 μm in minimum dimension (typically and hereafter zooplankton); (ii) <10 viable organisms mL^{-1} that are ≥10 μm and <50 μm in minimum dimension (typically phytoplankton) and (iii) set limits on abundance for three microbial indicators (IMO, 2004). All of these numerical limits represent a substantial reduction in population abundances of targeted groups versus typical field densities. IMO D-2 was globally ratified in September 2017 but will not be fully implemented until August 2024 (IMO, 2018).

Risk reduction associated with IMO D-2 is based on reducing the collective abundance – which we term 'community propagule pressure (CPP)' – to a low level for each of the two size classes. The number of individuals released of a species – which we term 'individual propagule pressure (IPP)' – is a key predictor of invasion risk (Colautti et al., 2006; Lockwood et al., 2005; Simberloff, 2009; Stringham & Lockwood, 2021; Williamson & Fitter, 1996), thus reducing population abundances to low levels should reduce risk. However, theory pertaining to propagule pressure is limited to the risk–release (i.e. dose:response) relationship for individual species and not for entire communities (Drake & Lodge, 2006; Johnston et al., 2009), whereas IMO D-2 is based on the entire community of similar-sized organisms. It is not clear whether this community-based metric can be extended from individual, species-based ones.

More importantly, the IMO D-2 regulation was silent on the topic of colonization pressure – the number of species introduced in a single release. Colonization pressure is also a strong predictor of invasion risk (e.g. Blackburn et al., 2020; Duncan et al., 2019; Dyer et al., 2017; Lockwood et al., 2009; Lonsdale, 1999; Pyšek et al., 2020), thus ignoring it could under-estimate overall risk of at least one species establishing. For example, introduction of multiple species should increase the likelihood that at least one will find conditions acceptable for colonization in the recipient port (Blackburn et al., 2020; Lockwood et al., 2009). On the other hand, multiple-species releases would require proportional decreases in individual propagule pressures in order to remain compliant with IMO D-2 standards. Such reductions in individual propagule pressures would, in turn, increase the likelihood that some or all species would suffer from problems associated with demographic stochasticity, Allee effects or genetic uniformity upon release (Gertzen et al., 2011; Lockwood et al., 2009; Tobin et al., 2011). Ballast water communities often have high colonization pressure, and knowledge of the importance of the trade-off between high individual propagule pressure and high colonization pressure may extend our understanding of invasion risk.

In this study, we evaluated whether communities with different combinations of individual propagule pressures and colonization pressures posed the same invasion risk at low community propagule pressure, and explored whether the IMO D-2 standard for community propagule pressure for zooplankton-sized organisms (10 ind. m^{-3}) optimally reduced risk. We also assessed the importance of colonization pressure by fixing individual propagule pressures for all species in a community; we then repeated the process across a spectrum of individual propagule pressures, which allowed us to determine the effect of colonization pressure as individual propagule pressure increased. Specific hypotheses tested include: (1) Communities with an IMO D-2-compliant community propagule pressure (10 ind. m^{-3}) have the same risk of establishment regardless of colonization pressure; (2) The IMO D-2 limit for zooplankton was optimal for reducing risk and (3) Colonization pressure and community propagule pressure have no effect on risk.

2 | METHODS

2.1 | Risk modelling

We applied mechanistic models to determine the establishment risk of non-indigenous species of zooplankton size (IMO D-2 group ≥50 μm in minimum dimension) at, below and above the legal discharge concentration by controlling the community propagule pressure, colonization pressure, and, indirectly, individual propagule pressure. While the IMO D-2 limit specifies a limit of <10 viable or living ind. m^{-3}, for simplicity we used exactly 10 ind. m^{-3} in our models.

To model establishment risk, first, we determined population sizes from discharge volumes obtained from Bradie et al. (2022), which consisted of 10,000 recorded ballast water discharges that ranged from 20 to 1,060,620 m^3 (13,871 ± 25,738, mean ± standard deviation). We used volumes from 29 vessels sampled in Atlantic (Halifax, Hamilton, Saint John, Sorel) and Pacific (Vancouver) ports in Canada in 2017 and 2018 by Fisheries and Oceans Canada as a reference for empirical community composition in treated ballast water (Bailey et al., 2022). Within each discharge volume, we set the colonization pressure and community propagule pressure while applying either unequal (hypotheses 1 and 2) or equal individual propagule pressures (hypothesis 3) between species to address each hypothesis (see Figure A1).

For hypotheses 1 and 2, we set a colonization pressure and community propagule pressure for a given discharge volume. Next, species-specific individual propagule pressures were generated, followed by probability of establishment, and determined if a species was established or not (Figure A1). Each combination of discharge volume, colonization pressure and community propagule pressure was iterated 100 times with a predefined pseudorandom number generator, also known as random seeds, to ensure reproducibility (Ahmed & Lofstead, 2022). Random numbers are generated in sequences by pseudorandom number generators, such that different generators return different outputs. Setting a pseudorandom number generator is critical to method reproducibility (Ahmed & Lofstead, 2022).

We tested the first hypothesis by holding community propagule pressure constant at the D-2 limit (10 ind. m^{-3}) across different colonization pressures (1, 2, 5, 10, 30, 50 and 100 species). We also determined whether the IMO D-2 limit optimized risk reduction by varying community propagule pressure around the prescribed limit (e.g. from 1 to 25 ind. m^{-3}) for different colonization pressures. As community propagule pressure divided by colonization pressure equals mean species' individual propagule pressure, these simulations always involved inverse patterns for the latter two parameters. This was done by randomly sampling individuals from a generated community for the colonization pressure tested. To ensure all species were present, first, we assigned one propagule to each species in the discharge (see Figure A1). Next, we generated a community to represent the entire ballast discharge for the desired colonization pressure by randomly drawing individuals from the generated community until the appropriate total number of individuals were sampled (i.e. discharge volume × community propagule pressure); this procedure provided the individual propagule pressures corresponding to the discharge's combination of community propagule pressure and colonization pressure. We ensured that the generated community was always larger than the discharge volume × community propagule pressure being modelled to ensure that species' individual propagule pressures were independent.

We then expanded the aforementioned analysis across a much wider range of community propagule pressures (1, 2, 5, 10, 30, 50, 100, 1000 and 5000 ind. m^{-3}). We allowed colonization pressure in each of these simulations to vary among 1, 2, 5, 10, 30, 50 and 100 species (Figure A1). Mean individual propagule pressure per species was determined as described above.

If risk varies in communities with covarying patterns of colonization pressure and individual propagule pressure, it is impossible to determine which of the variables was responsible for the effect. We sought to isolate the effect of colonization pressure from that of individual propagule pressure (hypothesis 3) by conducting simulations in which all species in a discharge had identical abundances, and repeating simulations across a range of individual propagule pressures and for different colonization pressures (1, 2, 5, 10, 30, 50 and 100). Individual propagule pressures tested were determined by using the set of community propagule pressures used to test the second hypothesis (above) and dividing by the colonization pressure; this resulted in individual propagule pressures ranging from 0.0002 to 5000 ind. m^{-3}.

Following the determination of individual propagule pressure for each objective, we determined species establishment probability (1 − probability of extinction) using the Leung et al. (2004) equation:

$$p_e = 1 - e^{-\alpha N^c} \tag{1}$$

where p_e is establishment probability, α is the probability that a single propagule will establish a viable population, N is initial population size (individual propagule pressure) and c is a shape parameter to accommodate an Allee effect (where $c > 1$). We assumed no Allee effect ($c = 1$), following Bradie et al. (2013) who showed this to be a reasonable assumption when modelling a heterogeneous group of species in an establishment pathway. As true α values are not known, we estimated species-specific α values using a beta distribution (beta distribution parameters $\alpha = 0.005$, $\beta = 5$; Drake et al., 2020). This distribution is suitable for a wide range of aquatic species under a variety of conditions (Bailey et al., 2009).

From species establishment probability values, we estimated risk of establishment as the probability of 'at least one species establishing' and as 'exactly one species establishing'. We calculated the probability of at least one species establishing, P_s, as:

$$P_s = 1 - \prod_{s=1}^{S} \left(1 - p_{e,s}\right) \tag{2}$$

where $p_{e,s}$ is the probability of establishment per species, s as determined by Equation (1) and S is the colonization pressure per trip (Wonham et al., 2013). We tested hypotheses 1 and 2 by controlling community propagule pressure in the model and applying Equation (2) which incorporated individual propagule pressure from Equation (1); simulations were then repeated for a series of colonization pressures. Risk of at least one species establishing was estimated as the complement of individual species' risk of establishment. We also calculated the probability of exactly one species establishing, though risks were similar to but lower than those for at least one species establishing, and thus are not shown.

As it is typically not clear what type of risk–release relationship exists with respect to individual propagule pressure for different species, we fit four different types to test each hypothesis (Ruiz & Carlton, 2003; Wonham et al., 2013): linear, hyperbolic (Michaelis–Menten), exponential and logistic. For hypotheses 1 and 2, we evaluated risk:release curves based on the controlled simulation parameters, colonization pressure and community propagule pressure. We applied the following respective equations: Linear: $\text{Risk} = \beta_1\text{PP} + \beta_2\text{CP} + \beta_3\text{CPP} \times \text{CP} + c$; Hyperbolic: $\text{Risk} = \frac{\beta_4\text{CPP} \times \text{CP}}{\text{CPP} \times \text{CP} + a}$; Exponential: $Risk = \beta_5 e^{(\beta_6\text{BPP} \times \text{CP} + a)} + c$ and Logistic: $\text{Risk} = \frac{1}{1 + e^{-\beta_7\text{CPP} \times \text{CP} + a}}$, where CPP is the community propagule pressure, CP is the colonization pressure and β, a and c represent constants. Each curve was fit with respect to risk of establishment per community propagule pressure and colonization pressure across all discharge volumes, while individual propagule pressure was used to determine the risk. For hypothesis 3, community propagule pressure was replaced by individual propagule pressure in each risk–release equation. This framework allowed us to test if changing individual propagule pressure and colonization pressure impacted establishment risk. We measured the accuracy of curve fit to actual simulated risk values by residual mean square error, mean absolute error and Pearson correlation of the observed simulated risk values and predicted risk per risk–release relationship. Statistical analysis of the risk–release relationship was completed on each metric by a mixed effects linear model in the lmerTest R package (Kuznetsova et al., 2017) following an ordered quantile normalization transformation. Risk–release relationship type was considered the fixed effect and discharge volume as a random effect. We conducted post-hoc tests using the emmeans R package (Length, 2023). We calculated each risk–release relationship per colonization pressure for community propagule pressure values of 1 to 5000 by increments of 1, or individual propagule pressure values of 0 to 5000 by increments of 0.1. We chose these values to simulate the risk–release relationship across a wide range of conditions.

The effect of colonization pressure and community propagule pressure (hypotheses 1 and 2) on the probability of at least one species establishing and exactly one species establishing were analysed with generalized linear mixed-effects models. To determine the effects of colonization pressure, we estimated risk when individual propagule pressures were held constant (hypothesis 3) with fixed effects of individual propagule pressure and colonization pressure. Discharge volume was applied as a random effect. We examined significance of the coefficients of generalized linear mixed-effects model using Type II Wald χ^2 tests. These coefficients identify the change in risk per unit increase of the corresponding independent variable. All simulations and analyses were completed in R v4.2.1 (R Core Team, 2021). All presented results pertain to the risk of at least one species establishing.

3 | RESULTS

Zooplankton-sized communities comprised different combinations of individual propagule pressure and colonization pressure had different establishment risks at the IMO D-2 limit of 10 ind. m^{-3}. Risk at the D-2 limit was directly and positively related to colonization pressure for each of the risk–release models (Figure 1, insets i–iv), though the effect was very weak for the exponential relationship (Figure 1, inset iii).

Across a range of low community propagule pressures (1–25 ind. m^{-3}), the pattern remained largely the same as that at the IMO D-2 limit: risk of at least one species establishing was strongly and positively related to colonization pressure for each of the risk:release models (Figure 1, insets i–iv). CP effects were strongest for the logistic relationship (Figure 1, inset iv). Community propagule pressure had little effect with exponential and logistic risk:release models (Figure 1, insets iii and iv respectively), though it interacted strongly with colonization pressure in the hyperbolic and less so in the linear model (Figure 1, insets ii and iii respectively). Overall, we observed that there was poor support for the IMO D-2 limit at 10 ind. m^{-3}, although the decline in relative risk increased with each unit decline in CPP in the hyperbolic model (Figure 1, inset ii).

Risk of at least one species establishing increased strongly as community propagule pressure increased from very low to very high levels (Figure 1, main panels i–iv). Colonization pressure also influenced risk very strongly across this broad range of community propagule pressures, and interacted significantly with it (Figure 1, main panels; Table 2). Risk was always highest in communities receiving the highest colonization pressure. Risk of at least one species establishing increased with increasing community propagule pressure and was most pronounced for the hyperbolic risk–release model when colonization pressure was high. In releases that contained few species, differences between risk:release models were relatively modest.

All three metrics revealed that the best fit of risk–release relationship was provided by the hyperbolic (Michaelis–Menten) model for community propagule pressure (above) and individual propagule pressure (below) models (Table 1). Even though the risk at very high community propagule pressure (5000 ind. m^{-3}) for a species-rich community (100 species) appeared higher for the logistic than for the exponential model, the former model had a slightly poorer fit (Figure 1; Table 1).

We explored the effect of colonization pressure by fixing individual propagule pressure in simulated ballast releases (Figure A2). Patterns were very similar to those observed for community propagule pressure (above), though because all species in multi-species communities were present at identical individual propagule pressures, overall risks were much higher and risk accelerated much more quickly than when judged against community propagule pressure (Figure A2 vs. Figure 1). For example, at a community propagule pressure of 10 ind. m^{-3} (i.e. the IMO limit; Figure 1), only 10 individuals m^{-3} were present across all

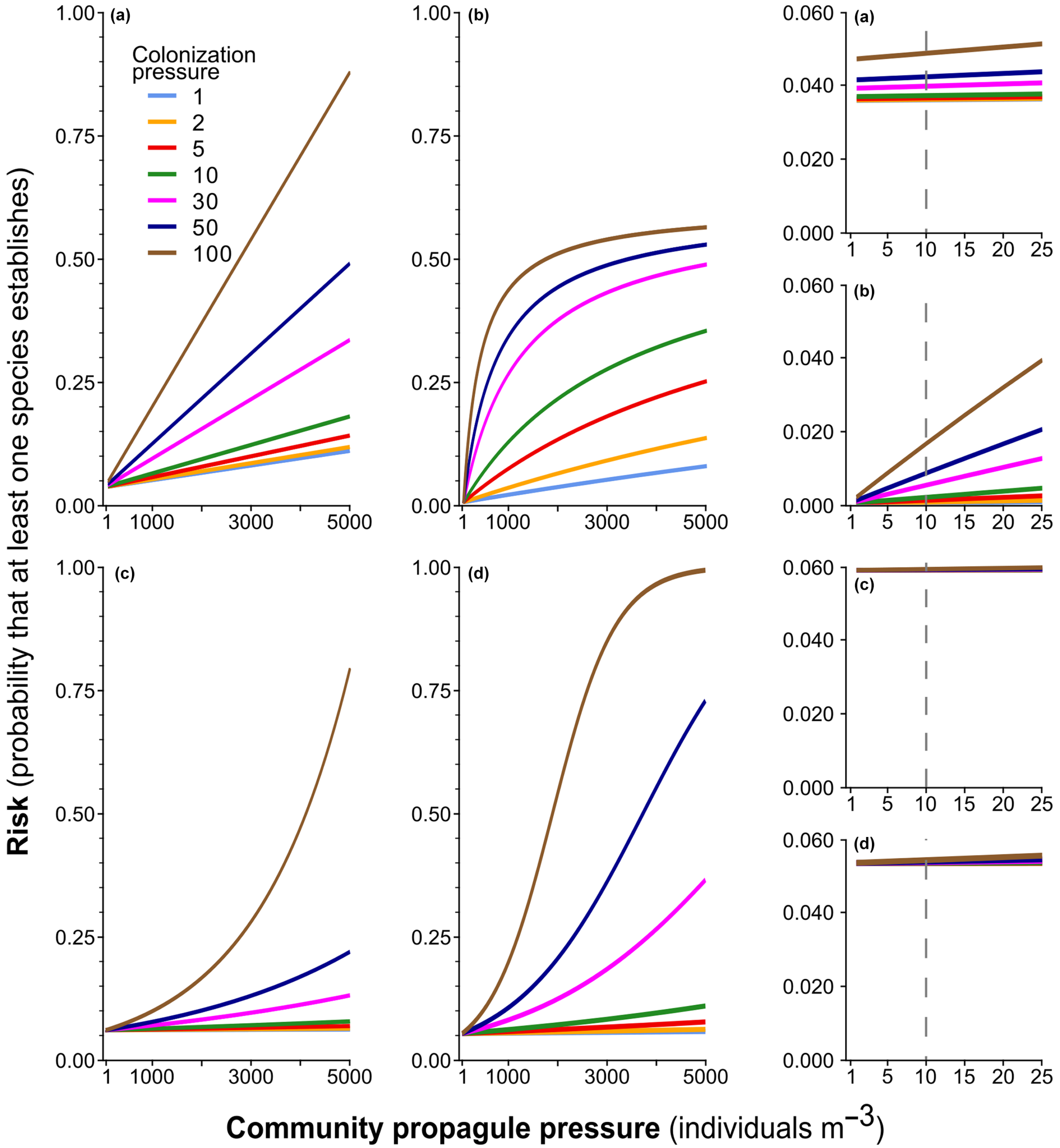

FIGURE 1 Risk of at least one species establishing in relation to community propagule pressure and colonization pressure of each fitted model. Colonization pressure is indicated by line colour. For each community propagule pressure, individual propagule pressure is inversely related to colonization pressure (not shown). Risk–release models utilized include: linear (a), hyperbolic (b), exponential (c) and logistic (d) fit for the relationship between risk and individual propagule pressure. Corresponding inset panels on the right indicate model patterns for community propagule pressure values near or at the IMO D-2 limit (vertical dotted line) for zooplankton-sized organisms (i.e. from 1 to 25 ind. m^{-3}). In cases where lines overlie, communities with higher colonization pressure always have slightly higher values. Three measures demonstrated that the hyperbolic and logistic risk–release relationships fit data best (Table 1).

colonization pressures explored, whereas at an individual propagule pressure of 10 ind. m^{-3}, the total number of ind. m^{-3} present ranged from 10 to 1000 for colonization pressures of 1 and 100 respectively.

4 | DISCUSSION

The IMO D-2 performance standards for each phytoplankton- and zooplankton-sized species mandate numerical limits on community

TABLE 1 Accuracy of curve fit for the community propagule pressure model risks.

	At least one species establishing		
Metric	MAE	RMSE	R^2
Linear	0.07	0.09	.31
Hyperbolic	0.05	0.08	.32
Exponential	0.07	0.10	.31
Logistic	0.08	0.10	.31

Abbreviations: MAE, Mean absolute error (lower is better); R^2, Pearson's correlation (higher is better); RMSE, Residual mean square error (lower is better).

TABLE 2 Per capita change in risk for colonization pressure (CP), community propagule pressure (CPP) and colonization pressure × community propagule pressure interaction (CP × CPP) as determined by generalized linear mixed-effects model coefficients ($\times 10^{-4}$).

Pressure	Risk at least one species establishes
CP	1.218
CPP	1.132e−2
CP × CPP	1.514e−4

Note: All *p* values were highly significant ($p < .0001$).

propagule pressure for living or viable organisms released. These limits apply to assemblages that may vary widely in composition with respect to colonization pressure and individual propagule pressures. Our study found that risk of at least one species establishing varied strongly according to community composition for zooplankton samples at the IMO D-2 limit (10 ind. m^{-3}). When community propagule pressure was at or below this limit, three of four risk–release relationship models (linear, exponential, logistic) predicted that risk was virtually insensitive to changes in community propagule pressure but critically affected by colonization pressure (Figure 1, insets i, iii and iv). Conversely, if the risk–release relationship was hyperbolic, risk of at least one species establishing was positively related to community propagule pressure as well as colonization pressure (Figure 1, inset ii). As community propagule pressure rose to very high levels (up to 5000 ind. m^{-3}), both colonization pressure and community propagule pressure influenced risk.

All four risk–release relationship models predicted dominance of colonization pressure over community propagule pressure (and, hence, individual propagule pressures) when the latter values were low (Figure 1). Duncan et al. (2019) reported that colonization pressure was key to understanding invasion risk and was more important than individual propagule pressure. Dominance of colonization pressure over individual propagule pressure at low community propagule pressure implies that environmental stochasticity may be more critical than demographic stochasticity. Both conceptual models and empirical data have demonstrated that invasion risk is related to colonization pressure (Blackburn et al., 2020; Duncan et al., 2019; Lockwood et al., 2009; Lonsdale, 1999). Indeed, Blackburn et al. (2020) argued that colonization pressure formed the basis for a second null model in invasion ecology.

Propagule pressure was previously proposed as the first null model to explain invasion success (Colautti et al., 2006). Individual propagule pressure has a well-established role in predicting establishment success of individual species (e.g. Chase et al., 2023; Colautti et al., 2006; Duncan et al., 2019; Lockwood et al., 2005; Simberloff, 2009; Smyth & Drake, 2022; Stringham & Lockwood, 2021; Williamson & Fitter, 1996). However, documentation of community propagule pressure as a reliable predictor of invasion success is limited, almost certainly because each species in an inoculum has a different individual propagule pressure and survival probability (Brockerhoff et al., 2014; Lawrence & Cordell, 2010; Lo et al., 2012).

The IMO focus on community propagule pressure during development of the D-2 regulation almost certainly relates to feasibility concerns regarding technology testing and, possibly, because of an inability to reliably predict risk or assess compliance for a multi-species community. In addition, when these standards were developed in 2004, the role of propagule pressure was much better understood than that of colonization pressure in affecting invasion risk (MacIsaac & Johansson, 2017). Nevertheless, two reviewers of a U.S. Coast Guard review of ballast water discharge standard options later expressed concern that the number of species released was not being addressed (pg. G-3, USCG, 2012).

High community pressure will, in most cases, include at least some species with high individual propagule pressures. These species are more likely to survive environmental and demographic stochasticity, to overcome Allee effects and to have sufficient genetic variation to adapt to the new environment (Blackburn et al., 2015). By reducing community propagule pressure, IMO D-2 necessarily lowers individual propagule pressures and, thereby, risk of invasion.

The species abundance relationship in the donor community and relative entrainment, survival, reproduction during transit (if any) and discharge from ballast water will determine the species abundance distribution for organisms introduced to recipient waters. Generally speaking, higher community propagule pressure in discharged ballast water should also include a higher colonization pressure as more 'rare' species are included in the inoculum (Briski et al., 2012, 2014; Lockwood et al., 2009). While we could not find any discussion of colonization pressure in IMO deliberations, its desire to strongly reduce community propagule pressure should nevertheless reduce colonization pressure and risk by eliminating species that were present at the lowest concentrations prior to treatment, assuming all species are similarly affected by treatment (see Briski et al., 2018).

A question arises of how risk is affected if species in ballast tanks experience selection during transit, resulting in high fitness – though possibly at low abundance – of one or a few species, while the majority of species die off (see Briski et al., 2018). Remaining species may have higher resistance to further stressors or to treatment. Alternatively, ballast water treatment itself may result in large overall declines in community propagule pressure and colonization pressure, though a small number of species may be unaffected or less affected

TABLE 3 Estimated risk of invasion for vessels visiting the port of Shanghai or ports across Canada.

Location	Compliant ships	Non-compliant ships	CP	CPP	Estimated probability of invasion	Reference
Port of Shanghai, China	9	8	3	5800	.17	Xiang et al. (2023), *Manage. Bio. Inv.*
			3	531	.04	
			4	22,840	~.26	
			4	666	.05	
			4	7100	.25	
			1	7876	.10	
			2	100	.01	
			2	100	.01	
Canadian ports	14	15	15	3822	.35	Bailey et al. (2022), *Mar. Poll. Bull.*
			12	223	.04	
			8	3573	.26	
			8	32	.01	
			7	929	.08	
			7	19	.01	
			6	43	.01	
			3	101	.01	
			2	22	.01	
			1	664	.02	
			1	15	.01	

Note: The number of ships with compliant, treated ballast water discharges is provided, though risk estimates for these vessels were not determined. Probability of invasion for non-compliant ships is based on Figure 1 ii and inset ii and assumes a hyperbolic risk:release relationship. In cases where immature stages of taxa were not identified to species, the 'species' was not added to the sample colonization pressure if adults from the same taxonomic group were present and identified to species. Colonization pressure included traditional microscopic identification or barcoding identification of species identity but excluded metabarcoded identifications since the eDNA analysed could have originated from living or dead individuals. As well, if immature stages and adults of a taxonomic group were present, we counted only one species. Bailey et al. (2022) observed 11 non-compliant vessels with colonization pressure >0 and 4 non-compliant vessels with colonization pressure of 0 (not included here). Estimated probability of invasion would be lower for the other risk:release relationships modelled in Figure 1.

(Gregg & Hallegraeff, 2007; Paolucci et al., 2017). In both cases, our models suggest that risk should be moderately to sharply reduced depending on the applicable risk:release relationship, and the community propagule pressure and colonization pressure prior to treatment. For example, if a sample had community propagule pressure of 2000 individuals m^{-3} and a colonization pressure of 30 species prior to treatment (e.g. pink curve, Figure 1ii), followed by application of a treatment that resulted in strong declines in both parameters, the resulting risk should be much lower (e.g. perhaps similar to the light blue line). However, if the remaining species was (were) selected for hardiness, the α value used in our models (Equation 1) may underestimate the actual per capita invasion risk. In this case, it is possible that a small number of propagules have higher risk (e.g. greater slope and/or higher asymptote, somewhat similar to the orange line in Figure 1ii).

Despite the tremendous importance of the new IMO D-2 standards that will apply globally, there exists a dearth of information regarding effectiveness of treatment systems on operational vessels. Only three studies exist that provide empirical data with respect to colonization pressure and community propagule pressure of zooplankton-sized taxa in treated ballast water. Dong et al. (2023) conducted five trials aboard a vessel moving between ports on the East China Sea and Yellow Sea and observed that a three-step treatment process effectively reduced >50 μm organism density to below the IMO D-2 requirement in all cases. In a second study conducted on treated ballast water from domestic and international sources that were discharged in the port of Shanghai, China, eight of 17 vessels exceeded the IMO D-2 standard for >50 μm organisms, with community propagule pressure exceeding 5000 ind. m^{-3} in four of the vessels (Xiang et al., 2023) (Table 3). Colonization pressure for these eight vessels for the >50 μm size class ranged between one and four species. Bailey et al. (2022) sampled 29 vessels in Canada and observed that 15 exceeded the permissible IMO D-2 limit for >50 μm species, with community propagule pressure exceeding 3500 ind. m^{-3} in three of the vessels (Table 3). Colonization pressure based on living organisms identified taxonomically or via DNA barcoding (but excluding those identified by DNA metabarcoding) in non-compliant, treated ballast water discharges varied from 1 to 15 species per vessel (Table 3) (Bailey et al., 2022). Some of the taxa (Rotifera, Ostracoda, Anomopoda, Diplostraca, and Ciliophora) recovered alive in treated ballast water reproduce parthenogenetically. These species also might have higher α values than those of strictly sexual species (Bailey et al., 2009; Branstrator et al., 2019; Gertzen et al., 2011). Extrapolation from our models using a hyperbolic risk–release relationship (Figure 1ii and inset ii) suggests that the probability of at least one species establishing ranged from 0.01 to ~0.26 for non-compliant vessels in the Xiang et al. (2023) study and from 0.01 to 0.35 in the Bailey et al. (2022) study (Table 3). Risk would be lower (maximum of 0.07 to 0.15) if any of the other three risk:release relationships were used. A fourth study that tested community propagule pressure (but not colonization pressure) of treated ballast water found only one of 28 vessels exceeded the IMO D-2 limit for organisms >50 μm (value was 600 ind. m^{-3}; Feng et al., 2023). Thus, the limited evidence available to date suggests mixed success for effects of treatment with respect to the >50 μm size class, and a small fraction of non-compliant vessels pose a non-insignificant invasion risk. Studies profiled in Table 3 that detected exceedances involved releases of multiple living species. Even if only a small fraction of vessels discharge ballast water that greatly exceeds IMO D-2 limits, these vessels do pose some risk of new invasions. More optimistically, Drillet et al. (2023) noted that in large-scale commissioning tests for treatment systems using 'indicative' indicators (i.e. adenosine triphosphate levels in ballast effluent) to assess compliance, failure rate declined strongly between 2019 and 2022, suggesting that improvements in treatment efficacy may have resulted from lessons learned.

Our model relied heavily on pseudorandom number generation to create communities, calculate alpha values, and in turn risk and species establishment or extinction. As such, the use of a single pseudorandom number generator potentially introduced artefact effects. For example, we observed a variation of 0.3 or more in risk at community propagule pressures under 25 (Figure 1 insets). This variation may owe to risk–release fit (linear, hyperbolic, exponential, logistic) interpreting biased risk values determined through a single pseudorandom generator. Picard (2021) applied 10,000 different pseudorandom number generators to a deep learning image classification model. Changing the pseudorandom number generator caused a 2% range in accuracy, which Picard (2021) concluded could be explained by the pseudorandom number generator selection. Our application of a single pseudorandom number generator may have biased the observed risk relationships with low community propagule pressure causing the observed range of predicted risk. Use of multiple or variation of the pseudorandom number generator may remove potential artefacts and potentially limit variation of risk at low community propagule pressure (Picard, 2021). Future studies should consider changing or varying the pseudorandom number generator to validate our results.

The IMO D-2 regulation was explicitly designed to reduce community propagule pressure, though we expect it to have similar effects on mean individual propagule pressure and – according to random sampling theory (Preston, 1948) – colonization pressure. Thus, regulation IMO D-2 should be highly beneficial in reducing future invasions so long as treatment systems on operational vessels meet their certification requirements. Three of four risk–release models (excepting hyperbolic) demonstrated that risk was neither higher nor lower when community abundance was slightly above or below the IMO D-2 standard (Figure 1, panels i, iii and iv). Hyperbolic risk–release models indicated that relative risk should decline faster for each unit of community propagule pressure decline (Figure 1, inset ii). If the hyperbolic relationship applies, then lower discharge limits result in enhanced risk reduction. Perhaps more importantly, additional empirical studies are required to determine the efficacy of treatment systems on operating vessels, as current sample sizes are too small to develop generalizations. As well, additional information is required regarding reasons underlying failures (Bailey et al., 2022) and whether communities discharged from these vessels pose different risks based upon their colonization pressure and individual propagule pressures.

AUTHOR CONTRIBUTIONS

Marco R. Hernandez (initial draft, editing, revision, graphics), **Justin R. Barker** (modeling, statistics, editing, graphics, revision), **Hugh J. MacIsaac** (conceptualization, initial draft, editing, revision, funding).

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

All data used are available via https://doi.org/10.5061/dryad.g4f4qrfvx.

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Appendix

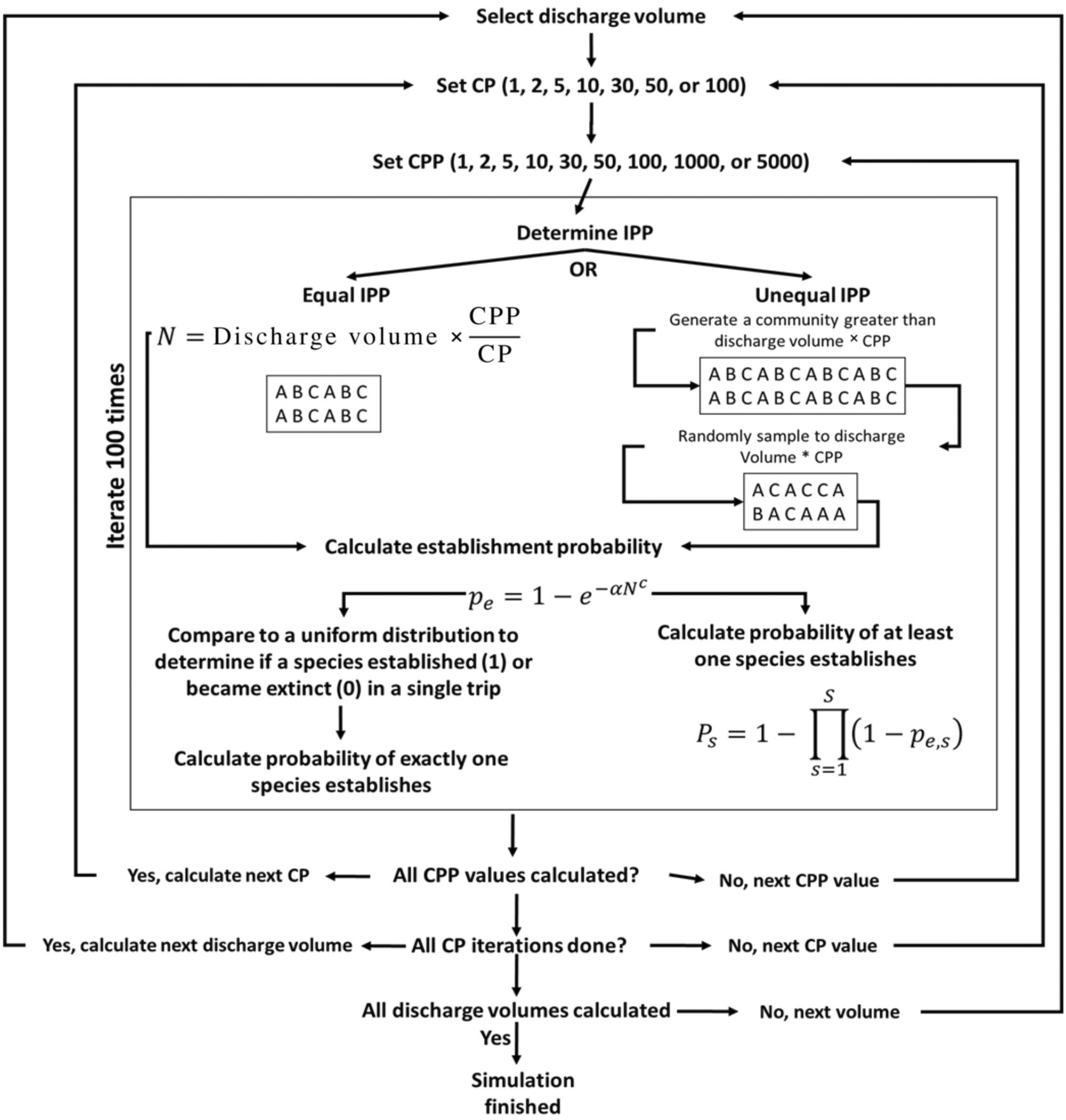

FIGURE A1 Workflow of the mechanistic model estimating invasion risk as a function of individual propagule pressure (IPP), community propagule pressure (CPP) and colonization pressure (CP). Simulations utilized empirical data for vessels discharging ballast water in Canada (Bailey et al., 2022). Within each discharge volume, CP and CPP, IPPs were unequal (hypotheses 1 and 2) or equal (hypothesis 3) to represent initial population size (*N*) for calculating establishment probability. A, B and C represent individuals of different species.

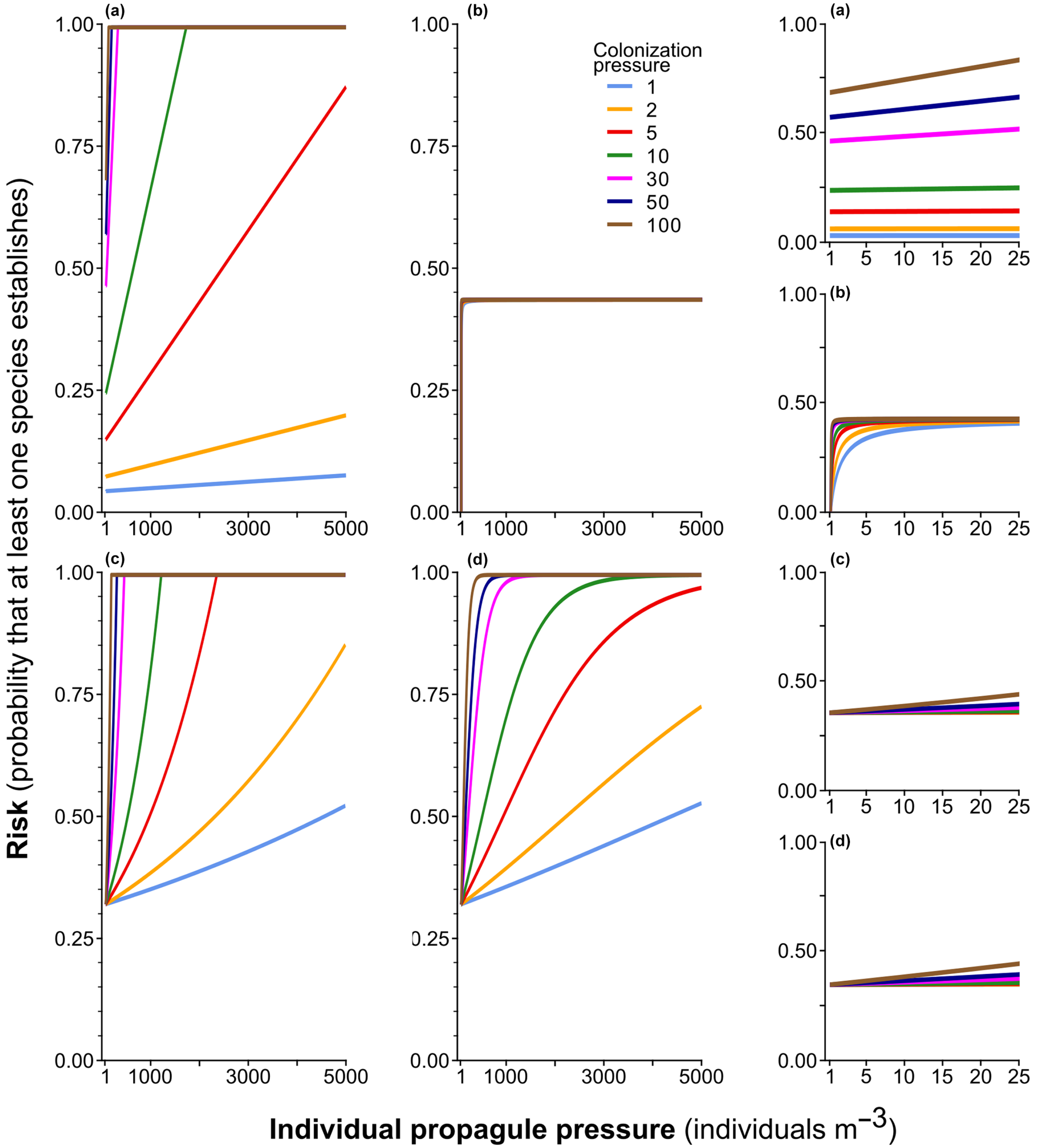

FIGURE A2 Risk of at least one species establishing in relation to species' individual propagule pressure and colonization pressure. Community propagule pressure (not shown) is equivalent to individual propagule pressure multiplied by colonization pressure. Colonization pressure lines in panel b overlie as they achieved a plateau at very low individual propagule pressure (inset b).