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# PREVENTING BIOLOGICAL INVASIONS BY UNDERSTANDING THE PROCESSES LEADING TO ESTABLISHMENT 

## By

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Invasive species are a leading cause of animal extinctions and result in billions of dollars (\$US) in economic damages globally. Understanding the processes involved in biological invasions can aid in finding efficient and effective policy and management solutions. In this dissertation, I explore three mechanisms that can prevent invasive species from establishing. First, within the context of the most common pathway for invasive vertebrate species, I document factors related to the release of exotic pets into the wild by their owners. Second, I develop a method to calculate the reduction of propagule pressure required to lower the establishment probability for introduced non-native populations. Last, I explore an overlooked assumption of the propagule pressure effect and calculate the how establishment probability is altered when spatial and temporal independence of introduction events is violated. The results I highlight, and the methods I developed, are critical in slowing the rate at which invasive species are establishing worldwide.

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## Introduction

Biological invasions cause massive socio-economic damage and ecological impacts that can sometimes drive entire suites of native species toward extinction (Pyšek and Richardson 2010). In the United States, invasive species cause an estimated \$120 billion/year in losses, damages, and control costs (Pimentel et al. 2005). For example, invasive weeds compete with crop plants and result in a loss in crop yield, thus a loss in profits for farmers (Neve et al. 2018). Some invasive species threaten human health by being vectors for human pathogens. For instance, a mosquito species (Aedes albopictus), known to carry the Dengue virus, has recently invaded parts of Europe (Medlock et al. 2012). Along with other major drivers of biodiversity loss (e.g., habitat loss), invasive species are a major conservation concern because they cause a wide range of negative ecological impacts (Simberloff et al. 2013). They can become novel predators for which native prey species have limited evolutionary defenses. Well known examples include rats established on oceanic islands that kill evolutionarily naïve seabirds (Blackburn et al. 2004), and the Burmese python established as a non-native species in the Florida Everglades causing the severe declines of native mammalian prey (Dorcas et al. 2012). Invasive species can have defenses that kill native predators, such as the case for the cane toad in Australia (Shine 2010). The cane toad produces toxic compounds on its skin and evolutionary naïve predators can die if they eat the toad. Invasive vertebrates can outcompete native fauna as is the case for European starlings in the US, which outcompete several native bird species for nesting sites (Linz et al.
2007). Overall, in the United States, impacts from invasive species are the primary cause for the listing of $42 \%$ of Threatened or Endangered species (Pimentel et al. 2005). Given these severe negative impacts, it is essential to understand the process of biological invasion to ensure effective management of current invasive species and prevent new invasions from occurring (Lodge et al. 2016).

The process of biological invasions can be described as a progression through several discrete stages, each stage with an independent probability of transition. The stages are: (1) transport, (2) release, (3) establishment, and (4) spread (Blackburn et al. 2011). Transport involves human actions moving individuals beyond the boundaries of their native range. Once transported, these individuals may remain in captivity or confinement never being released into a non-native environment. These individuals may, or may not, survive or reproduce after release. The establishment stage refers to the probability that enough released individuals survive and reproduce that they form a self-sustaining population. Established non-native populations may, or may not, spread beyond their initial point of release under their own dispersal powers. Management interventions differ for each stage, where management of earlier stages (transport and release prior to establishment) is focused on prevention, whereas in later stages it is focused on eradication, containment, and mitigation of damages (Blackburn et al. 2011). Prevention is widely considered to be the most cost-effective and desirable management option (Lodge et al. 2006). In this dissertation I explore patterns in release and how knowledge of these patterns can be used to inform policy formation and management solutions. The dissertation, is divided into three chapters, each of which I
introduce below. All publications that result from this work are co-authored by my advisor, Julie Lockwood.

Pet problems: Biological and economic factors that influence the release of alien reptiles and amphibians by pet owners

Non-native species arrive to novel environments through a variety of different mechanisms, termed pathways (Hulme et al. 2008). One of the most significant modernday pathways and the one that supplies the majority of exotic vertebrate species today, is the exotic pet trade (Padilla \& Williams 2004; Kraus 2009; Rhyne et al. 2012; Bush et al. 2014). Exotic pets are species without a long history of domestication, thus it excludes species such as cats, dogs and hamsters. Exotic pet individuals are often legally captured from within their native range, or are bred within facilities, and then are sold to consumers as household companions. The number of species involved in the exotic pet trade is vast. For aquarium fish, there were around 1,800 species imported in one year (2004-2005; Rhyne et al. 2012). In terms of terrestrial vertebrates, there have been at least 3,900 species imported since 1970 (Romagosa 2015). Furthermore, the composition of species is highly dynamic over time. For terrestrial vertebrates, there has been about a 60\% turnover rate in species composition since 1970 (comparing 19681972 to 2006-2010; Romagosa 2015). Thus, more than half of the species imported ca. 1970 were no longer imported in late 2000s. This suggests that demand for most species is highly elastic. Therefore, if native populations dwindle or if trade restrictions are put
in place, new species (to the pet trade) will easily take the place of the old (Carpenter et al. 2004).

In addition to the high diversity of species, the absolute number of individuals imported is immense. Between 2000 and 2006, 1.3 billion live animals designated for the pet trade were imported into the US (Smith et al. 2009). Aquarium fishes comprised a large majority of these imports (90\%). There were at least 85 million individual terrestrial vertebrates imported into the US between 1998 and 2010, which on average is 7 million/year (Romagosa 2015). As an example, for one terrestrial taxon, there were ~21,000 ball pythons imported into the US for the pet trade per year on average, from 2006 through 2010 (Romagosa 2015). To put this into the perspective of invasion risk, theoretical population models for non-native species establishment demonstrate that a founding population of 100-200 individuals has a $>90 \%$ probability of successful establishment (Cassey et al. 2014). Therefore, it is apparent that ball pythons and many other species found in the pet trade could easily establish non-native populations, even if a trivial fraction of them are released in geographic proximity.

One of the primary barriers that non-native species must transit early in the invasion process is being released as free-living individuals within the non-native environment (Figure 1). For species that tend to be accidentally transported out of their native range, this release event may be automatic. For instance, hitch-hiking species may escape from packing material on the tarmac after being transported within airplane cargo. Or, species transported in ship ballast water will escape once the ballast water is discharged. In these cases, the release stage of the invasion process is trivial and can be
reasonably concatenated with the transport phase in studies that examine transitions through these invasion barriers (Hulme 2009). In accidental-release scenarios, the volume of cargo, number of ships calling at one port, or other measures can adequately describe the probability that a transported species will become free-living and where it will be initially released.

We cannot take the same analytic approach to vertebrates imported for the exotic pet market. Individuals of these species arrive in a non-native range either through direct capture or breeding in their native range followed by transportation directly to a wholesaler or consumer. Individuals of these species may also be bred within the non-native range by breeders. No matter their provenance, these individuals are then sold to consumers and kept within households that are dispersed across the non-native range. Release under these circumstances occurs either when the wholesaler, breeder or consumer fails to keep the individual in a secure enclosure (escape), or when the owner (a consumer, breeder or the wholesaler) purposefully removes the individual from captivity and allows it to become free-living. We know very little about the way by which exotic pets become non-native species, in large part because pet release events are geographically dispersed and are known to be rare (e.g., < $10 \%$ of all pet owners admit to have released their pets into the wild; (Gertzen et al. 2008; Marson et al 2009; Strecker et al. 2011). However, the regular observation of pet species as free-living suggests that a non-trivial fraction are either accidentally released by escaping confinement or are deliberately released through owner-assisted means (Krysko et al. 2016; Hulme 2015).

The process of release for exotic pets involves spatial dynamics and is influenced by human behavior. Add to this the difficulty of documenting the dynamic composition of the exotic pet market (Romagosa 2015), and it becomes clear that the task of connecting trade and consumer behavior to the occurrence of invasive exotic pets is a formidable challenge. Nevertheless, with the massive taxonomic breadth and quantity of species sold as pets worldwide, this process has taken on increased importance in conservation. As is evident from the widespread ecological and economic damage that once-pet species like Burmese python (Python bivittatus) and Pacific lionfish (Pterois volitans) can produce (Dorcas et al. 2012; Whitfield et al. 2002), the need to better understand the release stage of invasion is critical.

In the first chapter in this dissertation, I explicitly explore the release stage of biological invasions for the exotic pet trade pathway. I set out to identify broad-scale and easily measured biological and economic factors that influence the release of these exotic pets by their owners. I hypothesize that biological factors reflect the cost of care, and economic factors reflect the value that owners place on their pet, both of which can influence the probability when a pet is released. I collected-life history and economic data on the 1,722 species of reptiles and amphibians sold within the US as pets over the last two decades. I also compiled a list of pet trade-attributed releases in the US and used boosted regression trees to correlate species release status with their life-history traits and economic attributes.

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#### Abstract

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Reducing propagule pressure to lower the establishment probability of potential invasive species

After the introduction/release stage, a non-native population has the potential to form a self-sustaining population (i.e., establish). The heavy economic and ecological costs of invasive species imply that policies that prevent non-native species from establishing in the first place are more efficient than post-establishment control and management (Keller \& Springborn 2014). Prevention research focuses on the early invasion stages of introduction and establishment (Blackburn et al. 2011). If such research can isolate principal ecological processes that elevate initial population establishment, then policy and management can be targeted accordingly (Hulme 2015, Finnoff et al. 2007, Lodge et al. 2016).

The initial establishment of a non-native species is a population-level process. Individuals of a species are introduced (released) into a novel location (making them non-native), and these individuals either begin breeding, or they do not breed and fail to establish (Sakai et al. 2001). Accordingly, the most consistent predictor of successful establishment is propagule pressure (Lockwood et al. 2005, Cassey et al. 2018).

Propagule pressure is defined as the number of individuals introduced to a location where they are non-native (Lockwood et a. 2005). As propagule pressure increases, so does establishment probability (Cassey et al. 2018). Reducing propagule pressure is a recognized solution to lowering establishment probability (Albert et al. 2013). In this chapter, I develop a method for a propagule-pressure reduction sensitivity analysis, which can reveal how much propagule-pressure reduction is required to reach a desired level of establishment probability. I use a probabilistic model of establishment probability to simulate realistic values of propagule pressure. I then systematically simulate reductions in propagule pressure and record the resulting marginal change in establishment probability. The methods presented here, in combination with information on costs of propagule-pressure reduction, can be used to determine the most cost-effective way to lower establishment probability via a reduction in propagule pressure.

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Spatial or temporal overlap in introduction events can elevate establishment probability through rescue effects

One critical assumption of propagule pressure that is extended to establishment calculations is the assumption that each introduction event is spatially and temporally
independent of all other events (Wonham et al. 2013). If this assumption is violated, functional propagule pressure will be higher and, thus, establishment probability will be higher than if calculated without regard to spatial and temporal independence of introduction events. However, it remains unclear when and by how much violating spatial and temporal independence alters establishment probability. Here I use a spatially explicit, discrete-time, stochastic population model to document when and if non-independence can safely be ignored in management and policy formulation and record the associated increase in establishment probability due to non-independence. I found that non-independence follows intuitive patterns and can cause establishment probability to be under-estimated by up to $70 \%$. I suggest that risk assessments, policy development, and academic investigations must explicitly consider the likelihood of propagule pressure rescue effects.

This chapter is formatted for Conservation Letters and will be submitted there (Stringham \& Lockwood, in prep).

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Pet problems: biological and economic factors that influence the release of alien reptiles and amphibians by pet owners

## Abstract

1. The number of alien reptiles and amphibians introduced and established worldwide has increased over the last decades. The legal pet trade is the now the dominant pathway by which individuals of these species arrive in their non-native locale. Despite its importance, pet trade pathway specific factors that influence the release (introduction) of exotic reptiles and amphibians have not yet been examined.
2. We set out to identify broad-scale and easily measured biological and economic factors that influence the release of these exotic pets by their owners. We hypothesize that biological factors reflect the cost of care and economic factors reflect the value owners place on their pet, both of which can influence the probability a pet is released. We collected life-history and economic data on the 1722 species of reptiles and amphibians sold within the US as pets over the last 18 years. We also compiled a list of pet trade-attributed releases in the US (i.e., all free-living species regardless of whether they successfully established). We used boosted regression trees to correlate species release status to their life history traits and economic attributes $\left(r^{2}=0.51, A \cup C=0.89\right)$.
3. We found that species with a high probability of being released were imported at higher quantities over our period of record, have a relatively large adult mass, and commanded cheaper retail prices. The number imported and price interacted with longevity and adult mass to produce non-linear increases in release probability. The most important interaction revealed that large-bodied species imported in high quantities have a three times higher release probability compared to large-bodied species imported in lower quantities.
4. Policy implications. Our results provide guidance toward targeting exotic pet reptile and amphibian species that are at a high risk of being released. Species that are both prevalent
in the pet trade and large-bodied or long-lived have the highest probability of being released. This will aid in developing education and policy solutions aimed at decreasing the rate at which these pets are released, thus curtailing the invasion process before these species can establish and impacts can occur.

## Introduction

Invasive reptiles and amphibians impose severe ecological and socio-economic costs including sometimes driving entire suites of native species toward extinction (Shine 2010; Wiles et al. 2003). Over the past two decades, the trade in 'exotic' pets has become the main source of alien reptile and amphibian species worldwide (Kraus 2009; Capinha et al. 2017; Krysko et al. 2011). 'Exotic' pets are species without a long history of domestication that are legally captured from their native range or bred within facilities and sold to consumers as household companions. Individuals sold as exotic pets are never intended for release, however the regular observation of traded species as free-living suggests that a non-trivial fraction are released (Hulme 2015). These released individuals then have the opportunity to establish a local population, with some further probability of an established population imposing negative impacts on co-occurring native species (Blackburn et al. 2011). Despite release being the initiating step of invasions, we know very little about the process by which exotic pets are released, in large part because pet release events are geographically localized and are known to be rare relative to the number of people that own exotic pets (Strecker et al. 2011). Add to this the difficulty of documenting the dynamic composition of the exotic pet market (Romagosa 2014), and it becomes clear that the task of connecting trade, species life history, and consumer behavior to the occurrence of freeliving pet reptiles and amphibians is a formidable challenge. Here, we generate hypotheses about how these species' biological traits, and the economic factors related to their trade, influence the release decisions of pet owners. We test these hypotheses by combining pet market data with in-depth records of documented released free-living reptiles and amphibians within the United States (US).

Research on invasion vectors and pathways makes clear that the suite of species transported via human actions is set by the interplay of socio-economic factors and species' biology (Essl et al. 2011; Hulme et al. 2008). One of the primary filters (or barriers) that alien species must transit early in the invasion process is being released as free-living within a nonnative environment. In the pet trade pathway, release occurs either when the wholesaler or consumer fails to keep the individual in a secure enclosure (escape), or when the owner (a consumer or the wholesaler) purposefully removes the individual from captivity and allows it to become free-living (Su et al. 2016; Vall-Ilosera et al. 2017). Since the pet trade pathway is quite distinct in the degree to which human behavior influences the release event itself, we should expect that drivers of release are specific to this pathway (Hulme et al. 2008). For example, smaller-bodied cargo hitchhikers may be more likely to be released (accidentally) because they are more likely to go undetected. However, the reverse relationship may be true for the pet trade pathway given that larger-bodied species tend to be released more often due to them outgrowing their housing (termed 'tankbusters' for fish: Holmberg et al. 2015). Thus, independent analyses of release pathways are imperative to producing meaningful insights for policy development (Hulme et al. 2017).

Despite the importance releases play in the invasion process for the pet trade pathway, most of the research to date has focused on factors influencing the establishment of exotic pet populations and not on the factors related to their initial introduction (or release; Van Wilgen \& Richardson 2012; Mahoney et al. 2015; Fujisaki et al. 2010; Bomford et al. 2009). The few published studies on pet species release are lacking in both taxonomic and analytical breadth (e.g., Duggan et al. 2006; García-Díaz and Cassey 2014; Su et al. 2016; Tingley et al. 2010). Consequently, the release stage is frequently ignored in risk assessment (Leung et al. 2012) even though there is considerable evidence that if alien species are not released, or are released in
small enough numbers, they are far less likely to become established (Lockwood et al. 2005; Cassey et al. 2018).

Here we seek to close this research gap by exploring the ability of biological and economic drivers to explain releases of pet reptiles and amphibians (Table 1). For biological drivers, we hypothesize that the probability of release will increase when there is a mismatch between the perceived and actual level of care needed to maintain the individual in captivity. We expect that well-meaning consumers purchase a pet but find it difficult to care for it over the long-term, and that some fraction of these owners will choose to release their pet rather than sell or euthanize it. We posit that care costs will be higher for species that grow to large adult sizes, live for a long time, and are capable of producing many young while in captivity. For economic drivers, we hypothesize that the more abundant and less expensive a species within the pet market, and the longer the species remains on the market, the more likely individuals of this species are to be released. Owners may place less value on low-cost pets and therefore be more likely to release them when care becomes costly or inconvenient. Furthermore, all else being equal, the probability that at least one individual of an exotic pet species will be released will increase if the species is commonly sold to consumers, some fraction of which will resort to release when the pet is no longer wanted. By attempting to quantify the factors related to the release of exotic pets, we seek to help guide efforts aimed at curbing pet animal releases.

## Materials and Methods

Pool of species available for purchase as pets

We identified the range of species that are available for purchase as pets in the US by combining two data sources. The first is import records kept by the US Fish and Wildlife Service (Law

Enforcement Management Information System, LEMIS; see Romagosa 2014 for more details). This data is collected by trained inspection agents at airports across the US. We focused our analysis on the conterminous US and therefore excluded import records from Hawaii, Alaska, and US territories. LEMIS data from 1999 to 2016 indicated that 1613 reptile and amphibian species were imported into the US for the pet trade.

Our second data source was a list of species available for purchase on highly-trafficked nationwide internet vendors from 2012 to 2016. We expected this inventory to overlap substantially in species composition with the LEMIS data. However, the web retailer sites also include species that are bred domestically and thus serves to expand our pool of species that had the opportunity to be released by pet owners. The vendors we chose to include in our survey are the top three most trafficked reptile and amphibian internet-based pet stores, each of which offers to ship individual pets to any consumer in the conterminous US. From these online pet retailers, we collated 94,230 unique individual pet listings representing 652 species (see Supporting Information S1 for details on our web-based data collection protocol).

## Variables that influence release

Next, we gathered information on biological factors that we hypothesized to be related to release probability (explanatory), which included mean adult body size (mass), mean reproductive output (eggs/year), and maximum longevity (years; Table 1). We expect that as each of these biological factors increases in magnitude, the incurred costs of care will also increase, thus increasing release probability. We collected this information from five published databases of vertebrate life history traits (see Supporting Information S2 for details on compiling databases). Additionally, following Holmberg et al. (2015) we compared the difference between age and body mass at time of sale (retail size and age) with maximum age and adult body mass
for species appearing on the web vendor sites (see Supplemental Information S4 for details on estimating age and mass at sale). Data coverage for maximum longevity and adult mass was substantially higher than retail mass and age, and the two measures were highly correlated (Supporting Information S3). Thus, we only included maximum longevity and adult mass per species in the boosted regression tree (BRT) model described below.

For the economic explanatory factors, we calculated the length of time that each species appeared in the US pet market by tallying the number of years each species was listed at least once across any of the three websites and/or within the LEMIS data. We calculated the number of imports for each species by summing across all years the number of live individuals designated for the pet trade in the LEMIS data (available for 1999-2013). We also estimated the price that an individual of each species commands on the retail market. We collated price information from all web listings per species, corrected all prices to represent December 2016 US\$, and calculated the median of this distribution (Supporting Information S1).

## Testing for release patterns

We compiled a list of documented released (also known as introduced or free-living) exotic reptiles and amphibians primarily using Kraus (2009), which is the most comprehensive dataset of releases available on these taxa for the US. We only included species from Kraus (2009) if he listed them as having arrived in the US via the pet trade. Corresponding with the temporal span of our species pool, we only recorded as 'released' species that Kraus indicates as having been observed as free-living after 1999. Because Kraus (2009) only had access to information up to about 2008, and to ensure comprehensive accounting of released species, we included species recorded as free-living from 1999 to 2016 within EDDmaps (www.eddmaps.org). EDDmaps is a citizen-science effort to provide real-time information on
alien species occurrences across the US, where each listing is verified by taxonomic experts. There were 114 more species recorded as released from EDDmaps that were not in Kraus (2009) within our period of record. We excluded all recorded releases from Hawaii and Alaska to match our geographical scope of species availability (above). Note that we included species as 'released' regardless of whether they have now, or ever will, establish self-sustaining populations in the US. Our interest is with the set of pet species that were released or escaped from captivity regardless of their longer-term fate once free-living. This effort resulted in 126 species recorded as free-living somewhere in the conterminous US between 1999 and 2016. We designated these free-living species as 'released' in our analyses below, and the species that were not recorded as free-living to be 'not-released' (our binary dependent variable).

We used boosted regression trees (BRT) to explore the relationship between our explanatory variables and the release status of reptiles and amphibians sold as pets the conterminous US. BRT is a machine learning technique that can fit complex nonlinear relationships and handle different types of data all while potentially yielding higher predictive performance than traditional statistical models (Elith et al. 2008; see Supporting Information S5 for BRT parameters used and testing of simpler models). Our reason for choosing BRT over more traditional statistical methods such as GLMs is its ability to accommodate for missing data. While we used the most up-to-date databases (to our knowledge) to compile life history traits, there was still missing data for all traits (Table 1). The BRT algorithm handles missing data by skipping the node with missing data during tree building (i.e., data is not imputed, but rather not included; (Elith et al. 2008)). BRTs were modelled in R v. 3.3.1 using the packages gbm v. 2.1. and dismo v. 1.1.

To assess for phylogenetic correlations between species (i.e., Allen et al. 2017; Capellini et al. 2015), we performed two additional BRT models that included taxonomy (Family and Order)
as a proxy for phylogeny (i.e., van Wilgen \& Richardson 2012, Schmidt and Drake 2011). This analysis does not directly measure phylogenetic correlations (e.g., Pagel's $\lambda$ ), which is a shortcoming of machine learning techniques in general (Supporting Information S6). Thus, we recommend that methods be developed to incorporate phylogenetic information into machine learning techniques including boosted regression trees. With this caveat, from our analysis we found little evidence for a phylogenetic signal in release probability (Supporting Information S6) and given that taxonomy or phylogeny alone does not reveal which life history traits are important predictors of release, we focus our interpretation of results below on the BRT without taxonomy.

To evaluate the performance and fit the BRT model, we used two metrics. First, we calculated the area under the Receiver Operating Characteristic curve (AUC) for both the training (all data) and cross-validated models (average of all cross-validated data folds). Second, we calculated $r^{2}$ (percent deviance explained) for both the training and cross-validated models.

To explore how each explanatory variable influenced release probability, we examined four different metrics. First, we calculated the relative contribution metric for each explanatory variable, calculated as the number of times a variable is selected for splitting a tree, weighted by the improvement resulting from that split, averaged over all trees. Second, we generated partial dependency plots to visualize the relationship between each explanatory variable and release probability. Third, for each explanatory variable, we measured the magnitude of its influence on release probability, calculated as the range ( $\max -\min$ ) of the values in the partial dependency plots. We termed this value $\Delta P$ (release), which is essentially a measure of effect size. Finally, we examined the relative strength of variable interactions by calculating the interaction size between explanatory variables (values near zero represent negligible interactions) and visualized these interactions in heatmaps (Elith et al. 2008).

## Results

Of the 1722 species recorded either in LEMIS or on the web sites, Lacertilia (lizards) were the group with the most species for sale (739 species), followed by Serpentes (snakes) with 490 species (Figure 1a). Over half of the species (1106) were available on the market for $\leq 5$ years (Figure 1b), while $\sim 10 \%$ of species were available for the full duration of this analysis, 18 years. Most web listings sold pets for under \$100 although some species commanded substantially higher prices (Figure S1). For all taxa, the age at the time of sale (retail age) was markedly less than the species longevity (Figure 2a). A similar trend was observed for retail mass and maximum adult mass (Figure 2b).

The BRT was effective at explaining release status, with a cross-validated AUC score of 0.89 and $\mathrm{r}^{2}$ of 0.51 . As anticipated, the AUC and $\mathrm{r}^{2}$ are somewhat higher for the training data (AUC of 0.94 and $r^{2}$ of 0.66 ), since overfitting is likely without cross-validation.

Three variables had the largest effect on release probability: quantity imported, price, and adult mass with a $\Delta P$ (release) of 48,23 , and 21 percentage points, respectively. In terms of model fit, these same variables had the largest relative contribution to release probability (ranging 17-30\%) (Table 2). The three other factors explored, time on market, longevity and reproductive output, had less of an effect on release probability and model fit.

Partial dependency plots showed that quantity imported, longevity, reproductive output, and time on market had a positive relationship with release probability, whereas price had a negative relationship (Figure 3). Adult mass had an unequal ‘U’ shaped relationship with release probability, where intermediate values saw the lowest release probability, while larger massed species had higher release probability compared to smaller massed ones (Figure 3). In terms of variable interactions, the strongest was between adult mass and quantity imported (interaction size of 56), where large-bodied species imported in high quantities have three times higher
release probability compared to large-bodied species imported in lower quantities (Figure 4a). There was a less strong but similar relationship between quantity imported and longevity whereby long-lived species imported in large quantity have higher release probability compared to long-lived species imported at low quantities (Figure 4c). Finally, we show that adult mass and price interact so that low price and large relative adult mass combine to produce a substantial rise in probability of release (Figure 4b).

## Discussion

The pet trade has taken on increased importance in conservation with regards to invasive species (Smith et al. 2009), as is evident from the widespread ecological and economic damage that once-pet species like Burmese python (Python bivittatus) and Pacific lionfish (Pterois volitans) can produce (Dorcas et al. 2012; Whitfield et al. 2002). Here, we set out to examine the role of biological and economic factors in explaining the first step in the reptile and amphibian invasion pathway, release probability. Our results indicate that there are clear biological and economic factors that increase the probability that exotic pet reptiles and amphibians will be observed as free-living (but not necessarily established) in the conterminous US. These factors reflect the cost of pet care that owners bear over the span of the pet's life and the value that these owners place on the pet's themselves. Notably, we demonstrate that considering both life history traits and economic characteristics is necessary to determine release probability as the two factors often interact to elevate release probability. This knowledge allows for the proactive development of policy and education tools that can serve to decrease either the prevalence of likely released exotic pets in the market and in homes or encourage owners to responsibly dispose of unwanted pets.

The set of species we record as released are the product of a complex set of individual owner decisions. Our approach seeks to identify broad-scale and easily measured factors that effectively capture and describe these decisions. In the absence of extensive pet owner surveys, our approach serves as a reasonable first step to elucidating mechanisms that drive exotic pet releases. We found that reptiles and amphibians that are more abundant on the pet market and are sold at cheaper prices are more likely to be released. This result is consistent with previous research on releases that concludes that pet abundance is a major factor for explaining releases in other exotic pet groups (Duggan et al. 2006; García-Díaz et al. 2015). Our finding that large adult mass increases release probability is also consistent with previous research for other taxonomic groups (Holmberg et al. 2015; Tingley et al. 2010). Therefore, it is likely that larger species may be a particular cause of concern for releases among most exotic vertebrate pet taxa (birds might be an exception: Su et al. 2015). Furthermore, we show that adult mass and longevity interact with economic factors to either diminish or augment release probability. For instance, long-lived species that are pervasive on the pet market are over three times more likely to be released compared to less commonly sold species of comparable longevity. Similarly, species that achieve a high adult mass while also being common in the market and low-priced are much more likely to be released than species of similar mass that are rare on the market or expensive. One caveat of machine learning methods is that they do not allow explicit testing for phylogenetic signal, which is a shortcoming to our results. Phylogeny was found to be important in a separate study on alien reptiles and amphibians (species not unique to the pet trade; Allen et al. 2017), suggesting that the same may be true with release.

Cross-stage differences in the importance of life history and socio-economic factors are a common feature across all biological invasions (Lockwood 2017) and our results further highlight the importance of compartmentalizing each stage of the invasion process when
quantifying risk (Leung et al. 2012; Blackburn et al. 2011). For instance, we show that larger bodied reptiles and amphibians are more likely to be released, however after release, other research suggests that smaller bodied species are more likely to establish self-sustaining populations (from global establishments: Mahoney et al. 2015; Allen et al. 2017). Similarly, our results suggest that import quantity strongly increases release probability for reptiles and amphibians but Fujisaki et al. (2010; Florida only) indicate this same variable does not translate into higher probability of successful establishment in these same taxa. Similarly, there is no reason to suspect that traits that are known to elevate establishment success or invasive spread, such as habitat breadth or competitive ability (van Wilgen and Richardson 2012), will have a strong influence on release probability.

Current management options aimed at reducing exotic pet releases include educating the pet-owning public of the ecological risks of releasing their pets (Reaser and Meyers 2007), or implementation by local agencies of 'buy backs' and 'amnesty events' for owners seeking to relinquish their pet (Hardin 2007). Our results provide an initial evidence base to allow such approaches to target particular species, and their owners, making these efforts more effective and efficient in their mission. Specifically, targeting species that are commonly sold and largebodied or long-lived will have the greatest effect in reducing the number of releases. Warning consumers about the zoonotic risks of exotic pets has been shown to decrease the probability a pet is purchased (Moorhouse et al. 2017). We therefore suggest that a similar strategy of making resources and information available about how a pet's adult size and longevity increases care requirements could help steer consumers away from purchasing reptiles and amphibians they are likely to release after initial purchase (Seekamp et al. 2016). In addition, to further help prevent consumers from releasing their exotic pets, it could be beneficial if retailers informed
consumers about safe places to surrender their pets such exotic pet shelters, amnesty events, or returns/buy backs to the retailers.

Integrating the release stage into risk management can result in a more robust and accurate assessment of invasion risk (e.g., Leung and Mandrak 2007). Our approach utilizes information common to existing invasion risk assessments (e.g., life history traits), or can be easily aquired (e.g., current price or popularity), allowing for easier and immediate integration of release risk factors. Such risk assessments have been used to guide legislation aimed at curbing invasions through import bans of high risk species (e.g., through the Lacey Act in the US: Fowler et al. 2007). Our results are particulary helpful in this context as the diversity of reptile and amphibian species sold as pets has been steadily increasing over the last two decades (Romagosa 2014). Finally, our results can be used to craft legislation targeted at reducing the probability of release of species. For example, our results can be used to target taxing and licensing efforts towards high release-risk species, requiring retailers to only sell single-gendered individuals of a high-release risk species, and 'tagging' (via microchips) individuals from high riskrelease species. No matter the approach, a data-driven effort to document factors that result in exotic pet releases can advance a more comprehensive, evidence-based approach to risk management and policy implementation.

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## Tables

Table 1. Biological and economic factors hypothesized to influence the probability that a pet reptile or amphibian will be released as free-living by their owners. Sample size represents the number of species that have data for the variable (out of a total of 1722 species).

| Name | Description | Sample Size | Expected Effect on Release Probability |
| :---: | :---: | :---: | :---: |
| Life History |  |  |  |
| Adult Mass | mean body mass of adults (g) | 1115 | $\uparrow$ |
| Longevity | maximum number of years known to survive either in wild or in captivity | 909 | $\uparrow$ |
| Reproductive <br> Output | number of eggs per year, calculated by multiplying clutch size by clutch frequency | 748 | $\uparrow$ |
| Economic |  |  |  |
| Quantity <br> imported | total number of live individuals imported into the US (designated for the pet trade) from $1999 \text { to } 2013$ | 1426 | $\uparrow$ |
| Price | five-year median of the retail price of a species (US\$) | 627 | $\downarrow$ |
| Time on Market | number of years that a species was available for sale on the pet market (from 1 to 18 years) | 1722 | $\uparrow$ |

Table 2. Results from boosted regression tree model. $\Delta P$ (release) is a measure of the effect size of the variable and is calculated as the range of the partial dependency plots (Figure 4). Relative contribution is a measure of variable fit and is scaled so that the contributions of all variables adds up to $100 \%$, where higher numbers indicate stronger contributions.

| Variable | $\Delta$ P(release $)$ | Relative |
| :--- | ---: | :--- |
|  |  | Contribution (\%) |
| Quantity imported | 0.48 | 29.7 |
| Price | 0.23 | 22.1 |
| Adult mass | 0.21 | 17.2 |
| Time on market | 0.10 | 8.5 |
| Longevity | 0.09 | 11.5 |
| Reproductive | 0.04 | 11.0 |

## Figures



Figure 1. (a) Species for sale in the US exotic pet market by taxonomic group. The groups in order from left to right are: Anura, Caudata, Crocodylia, Testudines, Lacertilia, and Serpentes.

The percentages of species in each taxonomic group recorded as released are listed above each bar. (b) Number of years species were available for purchase within the US exotic pet market.


Figure 2. Comparison of retail age/size (vertical lines) and longevity/adult size (histograms) for each taxa. (a; left column) Longevity of species sold on the US exotic pet market by taxonomic group. (b; right column) Adult mass of species sold on the exotic pet trade by taxonomic group. Vertical solid lines indicate the median retail age (a) or retail mass (b) of all species in the specified group. Dashed vertical lines represent the 5 and 95 percentiles of retail age (a) or retail mass (b). Note for Caudata, there was no data for retail age, and for Crocodylia the retail mass was recorded for only one species, hence no visible percentile lines.


Figure 3. Partial dependency plots showing effects of biological and economic factors on release probability for exotic pet reptiles and amphibians in the US generated from our boosted regression tree analysis. Partial dependency plots show the effect of a given explanatory variable on release probability, while holding the effects of other explanatory variables at their average. We used 500 bootstrap replicates to calculate the $95 \%$ confidence intervals, depicted in grey. Note that several of the $x$-axes are on a $\log _{10}$ scale. Across the top of each plot is a rug plot showing the distribution of data points.


Figure 4. Interactions in our boosted regression tree (BRT) model explaining release probability of exotic pet reptiles and amphibians in the US, including (a) quantity imported and adult mass, (b) price and adult mass, and (c) quantity imported and longevity. Contour lines with associated numbers represent factor of $10 \%$ increases in release probability. Darker shades indicate higher probability of release as predicted from the BRT model. Interaction sizes for each interaction are 56 (a), 16 (b), and 4 (c).

## Supplemental Material

Supporting Information S1. Methods for collecting information from online pet stores

Supporting Information S2. Methods for compiling life history databases

Supporting Information S3. Details of the relative price between species

Supporting Information S4. Methods of retail age and mass classification

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Table S1. Translation of word description of age and mass to numeric values

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Figure S3. Bar plot of probability of release for each Family

Figure S4. Boxplot of probability of release for each Order

## References

## Supporting Information S1. Methods for collecting information from online pet stores

We selected the three most trafficked (Alexa Website Traffic, May $17^{\text {th }}, 2017$, www.alexa.com) reptile and amphibian internet-based pet stores for our analysis (UndergroundReptiles.com, LLLReptile.com, and BackwaterReptiles.com). We collected information from each vendor using web scraper code, optimized for each vendor website. The web scraper recorded for each pet type listed the individual's scientific name, common name, and price. We excluded information that pertained to hybrid species or for those individuals listed only according to their Genus. Some of the species for sale were labeled "out of stock" and therefore were not available for immediate purchase. However, we assumed that if the vendor keeps the listing on their website they intend to refill the "stock" in the near future and we included these species in our analysis.

We used the web archive (http://archive.org/web) to access 556 archived 'snapshots' of these websites dating back to 1998 (accessed March 2017 to May 2017). Not all websites were archived across all years, with the vast majority of snapshots occurring after 2011. Therefore, we kept snapshots from years where all three vendors were archived (2012 to 2016) resulting in 126 snapshots. Temporal coverage in snapshots were evenly distributed among vendors, and over $80 \%$ of months had snapshots from at least two vendors and only three months had no snapshots (Figure S2). We coded the web scrapers in R , using the package RSelenium v 1.7.1.

From these online pet retailers, we collated 94,230 unique individual pet listings representing 652 species, of which 167 were not listed in the 1999 to 2016 LEMIS import dataset above. Half of those species (83) were available from online pet retailers but not found in the LEMIS import database are native to the US or have established non-native ranges in the US. On the whole, however, the web vendor data was a close match to the LEMIS information collected
in the same years (2012 to 2016). We found that $85 \%$ of species recorded in LEMIS were also recorded by the web vendors, after having excluded species native to the US listed by vendors.

For all 1722 species we verified the scientific name listed by the vendors or by LEMIS by matching it to the Catalogue of Life taxonomy database (Roskov et al. 2017, via the R package taxize v 0.8 .4$)$. We did not use pictures provided on websites to verify species identification. If the scientific name could not be verified as above, we matched the given scientific name with synonyms. If neither a scientific name nor the synonym could be verified, we used the common name listed by the vendor or LEMIS to identify the species using Encyclopedia of Life: trusted common names.

## Supporting Information S2. Methods for compiling life history databases

For our explanatory variables that were life history traits, we compiled data from five published databases: AnAge (de Magalhaes and Costa 2009), Mahoney et al. (2015), Amniote (Myhrvold et al. 2015), Allen et al. (2017), and AmphioBIO (Oliviera et al. 2017). Within a database, if data was available for males, females and/or 'no sex', we calculated the arithmetic average across categories and used this in our models. Within a database if clutch size was reported as two values, max and min, we used the average of these in our models. To compile these databases, we first used the AnAge database as the default for longevity data and the Amniote database as the default for all other life history trait data. Next, we used the remainder of the databases to fill in missing values for traits in the following priority (from first to last priority): AmphiBIO, Allen, Anage (non longevity traits), and Mahoney.

## Supporting Information S3. Details of the relative price between species

Price data was collected from the web vendor listings (Supporting Information S1; available from 2012 to 2016). Since the price of imported individuals is not available to us from the LEMIS database, we could not track price changes that occurred prior to 2012. However, we ensured that the price information collected from the web vendors adequately differentiated the value of each species relative to each other through time, thus providing assurance that the price differences between species calculated since 2012 are a robust indicator of pricing across our entire time series. Median prices did vary across vendors for a single species, however, this variation was significantly less compared to prices across species (Mann-Whitney $U$ test, $n_{\text {across }}=$ $592, n_{\text {within }}=590, p=0.01$, one-tailed, mean coefficient of variation across vendors $=0.23$, mean coefficient of variation across species $=0.32$ ). The year to year variation in price within a species was significantly different for most species with complete data (i.e., > 30 listings for $\geq 3$ years; ANOVA, $\mathrm{n}_{\text {species }}=329, \mathrm{p}<0.05$ for $88 \%$ of species), yet the relative ranking of the median price among species was stable for most species ( $85 \%$ of species stayed within $10 \%$ of their median price relative rank from year to year, $n_{\text {species }}=317$ ).

## Supporting Information S4. Methods of retail age and mass classification

To characterize the retail age and mass of species on the pet market, we used web scraper software (Web Scraper, Google Chrome Extension) to record information word descriptions of retail age and mass. We translated these word descriptions into numeric values (Table S1) by using life history traits collected for the BRT analysis. Given the difficulty in automating this process, this translation was only done for one-time period from information collected on June 16, 2016 under the assumption that retail age and mass has not changed drastically through time. This analysis resulted in a sample size of 143 species for retail age for 116 species for retail mass.

From this translation, we were able to calculate the variables 'years lived after purchase' and 'mass grown after purchase' by subtracting the median retail age and median retail mass of a species from their maximum longevity and adult mass, respectively. We believe these two variables represent a more causal relationship as to why pet owner may no longer be able to care for their pets compared to maximum longevity and adult mass. Yet, we found that 'years lived after purchase' and 'mass grown after purchase' were nearly perfectly correlated with longevity and adult mass since most species are sold young and small (linear regression $r^{2}=0.92$ and 0.99 , respectively). Therefore, taking into consideration that more data is available for longevity and adult mass, we used these variables in the analysis.

## Supporting Information S5. Details of Boosted Regression Trees algorithm, parameters used and testing of simpler models

## BRT algorithm and handling of missing data

BRTs use decision trees to explore explanatory variable parameter space to identify which parameter values minimize predictive error. BRT further increases predictive performance through boosting, which combines many simple decision trees in a stage-wise updating manner, where each sequential tree is fitted to residuals of the previous tree. The final model is an average across all sets of trees (Elith et al. 2008). To evaluate model performance BRT uses kfold cross-validation (see De'ath \& Fabricius, 2000 for details). In BRT, $r^{2}$ is calculated as (null deviance - residual deviance)/null deviance.

Parameters used and testing of simpler models
For the boosted regression tree models, we used a tree complexity of 3, learning rate of 0.001, and a bag fraction of 0.5 . We used 10 -fold cross-validation to avoid overfitting. Slower learning rates and higher tree complexities resulted in negligible increases in model performance. We tested simpler models by iteratively removing explanatory variables, but all simpler models resulted in a decrease in model performance (a decrease in $r^{2}$ ).

## Supporting Information S6. Details of Boosted Regression Trees models that included taxonomy and testing for a phylogenetic signal

## Rationale and Methods

Accounting for phylogenetic correlations is necessary in cross-species comparative analyses to avoid treating species with shared ancestry as statistically independent data points (Felsenstein 1985, Freckleton et al. 2002, Dunham \& Miles 1985). Ignoring phylogenetic correlations can result in incorrect or misleading conclusions (e.g., Felsenstein 1985). To the best of our knowledge, there are currently no methods to account for or measure phylogenetic correlation (i.e., Pagel's $\lambda$, Freckleton et al. 2002) for machine learning techniques such as the boosted regression trees. However, among comparable papers that used boosted regression trees with trait data we found that they used taxonomy as proxy for phylogeny (i.e., van Wilgen and Richardson 2012, Schmidt and Drake 2011). We therefore followed their protocol and conducted an additional BRT model that included the taxonomic level of Order (we split the Order of Squamata into the Suborders Lacertilia and Serpentes yet continued to call this variable 'Order' for simplicity). We compared the results of the BRT models with and without taxonomy to determine the degree to which phylogeny explains differences in release probability.

As a further check to determine the degree of phylogenetic pseudo-replication in our analysis, we compared the 'within' and 'across' variation in release probability (our response variable) between Orders. We chose the taxonomic level of Order because this is the level of phylogenetic detail found in comparable studies on alien reptiles and amphibians (Allen et al. 2017, Van Wilgen and Richardson 2012). If there is a strong phylogenetic signal, we would expect the 'across' Order variation in release probability to be larger than the 'within' Order variation. If there is a weak phylogenetic signal, we would expect the 'across' Order variation in release probability to be smaller than the 'within' Order variation. Finally, if there is no
phylogenetic signal we would expect no 'across' Order variation. To perform this comparison, we calculated the release probabilities for each Family as predicted from a separate BRT model that included Family (Figure S3) and grouped each Family by their Order (Figure S4). We then performed a one-way ANOVA between Order and release probability.

## Results

The model performance of the BRT model (cross-validated $r^{2}$ and AUC) with taxonomy was similar to the model without taxonomy (Table S2). In the model that included taxonomy, Order showed low relative contribution and low $\Delta \mathrm{P}($ release) (Table S2), where the differences in release probability between Orders was small, ranging from 10 to $18 \%$ (Table S3).

For the comparison of the 'across' and 'within' variation in Order release probability, we found the F -value was 0.948 (ANOVA, $\mathrm{p}=0.45$, indicating means across Orders are not significantly different). Since the F-value in an ANOVA is a ratio of the variance of the 'across' Order means vs. the 'within' Order variances, we conclude there is a relatively weak phylogenetic signal in our analysis.

## Discussion

The BRT model suggests that the broad taxonomic group of Order does not play an important role in explaining releases. Importantly, the model performance for the BRT model with taxonomy was not improved in relation to the model without taxonomy. This result suggests that taxonomy does not add to substantially to explaining variation in probability of release pet reptiles and amphibians. Our additional check for phylogenetic correlation confirmed that there was a weak phylogenetic signal across Orders.

Table S1. Translation of word description of age and mass given by a web vendor to numeric values. We reviewed each pet listing for a word description then translated this to a numerical value of years and/or grams. If there was no data for the variable needed for the translation, another variable was used, indicated by "OR" in the translation columns. While these translations are approximate, we believe that they are within a margin of error acceptable enough to for the qualitative comparison of retail age to maximum age and retail mass and adult mass (shown in Figure 2).

| Word Description | Age translation | Mass translation |
| :--- | :--- | :--- |
| 'Baby' or 'hatchling' | $25 \%$ age at sexual maturity OR <br> $10 \%$ longevity OR <br> 0.5 years old | $100 \%$ birth mass <br> OR <br> $10 \%$ adult mass |
| 'Yearling' | 1.5 year old | $50 \%$ adult mass |
| 'Young adult', 'young', <br> 'juvenile', or 'sub-adult' | $50 \%$ age at sexual maturity OR <br> $25 \%$ longevity | $50 \%$ adult mass |
| 'Adult' | $50 \%$ longevity | $100 \%$ adult mass |
| 'Small' | - | $20 \%$ adult mass |
| 'Small - medium' | - | $40 \%$ adult mass |
| 'Medium' | - | $60 \%$ adult mass |
| 'Medium - large' | - | $100 \%$ adult mass |
| 'Large' | - |  |

Table S2. Results of a boosted regression tree model evaluating the influence of biological and economic factors in probability that a pet reptile or amphibian is released in the US, excluding and including taxonomy.

|  | without taxonomy |  | with taxonomy (Order) |  |
| :---: | :---: | :---: | :---: | :---: |
| variable | variable magnitude | relative contribution (\%) | variable magnitude | relative contribution (\%) |
| Taxonomy |  |  | 0.07 | 6 |
| Quantity imported | 0.48 | 30 | 0.5 | 27 |
| Price | 0.23 | 22 | 0.26 | 21 |
| Adult mass | 0.21 | 17 | 0.28 | 17 |
| Time on market | 0.1 | 9 | 0.84 | 8 |
| Longevity | 0.09 | 12 | 0.13 | 11 |
| Reproduction | 0.04 | 11 | 0.06 | 10 |
| CV r ${ }^{2}$ | 0.5 | 51 | 0.5 | 51 |
| CV AUC | 0.8 | 89 |  | 89 |

Table S3. Probability of release pet amphibian or reptile release in the US for each Order as calculated from the BRT model that included Order.

| Order | Prob. release | Number of species |
| :--- | ---: | ---: |
| Lacertilia | 0.18 | 739 |
| Crocodylia | 0.16 | 11 |
| Serpentes | 0.11 | 490 |
| Testudines | 0.11 | 196 |
| Caudata | 0.10 | 45 |
| Anura | 0.10 | 237 |



Figure S1. Price distribution for web vendor listed pets. This histogram includes the price of 91,985 individual web listings of pet reptiles and amphibians sold in the US from 2012 to 2016.


Figure S2. Monthly coverage of web of archive snapshots for the three amphibian and reptile pet vendors operating in the US. A snapshot represents an archived version of the vendor website.


Figure S3. The probability that pet reptiles and amphibians sold in the US being released as freeliving as predicted from the boosted regression trees that include taxonomic Family affiliation.


Figure S4. Amphibian and reptile pet release probability as predicted by the boosted regression trees analysis by Family, grouped by Order. Each dot represents the release probability of one Family. ANOVA analysis demonstrate that variation within an Order is greater than across Orders (F-value $=0.948$ ), indicating a weak phylogenetic signal in our analysis. In addition, there was no significant difference between Orders ( $p=0.48$ ).

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Reducing propagule pressure to lower the establishment probability of potential invasive species


#### Abstract

Biological invasions cause massive economic and ecological damages. Preventing non-native species from establishing is a cost-effective way to avoid the negative impacts of potential invasive species. Reducing propagule pressure is a recognized solution to lowering establishment probability. Here, we develop a method for a propagule-pressure reduction sensitivity analysis, which can reveal how much reduction in propagule pressure is required to reach a policy relevant level of establishment probability. We use a probabilistic model of establishment probability to simulate realistic values of propagule pressure. We then systematically simulate reductions in propagule pressure and record the resulting marginal change in establishment probability. Importantly, we note the presence of nonlinear threshold values that must be surpassed before establishment probability can be reduced. In addition, we show that predicting the required reduction in propagule pressure is highly dependent on knowledge of propagule-pressure levels (propagule size and number) and the risk-release relationship of the species in question. The methods presented here, in combination with information on costs of propagule-pressure reduction, can be used to determine the most costeffective way to lower establishment probability via a reduction in propagule pressure.


## Introduction

Our capacity to prevent future biological invasions depends on our ability to assess the establishment probability of likely invasive species and develop strategies to lower this risk (Lodge et al. 2016, Genovesi et al. 2015). Predicting establishment probability requires information on environmental suitability, species traits, propagule pressure, and population dynamics (Catford et al. 2009, Leung et al. 2012). From a risk-reduction perspective, lowering or eliminating propagule pressure is the only active option that will reduce establishment probability as species traits and environmental suitability are fixed (Albert et al. 2013). While methods to incorporate propagule pressure into establishment probability calculations have existed for over a decade (Leung et al. 2004, Leung \& Mandrak 2007), a method to determine the amount of propagule-pressure reduction required to reach a desired establishment probability has yet to be developed. Similar analyses are routine in other fields, such as the sensitivity/elasticity analyses used alongside endangered-species population models (Morris and Doak 2002). In this context, sensitivity analyses have allowed for improved understanding between vital rates (model inputs) and extinction probability (model output) and, in conjunction with simulating increases in different vital rates (management actions), have yielded improved management outcomes (e.g., Crowder et al. 1994). Likewise, the knowledge gained from a sensitivity analysis on propagule-pressure reduction can guide practitioners and policymakers toward context-specific management plans and/or policy standards to lower establishment probability while still allowing associated trade to persist (e.g., ballast-water standards; Wonham et al. 2005).

Reducing propagule pressure is a recognized solution to lowering establishment probability (Albert et al. 2013). Accordingly, propagule-pressure reduction is either an implicit or explicit component of many policy measures (e.g., standards) aimed at lowering the
establishment probability of alien species (NRC 2011, Albert et al. 2013). However, a commonality of these standards is their lack of specificity in one or more components of establishment probability calculation. For example, the International Maritime Organization standard for ballast-water discharge addresses propagule size (discharge to be less than 10 viable organisms per $\mathrm{m}^{3}$; IMO 2004), yet, that standard does not incorporate the number of introduction events or take into consideration the influence of different species. Another standard aimed at preventing the establishment of wood-boring insects (International Standards for Phytosanitary Measures No. 15; ISPM15), specifies treatment of wood-packing materials via heat or fumigation (IPPC 2002) and does not directly include any information on propagule pressure by assuming treatment will reduce propagule pressure to zero. While the implementation of ISPM15 has effectively halved the infestation rate of wood-packing material (Haack et al. 2014), it is still predicted that over 200 establishments of wood-boring insects from wood-packing materials will occur in the US through 2050 (Leung et al. 2014). This lack of specificity in policies may result in either more spending than needed for management (overestimation of risk), or it may fail to prevent establishments (underestimation of risk). To make more specific and effective policies, there needs to be a method to calculate the amount of propagule-pressure reduction needed to reach a desired establishment probability.

Here, we develop a method that incorporates a propagule-pressure reduction sensitivity analysis into establishment probability calculations. We aim to demonstrate the utility of this sensitivity analysis, which can reveal the magnitude of reduction of propagule pressure required to reach a policy-relevant level of establishment probability. We use a probabilistic model of establishment probability to simulate realistic values of propagule pressure along its two components: propagule size and the number of introduction events. We then systematically simulate reductions in propagule pressure and record the resulting marginal change in
establishment probability. We explore the effects of different species traits and levels of environmental suitability (i.e., risk-release relationships; Wonham et al. 2013) on the efficacy of propagule-pressure reduction. Our methods, in combination with bioeconomic analyses of management costs (Lodge et al. 2016), can provide practitioners and policy makers a specific and practical path to lower establishment probability via propagule-pressure reduction.

## Methods

Calculating establishment probability: three essential components

We adopted previous methods that calculate establishment probability (Leung et al. 2004, Wonham et al. 2013, Duncan et al. 2014, Pigot et al. 2017) and distilled this calculation into three main components (e.g., model parameters; Table 1). The first two components are encompassed in the definition of propagule pressure (Lockwood et al. 2005): (1) propagule size (PS), defined as the number of individuals of a single species introduced into a specific nonnative locale and (2) the number of introduction events (NI), defined as the total number of occasions an introduction event occurs in a given location across time, where each introduction event has an associated propagule size. The third component is the within-species relationship between propagule size and probability of establishment, referred to as the risk-release curve (Wonham et al. 2013). The risk-release curve is determined by species traits, population growth dynamics (i.e., Allee effects; Tobin et al. 2011), environmental suitability, and potential biotic interactions (Catford et al. 2009, Bradie and Leung 2015, Cassey et al. 2018).

We calculated the overall probability of establishment, henceforth $P E$, using the following equation (see Figure 1 for illustrative representation of calculation):

$$
P E=1-\prod_{n=1}^{N I}\left(1-w_{n}\right)
$$

where $w$ is the probability of establishment for one given introduction event ( $n$ ), as determined by the risk-release curve, which is a function of propagule size $(P S)$ and species-specific characteristics (see equation 2 ). NI is the total number of introduction events. The term $1-w_{n}$ refers to the probability that one given introduction event fails to result in establishment. Thus, the term $\prod_{n=1}^{N I}\left(1-w_{n}\right)$ yields the probability that all introduction events fail to result in establishment. When subtracted from 1, it yields the probability that at least one introduction event will successfully establish (i.e., result in a persistent population). This calculation of $P E$ conservatively assumes that that all introduction events are spatially and temporally independent, so that no individuals survive between introduction events.

## Modelling different risk-release curves

The risk-release curve is the within-species relationship between propagule size and establishment probability for a given location of introduction (Wonham et al. 2013). Many factors can alter the risk-release curve including the environmental suitability of the location of introduction, biotic interactions, species traits, and population growth dynamics such as Allee effects (Catford et al. 2009; Cassey et al. 2014, Tobin et al. 2011, Duncan et al. 2014, Sol et al. 2012, Allen et al. 2017, Cappellini et al. 2015, Koop et al. 2012, Hayes and Barry 2008, Bomford et al. 2009). The slope of the risk-release curve is affected by differences in survival and reproduction for any given propagule size (Wonham et al. 2013). Risk-release curves can be derived from a variety of methods (Table 1), including from lab/mesocosm dose-response experiments (e.g., Berggren 2001), statistical correlations between propagule pressure and establishment records (e.g., García Díaz et al. 2015), and simulated population models (e.g., Cassey et al. 2014). The risk-release curve is positive and generally nonlinear (Cassey et al. 2018), and changes in shape and magnitude depending on the aforementioned factors (Leung et
al. 2004). Although incorporating the risk-release relationship has clear implications in the calculation of establishment risk (equation 1), it is rarely quantified (Cassey et al. 2018). A recent meta-analysis found that only 56 studies have quantified the risk-release relationship and only 11 of those studies were experimental (Cassey et al. 2018). While there are certainly logistical, ethical, and monetary obstacles to measuring this relationship, this information has the potential to alter the calculation of establishment probability and, thus, is highly relevant to policy makers (Cassey et al. 2018).

Notwithstanding the importance of the risk-release relationship to establishment probability, understanding how different risk-release curves may alter the efficacy of propagulepressure reduction remains untested. Here, we assessed the influence of the risk-release relationship in the context of propagule-pressure reduction by exploring two distinct risk-release curves differing in their 'establishment potential'. We modelled one risk-release curve that was 'amenable' to establishment (high establishment potential) and another curve that was relatively 'unamenable' to establishment (low establishment potential). We parameterized these curves by using risk-release curves derived by Cassey et al. (2014), themselves derived from population models of a short-lived songbird species with and without factors that negatively affect survival/reproduction (i.e., Allee effects and environmental stochasticity). While we used risk-release curves derived from a songbird species, the curves may describe are characteristic of other species in different invasion pathways and different introduction locations (Cassey et al. 2018). We fitted these curves using nonlinear least squares to the following equation for risk-release relationship (Leung et al. 2004):

$$
\begin{equation*}
w=q^{P S^{c}} \tag{equation2}
\end{equation*}
$$

where $q$ is the fitted probability of a single propagule establishing, $P S$ is the propagule size of the given introduction event, and $c$ is a shape parameter that can accommodate for shifts in the curve due to any of the aforementioned factors. The amenable risk-release curve had a $q$ value of 0.9993 and $c$ value of 1.2171 , and the unamenable risk-release curve had $q$ value of 0.9918 and $c$ of 1.1802 (Figure 3a,c, Figure S).

## Values of propagule pressure explored

For this analysis, we explored realistic combinations of values of propagule size and the number of introduction events. PS ranged from 0 to 300 individuals per event, and NI ranged from 0 to 50 events. These values represent an empirically derived range of propagule pressure values for different invasion pathways (Hulme 2015). In particular, the escape pathway (e.g., pet releases) is characterized by having many introduction events with small propagule sizes (Kraus 2009; Dyer et al. 2017) while the stowaway pathway (e.g., ballast water) is characterized by having moderate to high number of introduction events with potentially high propagule sizes (Briski et al. 2011). The contaminant pathway (e.g., insect pests in wood packaging materials) falls somewhere between with relatively moderate propagule sizes and number of introduction events (Brockerhoff et al. 2014).

Sensitivity analysis: marginal change in probability of establishment from reducing propagule pressure

To implement the propagule-pressure reduction sensitivity analysis, first we calculated the PE for each combination of parameter values of PS and NI mentioned above (via equation 1 and 2) and visualized the results (Figure 3b,d). Next, we implemented the sensitivity analysis by lowering either PS or NI by a value of 1 while holding the other parameter constant, and then
calculated the marginal change in PE. This process was repeated for all explored values of PS and NI. This sensitivity calculation is an approximation for the partial derivative of each parameter:

$$
\begin{align*}
& \frac{\Delta P E}{\Delta P S}=P E\left(P S_{i}, N I_{j}\right)-P E\left(P S_{i-1}, N I_{j}\right) \\
& \frac{\Delta P E}{\Delta N I}=P E\left(P S_{i}, N I_{j}\right)-P E\left(P S_{i}, N I_{j-1}\right) \tag{equation3b}
\end{align*}
$$

where PE is a function of PS and $N I$, as defined in equation 1 and $2, i$ is a given value of PS, and $j$ is a given value of NI. The calculation was performed for values of $i$ from 1 to 300 and $j$ from 1 to 50. We visualized the results in two separate heatmaps, one of the marginal change in PE (termed $\triangle \mathrm{PE}$ ) with respect to PS and the other with respect to NI. This procedure was conducted for both risk-release curves. We characterized the resulting heatmaps by identifying thresholds, nonlinearity, and changes in $\triangle P E$. We compared how the two different risk-release curves affected the efficacy of propagule-pressure reduction.

In addition, to test the influence of each model parameter on the calculation of establishment probability, we performed a parameter uncertainty analysis (Wu and Li 2006), where the resulting variation in PE is measured when a given parameter is unknown. Details of the methods and results for the uncertainty analysis are reported in Supporting Information S1.

## Results

Overall, the sensitivity analyses revealed a complex relationship between propagule-pressure reduction and $\triangle P E$ that involved thresholds and nonlinearity that were altered by different riskrelease curves (Figure 3). We found that reducing propagule pressure (either propagule size or the number of introduction events) lowered PE only after certain thresholds were passed. For any reductions in propagule size (PS) or number of introduction events ( NI ) that occurred prior
to the thresholds, $\triangle$ PE was 0 and PE remained at 1 (Figure 3, Figure $2 b, c$ ). Moreover, the thresholds were nonlinear, meaning $\triangle$ PE differed for the same reduction in propagule size depending on the number of introduction events (and vice versa; Figure 3). The location of the thresholds was influenced by the nonlinearities found in the risk-release curves (Figure 2a, c, Figure 3), as well as the nonlinear effects of multiplying probabilities together (equation 1). The nonlinear behavior was most pronounced towards the lower ends of the parameter values (for PS reduction, nonlinear behavior occurred at $\mathrm{NI}<10$ and for NI reduction, at $\mathrm{PS}<50$ ). One consequence of this nonlinear behavior was that establishment probability began to decrease at higher values of propagule size under low number of introduction events compared to high number of introduction events, and vice versa. For instance, for propagule-size reductions, PE began to decrease at PS $=300$ for $\mathrm{NI}=1, \mathrm{PS}=120$ for $\mathrm{NI}=15$, and $\mathrm{PS}=90$ for $\mathrm{NI}=30$ (for unamenable risk-release curve; Figure 4c).

The unamenable risk-release curve resulted in PE reductions occurring at higher values of PS or NI in comparison to the amenable curve (i.e., the threshold values occurred at higher values of PS or NI when survival and/or reproduction of introduced individuals are relatively lower; Figure 3). For the unamenable curve, PS reduction yielded PE reductions at PS $<250$, while the species without Allee effects yielded PE reductions at PS $<50$ (for $\mathrm{NI}=5$; Figure 3a,b). Similarly, for the unamenable curve, NI reductions yielded PE reductions at $\mathrm{NI} \leq 50$, while the species without Allee effects realized PE reductions at $\mathrm{NI}<10$ (for PS = 50; Figure 3b,d). In addition, the magnitude of $\triangle$ PE increased as the reduction in PS or NI neared their lower bounds (i.e., $\mathrm{PS}<50$ or $\mathrm{NI}<10$ realized the largest $\triangle \mathrm{PE}$; Figure 4). In addition, the uncertainty analysis revealed that PE could be miscalculated by as much as 0.35 with an unknown propagule size, 0.45 with an unknown number of introduction events, and 0.80 with an unknown risk-release curve (Figure S1, S2, S3, respectively).

## Discussion

Given the severe social, economic, and ecological damages incurred by invasive species, and the continual introduction of new potential invasive species (Early et al. 2016, Seebens et al. 2017, Seebens et al 2018), it is essential to be able to predict which species have a high probability of establishment and be able to evaluate the efficacy of potential management strategies in lowering that probability. Here, we present a sensitivity analysis capable of determining the reduction in propagule pressure required to reach a desired establishment probability. Importantly, we note the presence of threshold values that must be surpassed before establishment probability can be reduced. These thresholds were nonlinear and influenced by both the risk-release relationship and the exponential nature of multiple introduction events. In addition, we show that predicting the required reduction in propagule pressure is highly dependent on knowledge of propagule-pressure levels (propagule size and number) and the risk-release relationship of the species in question. Otherwise, if one component is unknown, our results reveal that establishment probability can be miscalculated by as much as 80 percent.

While the relative importance of propagule size versus the number of introduction events (Sinclair and Arnott 2016, Drolet and Locke 2016, Cassey et al. 2014) and quantifying the risk-release relationship (Bradie et al. 2013, Duncan 2016) have been evaluated, methods to incorporate this information into policy are rare (Wonham et al. 2013, Pigot et al. 2017). Even though both propagule size and the number of introduction events may differ in their relative importance, depending on the context, for determining establishment success (Sinclair and Arnott 2016), our results show that reducing either component can lower establishment probability. Further, our results indicate that reducing propagule size or the number of introduction events is most effective when the other component is already low. For propagule-
size reduction, our results indicate that establishment begins to be lowered only when propagule size is relatively small. In the context of modern global trade and the unintentional release or 'escape' of alien species (e.g., exotic pet trade or horticulture trade), the number of introduction events may be especially important, as introduction events are likely to consistently occur in the same place (Hulme 2015). Pertinently, our results show that reducing the number of introduction events can be an effective way to lower establishment probability as long as the propagule size of those introductions remains low, as is the case in pet releases. Thus, reducing the number of exotic pet introductions can be effective way to lower establishment probability (Stringham and Lockwood 2018).

Policies aimed at lowering the establishment probability of non-native species generally do not set specifications for one or more of the components needed to calculate establishment probability (Albert et al. 2013). For example, standards for ballast-water discharge specify a limit on propagule size (IMO 2005) yet does not set a limit on the number of introduction events nor specify context-specific risk-release curves. We found, using uncertainty analyses, that excluding one of these components results in an uncertainty in establishment probability up to 35 to 80 percent, potentially rendering policies aimed at reducing establishment probability ineffective. Our findings suggest that a more holistic approach of explicitly incorporating all three components of establishment into policies is necessary to determine the amount of propagulepressure reduction required to reach a desired establishment probability. In addition, when all components needed for establishment calculations are known, the sensitivity analysis method we present can serve as a guide on how to calculate the amount of propagule-pressure reduction required.

Although the sensitivity analysis presented here can inform policy options, implementing such options will require an economic cost-benefit analysis. The methods
presented here, in combination with information on costs of propagule-pressure reduction, can be used in bioeconomic optimization models (Clark 2010, Lodge et al. 2016) to determine the most cost-effective way to lower propagule pressure. In some cases, if the cost of reducing propagule pressure is too high, then money may be better spent on another species whose cost to reduce propagule pressure is within budget (Epanchin-Niell 2017). On the other hand, several ecological factors may negatively affect introduced individuals (e.g., severely intolerant to the local environment), thereby naturally lowering establishment probability and rendering propagule-pressure reduction unnecessary. For these situations where the risk-release curve is highly unamenable to establishment, managers need not to focus on lowering propagule pressure since the establishment probability may already be low enough. Contingent upon successful management and cost-optimization calculations are knowledge of current propagule pressure levels and risk-release curves for the species in question. We have demonstrated that knowledge of these components is necessary to determine establishment probability, which also extends to predicting the most cost-effective management route to lowering risk.

Given the need for data on propagule pressure and the hazards of using proxies (Pigot et al. 2017), we advise parties interested in managing invasive species to set up monitoring protocols to measure actual propagule pressure (Latombe et al. 2017). Some monitoring systems, which are already in place, can serve as a tool for estimating propagule pressure. For instance, border interceptions have the potential to estimate propagule pressure of alien insects arriving through trade (Brockerhoff et al. 2014, Caley et al. 2015). Importantly, these monitoring programs should include taxonomic experts that can identify individuals down to the species level (Saccaggi et al. 2016). Since establishment is a population process, almost all useful information is lost if propagule pressure data is grouped by taxonomic levels higher than species (i.e., genus, family, etc.) (Smith et al.2009, Rhyne et al. 2012, Lockwood et al. 2009). In addition,
emerging technological advances in environmental DNA analyses (Valentin et al. 2018) may be adapted to estimate propagule pressure levels. While eliminating invasion risk entirely via species or trade bans are the safest ways to avoid biological invasions (Keller and Springborn 2014), these bans may not be compatible with modern globalization and global trade, which affords vast economic benefits (Hulme 2015). The management strategy of reducing propagule pressure can provide an alternative to bans if the net economic benefits of trade is outweighed by the cost of monitoring and managing for propagule pressure.

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## Tables

Table 1. Components of the probabilistic model used to calculate probability of establishment.

| Component | Abbre- <br> viation | Description | Sources of data (and examples from <br> the literature) |
| :--- | :--- | :--- | :--- |
| number of <br> introduction <br> events | NI | The number of times an <br> introduction event occurs | From recorded data or proxies ${ }^{1}$ |$|$| propagule size | PS | The number of introduced <br> individuals for a given introduction <br> event | From recorded data or proxies ${ }^{1}$ |
| :--- | :--- | :--- | :--- | | The relationship between propagule |
| :--- |
| risk-release |
| relationship |

1 Leung et al. 2014, 2 Cassey et al. 2018, 3 Bradie and Lueng 2015, 4 Cassey et al. 2014, 5 Wonhan et al. 2013

## Figures



Figure 1. Overview of the process to calculate probability of establishment. Blue borders indicate 'raw' data needed from system. Purple border indicates calculated values. When the propagule size is not known for every introduction event (such in the case of accidental or introductions not recorded), then a distribution can be used (as shown). Using a distribution for propagule size allows for inclusion of uncertainty, which is reflected in the calculation of probability of establishment.


Figure 2. Risk-release curves showing the relationship between propagule size (PS) and probability of establishment (PE): (a) amenable risk-release curve where survival/reproduction of introduced individuals are not negatively affected and (c) relatively unamenable risk-release curve to establishment, where negative factors decrease the survival and/or reproduced of introduced individuals. The resulting PE for all combinations of propagule size and number of introduction events (NI) under (c) the amenable risk-release curve and (d) the 'unamenable' risk release curve. Darker shades of red indicate a higher PE.


Figure 3. Marginal change in establishment probability resulting from reducing propagule size (PS; panels a and c) or the number of introduction events (NI; panels band d) by increments of 1 (equation 3). Darker colors indicate a higher marginal reduction in PE per unit reduction in propagule pressure (e.g., higher $\Delta \mathrm{PE}$ ). Gray areas indicate $\triangle \mathrm{PE} \approx 0$. Panels (a) and (b) were calculated from the amenable risk-release curve and panels (c) and (d) from the unamenable risk-release curve. The direction of the arrow indicates the direction to read the plot. For example, in panel (a) PS was reduced by increments of 1 starting at 300 and ending at 0 . The resulting heatmap shows the $\triangle$ PE for that reduction of 1 individual of PS for each value of NI. Contour lines are in increments of $0.2 \%$. We used a blue color palette to highlight the negative marginal change in establishment probability.

## Supplemental Material

Supporting Information S1. Methods and results for uncertainty analysis
Figure S1. Results from the uncertainty analysis of an unknown propagule size
Figure S2. Results from the uncertainty analysis of an unknown number of introduction events
Figure S3. Results from the uncertainty analysis of an unknown risk-release curve
References

## Supporting Information S1: Methods and results for uncertainty analysis

## Methods

To test the influence of each model parameter on the calculation of establishment probability, we performed a parameter uncertainty analysis (Wu and Li 2006), where the resulting variation in PE is measured when a given parameter is unknown. We explored three different scenarios of uncertainty: (1) an unknown propagule size, known number of introduction events, and known risk-release curve; (2) an unknown number of introduction events, known propagule size, and known risk-release curve; and, (3) an unknown risk-release curve, known propagule size, and known number of introduction events. These scenarios are reflective of real-world data limitations and policy standard specifications aimed at avoiding establishment (Albert et al. 2013).

To implement the parameter uncertainty analysis for PS and NI, we assumed the 'unknown' parameter followed a uniform distribution around the values explored in this study (1 to 300 for PS and 1 to 50 for NI). Next, we used 10,000 iterations of Monte Carlo sampling for the 'unknown' parameter to generate a distribution of values for PE (via equation 1 and 2 ) for each combination of 'known' parameters (Wu and Li 2006). Then, we took the difference between the 75 and 25 percentile values in PE (approximately two standard deviations) and called this metric the 'uncertainty in PE' (Figure S1, S2). This metric represents the variation in establishment probability when the parameter in question is 'unknown'. For example, to implement the uncertainty analysis when PS is unknown, we sampled PS from a uniform distribution from 1 to 300 and calculated the distribution of PE for every combination of NI and risk-release curve (Figure S1, top row). Then, we subtracted 75th percentile from the 25th percentile of PE values to obtain the 'uncertainty in PE' metric (Figure S1, bottom row). For the scenario with an unknown risk-release curve, to obtain the 'uncertainty in PE' metric, we
calculated the PE for each combination PS and NI for each risk-release curve, then subtracted the PE values of the amenable curve from the unamenable curve (Figure S3).

## Results

Establishment probability had little variation towards the upper ends of the parameter values, where $P E \approx 1$ for all values of the unknown parameters. However, towards the lower ends of parameters values, where PE was less than 1 , there was notable variation in the calculation in of PE. Here, the 'uncertainty in PE' was as high as 0.35 with an unknown propagule size, 0.45 with an unknown number of introduction events, and 0.80 with an unknown riskrelease curve (Figure S1, S2, S3, respectively). For an unknown risk-release curve, the uncertainty in PE was highest when PS and NI values were low (<10).

The unamenable risk-release curve caused the uncertainty in PE to affect a wider range of parameter values in comparison to the amenable risk-release curve. For example, under an unknown NI (Figure S2), under the amenable risk-release curve, uncertainty in PE was greater than zero for PS values from 0 to 20 but was expanded for the unamenable risk-release curve to PS values from 0 to 150 .


Figure S1. Results from the uncertainty analysis of an unknown propagule size (PS), known number of introduction event (NI), and known risk release curve (either amenable or unamenable). Top row: the distributions in PE for each value of NI when PS is unknown. Bottom row: the 'uncertainty in PE' for each value of NI, calculated as difference between 75th percentile and the 25th percentile in PE.


Figure S2. Results from the uncertainty analysis of an unknown number of introduction events (NI), calculated at each value of propagule size (PS). Top row: the distributions in PE for each value of PS when NI is unknown. Bottom row: the 'uncertainty in PE' for each value of PS, calculated as difference between 75 th percentile and the 25 th percentile in PE.


Figure S3. Results from the uncertainty analysis of an unknown risk-release curve. To obtain the 'uncertainty in PE' metric, we calculated the PE for each combination PS and NI for each riskrelease curve, then subtracted the PE values of the amenable curve from the unamenable curve. Darker shades of red indicate higher uncertainty of PE for those combinations of PS and NI.

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Spatial or temporal overlap in introduction events can elevate establishment probability through rescue effects


#### Abstract

Preventing additional establishments of non-native species is considered the most effective way to avoid the negative impacts of invasive species. Propagule pressure is the most consistent indicator of the establishment probability and has been incorporated in models of establishment probability used in policies focused on preventing establishments. Long standing in the definition of propagule pressure and in establishment calculations is the assumption that each introduction event is spatially and temporally independent of all other events. If this assumption is violated, establishment probability will be underestimated. However, it remains unclear when and by how much violating spatial and temporal independence alters establishment probability. Here we use a spatially explicit, discrete-time, stochastic population model to document when and if non-independence can safely be ignored and record the associated increase in establishment probability due to non-independence. We find that nonindependence follows intuitive patterns where spatial non-independence becomes more prevalent as the distance between initial introduction locations decreases and temporal nonindependence becomes more prevalent as the time between introduction events decreases. Furthermore, we find that non-independence can cause establishment probability to be underestimated by up to $70 \%$. We suggest that risk assessments, policy development, and management actions must explicitly consider the likelihood of propagule pressure-rescue effects.


## Introduction

The heavy economic and ecological costs of invasive species support that policies that prevent non-native species from establishing in the first place are more efficient than postestablishment control and management (Keller \& Springborn 2014). Prevention sharply focuses research on the early invasion stages of introduction and establishment (Blackburn et al. 2011). If such research can isolate principal ecological processes that elevate initial population establishment, then policy and management can be targeted accordingly (Hulme 2015, Finnoff et al. 2007, Lodge et al. 2016). A consistent factor in raising establishment success is high propagule pressure, where pressure is defined as the number of individuals initially released at a single location (an introduction event; Cassey et al. 2018). High propagule pressure can be achieved by having one introduction event of many individuals or several independent events with few individuals (Lockwood et al. 2005). Most models of establishment include a propagule pressure effect (Leung et al. 2004, Wonham et al. 2013), including those used in academic research (Pigot et al. 2017, Duncan et al. 2014), risk assessments (e.g., Leung et al. 2014), and policy formulation (Albert et al. 2013). A critical assumption of these models is that each introduction event is spatially and temporally independent of all other events (Wonham et al. 2013). If this assumption is violated, establishment probability will naturally be underestimated since the functional number of individuals available to form a self-sustaining population will be higher than the number recorded as introduced. However, it remains unclear when and by how much violating spatial and temporal independence alters establishment probability. Here, we use a spatially explicit, discrete-time, stochastic population model to document when and if non-independence can be ignored. Related, we document the extent to which risk assessments and policy standards may be under-estimating establishment risk by using propagule-pressure information and models that fail to capture true non-independence.

The initial establishment of a non-native species is a population-level process.

Individuals of a species are introduced (released) into a novel location (making them nonnative), and these individuals either begin breeding, or they do not breed and fail to establish (Sakai et al. 2001). If individuals initiate breeding, the population still may not be self-sustaining if the rate at which individuals die is higher than the birth rate. The plethora of ecological and behavioral factors that influence individual birth and death rates within very small populations will dictate how likely it is that this incipient non-native population will become self-sustaining (Lockwood et al. 2013). The key insight that propagule-pressure research brings to invasion biology is that these small population problems (e.g., Allee effects) combine to substantially elevate incipient non-native population extinctions (Simberloff 2009, Cassey et al. 2018). Yet, the influence of spatial and temporal non-independence of introduction events on establishment success has not been comprehensively investigated despite the ample evidence that, at a minimum, spatial dynamics matter greatly in population persistence. For example, it has been long known that small sub-populations within a meta-population can be 'rescued' by the arrival of dispersing individuals from another sub-population (Gotelli 1991). If we view nonnative species' introductions in this light, then spatial and temporal non-independence of introduction events may mimic meta-population rescue effects (Lenda et al. 2010). If so, we should expect propagule-pressure rescue effects to, at times, substantially alter non-native species' establishment probability.

How often should we expect such propagule pressure 'rescue effects' to occur within real-life species introduction scenarios? Through careful documentation of the pathways by which non-native species are transported, and then released, invasion scientists have shown that spatial and temporal non-independence of introduction events can be common (e.g., Krysko et al. 2016). For example, exotic pets can establish non-native populations if they are
released by their owners or by pet wholesalers. Initially, one may count each pet-release event as an independent introduction event, and thus unless the owner or wholesaler released a large number of individuals at once, the establishment probability of these releases will be judged by models as quite low. However, if owners are spatially grouped (e.g., in urban areas; Edwards et al. 2016), and the released pets disperse far enough so that they encounter each other, then the actual propagule pressure count is the combined number of release events within a geographical extent dictated by the dispersal range of the species (Garnier et al. 2012). Similarly, some invasion pathways may stack introduction events close enough together in time that individuals from a prior introduction event remain alive to effectively assimilate all newly released individuals into the incipient non-native population. This scenario may be particularly common when non-native species are accidentally transported within, and released from, ship ballast or on ship hulls; or from stowing away in the cargo moved by ships, airplanes or trucks. If these vectoring mechanisms are consistent in the species they move, and they frequent particular locations, then individuals of the same species may be repeatedly introduced to the same locations (Verling et al. 2009, David et al. 2013, Sinclair \& Arnott 2016). In these cases, to correctly estimate propagule pressure, all vector activity within a given time interval dictated by the longevity of the species should be summed to index true propagule pressure.

If propagule pressure information is to be used to generate risk assessments and policies, it is critical to understand how and when information sources lead to mis-estimation of establishment probability. There are two sources of empirical propagule-pressure information. First is direct information on propagule pressure that stems from observational and often historical records of acclimatization societies, biocontrol programs, or releases to enhance hunting and fishing opportunities. There are well-known information gaps in these records, with some gaps related to how exactly one should divide the records so that they accurately
represent spatially and temporally independent introduction events (Blackburn \& Duncan 2001, Blackburn et al. 2013). Failure to correctly capture spatial and temporal non-independence in these records can result in misleading conclusions relative to the broader propagule-pressure effect (Blackburn et al. 2013). Second, for most species introductions, the information available on propagule pressure comes from surrogate variables that are relatively easy to record but have an unknown relationship to true propagule pressure (e.g., port-level shipping activity, frequency of recreational boaters moving between lakes; Bradie \& Leung 2013, Wonham et al. 2013). Relative to our goals here, the question is to what extent do surrogate measures consistently mis-estimate establishment success because they fail to capture true spatial and temporal non-independence of introduction events.

Here, we systematically track how establishment probability of a single species' population responds to decreasing spatial distance and time between introduction events. We also explore how increases in initial propagule size interact with spatial and temporal nonindependence to dictate establishment probability. We keep several underlying population parameters constant across model scenarios and assume complete environmental suitability. We consider environmental stochasticity and Allee effects as the only factors elevating population extinction probability. Although simplistic, our model generates several insights that highlight under what circumstances temporal and spatial non-independence of propagule pressure substantially influence establishment probability.

## Methods

We constructed a spatially explicit, discrete-time, stochastic population model (i.e., cellular automata model, Pitt et al. 2009, Lustig et al. 2017) that incorporated information on dispersal
and population growth. We explored two model scenarios, where each was designed to violate either spatial or temporal independence between introduction events at varying magnitudes (Table 1, Figure 1). In Scenario 1, we decreased spatial independence between introduction events by increasing the clumping of initial introduction locations. We then measured how often individuals released in the unique locations dispersed sufficiently to encounter one another and tracked how these events increased establishment probability. In Scenario 2, we decreased temporal independence by allowing multiple introduction events through time in the same location. We measured how often individuals from prior introduction events remained alive to encounter individuals released in the subsequent introduction event(s) and tracked how such events influenced establishment probability. Across model realizations, we varied the number of individuals introduced within each event (propagule size) as this value is well-known to influence establishment probability (Cassey et al. 2018; Table 1).

## Model procedure

We simulated introduction events across space by establishing a grid of cells, all of which were equal in size and provided suitable conditions for modest population growth $\left(\lambda_{\max }=1.1\right)$ when numbers of individuals are above an Allee Effect (Figure 2; see below). Thus, a single populated cell could be self-sustaining. If any populated cells physically adjoin, we considered those cells to be a single panmictic population (see below). To simulate introduction events, we chose the location of the initially populated cell(s) at random for each model realization (Figure 2). Each year after the initial introduction event, each incipient population grew according to equation 1 and individuals dispersed from this population into unoccupied cells after a population size threshold was reached following equation 2 . We simulated additional introduction events (when applicable) by allowing new individuals to be released into a cell that was populated in the beginning of the model realization. We ran each model realization for 50 time steps where one
step represents a single breeding event (i.e., one time step equals a 'year'), and implemented 1,000 realizations of each scenario variation.

## Population growth

We modelled population growth as a discrete exponential growth function with Allee effects (Berryman 2003, Courchamp et al. 2008) as follows:
$\lambda_{x, y, t}=e^{r\left(1-\frac{N_{c, t}}{K}\right)^{Q}\left(1-\frac{A+V}{N_{c, t}+V}\right)^{P}}$ equation 1
where $\lambda_{x, y, t}$ is the population growth rate of a cell for the current time step (used to project the population into the next time step) and $e^{r}$ is the maximum population growth rate, which we set to 1.1 (Cassey et al. 2014). We defined population growth as a function of the collective population size of a 'cluster' of cells ( $N_{c, t}$ ). We defined a cluster as any group of adjacent cells where each had a population size greater than zero. Cluster size can vary between 1 and the maximum number of cells in a grid in any model realization, and the size of clusters can change through time. Note, in scenarios with multiple initial introduction locations, the grid can harbor more than one population cluster at the same time, dispersed across the grid. We incorporated environmental stochasticity in the model by sampling values for the growth rate ( $\lambda$ ) from a normal distribution with a standard deviation of 0.15 .

The remaining parameters in equation 1 affect the severity of Allee effects where $A$ is the population below which $\lambda<1, V$ is $30, K$ is $10^{6}, P$ is 3 and $Q$ is 0.01 . By setting $A=20$ we are including a strong Allee effect (Courchamp et al. 2008, Fagan \& Holmes 2006), meaning that population sizes ( $N_{c, t}$ ) below 20 will experience increasingly negative population growth rates ranging from $\lambda$-values just below 1 down to 0.6 at very low population sizes (Figure 3a). We did not include density dependence as we are tracking the fate of populations that initially begin
with very small numbers of individuals. As a simplifying assumption, we did not include stage or age structure. We kept the dispersal and growth-rate parameters constant across all model realizations, effectively modelling a single species.

## Dispersal

We allowed individuals in a cluster to disperse away from that cluster if population size exceeded a threshold ( $d_{\text {threshold }}$ Matthysen 2005). We set $d_{\text {threshold }}$ to be 50 individuals, which represented a population size more than twice that of the largest propagule size we simulated (Table 1). We calculated the number of individuals dispersing after surpassing the dispersal threshold ( $M$ ) using:
$M_{x, y, t}=N_{x, y, t}-d_{\text {threshold }}, \quad$ for $N_{x, y, t}>d_{\text {threshold }}$
equation 2
where $x$ and $y$ refer to the coordinates of a cluster, $t$ to the time step (in years), and $N_{x, y, t}$ to the population size of a cluster at time $t$. We modelled dispersal distance ( $d_{\text {distance }}$ ) as a negative binomial probability distribution (Nathan et al. 2012):

$$
d_{\text {distance }} \sim \text { negative binomial }(1,1)
$$

This dispersal function is representative of a species with short-range dispersal abilities (e.g., vertebrates, Trakhtenbrot et al. 2005), where dispersers have a $50 \%$ probability to disperse to a cell neighboring the population cluster, and a $25 \%$ probability to disperse to two cells away (Figure 3b). We assigned the direction of each disperser randomly from any of the eight possible surrounding directions (sampled from a uniform distribution from 1 to 8 ). We assumed that dispersing individuals did not suffer from an increase in mortality. Therefore, in cases where dispersal mortality increases with dispersal distance (Johnson et al. 2009), our results may represent an overestimation of establishment probability.

## Non-independence and probability of establishment

At the end of each model realization, we declared the species as being 'successfully established' within the grid if the total number of individuals across the grid exceeded the total number of individuals ever introduced. This outcome indicates that at least one of the populations within the grid realized positive population growth over the 50 years in the model. In accordance, failed establishment occurs when the number of individuals after 50 years is smaller than the number ever introduced. Failed establishments in our model can happen through two processes. First, failed establishments can result from random extinction of populations due to environmental stochasticity (Morris \& Doak 2002). Fluctuations in growth rate are more likely to cause smaller populations to go extinct compared to larger ones (Lande 1993) and, thus, if introduction events only tend to create one to several small spatially independent populations the species is unlikely to meet our definition of 'established'. Second, failed establishments can happen because Allee effects accelerate population decline in very small populations (Courchamp et al. 2008). If introduction events consistently produce nascent populations that are below Allee thresholds, then the species is very unlikely to establish according to our definition.

We varied propagule size systematically between 5 and 20 to explore how it interacts with violations of spatial and temporal independence to determine establishment probability. We defined a violation of spatial independence as any instance in which a cell populated in year 1, or its associated cluster of connected cells, is incorporated into another cell also initially populated in year 1. In other words, if two or more cells that were populated at the beginning of the realization 'touch', we considered spatial independence to be violated. We defined a
violation of temporal independence as any instance when individuals are introduced into a cell already populated via a prior introduction event. The maximum number of violations for either spatial or temporal scenarios was one less than the total number of introduction locations/events.

We recorded the total number of violations in spatial or temporal independence for each model realization and calculated the distribution of the number of violations across scenario variations. To explore the relationship between establishment probability and nonindependence, we fit a logistic regression model with a binomial error term for establishment success, where a value of 1 was assigned to realizations with a successful establishment and a value of 0 was assigned to realizations with a failed establishment. We assigned the independent variables to be the number of violations of independence and the propagule size. We ran separate a separate logistic regression model for the spatial and temporal scenarios. We interpreted the intercept of the 'number of violations' variable to be an estimate of the establishment probability under no violations of independence. We measured model performance by calculating McFadden's pseudo $\mathrm{R}^{2}$.

We coded and implemented the model in R v. 3.5.1 (R Core Team 2018) and used the packages raster v. 2.8-4 (Hijmans 2018), igraph v. 1.2.2 (Csardi \& Nepusz 2006), dplyr v. 0.7.7 (Wickham et al. 2018), ggplot2 v. 3.1.0 (Wickham 2016). We will make the code for the model publicly available upon publication.

## Results

We found that as the number of introduction events increased and the size of the grid decreased, the number of violations of spatial independence increased (Figure 4a). Similarly, as
the number of introduction events increased and these events were more closely spaced in time, the number violations of temporal independence increased (Figure 4b). Overall, for both spatial and temporal scenarios, as the propagule size per introduction location/event increased, the number of violations of independence increased.

Spatial independence was only violated under specific conditions of either a propagule size per location of 20 and/or 8 or 12 introduction locations (Figure 4a). Under all other conditions, there were no violations in spatial independence. When spatial independence was violated, the number of violations was small (relative to the maximum amount of violations possible). For instance, under 12 introduction locations, most model variations had a median of 1 violation of spatial independence even though the maximum number of possible violations was 11. As the number of introduction locations increased, the number of violations increased by about 0.5 violations for every 4 additional introduction locations (where violations already occurred). Likewise, as the propagule size per introduction location increased, the number of violations increased slightly. For instance, when comparing a propagule size per introduction location of 5 to 20 , there was an average increase of 1 violation (with 12 introduction locations).

Temporal independence was more readily violated compared to spatial independence (Figure 4b). Under most model variations with a propagule size per introduction event of 15 or $20,100 \%$ of the realizations had the maximum number of violations of temporal independence (except at 8 'years between introduction events'). Under a propagule size per event of 5 and 10, as the 'years between introduction events' increased, the number of violations in temporal independence increased in a logistical fashion, eventually reaching the maximum number of violations at 2 or 3 'years between introduction events'. As the number of introduction events increased, the number of violations in temporal independence increased by about 2 violations for every 2 additional events (where violations already occurred).

The logistic regression models were effective at explaining the correlation between establishment probability and the explanatory variables, with a pseudo $R^{2}$ of 0.54 for the spatial model and 0.46 for the temporal model. The relationship between the number of violations of independence and establishment probability was positive and nonlinear (Figure 5). Under no violations of independence, establishment probability varied from near 0 under low propagule sizes (5 and 10) to 0.75 and 0.40 for propagule sizes of 20 , for spatial and temporal models respectively (y-intercepts of Figure 5). Violations in spatial independence increased establishment probability for each propagule size at around the same rate (i.e., slope of curve and slightly different rates for violations in temporal independence).

Under the temporal scenario, a propagule size per introduction event of 10 had the steepest slope. Since each propagule size had different establishment probabilities under no violations (difference y-intercept), the amount of increase of establishment probability due to violations differed across propagule sizes. Under the spatial model, with a propagule size of 15, establishment increased by nearly 0.4 when comparing no violations of independence to 1 violation (the average number of violations of spatial independence). Likewise, under the temporal model, with a propagule size of 10, establishment probability increased by over 0.7 when comparing no violations of independence to 5 violations (the average number of violations of temporal independence). Because the model variations with a propagule size of 20 started at a higher establishment probability with no violations, there was a smaller increase in establishment probability, as the number of violations increased, even though it reached the same or higher establishment probability at 5 violations of independence (compared to other propagule sizes). When the propagule size was 5 , there were no successful establishments under the spatial model, therefore no increase in establishment probability as the number of
violations increase. For a propagule size of 5 under the temporal model, establishment probability increased from zero after 3 violations to maximum of 0.25 with 5 violations.

## Discussion

In the face of ongoing introductions of non-native species (Seebens et al. 2017, Early et al. 2016), models of establishment probability are pivotal to developing management actions and setting policy standards to prevent establishment of invasive species (Lodge et al. 2016). Here, we show that violations of spatial and temporal independence in propagule pressure can at times substantially elevate establishment success. This increase reflects temporal and spatial 'rescue effects' whereby individuals introduced to different spatial locations or at different times combine to functionally elevate founding population size and concomitantly decrease extinction probability. As temporal and spatial patterns of introduction overlap a species' longevity or maximal dispersal distance, the degree to which establishment success will be under-estimated rises. However, these propagule-pressure rescue effects are tempered by the propagule sizes associated with each introduction event. At low propagule sizes, the influence of rescue effects on establishment success are swamped by underlying population dynamics dictated by Allee effects and environmental stochasticity. To the extent that our model represents real invasion scenarios, we suggest that risk assessments, policy development, and management actions must explicitly consider the likelihood of propagule pressure rescue effects.

We show that the probability of a rescue effect is a non-linear function of how the dispersal distance and longevity of a species compared to the timing and location of introduction events. As introduction locations increasingly fall within the species' dispersal
range, the functional founding population size increases. Similarly, as the temporal rate of introduction events increasingly overlap with the species' longevity range, founding population size increases. However, establishment probability responds strongly to rescue effect boosts in founding population size if the number of individuals released lies just below an Allee effect threshold (Figure 6). We further demonstrate that, if such situations are not identified and each of these introduction events are erroneously considered spatially and temporally independent, then species' establishment probability can be under-estimated by up to 40 to $70 \%$. Perhaps more worrying is that, in certain circumstances, a species' establishment success may be falsely assumed to be near zero when it is instead approaching 40 to $70 \%$.

We further suggest that such situations will arise most commonly for species that are long-lived or have strong dispersal abilities since there is a high chance that the vectors that introduce them will have temporal or spatial 'footprints' that create rescue effects (Wilson et al. 2009, Cassey et al. 2014). Likewise, we suggest that invasion vectors that repeatedly transport the same species to the same location (e.g., ballast-water discharge, accidental hitchhikers; Albert et al. 2013) are at a higher risk of mis-estimating establishment risk. Even short-lived species may be subject to temporal rescue effects if its principle vector arrives frequently enough to the same location. Such situations may be quite common in pathways that create invasion bridgeheads since these produce frequently traveled vector connections at local spatial scales (Lombaert et al. 2010). The species most likely to have their establishment risk underestimated are those long-lived or strongly dispersing species that arrive via invasion vectors that repeatedly release into the same or nearby locations. For example, in the exotic pet pathway, introduction events are centered near large cities and the species released are relatively longlived (Krysko et al. 2016, Stringham \& Lockwood 2018). In these circumstances, rescue effects from temporal non-independence may be commonplace.

Gathering information on propagule pressure is very difficult in practice since the cultural and economic context of introduction events differ markedly across invasion vectors. Therefore, incomplete observational records and surrogate proxy variables are frequently used in establishment calculations (Wonham et al. 2013). There are persistent anomalies in observational records where species introduced at low propagule pressure nevertheless succeed in establishing a non-native population (Blackburn et al. 2013; Cassey et al. 2018). There are several plausible ecological mechanisms that can explain these cases, but our results provide the more prosaic explanation that propagule pressure was simply under-estimated in these cases because records failed to incorporate spatial and temporal non-independence. More practically, when management or policy is based on proxy measures of propagule pressure, there are persistent concerns about bias in the proxy relative to true propagule counts (Wonham et al. 2013). We extend this concern to include an assessment of how well proxy measures capture spatial and temporal non-independence in the introduction events they represent. Given the difficulty in quantifying the relationship between proxies and true propagule pressure (Wonham et al. 2013), we suggest that future research efforts focus on creating proxy variable 'rules of thumb' that allow adjustment of establishment probability according to the invasion vectors and species combination.

Our model represents an initial exploration of propagule-pressure rescue effects, and thus it leaves considerable room for exploring across a greater variety and more realistic suites of species' traits and vector dynamics. In particular, we did not consider how spatial and temporal rescue effects combine to raise establishment probability. In addition, we considered a very simplified habitat landscape over which introductions occur. Certainly, realistic landscapes will incorporate patches of 'good' and 'bad' habitat, and how these patches are configured relative to locations of introductions can have strong implications for establishment
success (Schreiber and Lloyd-Smith 2009). Also, the details of dispersal such as seasonality and different dispersal modes can greatly affect the probability rescue effects occur (Carson et al. 2011). Lastly, the possibility for gene flow or local adaptions prior to establishment may diminish the severity of Allee effects, and thus elevate establishment probability (Briski et al. 2018). Each of these complexities will provide the realism needed to fully identify when the assumption of spatial and temporal independence in establishment models and analyses will produce biased recommendations and results.

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## Tables

Table 1. Parameter values for model scenarios exploring spatial and temporal nonindependence. Scenario 1 evaluates the influence of increasing spatial non-independence on establishment probability by varying the size of the grid relative to the number of introduction locations. For example, small grid size and high number of introductions leads to high spatial non-independence. Scenario 2 evaluates the influence of temporal non-independence on establishment probability by varying the number of introduction events and the years between these events. For example, many introduction events spaced so that they are a year apart will increase temporal non-independence. In both Scenarios propagule size is varied systematically between 5 and 20. We ran 1,000 model realizations of each combination of parameters values, reporting the distribution of establishment probability for each (Figure 4).

| Scenario | Spatial Non-Independence |  | Temporal Non-Independence |  | Propagule <br> size per <br> event |
| :--- | :--- | :--- | :--- | :--- | :--- |
|  | Grid size <br> (cells) | Number of <br> introduction <br> locations | Years between <br> introduction <br> events | Number of <br> introduction <br> events |  |
|  | $20,30,40,50$ | $4,8,12$ | Single Year | Single Event | $5,10,15$, |
| Scenario 2 | Single Grid <br> Size (50) | Single <br> Location | 1 to 8 | $2,4,6$ | 20 |

## Figures


(average distance between introduction locations)
Figure 1. Conceptual representation of the model scenarios exploring spatial and temporal nonindependence. Scenario 1 evaluated the influence of spatial non-independence on establishment success by simulating multiple introduction locations at year 1 with no addition introduction events in the following years. Scenario 2 evaluated the influence of temporal nonindependence by simulating multiple introduction events at the same locations with a varying number of years between each event. In each scenario we estimated establishment probability across a range of propagule sizes according to Table 1.


Figure 2. Conceptual overview of the modelling procedure. An establishment was considered successful if the final population size at year 50 exceeded the total number of individuals ever introduced. For Scenario 1, where spatial non-independence was investigated, introduction events occurred only in year 1 but at varying numbers of cell locations. For Scenario 2, where temporal non-independence was investigated, all introduction events occurred in the same location but the multiple introduction events where spaced from 1 to 8 years apart. We checked for and recorded any violations in spatial or temporal independence at the end of each year.


Figure 3. (a) Growth rate $(\lambda)$ as a function of population size used in the model. The Allee threshold was a population size of under 20 . Each year of every realization we sampled $\lambda$ from a normal distribution to simulate environmental stochasticity. Dispersal and growth functions did not vary between or within model scenarios (except for stochasticity). (b) Probability distribution of dispersal distance used in the model. Individuals in a cell will disperse if the population size of the cell is greater than the dispersal threshold ( 50 individuals). The distance they will disperse follow the probabilities in the figure. The direction of dispersal is assigned randomly from any of the 8 possible intermediate directions ( $N, N E, E, S E, S, S W, W, N W$ ).


Figure 4. (a) The number violations of spatial independence across variations of model scenario 1. The degree of spatial non-independence is defined as the proportion of initial locations that assimilate together (through population growth and dispersal). The top gray ribbon denotes the propagule size per introduction location and the right-hand side gray ribbon denotes the number of introduction locations (not labelled on plot). (b) The number of violations of temporal independence across variations of model scenario 2 . The top gray ribbon denotes the propagule size per introduction location and the right-hand side gray ribbon denotes the total number of introduction events (not labelled on plot). Note the x-axis for both (a) and (b) are in descending order for grid length and years between introduction events. Therefore, as either grid length or the years between introduction events decreases, the number of violations of independence increases. Also note that the maximum number of violations for either spatial or temporal scenarios is one less than the total number of introduction locations/events.


Figure 5. The effects of the degree of (a) spatial non-independence and (b) temporal nonindependence on establishment probability. Curves are generated from a logistic regression with binomial error term for establishment success. PS (in the legends) is an abbreviation for propagule size. Dark grey areas around curves indicate 99\% confidence intervals. The yintercepts are interpreted as the establishment probability under no violations of independence. Under the spatial model, the propagule size of 5 had no realizations with a successful establishment and therefore could not be fit in a regression, however it was plotted for visualization purposes.


Figure 6. Conceptual diagram of the observed 'rescue effect' of propagule pressure from spatial or temporal non-independence. Shades of red represent probability of establishment, where darker shades indicate higher probability. The dotted line represents the Allee threshold, where if the population size is above this threshold, population growth is positive, and extinction is less likely. The solid lines represent the propagule sizes explored in this study and the length of the line represents the degree of the rescue effect. While higher initial propagule sizes experienced more of a rescue effect, since the initial establishment probability was high, the rescue effect only slightly increased establishment probability. Similarly, small propagule sizes had a small rescue effect and thus realized a minor increase in establishment probability. Intermediate propagule sizes started at a low establishment probability, but since they were close to the Allee threshold, the moderate rescue effect they received resulted in a large relative increase in establishment probability.

