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HOW TO BECOME A SUCCESSFUL INVADER[§]

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ABSTRACT

Most invasive species hitchhike on human transportation, and their close associations with human activity increase their chances of uptake. Once aboard, potential invaders have to survive the journey, and those with traits such as being a general feeder or tolerance to a wide range of environmental conditions tend to survive the transportation better. Similar traits are generally considered to also aid their establishment in new habitats, but studies showed that the propagule pressure, not any of the species-specific traits, is the most important factor contributing to their successful establishment. Higher propagule pressure, i.e., repeated invasions of larger numbers of individuals, reduces Allee effects and aids the population growth of invasive species in alien lands. Coined as the invasive bridgehead effect, repeated introduction also selects a more invasive population that serves as the source of further invasions to other areas. Invasive species is the consequence of homogenocene (our current ecological epoch with diminished biodiversity and increasing similarity among ecosystems worldwide) that began with the Columbian Exchange of the 15th century and possibly the Pax Mongolica of the 13-14th century. Anthropogenic movement of goods among major cities will only accelerate, and the heightened propagule pressure will increase the number of invasive species for as long as the current practices of global commercial activities continue.

Key Words: propagule pressure, invasive bridgehead effect, homogenocene, Columbian Exchange

RESUMEN

La mayoría de las especies invasoras entran los países conjuntamente con el transporte humano y sus estrechas asociaciones con las actividades humanas aumentan sus posibilidades de admisión. Una vez a bordo, los invasores potenciales tienen que sobrevivir el viaje y las species con características tales como ser un consumidor general o una tolerancia a una amplia gama de condiciones ambientales tienden a sobrevivir el transporte mejor. También, por lo general se considera que las características similares ayudan su establecimiento en nuevos hábitats, pero los estudios muestran que la presión de propágulos, no unas de las características específicas de la especie, es el factor más importante que contribuye a su establecimiento exitoso. Mayor presión de propágulos, es decir, repetidas invasiones de un mayor número de individuos, reduce los efectos de Allee y ayuda en el crecimiento de la población de las especies invasoras en paises exóticos. Llamado como el efecto invasivo de la cabeza de puente, la introducción repetida también selecciona una población más invasiva que sirve como una fuente para más invasiones a otras áreas. Las especies invasoras son la consecuencia de homogenocene (nuestra época ecológica actual con la disminución de la biodiversidad y el aumento de similitud entre los ecosistemas en todo el mundo), que comenzó con el Intercambio Colombiano del siglo 15 y posiblemente la Pax Mongolica del siglo 13 al 14. El movimiento antropogénico de mercancía entre las principales ciudades seguirá acelerarandose, y la elevada presión de propágulos aumentará el número de especies invasoras por el tiempo que las prácticas actuales de actividades comerciales globales continúen.

Palabras Clave: presión de propágulos, efecto invasivo de la cabeza de puente, homogenocene, Intercambio Colombiano

Of the over 12,500 insect species found in Florida in 1995, 988 (7.9%) were listed as "non-native" species (Frank & McCoy 1995), but not all of them are considered "invasive." Invasive species are defined as the non-native "pest" species, i.e., those that adversely affect environment, economy and human health (Anonymous 1999). Pest status is determined primarily by human value and perception. Following its successful introduction to control cacti (*Opuntia* spp.) (Caryophyllales: Cactaceae) in Australia in 1925, for example, the moth *Cactoblastis cactorum* Berg (Lepidoptera: Pyralidae) was intentionally introduced to several Caribbean islands in 1957 (Frank & McCoy 1995) to control *Opuntia* weeds. By 1989, *C. cactorum* had spread to the Florida Keys where it became a "pest" because it began to attack two cati, *O. spinosissima* Martyn (Mill.) and *O. triacantha* (Willdenow), which are considered to have value because they are designated rare (Habeck & Bennett 1990).

Certain species-specific characteristics are often regarded as traits that render some species more "invasive." These include, among others, high dispersal ability (better survival of transportation), association with human activity (increasing opportunities for migration), ecological competence (better survival in a new environment), rapid and/or placid reproduction (e.g., sexual and asexual reproduction), and rapid population growth. The usefulness of the list of such "invasive" traits has been questioned because many species with these traits have never become invasive (Kolar & Lodge 2001). These traits may be "necessary" instead of "sufficient," but they still serve as the guide to understand the likelihood of a species to become invasive.

Steps Toward Successful Invasion and Establishment

Uptake and Migration

Most cases of species invasions are human-mediated. Living organisms extend their ranges naturally, but natural extension of most species occurs less frequently and at much shorter distances than anthropogenic events. Because most invasive species hitchhike on human transportation, a close association with human activity increases their chances of uptake. Cockroaches, rodents and some termite species tend to live near human habitat and are frequently transported. The Formosan subterranean termite, *Coptotermes formosanus* Shiraki (Isoptera: Rhinotermitidae), for example, tends to infest man-made structures (hence the common name in its native China is "house termite"), and is one of the most widely distributed subterranean termites (Rust & Su 2012). The West Indies powderpost termite, *Cryptotermes brevis* Walker (Isoptera: Kalotermitidae), often hitchhikes in wooden furniture or picture frames (and thus nicknamed "furniture termite"), and is found in more regions in the world than any other termite species.

Once aboard, the stowaway has to survive the journey (Fig. 1). General feeders that can tolerate a wider range of temperature and humidity tend to survive better during the transportation, but some species may create conditions suitable for their survival. Incipient colonies of *C. formosanus*, for example, may seal off the nest after tunneling into wet wood, and create moist conditions in their food source to survive the journey.

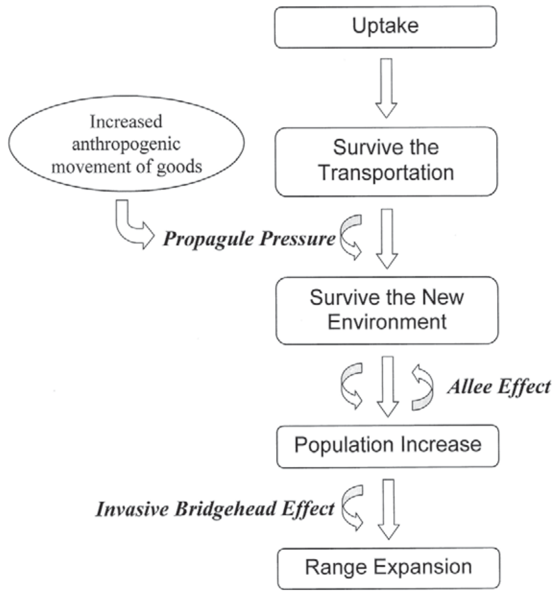

Fig. 1. Steps for a species to become a successful invader in alien lands.

Surviving in a New Environment: Propagule Pressure

Species-specific traits that better serve for survival during transportation (i.e., generalist feeders, and tolerance to a wide range of environmental conditions) are usually considered to aid the invaders to survive in new environment. Colautti et al. (2006) who studied 14 invasive characteristics (i.e., features associated with invasive species), however, found that propagule pressure was the only consistent predictor of invasiveness. Physiological tolerance and body size did not have any effect on a species' ability to invade a foreign land. Propagule pressure is defined as the measure of the total number of individuals being introduced, and is the function of the number of introduction events and the mean number of introduced individuals per event (Lockwood et al. 2005) (Fig. 1). Generally speaking, more introduction events with more individuals per event increase the propagule pressure and hence the chance of successful establishment (Colautti et al. 2006). Propagule pressure is affected by invasion pathways that are closely associated with human activities. Using the mitochondrial DNA sequences, Yang et al. (2012) examined the invasion pathways of the fire ant, *Solenopsis invicta*

Buren (Hymenoptera: Formicidae), into China and showed that this species was most likely imported from Austin, Texas, which also ranked the highest in exporting goods to China. The frequent traffic of goods from Austin to China apparently increased the propagule pressure and aided its successful invasion.

Population Growth and Allee Effect

The notion that density dependent factors govern the upper limit of population size goes back as far as Malthus and forms the backdrop for natural selection. However, low population density during the early stage of species establishment may also inhibit population growth due to infrequent intra-species encounters. Coined the "Allee effect," this principle was demonstrated in a series of studies using goldfish (Allee 1931; Allee & Bowen 1932) during the time when most ecologists were focusing on the adverse effects of overcrowding and competition on individual survival. Overcrowding increased individual competition and mortality thus inhibits population growth, but according to the Allee effect, undercrowding also deters population growth due to these aggregation-related consequences. Mechanisms contributing to the Allee effect may include mate limitation, cooperative defense, cooperative feeding, and environmental alternation through aggregation. Leung et al. (2004), for example, used prediction models to study zebra mussel invasions in 1,589 inland lakes of Michigan and found that models that included the Allee effect were better in predicting its invasion. Due to the Allee effect, higher propagule pressure increases the probability for invasive species to establish in a new environment, and to increase its population (Fig. 1).

Range Expansion and Invasive Bridgehead Effect

Many species do not establish in alien lands despite being frequently transported by man, be it intentionally or accidentally (Lockwood et al. 2005). The frequent anthropogenic movement of these species may act as a process to select a particular population that is more invasive than others. Once established, the selected population, instead of the populations in the native land, may become the source of further invasions to other regions and range expansion (Fig. 1). This phenomenon was termed "invasive bridgehead effect" by Lombaert et al. (2010) who tracked the invasive pathways of the Asian ladybeetle, *Harmonia axyridis* (HA) by analyzing the microsatellite genetic variation among its populations worldwide. There have been repeated attempts to release *H. axyridis* as the biological control agent against aphids since early 1900s, but all failed. Since 1988, *H. axyridis* has been found unexpectedly in multiple areas. Some of these populations were eventually successful in the control of soybean aphids, but others became nuisance pests due to their unpleasant odors when they overwinter indoors in large numbers. A genetic study by Lombaert et al. (2010) showed that *H. axyridis* from its native Asia established its bridgehead in eastern U.S. in 1988, from which it was later introduced to South America, South Africa and Europe. The study of *S. invicta* invasive pathways to China offers another example of bridgehead effect (Yang et al. 2012). A comparison of the genetic variations among 27 populations of *S. invicta* (10 in China and 17 in the U.S.) showed that most populations in China appeared to have originated from Wuchuan in southwest Guangdong Province, P.R. China, in which this ant species first established, and served as the bridgehead population to other populations in China.

Homogenocene

The process of successful establishment by invasive species as shown in Fig. 1 is part of a larger trend of "homogenocene" which was termed by Samways (1999) to characterize our current ecological era as an epoch with diminished biodiversity and increasing similarity among ecosystems worldwide. Homogenocene results from anthropogenic movement of organisms worldwide, and most attribute its beginning to the "Columbian Exchange," i.e. the large scale exchange of goods, and macro- and microorganisms following the 1492 voyage of Christopher Columbus to the New World (Mann 2011). Connection of 2 once-separated Hemispheres prompted the movements of numerous organisms, but before the Columbian Exchange, there was another dramatic connection of 2 largely separated worlds during the Pax Mongolica via the Silk Road.

Pax Mongolica: 13th-14th Century

Following a series of wars waged through most of the 11th century, Genghis Khan and his descendents built the largest continuous empire in human history that stretched from the Pacific Ocean to the Caspian Sea and today's Moscow. The Mongol Empire was partitioned into 4 branches, and despite political tensions and constant squabbles among them, trade routes were kept open, and exchanges of goods, people, and ideas changed the lives of those inhabited within the Mongol Empire and the neighboring nations. The Silk Road (started in the Han dynasty, 206 BCE – 220 CE) was reopened as the main land route connecting China with Europe. The Maritime Silk Road connected China through SE Asia, the Indian Ocean, the Arabian Sea, the Persian Gulf, and the Red

Sea to East Africa. Through these networks of trade routes, a global commerce flourished for the first time in human history, and productivity and populations of nations within the trade zone grew rapidly (Abu-Lughod 1989). The *Yum* system (a series of relay stations at every 32-40 km along the major routes to supply fresh horses and other travel accommodations) that was originally established to secure communication among Mongol troops, provided vital needs for traveling merchants, and the trade routes were manned by Mongol soldiers for safe passage. Chinese silk, exotic spices, Indian cotton, sugar and new crops such as carrots, turnips and buckwheat were introduced to Europe by merchants from the East.

In addition to commodities and products, people and information also flowed through the Silk Road. The Venetian merchant, Marco Polo traveled with his father and uncle to China (Cathay) and the book of his travel and adventure, "The Travel of Marco Polo" introduced Europeans to the exotic countries in the east, and stirred imagination of many including Christopher Columbus (Latham 1958). Introduction of Chinese innovations such as paper, printing, gunpowder, firearms and the magnetic compass were considered underlying factors for the emergence of Renaissance in Europe (Weatherford 2004). Through the same trade routes, the pathogen of Plague, the bacterium *Yersinia pestis* (Lehmann and Neumann 1896) van Loghem 1944, was also brought to Europe by its carrier, the Oriental rat flea, *Xenopsylla cheopis* (Rothschild) (Siphonaptera: Pulicidae) on rodents that hitchhiked trade ships from the Orient. The disease ravaged Asia with an estimated 25 million victims before entering Europe (Kohn 2008). Between 1347 and 1353, Plague killed one third of the European population, and profoundly altered the course of European history. The most significant impact of Pax Mongolica to homogenocene, however, is that stories of lands with abundance of gold, treasures, and exotic spices flowing through the Silk Road led Europeans to the age of discovery, and the Columbian Exchange.

Columbian Exchange

Columbus' voyage in 1492 connected 2 Hemispheres and promoted a dramatic and widespread exchange of organisms between them. New World crops such as maize, potato, tomato, tobacco, sweet potato, cacao, vanilla, pineapple, chili pepper, peanut, sunflower, and papaya were spread to and deeply affected lives of those in the Old World. Introduction of maize, potato and sweet potato to China, for example, turned marginal lands of mountainous terrains (which were unsuitable for cultivating traditional crops such as rice and wheat) into productive lands that contributed to the doubling of the Chinese population (Mann 2011) in the Qing dynasty (1644 to 1912). Potato was singularly responsible for the population explosion in Ireland as well as the Great Irish Famine (1845-1852) when the crops were decimated by potato blight. Before the 1500s, there were no tomatoes in Italian cuisine, no chocolate in Switzerland, no pineapples in Hawaii, no chili peppers in Thai or Indian food, no potatoes in the German diet, and no rubber trees in Malaysia. Almost as many plant species were also brought from the Old to New World, including apple, banana, black pepper, coffee, citrus, garlic, onion, peach, soybean, sugarcane, rice, wheat, and watermelon. Domesticated animals such as horse, chicken, donkey, pig, earthworm, honey bee and silkworm were introduced to the New World and changed the life style of Native Americans. As with Plague during the Pax Mongolica, many infectious diseases including malaria, small pox, chicken pox, cholera, leprosy, bubonic plague, yellow fever, typhoid, and measles were also brought from the Old to New World. Of these, the most devastating was small pox that killed 80-90% of Native American populations (Mann 2011). Columbus' crews who contracted syphilis spread it to European populations when some of them later joined the Spanish army to invade Italy. Edible plants and domestic animals were intentionally introduced, but diseases and other organisms were accidentally transferred, and many became invasive, e.g., brown rats, zebra mussels, tumbleweed (*Salsola* spp.; Caryophylalles: Amarantaceae), wild oat, and ascomycete microfungi (*Ophiostoma* spp.) responsible for Dutch elm disease. Some species such as Kudzu that was intentionally introduced (to prevent soil erosion) became a pest species, while others such as the yeast, *Saccharomyces bayanus* Saccardo, which was accidentally introduced from South America was later used for producing lager beer.

Conclusion

As shown in Fig. 1, propagule pressure is the major factor contributing to the increase of invasive species across the globe. Beginning with Pax Mongolica, and later the Columbian Exchange, anthropogenic movement of goods among major cities has increased over time, and this trend will only accelerate. This will heighten propagule pressure to provide more opportunities for potential invasive species, and to select for a more invasive population within a species. The number of invasive species, thus, will only increase for as long as current practices of global commercial activities continue. Between cities with heavy traffic, a more targeted quarantine/inspection measure focusing on potential invasive species of the source region may be one solution to intercept their shipments and reduce propagule pressure.

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