A framework for predicting which non-native individuals and species will enter, survive, and exit human-mediated transport

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Abstract Determining which non-natives are likely to be introduced is integral for understanding and predicting biological invasions. However, the hypotheses and research regarding invasive species have largely focused on processes occurring post-introduction. Improving predictions of non-native transport and generating new hypotheses about the drivers of species invasion requires a better understanding of the 'pre-introduction' mechanisms that determine whether propagules successfully enter, survive, and exit human vectors. We propose that the subset of non-natives successfully introduced are determined by two primary filtering mechanisms: (1) the characteristics of organisms, and the way in which these characteristics are shaped by and interact with their environment; and (2) the attributes, movement, and behavior of human vectors. We review how species distribution, individual phenotype, environmental conditions, and ecological interactions filter organisms between each pre-introduction stage of non-native transport. Additionally, we apply a modified version of the vector science framework to elucidate mechanisms driving patterns in human movements, which also determine the subset of individuals transported and introduced as non-natives. Our framework distills the human-mediated transport process to its most critical components, providing a simple approach for creating new hypotheses of the drivers of biological invasions.

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Introduction

Human activities, movements, and trade intentionally and unintentionally transport millions of species outside of their native range every year (Mack and Lonsdale 2001; Perrings et al. 2005; Bush et al. 2014; Hulme 2015). Of these transported species, a subset

become invasive in the habitats to which they are introduced, inflicting both economic and ecological harm (Blackburn et al. 2011; Bradshaw et al. 2016; Early et al. 2016; Paini et al. 2016). A primary goal of invasion research is to prevent and control these effects. This global research effort has stimulated a diverse array of hypotheses (e.g., Catford et al. 2009; Jeschke and Heger 2018), which have provided valuable insights into the drivers of invasion. However, there is a clear bias in invasion research favouring 'post-introduction' hypotheses, which seek to mechanistically explain which species establish as non-natives and which subset of those become invasive (Floerl and Inglis 2005; Puth and Post 2005). The lack of a mechanistic framework for 'pre-introduction' invasion dynamics (i.e., those events occurring before a non-native is introduced) restricts progress in the field as these processes often produce the ultimate drivers of invasibility, such as the identity, abundance, phenotype, and standing genetic diversity of established non-native species (Rejmánek and Richardson 1996; Colautti et al. 2006; Lockwood et al. 2009; Forsman 2014; Blackburn et al. 2015). Here we develop a pre-introduction mechanistic framework for invasions that can improve our understanding of the early invasion process and aid development of more robust methods for predicting future invasions.

The call for a greater pre-introduction focus in invasion research is not new (e.g., Carlton 1996; Ruiz and Carlton 2003; Colautti and MacIsaac 2004; Puth and Post 2005), and efforts have increased over the last two decades to incorporate mechanisms operating prior to non-native arrival (e.g., Colautti and MacIsaac 2004; Carlton and Ruiz 2005; Hulme et al. 2008; Wilson et al. 2009; Essl et al. 2015; Hulme 2015). These efforts have added substantially to our ability to prevent species invasions by enabling the categorisation of certain transport pathways as 'riskier' than others based on observed differences in the quantity and identity of transported non-natives (e.g., Bradie et al. 2013; Cope et al. 2019). But we currently cannot predict what subset of species or individuals are most likely to enter a vector, which individuals will survive transport, and which of the surviving individuals will successfully exit.

Existing research describes key components of the early invasion process, such as the likely stages and filters through which transported propagules transition (e.g., Colautti and MacIsaac 2004) or the

characteristics of human vectors that influence the quantity and identity of introduced non-natives (e.g., Carlton and Ruiz 2005). However, such studies detail only some of the processes operating during pre-introduction. In this manuscript, we combine existing frameworks and research to develop a single, integrative framework of the pre-introduction invasion process. We review how the three principal, pre-introduction filters that determine the likely subset of non-natives eventually introduced—the entrance, survival, and exit filters (Fig. 1)—are structured by the interplay between two independent transport mechanisms: (1) the characteristics of organisms, and the way in which these characteristics are shaped by and interact with their abiotic and biotic surroundings; and (2) the characteristics of human vectors (e.g., clothing, cars, boats, airplanes), and the way in which these characteristics are affected by external, socioeconomic factors.

For organism characteristics, we review research on how distribution, phenotype, environmental conditions and ecological interactions can influence which individuals pass through the entrance, survival, and exit filters (the biological processes in Fig. 2). For human vectors, we apply a modified version of the vector science framework developed by Carlton and Ruiz (2005), which characterizes vectors by various attributes such as the route they travel and their timing of movement. We modify this framework by only focusing on the four main questions that characterize vector movements: (1) *why* a vector is moving, (2) *how* it is moving, and (3) *when* and (4) *where* it is
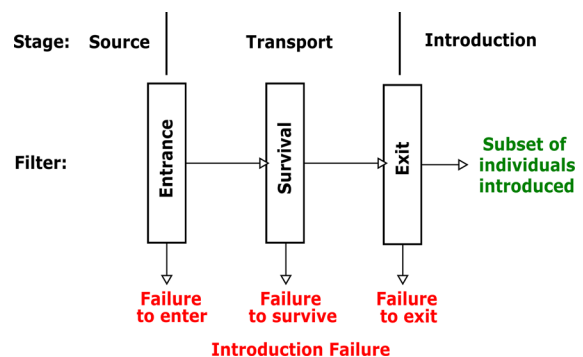

Fig. 1 Stage- and filter-based invasion framework of the first three stages of the invasion process (source, transport, and introduced). Framework structure and terminology has been adapted from those detailed in Colautti and MacIsaac (2004), Catford et al. (2009) and Blackburn et al. (2011)
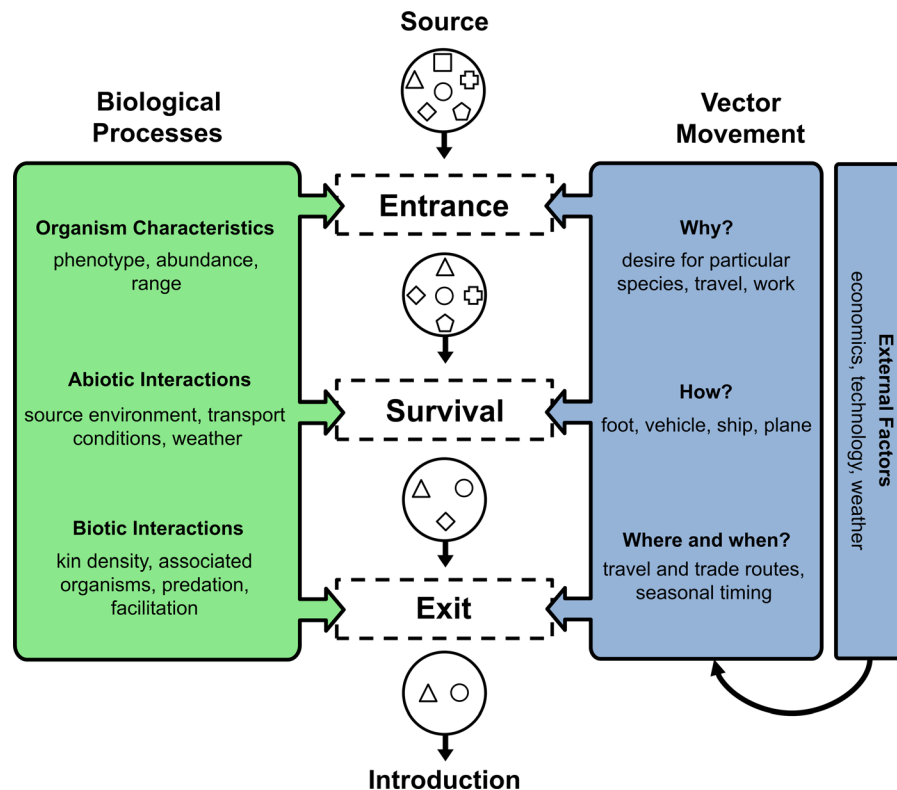
Fig. 2 Conceptual interaction between biological processes and vector movement that determine which individuals or species (both represented by different shapes) will successfully pass through the entrance, survival, and exit filters of the non-native pre-introduction process. The non-bolded text in the figure details a few examples for each sub-section of the framework. Each section of the framework does not necessarily apply to all possible situations and types of vectors (e.g., for some vectors there will be few or no biotic interactions), but all should be considered when evaluating potential mechanisms structuring the filters. This framework structure has been modeled after other similar stage-based invasion frameworks (particularly Colautti and MacIsaac 2004; Catford et al. 2009; Blackburn et al. 2011)

moving. We also add to this framework the factors *external* to a vector, such as changes in global trade networks, which affect why, how, when, and where vectors move (the vector movement components of Fig. 2). These modifications produce simple mechanistic hypotheses describing the drivers of human vector movements that can be tested using empirical data within invasion science (see examples in Table 1).

Biological processes influencing introduction

Entrance into, survival within, and exit from a human vector is influenced by the characteristics of individuals, populations, and species and how these characteristics are affected by both abiotic and biotic interactions (e.g., trait, distribution or source bias; Table 1).

Entrance filter

In the source region, species- and individual-level characteristics affecting entrance can be broadly divided into characteristics of distribution and phenotype. Species, populations, and individuals with geographical distributions that overlap human movement networks, or that closely associate with urban areas, are more likely to enter human vectors (i.e., distribution bias; Table 1; Carlton 1996; Floerl and Inglis 2005; Liebhold et al. 2016; Cardador and Blackburn 2019). Distribution can also probabilistically bias entrance geographically and taxonomically towards species that are, for example, abundant and

Table 1 Example hypotheses generated from our framework. Mechanistic hypotheses can be produced for each pre-introduction filter and tested individually or as a group for a filter or series of filters of interest

Name	Hypotheses and example questions
Distribution bias	*Hypothesis* widespread and abundant species, or those with ranges closely associated with urban centers and transport corridors, are more likely to be introduced and therefore become invasive
	Example questions Are abundant species more likely to be unintentionally collected compared to less abundant species? Are species more closely associated with people or urban areas more likely to be introduced? Is survival during transportation linked to the extent of a species' distribution is in its native habitat?
Trait bias	*Hypothesis* Species with traits that promote successful entrance, survival, and exit are more likely to become invasive
	Example questions Are there behaviors that drive individuals to enter human vectors of their own volition? Which phenotypes are associated with a higher likelihood of escape from captivity?
Source bias	*Hypothesis* Certain source habitats produce organisms with a higher likelihood of introduction and thus invasion
	Example questions Do good and poor-quality habitats vary in the propensity or ability of their propagules to enter human vectors? Are individuals from poor quality habitats in poor physiological condition, and is this linked to their ability to survive vectored transport?
Conveyance bias	*Hypothesis* Certain methods of transport will successfully introduce a greater quantity or diversity of propagules, subsequently increasing the chance of invasion
	Example questions Does the quantity and diversity of accidentally collected propagules vary between different vector types? How do different vector types vary in their transport conditions, and how does this affect non-native survival during transport?
Route bias	*Hypothesis* Certain vector travel routes will introduce a greater quantity or diversity of propagules, subsequently increasing the chance of invasion
	Example questions Do different routes of the same vector type vary in policy or regulations that subsequently affect the chance of non-natives successfully exiting the vector? Do transported non-natives survive better in certain vector routes compared to others, and if so why?

widespread (Cassey et al. 2004; Gravuer et al. 2008; Ansong and Pickering 2014).

Phenotypic characteristics can be subdivided into morphology, behavior, life-history, and physiology (Clobert et al. 2009), each of which could affect entrance. For example, individuals and species with seed structures that can attach to clothing, those that are bold and explorative, or organisms with life-histories associated with other intentionally or unintentionally transported species (e.g., parasites, mutualists, or commensalists) and materials could have a greater probability of entering human vectors (Colautti et al. 2006; Chapple et al. 2012; Auffret and Cousins 2013). Similarly, species intentionally transported and introduced as non-natives often have specific traits that increase their probability of entrance. These traits are tightly associated with human usage, such as traits related to aesthetics, hardiness, novelty, cultural value, susceptibility to capture, or the suitability of a species for an intended recipient environment (Ruiz and Carlton 2003; Cassey et al. 2004; Alcaraz et al. 2005; Mack 2005; Thuiller et al. 2006; Theoharides and Dukes 2007; Vall-llosera and Cassey 2017a).

Distribution and phenotype are not constant. Predicting the quantity and identity of non-native species likely to enter a vector therefore requires consideration of the abiotic and biotic context in the source environment. Individuals may only be active in suitable seasons, reproductive structures (e.g., seeds or larvae) may only be produced under particular conditions (Ansong and Pickering 2014), and ranges may overlap vector routes only in certain years. Additionally, abiotic and biotic conditions influence the development of phenotypes with a higher ability or propensity to enter human vectors. For example, possessing attachment structures for dispersal or a bolder personality can increase an individual's likelihood of entrance into a vector, and individuals can vary in their possession of these traits according to the availability of resources or kin density in the natal habitat (Matthysen 2005; Benard and McCauley 2008; Cote et al. 2010).

Survival filter

The survival filter 'weeds out' individuals and species unable to tolerate conditions experienced during transport. The geographic distribution of species can affect survival in unintentional and intentional pathways. More widely distributed species may exhibit broader environmental tolerances (McKinney and Lockwood 1999), and these traits potentially improve survival during transport. In terms of phenotype, individuals that possess morphological, behavioral, life-history, or physiological traits that confer 'hardiness', or that reduce sensitivity to the stress of movement, handling, and captivity, will have a higher likelihood of persisting in harsh vector conditions. Challenging abiotic conditions in or on vectors can include extremes of temperature, water availability, and even toxic compounds applied to remove unwanted hitchhikers. Identified phenotypic traits advantageous for surviving such conditions include: (1) morphological structures that reduce desiccation (Franchi et al. 2011); (2) dormancy to outlast harsh environmental conditions (Franchi et al. 2011); (3) behavioral flexibility (Mason 2010; Chapple et al. 2012); (4) heat-shock proteins improving temperature tolerance (Zerebecki and Sorte 2011); or (5) body mass or energy reserves sufficient to sustain life functions during resource deprivation (Kobelt and Nentwig 2008).

Biotic interactions affecting transport conditions are not commonly studied, but negative interactions (i.e., predation, parasitism, and competition) are all likely to occur in vectors that transport multiple species (e.g., ballast water; Galil and Hülsmann 1997). Shared captivity can also cause crowding stress, which is a primary source of mortality in intentionally transported species (Teixeira et al. 2007). Conversely, positive biotic interactions, such as mutualism and facilitation, might improve survival during transit. For example, hull fouling species that are resistant to toxic paints can facilitate the attachment and survival of other, less tolerant fouling species (Floerl et al. 2004). Phenotypes that can withstand the negative biotic interactions, or that are better able to take advantage of the positive ones, are therefore more likely to survive.

Phenotypic influences of environment and biotic interactions in the source region can carry forward through all stages of vectored transport. Certain phenotypic traits not necessarily relevant for entrance (e.g., timidity, energy storage or body size) may instead be the key to survival during transit. Such traits are affected by natal habitat conditions (Bell and Stamps 2004; Daws et al. 2006; Benard and McCauley 2008). A better understanding of the link between source environment and traits relevant to withstanding the stresses of human-mediated transport will therefore improve predictions of which regions produce individuals with a higher likelihood of surviving transport and thus invading. Similarly, for some intentionally transported species, being raised in captivity (their 'source' habitat) may produce lower quality individuals that are less capable of surviving transport (Robinson et al. 2015), reducing the likelihood of invasion. Conversely, depending on the species, source captivity could improve survival during transport through acclimation to handling and crowding stress (Baker et al. 2013a).

Exit filter

The likelihood that an individual exits a vector is also affected by geographical distribution, phenotype, and abiotic/biotic interactions. Probabilistically, we may expect that more abundant or widely distributed species will be more commonly transported, and therefore will have more opportunities to be accidentally or intentionally released. Common species may also be less valued or carefully confined during transport and therefore more likely to be freed or escape (Cassey et al. 2004; Vall-llosera and Cassey 2017b). In the case of unintentional transport, an organism not trapped within a vector can actively choose to leave. Where and when this decision occurs can be affected by phenotype, such as individual behavior (boldness or exploration; Chapple et al. 2012) or habitat selectivity (Clobert et al. 2009). Similarly, an individual can passively affect its likelihood of departure through morphological (e.g., seed structure; Ansong and Pickering 2014) or life-history traits (e.g., timing of larval release; Acosta and Forrest 2009). For intentional transport, phenotype can also affect purposeful release or accidental escape. Life-history traits can determine whether plants escape from cultivation (Dehnen-Schmutz et al. 2007), morphology often determines the purposeful release of pets (e.g., those that grow too large to be kept; Stringham and Lockwood 2018), and individuals

that exhibit a higher stress response to humans can be more likely to escape (e.g., Cabezas et al. 2013).

Abiotic and biotic conditions can influence the exit of individuals or species from a vector. Departure can be triggered by conditions within the vector itself, conditions in the locations the vectors pass through (e.g., spawning in hull fouling organisms; Minchin and Gollasch 2003), or conditions experienced during captivity (e.g., acclimation to captivity reducing escape behaviors; Cabezas et al. 2013). The development of phenotypes associated with the ability or propensity to exit, such as body size or settlement preferences, is also influenced by the quality and conditions in the source habitat from which individuals originated (Matthysen 2005; Stamps 2006; Benard and McCauley 2008; Bonte et al. 2012).

Overall, the biological processes affecting the subset of non-natives eventually introduced is mechanistically linked to both a species' geographical distribution and species or individual phenotype. Introduction probability is also influenced by the ways in which these attributes are shaped by, or interact with, the abiotic and biotic environment of the source region, transport vector, and destination habitat. In the following section we now consider mechanisms of human movement and behavior that contribute to each of the pre-introduction filters.

Vector movement characteristics

Different vectors move for different reasons ('Why?' in Fig. 2). Unintentional transport is an accidental consequence of daily human movements, primarily motivated by needs for work, travel, recreation, or visitation (Bell and Ward 2000). Alternatively, intentional transport targets particular species, which is motivated by consumer demand and cultural connections (Perrings et al. 2005; Dehnen-Schmutz et al. 2007; Hulme 2009; Helmus et al. 2014). Each vector also has a physical agent for movement ('How?' in Fig. 2). Movement methods vary widely and can include individual people (e.g., clothing and footwear), vehicles (e.g., boats, cars, airplanes), or commodities (Wichmann et al. 2009; Wilson et al. 2009; Auffret et al. 2014). Movement methods can also be divided into subcomponents (e.g., outer surfaces vs. interior compartments), each of which transports a unique subset of organisms (Carlton and Ruiz 2005).

Vector movements have directionality and timing ('Where and When?' in Fig. 2). The where-and-when of human movements are dictated by the reasons and methods for movement, generally following travel networks between locations and schedules of peak activity. For example, trade movements follow economic connections between metropolitan areas (Ruiz and Carlton 2003; Kaluza et al. 2010; Colunga-Garcia et al. 2013). Non-trade movements, such as for travel or work, follow airline, road, and street networks with associated periods of high and low activity (e.g., Guimerà et al. 2005; Hillier and Iida 2005; Schneider et al. 2013; Cope et al. 2016).

Numerous factors external to an individual vector can in turn affect why, how, where, and when vectors move ('External Factors' in Fig. 2). Some external factors that affect human vectors are natural in origin, such as weather which can result in travel cancelations or adjustments in the methods, location and timing of travel (Cools and Creemers 2013 and references therein). However, human vectors also have unique external factors that are created by people, such as: (1) changes in technology, which affects the methods and speed of movement (Carlton 1996; Carlton and Ruiz 2005); (2) economics, which can change vector movement patterns at the whims of the market (Perrings et al. 2002; Duggan et al. 2006; Dehnen-Schmutz et al. 2007; Hulme 2009); and (3) policy and regulations (e.g., European Union ban on import of wild-caught birds which shifted trade relationships among countries and continents; Reino et al. 2017) which can influence transport methods and directionality at global (Perrings et al. 2005) and local (Chivers et al. 2017) scales. Changes in these external factors act to close old transport pathways or routes and open new ones.

However, it is not enough to simply recognise that humans can move for different reasons, via different methods, following different routes and timings, all of which are influenced by external forces. Crucially, if we are to create a testable pre-introduction framework for invasion science, we must also consider how these vector characteristics interact with biological processes (Fig. 2) to filter non-natives at each pre-introduction invasion stage (e.g., conveyance or route bias; Table 1).

Entrance filter

Vector characteristics determine which subset of global species diversity is collected or encountered by a vector. Unintentional transport can occur within any type of vector movement and is most likely to entrain small or microscopic organisms that could be more difficult to find and remove via management actions (e.g., arthropods and marine invertebrates; Lockwood et al. 2013). Conversely, intentional transport occurs to satisfy our desires for resources or to enhance our environment, recreate, or consume specific foods (Mack et al. 2000; Bush et al. 2014). Intentional transport specifically targets species used to satisfy these motivations, placing particular pressure on freshwater fish, amphibians, reptiles, and plants (Lockwood et al. 2013). There are often biases for intentionally transporting species from certain taxonomic families or orders, which has been observed in animals hunted as game, used as bait, or as aquarium pets (Lockwood 1999; Duggan et al. 2006; Drake and Mandrak 2014).

The method of vector movement can also create entrance bias. Only organisms that a given type of vector interacts with will have the opportunity to be collected. One can therefore make simple predictions about entrance bias based on vector type. We can posit, for example, that aquatic vectors are more likely to collect propagules that float close to the water surface where they encounter the surfaces of boats or their ballast intake pumps (Fofonoff et al. 2003). However, more refined predictions can be made by dividing vectors into subcomponents, such as exterior and interior sections of vehicles, with the species and quantity of collected propagules differing between each subcomponent (Veldman and Putz 2010).

Where and when vectors move also creates entrance bias by determining the regions within which they operate and the temporal window within which organisms can be encountered. Localities differ in their regulations for species collection (e.g., legality of wildlife harvest; Broad et al. 2003) and rigor of inspection (Bacon et al. 2012). Vectors moving through less heavily regulated areas may thus intentionally or unintentionally collect more, or a different subset of, species than more regulated or carefully inspected vectors. The quantity and subset of species available for unintentional collection is also determined by when and where vectors tend to move, in what temporal window they tend to be active, and their destination. Sources, routes, and destinations with a higher volume of use, such as commonly used movement networks or popular destinations, are more likely to transport a greater quantity and diversity of propagules (Floerl et al. 2009; Hulme 2009; Auffret and Cousins 2013).

Predicting the timing and routes of vector movement, and thus which organisms are likely to overlap with and become entrained within a vector, can be accomplished through a variety of tools, such as gravity models (Leung et al. 2006) or other models of human movement patterns (e.g., intervening opportunities, Stouffer 1940; or a random utility model, Block and Marschak 1960). Research on the predictability of human movements has progressed rapidly thanks to the recent expansion of trackable data, such as from mobile phones (e.g., González et al. 2008; de Montjoye et al. 2013). The ecological applications of big data on human movements are only just beginning (Meekan et al. 2017) but could be applied to predict not only where and when transport vectors tend to move, but also the set of species and number of individuals vectors are likely to collect along their way.

Any external factor that alters human motivations for movement, such as weather, can influence unintentional transport. Conversely, intentional transport is specifically conducted to satisfy human desires, which are influenced by changes in regulations, legality (Bush et al. 2014), species price, utility, or popularity (Duggan et al. 2006; Drew et al. 2010). Other external factors, such as technology, can also affect the method of movement and thus the entrance filter. For example, ships initially transported solid ballast in the form of rocks, soil, and debris, which biased entrance towards plant seeds and intertidal marine species. Technological advances in the 1800 s enabled the use of water ballast, shifting entrance towards entirely aquatic organisms (Mills et al. 1993). In terms of affecting where and when vectors move, changes in the attractiveness of a location or the opportunities available along potential routes to the location (e.g., sites for trade, recreation, or entertainment) could alter the selected route and timing of travel, subsequently determining which species could enter the vector.

Survival filter

Vector characteristics play an integral role in which individuals are likely to survive transport by dictating the abiotic and biotic conditions they experience and, in the case of organisms trapped within the vector, the duration of the transport process itself. The likelihood that an individual survives depends on whether vectors are driven by motivations for intentional collection or if transport is an unintended consequence of other motivations driving vector movements. Unintentional vectors potentially expose transported propagules to extremely harsh environments or biotic interactions, resulting in high mortality (e.g., Wonham et al. 2001). Conversely, survival may be higher if movement is motivated by intentional collection because such vectors may be equipped to provide transport conditions that are as optimal as possible. However, high mortality is still possible in intentionally transported species (Teixeira et al. 2007; Carrete et al. 2012).

The how, where, and when of vector movement dictates the conditions, directionality, and tempo of the transport process, which in turn affects survival. Vector types and their subcomponents can differ widely in their transport conditions (Verling et al. 2005; McNeill et al. 2011), ranging from harsh to mild. Transport methods that inflict harsher conditions are likely to transport a comparatively lower quantity of propagules and inflict greater selection pressure on transported individuals. Vector conveyance methods that travel faster, or that follow a more direct or shorter transit route, will also tend to successfully introduce more organisms because individuals do not have to survive stressful conditions for long periods (Carlton 1996; Carlton and Ruiz 2005; Teixeira et al. 2007). The directionality of vector movement also determines the conditions transported organisms are exposed to, and the duration of transport. Regions differ in their climatic conditions, countries initiating intentional transport can differ in their concepts of animal welfare (Baker et al. 2013b), and regulatory methods employed to remove or kill transported organisms can vary widely between countries (e.g., variation in border inspection strategies between European countries; Bacon et al. 2012). Movement routes that travel through more benign regions (based on climate, laws, regulations, etc.) will have a weaker survival filter, successfully transporting a greater quantity or diversity of non-native propagules.

Human movement motivations that affect the survival filter are subject to external influences. For example, advertising campaigns promoting awareness and removal of targeted non-native species can strengthen the survival filter in unintentional pathways (Rothlisberger et al. 2010), and the level of care provided in intentional pathways could be reduced if the demand for transported species declines (i.e., care is positively related to value; Cassey et al. 2004). External factors can also influence the survival filter via changes in the methods, directionality, or timing of the vector. New regulations or technological advances could make it harder or easier for transported individuals to survive (e.g., the implementation of animal welfare laws; Baker et al. 2013b). Additionally, changes in weather could affect the survivability associated with certain vectors or routes, and new laws or tariffs can alter trade routes (e.g., Reino et al. 2017), changing the conditions non-natives encounter during transit.

Exit filter

Vector characteristics determine the ease with which individuals exit a transport vector. Intentional transport pathways with the aim of purposeful release, such as the introduction of game animals or biocontrol organisms (Hulme et al. 2008), will have a weaker exit filter because organisms are intentionally set free. Conversely, species purposefully transported to be kept in captivity, such as for ornamentation or the pet trade, must exit human control primarily via escape (Hulme et al. 2008; Cassey and Hogg 2015), leading to a stronger exit filter. For unintentional transport, long-distance movements may tend to have stronger exit filters because management regulation is more likely (e.g., cross-border transit via airline or ship ballast water). In these instances, propagules must escape detection and successfully transition through multiple cargo transfer points to reach a habitat into which they can exit. Conversely, the exit filter for movements motivated by shorter-distance needs, accomplished via walking or vehicle travel, may offer fewer restrictions.

The vector can also affect the likelihood of introduction by determining how far from the source location individuals are likely to exit. Some vector types are slow, or move shorter distances, depositing most transported individuals closer to their source

environment (e.g., footwear or clothing, Fig. 3a), while others travel quickly over longer distances, increasing the probability that individuals are deposited outside of their native range (e.g., vehicle vectors, Fig. 3b). Propagules that exit within the native range will not be considered non-native. The likelihood of achieving non-native status therefore increases as vector speed and distance traveled increases. Some vectors may even trap transported individuals until the destination has been reached, which may occur in

ground, air, or ship cargo. In such cases, the likelihood of introduction would be low close to the source when transported organisms are confined and have few exit opportunities, then dramatically increased once the vector reaches its destination (Fig. 3c).

Where and when vectors move can vary according to conditions and regulations associated with vector travel, which in turn affects the probability of exit. For example, wet weather can increase the propensity with which seeds are deposited from vehicles (Taylor et al.
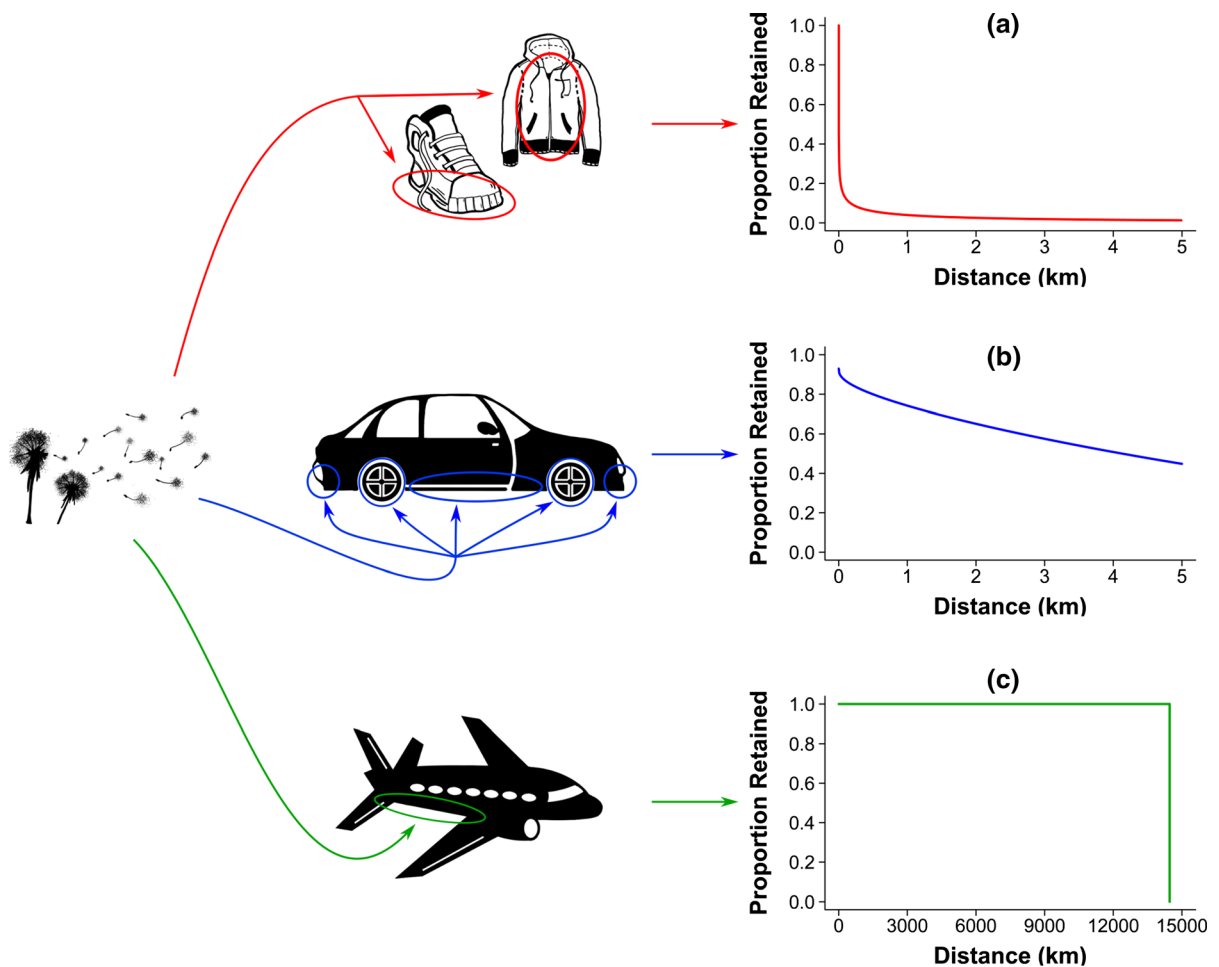

Fig. 3 Potential propagule deposition patterns for three types of vectors (clothing vector in red, car vector in blue, air vector in green) that are interacting with the same organism (plant seeds). In **a**, most propagules are deposited within tens of meters of the source environment. In **b**, propagules are more evenly deposited over several kilometers. In **c**, trapped propagules in cargo are deposited upon unpacking at the vector destination several thousand kilometers from the source region. Air vectors therefore potentially introduce the most non-native species or

individuals because the most propagules are deposited at the furthest distance from the source. Example dispersal curves in **a** and **b** were calculated using averaged coefficients from models of seed dispersal via foot and vehicle vectors from, respectively, Wichmann et al. (2009) and Taylor et al. (2012). The dispersal curve in **c** is hypothetical, with the distance traveled based on the distance between London, UK and Perth, Australia, one of the longest non-stop passenger flights
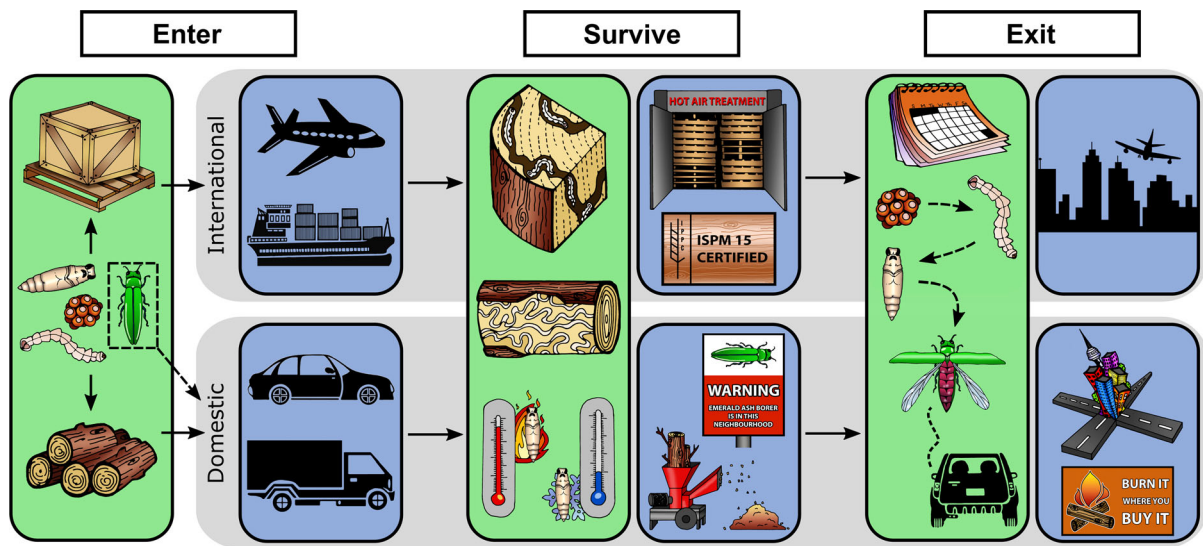
Fig. 4 Human-mediated transport of emerald ash borer (EAB) from its initial entrance into a vector to its eventual exit. Example biological processes of EAB that affect transport, such as its life history and physiological tolerances to heat and cold, are illustrated in green (following the design of Fig. 2) and further detailed in the case study text in Online Resource 1. Example characteristics of human vector movements that affect transport, such as movement via international versus domestic vectors or external regulations used to remove EAB or prevent transport, are illustrated in blue. Biological processes jointly influence both international (top grey horizontal box) and domestic (bottom grey box) transport pathways, which is why green boxes span top-to-bottom across pathways, while vector movement characteristics are unique to each pathway type

2012), and extreme weather events can be responsible for the escape of confined species (as is suspected to have occurred with *Python bivittatus*, the Burmese python; Engeman et al. 2011). Routes through or into locations in which such environmental conditions promoting exit are more common will subsequently have a higher likelihood of releasing transported organisms. Similarly, transport routes through regions with little or no regulations prohibiting release of non-native species, or during times that inspections do not occur (i.e., outside peak activity periods), will have a weaker exit filter, compared to routes that encounter more intensive quarantine or inspection.

In summary, the reasons why people move, how they move, where/when they move, and the external factors that affect each, combine to drive patterns and behaviors of human movements. By questioning the motivations, methods, directionality, and timing of human movements, we can improve predictions of which subset of species and individuals are likely to be moved, the conditions they experience during transport, and their probability of exit.

Case study: emerald ash borer

To illustrate how the biological processes and vector movement characteristics that we have outlined relate to an actual invasion, we apply our framework to the pre-introduction process of an example organism: the emerald ash borer (EAB; *Agrilus planipennis*). EAB is a wood-boring beetle that is invasive in North America. This invasion occurred not just due to post-introduction mechanisms, such as suitability of the habitats into which EAB was introduced, but also due to pre-introduction processes that involve a complex interaction between the life-history and physiological characteristics of the organism and the behavior of the vectors that collect, transport and introduce it. These pre-introduction mechanisms have been uncovered over the last two decades of research on the North American EAB invasion. We place this research into the context of our framework (detailed in Online Resource 1 and illustratively summarized in Fig. 4) to show that the broad mechanisms and filters we have reviewed match closely to the factors known to cause the introduction and subsequent invasion of a well-researched organism. Additionally, this case

study also highlights the principal message of our review: the pre-introduction process is an integral driver of invasion and a deeper understanding of it is also valuable for identifying effective targets for control and prevention. Our framework can be similarly applied to understudied, new or potential invaders both to better elucidate what is happening prior to introduction that could be driving invasion, and for identifying key mechanisms upon which to focus regulatory efforts.

Hypothesis generation

The ecological and economic damage caused by invasive species has inspired and driven research into the causes of non-native establishment and spread. While this work has provided considerable insight into invasion dynamics, prediction remains elusive. A major gap in the overall predictive framework for biological invasions is the absence of a complete, mechanistic framework for the pre-introduction invasion stages. Transported and introduced non-native species are not geographically, phenotypically, phylogenetically, or genetically random. They are instead the subset of individuals that successfully enter, survive, and exit human transport vectors. Predicting the amount and identity of introduced non-native individuals and species therefore requires that we uncover the mechanisms creating these initial biases.

Here, we have synthesized literature and other frameworks from invasion ecology, dispersal ecology, and human movement to outline the primary biological- and human-based mechanisms that interact to create the entrance, survival, and exit filters of the human-mediated transport process. By questioning how organism traits, abiotic/biotic conditions, and human movements may structure these filters, we can generate new hypotheses about the drivers of invisibility (Table 1). Not all aspects of this framework are equally relevant to every non-native species or transport pathway, but all should be considered when developing testable hypotheses about the mechanisms determining the quantity, identity, traits, and diversity of introduced non-natives, and for informing how best to prevent or control these introductions.

Glossary

Entrance	The intentional or unintentional entrance of an organism into or onto a human vector. Encompasses all terminology for this process, such as harvest, collection, capture, entrainment, uptake, or attachment
Exit	The intentional or unintentional exit of an organism from a human vector or human control. Encompasses all terminology for this process, such as escape, release, deposition, or detachment
Intentional	The purposeful human-mediated transport and introduction of non-natives (e.g., introductions for biocontrol or game animals). Note that the degree of intention can vary during the introduction process, such as cultivated plants or pets that are intentionally transported but whose release into the wild 'at-large' is unintentional
Invasive	A non-native species with demonstrable ecological or economic effects
Native range	The evolutionary geographic range of a species (i.e., range extent not established through human-mediated movement)
Non-native	Species moved outside their native range by human actions
Pathway	The variety of mechanisms by which non-native species are transported and introduced from one location to another (sensu Hulme et al. 2008)
Route	The geographic path over which vectors travel
Source	The specific location or region from which a non-native originates may or may not be the native range

Unintentional	Non-natives whose human-mediated transport and introduction is entirely accidental (e.g., hitchhiking insects or aquatic organisms trapped in ship ballast)
Vector	The physical agent by which a non-native individual is transferred

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