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RESEARCH ARTICLE

The role of propagule pressure in experimental bark beetle invasions

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Abstract

1. Although many non-native species arrive in novel environments, only a fraction successfully establish. A crucial factor affecting the colonization process of invading species is propagule pressure. The positive association between propagule pressure and colonization probability is driven both by stochastic dynamics and the 'Allee effect'. Although the role of Allee effects in invading populations is theoretically compelling, they are difficult to quantify in the field because the earliest phases of biological invasions are typically not observed.
2. We conducted parallel studies using two species of bark beetles, *Hylurgus ligniperda* in New Zealand and *Ips pini* in North America, to (i) assess the role of propagule pressure on colonization success, (ii) empirically test for Allee effects and (iii) estimate Allee thresholds. We evaluated each of these factors by experimentally testing the effect of propagule pressure (numbers released) on simulated tree colonization success in two different settings: (1) field conditions where beetles could disperse freely and (2) enclosed cages where dispersal loss was prevented.
3. Colonization success was positively associated with numbers released (i.e. propagule pressure) for both species, though colonization occurred at lower numbers for *H. ligniperda* than for *I. pini*. A demographic Allee effect was only detected in *H. ligniperda* and the Allee threshold was smaller when beetles were released 1 m from host billets than when they were released 10 m away. Greater colonization success at lower release densities may explain the invasion success of *H. ligniperda* worldwide. Higher release densities required for successful colonization may explain why *I. pini* is a poor establisher.
4. *Synthesis and applications*. Our results linking invasion failure to small founding population densities generally support the theoretical literature on the role of propagule pressure and Allee effects in biological invasions. Agencies such as the International Plant Protection Committee (IPPC) setting phytosanitary measures such as the International Standards for Phytosanitary Measures No. 15 (ISPM 15) should consider using the colonization thresholds estimated here to limit numbers of colonizing individuals below invasion thresholds. Additionally, agencies conducting trapping efforts at ports-of-entry should be aware of these thresholds and widely report when trapping numbers exceed these thresholds.

KEYWORDS
Allee effects, biological invasions, dispersal loss, *Hylurgus ligniperda*, *Ips pini*, point introductions

1 | INTRODUCTION

Invasive non-native species can have severe consequences for global biodiversity and economies (Clavero & García-Berthou, 2005; Simberloff et al., 2013). Fortunately, not all arriving non-native species become established (long-term foreseeable persistence of the population), with colonization failure being more likely when individuals arrive in small numbers (i.e. low propagule pressure; Leung et al., 2004; Lockwood et al., 2005; Simberloff, 2009; Brockerhoff et al., 2014; Cassey et al., 2018). A ubiquitous cause of the positive effect of propagule pressure on invasion success is stochastic dynamics. Low-density populations are strongly influenced by demographic and environmental stochasticity; such stochastic effects can lead to the extinction of small populations, but large populations are more robust to their effects (Duncan et al., 2014; Leung et al., 2004).

Another contributor to colonization failure in invading populations is the demographic Allee effect (Drake & Lodge, 2006; Liebhold & Tobin, 2008; Taylor & Hastings, 2005; Tobin et al., 2011), defined as increasing population growth with increasing abundance (Allee, 1931; Dennis, 1989). A component Allee effect occurs when a positive relationship exists between any component of individual fitness and population density, such as those associated with mate finding or predator satiation (Stephens & Sutherland, 1999). Depending how component Allee effects interact with other density-dependent processes, they may lead to a demographic Allee effect at the population level, which can ultimately determine whether a population persists or goes extinct at a given location (Berec et al., 2007). Theoretical studies have shown that multiple component Allee effects can interact with each other (Berec et al., 2007; Kanarek et al., 2013) and with other density-dependent processes (e.g. competition or predation; Courchamp et al., 2000) in ways that may or may not produce a demographic (i.e. population-level) Allee effect (Taylor & Hastings, 2005).

Demographic Allee effects can further be classified as weak or strong (Stephens & Sutherland, 1999) based on the presence of an Allee threshold – a population density below which population growth rates are negative and, unless there is reinforcement (i.e. immigration), local extinction occurs. Weak Allee effects are characterized by reduced but positive fitness at low population densities and the absence of an Allee threshold. Strong Allee effects are characterized by the presence of a critical Allee threshold below which per capita population growth is negative. Allee effects are not present in all species (Gregory et al., 2010), nor are Allee thresholds static in space or time (Walter et al., 2017).

During an invasion event, reinforcements are typically not present to support the invading population during the colonization phase. Therefore, for successful colonization to occur, the number of arriving individuals must arrive above an 'invasion threshold' (Lewis & Kareiva, 1993), which is defined as the minimum number of individuals required for colonization to occur. Though ecological theory predicts that elevated propagule pressure during the colonization process increases the probability of long-term establishment, attributing failed invasion events to insufficient propagule pressure is difficult because most failed colonization events go undetected. Some empirical studies relating propagule size and colonization have been conducted, either in mesocosms (Drake et al., 2005; Kaul et al., 2016; Ketola et al., 2017; Kramer & Drake, 2010) or in field conditions (Davis et al., 2004; Grevstad, 1999; Kramer et al., 2009; Williams et al., 2021), but such empirical quantification of invasion thresholds are generally rare.

Similarly, empirical documentation of demographic Allee effects is generally lacking. Most inference on the role of Allee effects in invasion success is based on theoretical studies (Boukal & Berec, 2002; Courchamp et al., 2008). Because Allee effects are largely limited to very small populations, their detection is typically obscured by measurement error as well as environmental heterogeneity (Gregory et al., 2010; Kramer et al., 2009).

Experimental invasions (releases) can be powerful tools for probing the effects of propagule pressure on colonization as well as quantifying Allee effects (Grevstad, 1999; Williams et al., 2021). In this study, we used bark beetles (Scolytinae), a globally important pest group (Lantschner et al., 2020), as model systems to experimentally test how propagule pressure and Allee effects influence population growth and colonization success. Specifically, we released varying densities of two bark beetle species in settings with varying constraints on dispersal (i.e. open vs closed environments) in regions with little or no background populations of beetles. We conducted these experiments to simulate the colonization phase of invasions in which individual beetles must disperse, locate hosts and find mates following emergence. Bark beetle species may show component Allee effects, arising either from mate-finding or resource-finding failure (Contarini et al., 2009; Fauvergue, 2013; Gascoigne et al., 2009) or from cooperative feeding (Berryman et al., 1985; Goodsman & Lewis, 2016). Since Allee effects can strongly influence bark beetle population dynamics in their native range, we expected greater colonization success with greater numbers of bark beetles released (Kanarek et al., 2015). To probe for the presence of Allee effects, we measured F1 output (first generation offspring) to estimate population growth for various initial population densities (number released). The information gathered here provides insights into the role of propagule pressure and Allee effects in the success of invading bark beetle populations, and we explore the biological traits that may permit or inhibit population colonization.

2 | MATERIALS AND METHODS

2.1 | Study system

We conducted studies using two bark beetle species, *Hylurgus ligniperda* in New Zealand and *Ips pini* in North America. *H. ligniperda* F. is a saprophytic bark beetle which feeds and mates in dead pine trees (*Pinus* spp.) that lack induced defensive responses. Therefore, beetles do not need to mass attack to overcome host resistance. There is no evidence that *H. ligniperda* uses sex or aggregation pheromones (Kerr et al., 2017); therefore, it is assumed mate-finding of emerged adults occurs through other cues. *H. ligniperda* is highly attracted to volatile organic compounds such as ethanol and α-pinene to locate host pine trees. It is not known if *H. ligniperda* mates pre- or post-emergence. Both males and females bore through the bark and into the phloem. Females create a nuptial chamber within the phloem where mating and egg laying takes place. This beetle species is native to Eurasia and has invaded many regions where pines occur, including New Zealand where pines are planted in large plantations. *H. ligniperda* was first detected in New Zealand in 1974 and is now widely distributed wherever pines occur (Brockerhoff et al., 2006).

I. pini Say is native to North America and has never established in any areas outside of that continent, although it has been intercepted at overseas port locations (Brockerhoff et al., 2003). This species can colonize freshly dead as well as stressed or otherwise compromised live pine trees (Wallin & Raffa, 2000). The stressed trees that *I. pini* colonizes may still have constitutive defensive chemical compounds and be able to respond to bark beetle attacks. When trees are still alive, they may respond to bark beetle attack with induced defensive compounds (Christiansen et al., 1987). Pioneer male *I. pini* are attracted to the plant volatiles produced by stressed host trees (Erbilgin et al., 2003), initiate tree attack by boring into the phloem and emit a sex pheromone (ipsdienol) that attracts both males and females (Schenk & Benjamin, 1969). A single male can mate with up to three females (Robins & Reid, 1997). Thus, *I. pini* can overcome tree resistance by aggregation and mass-attacking stressed trees (Wood, 1982) while it faces no induced defence when it attacks dead trees. By contrast, *H. ligniperda* only attacks dead trees and faces little to no tree resistance. Raffa (2001) provides a detailed overview of optimal colonization densities of a variety of bark beetles in both living and dead hosts and discusses the mechanisms behind chemical communication failure and success. We chose *I. pini* and *H. ligniperda* because of their contrasting biologies (host selection behaviour, quality of host material colonized and invasion history) and because they could be captured in high numbers and released in areas with little or no background populations of conspecifics (i.e. in areas where no pines are present or nearby; see Chase et al., 2017).

We conducted releases of both *H. ligniperda* and *I. pini* in field (open) and cage (closed) settings (see 'species release' sections below). All settings contained four pine billets (cut logs). By comparing colonization in the two different settings, we could assess the effects of dispersal loss on colonization because cages prevented dispersal loss. Closed settings also prevented colonization of billets by other species, allowing us to compare the effects of such colonization with those in field releases.

As dispersal loss decreases population density, possibly below Allee thresholds (Goodsman & Lewis, 2016; Hopper & Roush, 1993; Robinet & Liebhold, 2009; Taylor & Hastings, 2005), it is useful to measure this component of an invading population (see Kuussaari et al., 1998; Robinet et al., 2008). Releases in closed settings also allowed us to measure the strength of negative density dependence (if any exists) without the loss of propagules, which may impact colonization success. Because measurements only recorded persistence of the first generation of both species, it was not possible to determine long-term survival. Consequently, we apply the term 'colonization success' as opposed to 'establishment success' throughout the manuscript.

For all releases, we used field-trapped beetles. We did not use freshly emerged beetles because these insects may not be physiologically ready to colonize hosts (Turchin & Odendaal, 1996). In contrast, trap-captured beetles are most likely in the process of actively searching for hosts. Using trap-captured bark and wood-boring beetles for release experiments is common practice (e.g. Costa et al., 2013; Dodds & Ross, 2002; Torres-Villa et al., 2013; Zolubas & Byers, 1995).

2.2 | *Hylurgus ligniperda* releases

Our study did not require ethical approval prior to releases. We collected live specimens of *H. ligniperda* by capturing beetles in panel traps baited with the host attractants α-pinene and ethanol as described in Kerr et al. (2017). Traps were placed in a recently harvested pine plantation in West Melton, Canterbury, New Zealand (43°28′S, 172°23′E; WGS 84 Web Mercator) in the Austral summer of 2014–2015. Adults were stored at ~12°C in an environmental chamber and kept no longer than 2 weeks prior to experimental releases.

To supply host material for colonization, we harvested *Pinus radiata* D. Don (Monterey pine) billets from plantation forests near West Melton, Canterbury and Ikamatua, Westland (42°16′S, 171°34′E). We cut trees into ~32 cm long billets and the cut ends of all billets were double coated with paraffin wax on the same day to reduce moisture loss. Billet diameter ranged from 28.5–73.5 cm (mean = 47.2 cm). Billets were stored in a netted cage to prevent colonization by bark beetles and were randomly chosen for field releases. We stored all billets less than 3 weeks prior to use in experimental releases (range = 1–20 days). We also inspected all billets to confirm that they were clear of prior colonization (e.g. absence of frass or boring holes) immediately prior to releases.

We conducted field releases of *H. ligniperda* in six areas, with each area containing four sites ($N = 24$ total sites), in the South Island, New Zealand. *H. ligniperda* propagule numbers released ranged from 0 to 500 beetles (Table 1). Prior trapping in these areas confirmed that the local background density of *H. ligniperda* was either zero or very low (<0.29 beetles/trap/week; Chase et al., 2017). We separated field release sites by a distance >1.5 km to reduce risk of interference from neighbouring releases. *H. ligniperda* is widely distributed throughout both main islands of New Zealand (Brockerhoff et al., 2006); therefore, there were no biosecurity concerns regarding releasing *H. ligniperda* in remote areas with no host trees.

At each beetle release site, we placed four *P. radiata* billets horizontally on the ground in four cardinal directions, either 1 m or 10 m away from a central release point. We placed a platform made of

TABLE 1 Numbers of bark beetles released for establishment success experiments in open (field) and closed (cage) settings. Experimental releases of *Hylurgus ligniperda* occurred across the Canterbury region of New Zealand and releases of *Ips pini* occurred in southeastern Iowa, USA

Beetle species	Host tree species	Distance (m)	Environment	Release size (number of replicates)
Hylurgus ligniperda	*Pinus radiata*	1	Closed	0(3), 5(2), 7(2), 10(2), 25(2), 50(2), 100(2), 250(2), 500(1)
		1	Open	0(11), 10(6), 25(6), 50(6), 100(5), 250(5), 500(4)
		10	Open	0(11), 10(6), 25(6), 50(5), 100(5), 250(5), 500(6)
Ips pini	*Pinus strobus*	1	Closed	0(3), 2(2), 5(2), 7(2), 10(2), 15(2), 20(2), 25(2), 50(2), 75(1), 100(2), 500(2)
		10	Open	0(5), 2(1), 5(1), 10(1), 25(1), 50(1), 60(1), 75(1), 100(1), 125(1), 150(1), 200(1), 300(1), 500(1), 600(1), 1000(1)

fibreboard (80 cm long, 38 cm wide and 2.4 cm high) at the release point to observe beetles during each release. We conducted all field releases in grassy meadows with no tall objects (e.g. trees, shrubs) between billets and the release platform. We only released *H. ligniperda* on days with clear weather and temperatures ≥18°C. We used the same methods to conduct releases in an enclosed environment (a 2 m × 2 m × 2 m Biomesh™ cage) where billets were placed 1 m from a central platform. Cage releases were conducted outside on the campus of the University of Canterbury, Christchurch, New Zealand. We used approximately equal numbers of each sex for releases of ≤10 beetles; for all other releases, beetles were chosen at random. *H. ligniperda* sex was determined by the stridulatory chirp method (Bedoya et al., 2019; Mausel, 2002). All released *H. ligniperda* were checked to be mobile and active before each release.

To monitor for interference from background populations of *H. ligniperda* in field releases, we performed the following: (1) a control site with billets but no released beetles was implemented at one of the four sites within each area on every release occasion and monitored for external contamination from naturally occurring populations or released beetles from other sites; (2) panel traps (baited with α-pinene and ethanol) were placed ~2 km from the most distant release sites in each area to monitor for the presence of locally flying *H. ligniperda*.

We collected billets after 1 week of exposure in both cage and field releases. We individually separated and set aside any *H. ligniperda* adults found on the surface of billets for later re-introduction to the same billet on which they were found so that colonizing beetles were not lost during transport. Billets were transported to an enclosed dark room, placed in 20-litre polyethylene containers and laid horizontally, with mesh screens on the top and bottom to allow for airflow. We re-introduced all *H. ligniperda* that were set aside to the same billet within the container. At 6–8 weeks following initial release, allowing sufficient time for egg eclosion, we carefully removed the bark from all billets with a wood chisel and searched for the presence of F1 (first filial generation) larvae. We separated a subset of live adults (which we assumed to be released adults based on insufficient time for F1 members to reach the adult stage) to estimate their sex ratio using the stridulatory chirp method (see above). Although it would have been preferable to count teneral adults, we were only able to count larvae because of temporal and logistical issues with our rearing facility in New Zealand. Therefore, counts of *H. ligniperda* larvae were grouped into bins of 0, 1–10, 11–100 and 101–1000.

2.3 | *Ips pini* releases

We captured live *I. pini* in funnel traps baited with the pheromone ipsdienol (Synergy Semiochemicals Corp., Burnaby, BC, Canada) at various locations in south-eastern Greene County, Pennsylvania, USA (39°75′N, 80°02′W) in the boreal summer of 2015 (Table 1). We stored adult beetles at ~14°C and for <14 days prior to experimental releases. We selected only active *I. pini* immediately prior to each release. Numbers of *I. pini* released ranged from 0 to 1000 beetles (Table 1).

To provide host material with each release, we harvested *Pinus strobus* L. (eastern white pine) billets, a common host of *I. pini* (Erbilgin & Raffa, 2000), from a small plantation near Mt. Morris, Pennsylvania (39.78 N, 80.15 W). We cut trees into ~50 cm length billets and double coated the cut ends of all billets with paraffin wax to reduce moisture loss. Billet diameter of *P. strobus* billets ranged from 23–43 cm. We deployed all pine billets for releases within 5 days of harvesting. Storage and post-development inspection of billets was conducted in the same manner as for the experiments with *H. ligniperda* (above).

Field releases of *I. pini* took place across four sites near Oskaloosa, Iowa, USA (41°3′N, 92°65′W; Table 1), an area in the Midwestern USA that is not known to contain *I. pini* and has few potential host trees, based on a comprehensive trapping survey (Chase, 2016). Field release sites were located at least 2 km apart. The *I. pini* experiment followed the same methods as for the *H. ligniperda* experiment, with the following exceptions: we placed all billets 10 m from the center release point in the open environment and attached lures of the host primary attractants α-pinene and ethanol (30 ml of each compound) to each. Lures were not added to closed environment billets. Lures were added to open environment *P. strobus* billets because preliminary release trials in 2014 without lures resulted in complete colonization failure (i.e. no billets were colonized) for all release densities (Table 1). Primary attractants are present in all host material naturally colonized by *I. pini*, so adding lures increases pre-existing levels of host attractants. The release platform was a polystyrene slab (50.8 cm long, 38.1 cm wide and 3.8 cm high) and, after collection, we stored billets in enclosed cardboard rearing tubes (either 0.15 m diameter ×0.61 m length or 0.3 m ×1.22 m) modified to allow airflow to prevent fungal infestation. Billets were collected after 2 weeks (as opposed to 1 week for *H. ligniperda*). Lastly, because *Ips* spp. larvae cannot easily be identified to species and because a suite of other pine-feeding bark beetles could have potentially colonized the *P. strobus* billets, we waited at least 7 weeks between release date and dissection to allow for complete development of *I. pini* to enable identification and counting of teneral adults. We used the same billet dissection methods as for the *H. ligniperda* experiment. The numbers of teneral adult *I. pini* males and females were recorded using external morphological traits.

2.4 | Statistical analysis

We used a binomial generalized linear model to quantify the shape and strength of colonization success, defined as the presence of an F1 larvae or adult in at least one billet per release replicate (where each replicate represents four billets in all release scenarios), against the number of bark beetles released. Releases were classified as colonization failures if there was a complete absence of F1 beetles from all four billets per release replicate.

Data from these same experimental releases were also used to directly detect and quantify the presence of a demographic Allee effect by regressing per capita population growth (the sum of F1 larvae or adults per release replicate, including those billets that contained zero beetles, per numbers released) against numbers released (Table 1). This model describes the classic relationship between replacement rate and population size that quantifies a demographic Allee effect (Gregory et al., 2010). A positive slope indicates the presence of a demographic Allee effect. For population densities where the replacement rate increases above 1, it is assumed colonization will occur because the F1 output is positive. This population size where reproductive rate reaches $y = 1$ is the estimated Allee threshold. Equivalent analyses were conducted for *H. ligniperda* and *I. pini*, for which reproductive output was taken as the number of larvae or adults, respectively, produced per released beetle. For both beetle species, analyses were conducted separately using data from the open and closed caged settings. We conducted all data analysis using R (V. 3.2.3 R Development Core Team, 2015).

3 | RESULTS

3.1 | *Hylurgus ligniperda* releases in New Zealand

The summed sex ratio (females: males) of adult *H. ligniperda* found on billets after releases was 3.5:1 (300:85) from all 1 m field billets and 9.25:1 (148:16) from all 1 m cage billets. These adults were released beetles and not F1 adults due to insufficient development time. We did not find any adult *H. ligniperda* located externally on billets from 10 m field billets prior to collecting them. We detected only one occurrence of contamination in a field control billet (release size = 0), where we found a single male *H. ligniperda*. In all billets deployed, we never found any bark beetle species other than *H. ligniperda*. We did not catch any *H. ligniperda* in panel traps installed to monitor for interference.

By fitting the binomial generalized linear model to our colonization data, we found that, in both field (open) and cage (closed) releases, *H. ligniperda* colonization was positively related to the number of propagules released (Figure 1). The positive relationship

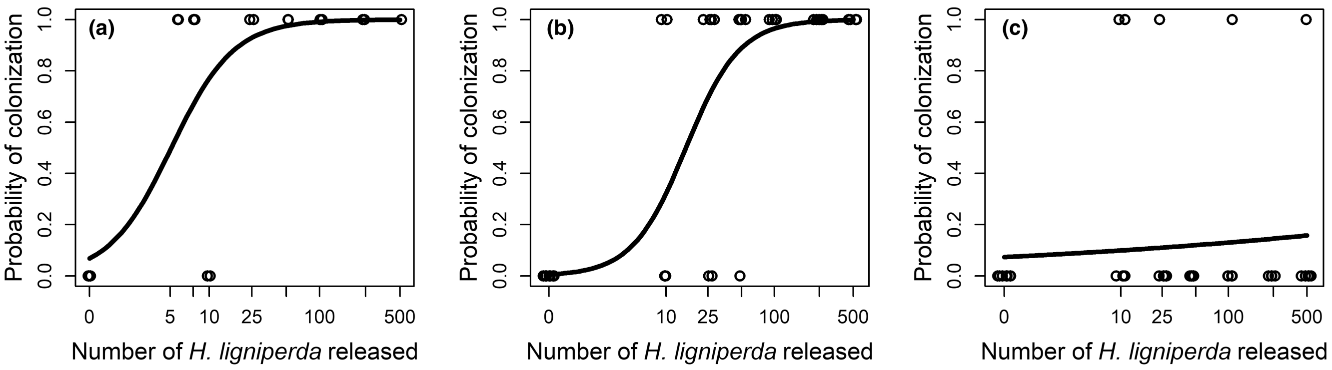

FIGURE 1 Colonization rates of *Hylurgus ligniperda* in relation to numbers of propagules released (log scale) in (a) 1 m caged, (b) 1 m field and (c) 10 m field scenarios. Colonization was defined as at least one billet out of four per release replicate having at least one F1 larvae present. Each data point represents one release replicate. A binomial generalized linear model was fit to the data to produce each line.

between the number of beetles released and their colonization success varied with distance from the release point to the billets and between the closed versus open environment (Figure 1). The smallest *H. ligniperda* release size to result in colonization occurred at 5 in the cage, 10 in the 1 m field and 10 in the 10 m field releases, respectively. In both the cage and field 1 m releases, colonization success approached 100% for the highest released population densities tested (Figure 1a,b). However, in the 10 m field releases, colonization rates generally remained low across the range of released population densities tested (Figure 1c) and the estimated number of propagules for per capita growth to be >1 was impossibly high (Table 2).

Regressions of per capita growth rate on initial population size based on all replicates (Figure 2) indicated a significant demographic Allee effect (positive slope) for *H. ligniperda* both for the 1 m cage release (Figure 2a, $F_{1,13} = 14.26$, $p = 0.002$, Adj. $R^2 = 49\%$) and the 1 m field release (Figure 2b, $F_{1,41} = 39.1$, $p < 0.001$, Adj. $R^2 = 48\%$). We did not detect a demographic Allee effect for the 10 m field release (Figure 2c, $F_{1,42} = 0.26$, $p = 0.614$, Adj. $R^2 = -0.02\%$).

3.2 | *Ips pini* releases in North America

In field releases of *I. pini*, some billets were also colonized by individuals of resident populations of the bark beetles *Ips grandicollis* Eichoff and *Orthotomicus* spp. Billets in six out of 15 (40%) release replicates (not including control releases of zero beetles) were colonized by *I. grandicollis* and four out of 15 (27%) replicates were colonized by *Orthotomicus* spp. Of the six individual billets that *I. pini* successfully colonized in field releases, *I. grandicollis* was present in three billets and *Orthotomicus* spp. was present in one billet. However, it is unlikely that *I. grandicollis* or *Orthotomicus* spp. influenced *I. pini* colonization because *I. pini* were released immediately after billet placement. Sex ratios (females: males) of reared F1 *I. pini* adults in 10 m field billets and 1 m cage billets were 1.2:1 (88:72) and 1.1:1 (524:469), respectively. The binomial generalized linear model fit to the *I. pini* colonization data indicated that colonization was positively associated with the number of beetles released, asymptotically approaching 100% colonization in both 1 m cage and 10 m field scenarios, but colonization at lower propagule densities was higher in the closed environment (Figure 3). The smallest *I. pini* release size to result in colonization was two beetles in the cage and 60 beetles in the 10 m field releases. Release densities associated with 50% colonization by *I. pini* were generally higher than for comparable experiments using for *H. ligniperda* (Table 2).

A demographic Allee effect was not detected from regressions of per capita growth rate on numbers released for *I. pini* cage releases (Figure 4a, $F_{1,22} = 0.02$, $p = 0.9$, Adj. $R^2 = -4\%$) or 10 m field releases (Figure 4b, $F_{1,18} = 0.63$, $p = 0.44$, Adj. $R^2 = -2\%$).

4 | DISCUSSION

We experimentally demonstrated that increased propagule pressure is positively related to colonization success for two bark beetle species with different host selection behaviours (Figures 1 and 3). Analogous relationships between initial population size and colonization success are commonly found in other types of organisms and may result simply from stochasticity – that is, low-density populations are prone to going extinct by chance (Dennis, 1989; Duncan et al., 2014; Jerde & Lewis, 2007; Leung et al., 2004). In the case of our experiment, colonization might have been influenced by stochastic behaviour of released beetles (e.g. random movement affecting the chance that males and females find each other on billets). In addition, demographic Allee effects are present in populations of certain species, and these may strengthen the relationship between propagule pressure and colonization (Courchamp et al., 2000; Taylor & Hastings, 2005; Tobin et al., 2011). Demographic Allee affects, if present, could potentially contribute to the positive effect of propagule pressure on colonization success seen here (Figures 1 and 3).

Our results indicate that the strength of Allee effects and their invasion threshold differed between the two species investigated. We conclude that a demographic Allee effect is present in invading populations of *H. ligniperda* as evidenced by the positive relationships between per capita growth and initial population size (Figure 2). However, there is little evidence for the presence of demographic Allee dynamics in *I. pini* through the range of initial population densities assessed here (Figure 4). If a strong demographic Allee effect exists in *I. pini* populations, it would appear that the Allee threshold is much larger than for *H. ligniperda*. There are caveats concerning our conclusion of differences in the Allee

TABLE 2 Estimated 50% colonization rates based on release size and release scenario and estimated Allee thresholds (back transformed number of propagules required to have a per capita growth rate = 1 obtained from regression equations). N/A: regression was not significant, so no estimate presented. For *Hylurgus ligniperda*, field 10 m, the calculated number of propagules for a growth rate >1 was extremely and unrealistically high and is shown as +∞

Species	Scenario	Release size associated with 50% colonization rate	Regression equation	Estimated number of propagules required to have a per capita growth rate >1
Hylurgus ligniperda	Cage (1 m, no lures)	5	$Y = -0.03 + 0.507X$	107
	Field (1 m, no lures)	16	$Y = -0.053 + 0.24X$	24,406
	Field (10 m, no lures)	>1000	$Y = 0.0178 + 0.0067X$	+∞
Ips pini	Cage (1 m, no lures)	27	N/A	N/A
	Field (10 m, with lures)	224	N/A	N/A

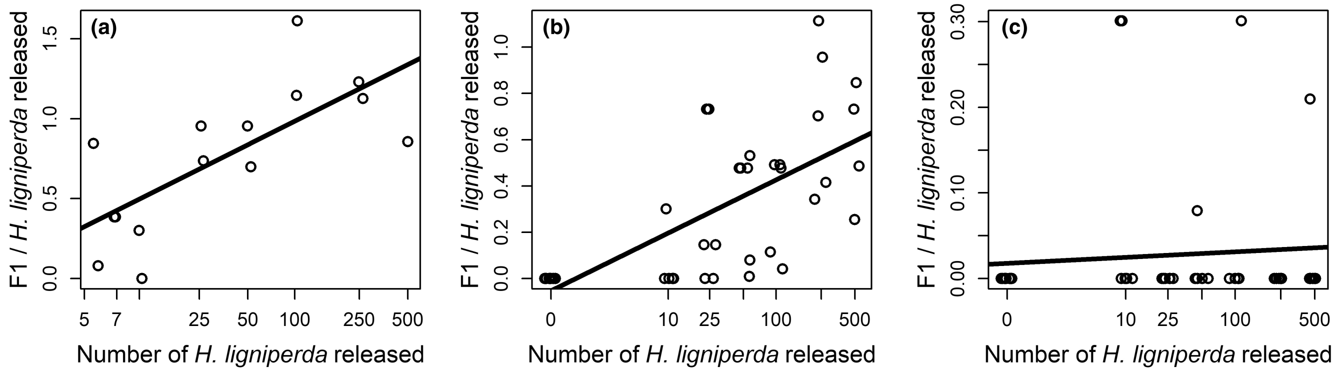

FIGURE 2 Plots of *Hylurgus ligniperda* per capita growth rate of F1 larvae vs numbers of *H. ligniperda* (log scale) released across all release replicates (where a release replicate represents four billets) in (a) 1 m caged, (b) 1 m field and (c) 10 m field scenarios. Lines were produced from a linear regression fit to the data.

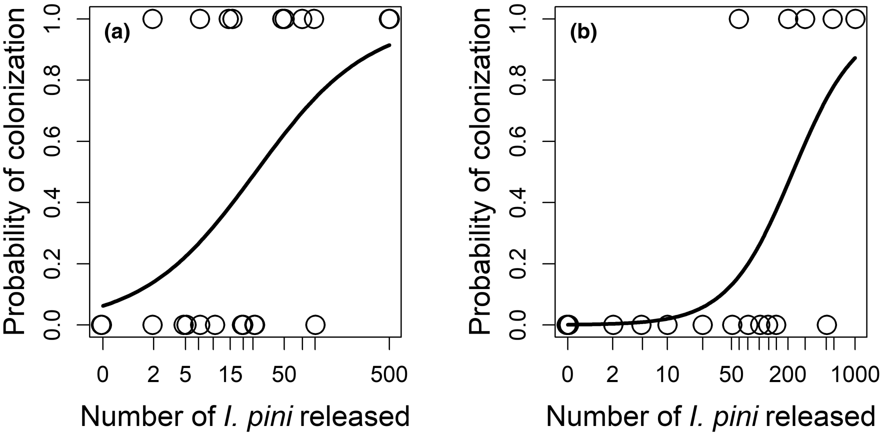

FIGURE 3 Colonization rates of *Ips pini* in relation to numbers of propagules released (log scale) in (a) 1 m caged and (b) 10 m field scenarios. Colonization was defined as at least one billet out of four per release replicate having at least one F1 adult present. Each data point represents one release replicate. A binomial generalized linear model was fit to the data to produce each line.

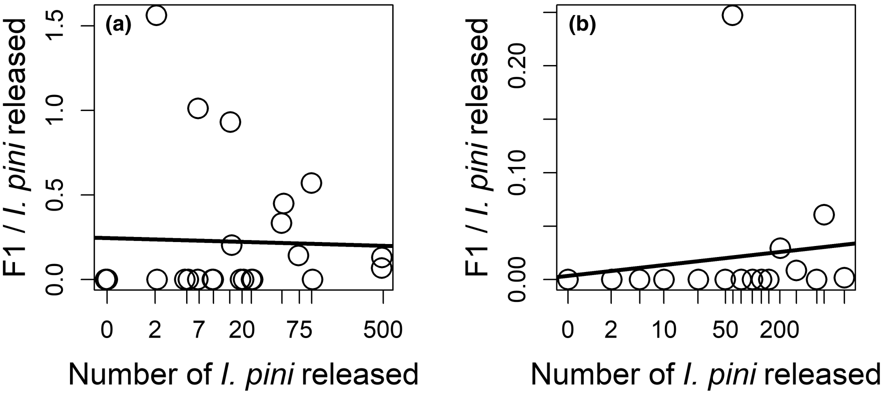

FIGURE 4 Plots of *Ips pini* per capita growth rate of F1 adults vs log-transformed numbers of *I. pini* released across all release replicates (where a release replicate represents four billets) in (a) 1 m caged and (b) 10 m field scenarios. Lines were produced from a linear regression fit to the data.

dynamics between these two species. First, our estimates of per capita replacement rate were based on the production of F1 adults in *I. pini* while for *H. ligniperda*, we were forced to rely on production of late-instar larvae for measuring replacement. Therefore, we could be underestimating the negative density dependent (i.e. competition) response on F1 adult output and overestimating the positive density dependent response of the per capita growth rate of *H. ligniperda*. Second, because we did not take into account adult mortality during hibernation, flight, mating or egg laying, we may be overestimating the number of propagules from the F1 output that contribute to colonization success in successive generations. Third, our failure to detect a positive relationship between replacement rate and population size does not necessarily mean that one does not exist. Fourth, because we used host volatile lures on the *I. pini* billets but not the *H. ligniperda* billets, our Allee threshold estimates are not directly comparable. Finally, it is possible that for *I. pini* a component Allee effect exists (e.g. related to mate-finding or host conditioning) but it is compensated by density-dependent factors (e.g. competition) so that it does not translate into a demographic Allee effect (Berec et al., 2007).

Even though a demographic Allee effect was present in *H. ligniperda* but not in *I. pini*, both species exhibited an asymptotic relationship between propagule pressure and colonization. However, colonization was generally observed at lower release densities for *H. ligniperda* compared to *I. pini* (Table 2; Figures 1 and 3). This latter result may partially explain why *I. pini* has not successfully established outside of its native range while *H. ligniperda* has invaded much of the southern hemisphere and parts of the United States and China; *H. ligniperda* is likely to establish at much lower propagule pressure. However, it is important to keep in mind that the successful colonization measured here (the production of at least some F1 larvae) is not equivalent to colonization. Successful colonization would only occur when the net reproductive rate is greater than 1. For the 1 m field releases of *H. ligniperda*, 50% colonization occurred at release densities of ~16 individuals whereas the Allee threshold estimate was > 1000; in cages, 50% colonization occurred at release densities of ~5, but the Allee threshold was estimated at 107 (Table 2). However, it is important to point out that our experimental releases represent an unrealistically unfavourable situation since solitary isolated billets were the only resource available for colonizing beetles. In a real situation where a port-of-entry is close to a forest setting, one or more entire trees may be available for colonization by founding beetle populations. In such realistic settings, beetles that leave the immediate release site may still locate a host and reproductive output would likely be much higher. Ports-of-entry with no host forests nearby will have a strong dilution effect (Meurisee & Pawson, 2017) and likely result in colonization failure. Consequently, Allee thresholds could be much lower than those estimated here. Nevertheless, it is most likely that numbers of individuals necessary for successful colonization of *I. pini* would be much higher than numbers required for *H. ligniperda* colonization.

Cassey et al. (2018) conducted a meta-analysis of 56 studies that related propagule pressure to the colonization success of non-native species and found that for most species, the critical colonization threshold ranged from 10–100 individuals. While we do not have a specific estimate of the *H. ligniperda* colonization threshold, it lies beyond that range and the threshold for *I. pini* is even higher.

There are several factors that may explain differences observed between these two species in both the strength of Allee effects and in the threshold number of individuals required for successful colonization. Several aspects of their life cycle and host relationships that affect component Allee effects could contribute to demographic Allee effects in these (and other) bark beetles. As in other sexually reproducing species, mate finding may limit reproductive success and lead to a component Allee effect. But density-dependence of host resistance is a unique characteristic of bark beetles that may also lead to a component Allee effect; several studies have documented greater reproductive success with increasing numbers of beetles attacking trees (and thereby overcoming host resistance; Raffa & Berryman, 1983; Nelson & Lewis, 2008). Neither of the two bark beetles studied here typically attack living, vigorous trees so host defences may not generate a component Allee effect in either species, and mate-finding failure may be a more likely source of a component Allee effect.

H. ligniperda is not known to produce an aggregation pheromone and, therefore, appears to rely on its strong orientation to host volatiles (Kerr et al., 2017) for both host location and mate-finding. In contrast, *I. pini* is only mildly attracted to host volatiles such as α-pinene and ethanol, whereas both males and females are strongly attracted to the males' aggregation pheromone (Chase et al., 2018). However, the aggregation pheromone is emitted by pioneer and subsequent male beetles only once they have located suitable host material and started excavating a gallery in the bark. Therefore, for the initial location and colonization of host material, *I. pini* may be less able than *H. ligniperda*. This may explain, in part, why *H. ligniperda* has historically had better invasion success than *I. pini* and possibly be related to differences in the strength of their demographic Allee effects. Future experiments should investigate if a stronger dependency on an aggregation pheromone is linked to reduced colonization and establishment success of invading populations.

Dispersal loss is known to potentially interact with Allee effects by diluting populations and reducing the local numbers of individuals; this may lead to a reduction of invasion success (Kanarek et al., 2013). Kuussaari et al. (1998) found that dispersal loss interacted with mate-finding (a component Allee effect) in metapopulations of the Glanville fritillary butterfly and thus helped explain variability in metapopulation persistence. The dispersal loss mechanism likely explains why colonization thresholds and Allee effects differed between field releases (Figures 1b,c and 3b), where individuals were not spatially constrained, and cage releases (Figures 1a and 3a), where beetles were confined. During field releases of both bark beetle species, we observed that many individuals flew past the billets, therefore immediately reducing the number of individuals available for colonization and reproduction. On windy days, beetles were less likely to fly and, instead, crawled off the release platform. In one field release of *H. ligniperda* at 1 m, we observed that the billet, located upwind from the release point on a windy day, was heavily colonized, and we suspect that beetles walked towards the volatile organic compounds released from this billet. In a study investigating host foraging by the Warren root collar weevil, short-distance walking appears to be an efficient strategy to find host material in forests where suitable and abundant host material (e.g. cut stumps and slash material) is available (Machial et al., 2012). We also found that a small increase of distance (9 m) between the point of release and the location of host material greatly decreased the probability of colonization for *H. ligniperda* (Figure 1b,c) and that preventing dispersal loss (i.e. by releasing in a cage) caused a further increase in the likelihood of successful colonization (Figure 1a).

By empirically releasing bark beetle propagules into areas where no reinforcements were available, we have been able to demonstrate that critical minimum thresholds affect the colonization success of founder populations to varying degrees. Due to excessive measurement error associated with sampling populations at low densities, detecting Allee effects and quantifying the role of propagule pressure on invasion success are often difficult (Gregory et al., 2010; Kramer et al., 2009). Experimental introductions provide a powerful method for accomplishing both. Aside from experimental releases of biological control agents (e.g. Grevstad, 1999; Williams et al., 2021) and historical intentional introductions by new settlers (e.g. bird introductions by naturalization societies [Veltman et al., 1996]), such experimental approaches have rarely been conducted. The present study, which exploited introductions of populations into artificial habitats, serves as a useful example that could be applied in future studies.

Although most transported non-native species fail to establish due to insufficient propagule pressure (Brockerhoff et al., 2014; Lange & Marshall, 2016), unfavourable climatic conditions, or lack of hosts, a few do establish. Dispersal via inadvertent human assistance has drastically increased the number of species moved among continents (Hulme, 2009). Agencies such as the International Plant Protection Convention setting phytosanitary measures (e.g. International Standards for Phytosanitary Measures No. 15) may consider using the colonization thresholds estimated here to guide development of policies aimed at limiting numbers of colonizing individuals below invasion thresholds (Allen et al., 2017; Ormsby, 2022). Additionally, biosecurity agencies conducting trapping at ports-of-entry should be aware of these thresholds and consider intensification of surveillance when trapping numbers exceed these thresholds, which vary among species.

AUTHOR CONTRIBUTIONS

Eckehard Brockerhoff conceived the initial project idea and wrote the proposal. Kevin Chase, Dave Kelly Andrew Liebhold and Eckehard Brockerhoff developed the detailed project plans and methodology; Kevin Chase collected the data; Kevin Chase and Andrew Liebhold analysed the data; Kevin Chase led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

We declare that no conflict of interests shaped or biased the data contained in this manuscript.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository: https://doi.org/10.5061/dryad.8sf7m0csf (Chase et al., 2022).

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