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Impact of repeated human introductions and the Allee effect on invasive species spread

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ABSTRACT

A strong Allee effect, or density dependent growth, has been proposed as a justification for early control of some spreading invasive species. A strong Allee effect implies that if the invader can be caught early in a low density area, then the invasive species will not be able to establish in the new environment and will die off. Yet, economic activity is often responsible for repeated human introductions, and can increase the density of the invader thereby allowing establishment. In this paper, we examine the implications of repeated human introduced invasive species and determine the benefits of policies that reduce introductions. We use the emerald ash borer (EAB) in Ohio as an example and model the relationship between this invasive species with the native environment, as well as economic activity in Ohio. We show that when accounting for a strong Allee effect, the population of the EAB can be managed to remain below endemic levels; we can slow ash tree decline. Understanding the interaction between human activity, repeated introductions, and the Allee effect can assist policymakers in effectively reducing the establishment and spread of invasive species.

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1. Introduction

The spread of invasive species cost the United States upwards of $120 billion a year in damages and losses (Aukema et al., 2011; Pimentel et al., 2005). A significant challenge in environmental policymaking is determining how much attention should be given to controlling invasive species. The problem of control is complicated when we recognize the ecological and economic relationships of invasive species (e.g. economic activity spreads invasive species and invasive species affect economic activity). However, most invasive species control recommendations reveal a common avoidance of ecological and economic realities (NISIC, 2012), which ultimately misleads policy decisions. Examples abound, but the two most common avoidances are that the invasive species exhibit density dependent growth rates (such as the Allee effect) and that economic activity contributes to the invasive species population through continued human reintroduction. We argue that management that accounts for these realities can keep invasive species damages low.

The Allee effect captures the decreased fitness and lack of reproductive success that occurs at low population densities (Suckling et al., 2012; Drake and Lodge, 2006; Taylor and Hastings, 2005; Taylor et al., 2004; Keitt et al., 2001). This is in contrast to most bioeconomic models that assume a constant growth rate (Burnett et al., 2007; Leung et al., 2002; Olson, 2006). The Allee effect, specifically a strong Allee effect, dramatically influences the dynamics of invading populations, which may have low density or experience slower population growth, decreasing the probability of the species establishing (Fig. 1, panel (a)). As a result, the cost of controlling the invasion may be significantly lower with a strong Allee effect because eradication can be achieved by controlling the population to a level at which the strong Allee effect takes over. Recent research has illustrated the consequences of the Allee effect in the invasion control context (Drake and Lodge, 2006; Taylor and Hastings, 2005; Taylor et al., 2004). However, a common missing element in this literature is the impact that repeated human introductions has on long-range spread and its impact on reaching the strong Allee effect threshold (BenDor et al., 2006).

Economic activity leads to repeated invasive species introductions (Lavergne and Molofsky, 2007; Perrings et al., 2002; NISIC, 2012). Repeated introductions increase the invader's probability of establishment by pushing the population over the critical threshold, or the strong Allee threshold, K_{crit} (Fig. 1, panel (b)).

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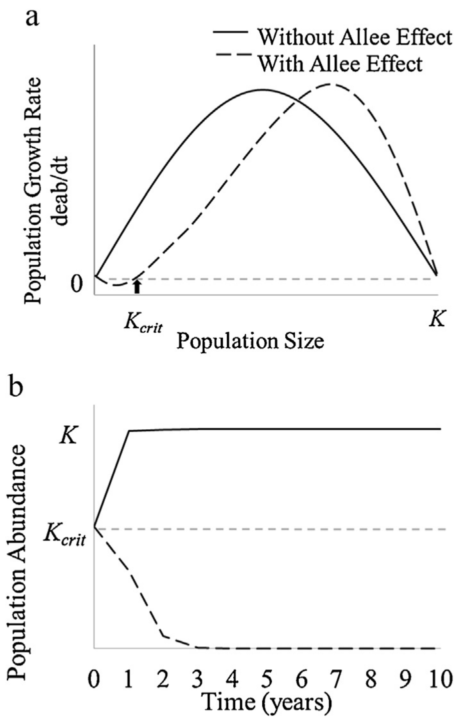

Fig. 1. Invasive species dynamics with a strong Allee effect. If the invasive species population is less than K_{crit}, which is the minimum population required for positive growth, then all of the invasive species die out. If the invasive species population is greater than K_{crit}, then the invasive species grow to their carrying capacity, K. (a) EAB growth rates. (b) EAB population abundance.

Examples of repeated introductions include aquatic invasive species, such as the zebra mussels that are spread through infected ballast water discharge by boats (Griffiths et al., 1991); invasive plants, such as the yellow star thistle that are often spread through hiker's boots and on the tires of cars (Kaufman and Kaufman, 2013); and invasive insects, such as the emerald ash borer (EAB) beetle that often hitchhike on cars or in consumer wood goods (Prasad et al., 2010).

There is also a timing consequence of repeated human introductions from economic activity. Over time, economic activity contributes to the invaders population, helping it explode long after initial introduction. As a result, Dehnen-Schmutz et al.'s (2007), Essi et al.'s (2011), and Epanchin-Niell and Liebhold (2015) research suggests that limiting economic introductions below the strong Allee threshold could provide effective control during the introduction-establishment time lag.

Herein our objective is twofold. First, we demonstrate the importance human activity has on pushing invasive species population above the strong Allee threshold. Specifically, we generate a deeper understanding of how repeated human introductions impact invasive species dynamics, something that is currently missing in the literature (Siegert et al., 2015). Second, we determine the benefits of an improved native population due to reduced repeated human invasive species introductions. Such information is valuable when determining whether or not to implement large-scale invasive species control projects.

2. Background of the emerald ash borer invasion

We use the invasive emerald ash borer (EAB) to illustrate the consequences of the strong Allee effect in EAB control because EAB and other beetles have been shown to exhibit strong density dependent growth (Herms and McCullough, 2014; Courchamp et al., 1999; Rutledge and Keena, 2012; Takasu, 2009). Originating in Asia, EAB were discovered in southern Michigan in 2002. Feeding on the inner bark of ash trees, EAB larvae destroy a trees ability to translocate water and nutrients (Poland and McCullough, 2006). For this reason, the EAB is known as one of the costliest forest pests to enter the United States and is projected to cost \$10.7 billion in damages (Kovacs, 2010).

Economic activity is likely to blame for introducing and spreading EAB throughout the United States. For example, most scientists hypothesize that the EAB entered the United States through the solid wood packing materials transported in cargo ships and on planes (Strutt et al., 2013). Economic activity has also accelerated the spread of EAB through driving, leisure (i.e. camping), firewood gathering, and gardening with infested nursery trees. Human activity leads to hundreds of new introduction points and is likely to blame for the blanket of infestation now seen in southeastern Michigan (BenDor et al., 2006). For instance, naturally, EAB can move an average of 9.84 km/year; however, they are currently moving over 20 km/year (Taylor et al., 2006). Most recently, Greene and Ulster County in New York have confirmed EAB infestations, yet the closest EAB-infested county is Steuben County, New York, which is over 350 km away (NYS Dept. of Environmental Conservation, 2011). This distance is well beyond the EAB's ability to fly, suggesting economic activity is contributing to EABs' spread (Muirhead et al., 2006). The EAB is now found as far east as New Hampshire and as far north as Ontario, Canada, and has caused the death of more than 30 million ash trees in Michigan alone (USDA Forest Service, 2009).

There has been little resistance to the spread of EAB. In fact, both healthy and damaged ash trees are impacted by EAB (Herms and McCullough, 2014). Early EAB control policies of destroying an 800 m radius of ash trees around an EAB infested ash tree (stopped in 2006 once EAB was discovered in numerous ash stands) and quarantining an infested county (prohibiting the movement of ash outside a confirmed EAB-infested area) have not been effective. While the (costly) practice of destroying an 800 m radius around an infested ash tree was beneficial for addressing the strong Allee effect, the consequence of repeated human introductions was ignored with the quarantine. Quarantines have intensified the short-run and long-run human dispersal of EAB as it is legal to move infested EAB ash within and between adjacent quarantined areas; making it more likely that the EAB will reach the minimum population size necessary for positive growth. In September 2010, Ohio officially announced that the entire state was under quarantine; this quarantine included 88 counties, of which only 69 were under quarantine prior to September and of which 53 were positive for EAB infestations. The allowed movement within the entire state increased the probability of EAB permanently establishing. In response to the quarantine, Dan Herms, an entomologist with the Ohio Agricultural Research and Development Center, wrote, "It's inevitable that all of the ash trees in Ohio are going to die" (Kovacs, 2010). Indeed, the previous literature suggests a complete loss of ash stock (Poland and McCullough, 2006; Sydnor et al., 2007).

Recent research has illustrated the connection between EAB infestation and human activity. BenDor and Metcalf (2006) and BenDor et al. (2006) examined ash density and EAB spatial dynamics in DuPage County, IL. Parameterizing a combined spatial modeling environment (SME) and a STELLA® simulation model augmented with human-assisted EAB introductions through firewood, these authors measure the severity of EAB spread, and consequently ash mortality. They assert that human activity leads to hundreds of new introduction points, which is likely to blame for the infestation now seen in southeastern Michigan. Prasad et al. (2010) estimated the EAB front is moving roughly 20 km a year using a spatially explicit cellular model, depending on economic activity, including driving, leisure activities such as camping, and wood industries known to use ash as inputs into production.

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