Primary and secondary invasion pathways: why the distinction matters

Susan Canavan*, Julian D. Avery, Jacob N. Barney, Evelyn M. Beaury, Kim Canavan, Diana Albuja Carbonell, Wesley Daniel, Leah Elwell, Peder Engelstad, Katelyn T. Faulkner, Leigh Greenwood, Heidi Himes, Catherine Jarnevich, Ivan Jarić, Amy Kendig, Julie L. Lockwood, Charles W. Martin, Heidi McMaster, Laura A. Meyerson, Kathryn A. O'Shaughnessy, Elliott W. Parsons, Alanna D. Richman, Katriona Shea, Daniel Simberloff, Helen R. Sofaer, Rochelle Sturtevant, Amanda Suzzi-Simmons, Ahmed Taheri, Emma van der Heide, Ava Waine, Deah Lieurance

**Corresponding author: Susan Canavan (sucanavan@gmail.com)*

Abstract

The pathways through which non-native species are introduced and spread help shape the rate and geographic patterns of biological invasions. These pathways can be classified as primary, where non-native species cross jurisdictional or biogeographic boundaries, or secondary, where species move within these boundaries after introduction. Despite fundamental economic, political, social, and ecological differences between these pathway types that affect the risk of species introductions and the prioritization of management responses, most classification schemes and regulatory frameworks do not explicitly distinguish between them. This lack of distinction is consequential: primary pathways are relatively well-defined and subject to biosecurity regulation, while secondary pathways remain poorly characterized and largely overlooked in policy and practice. Secondary pathways create multiple nodes from which non-native species spread, transporting individuals extensively and complicating containment efforts. Here we refine the distinction between primary and secondary pathways and explore their explicit separation in classification and management frameworks. We highlight how failing to recognize this distinction can limit the effectiveness of biosecurity systems, particularly by leaving secondary pathways inadequately addressed. Explicitly distinguishing these pathway types can help to improve invasive species control responses, strengthen cross-scale coordination efforts, reduce economic damage, and achieve global biodiversity goals.

Keywords: biosecurity; dispersal; invasive species management; pathway classification; pathway prioritization; primary pathways; secondary transport; spread; stakeholder engagement

1. Introduction

Introduction pathways help shape the rate, extent, and geographic patterns of biological invasions (Hulme et al. 2008; Essl et al. 2015). These pathways encompass the processes that facilitate non-native species movement into and within regions, and vary across spatial and temporal scales (Roy et al. 2023; Lieurance et al. 2025). We can classify these pathways as primary pathways (those that facilitate non-native species introduction to new regions) or secondary pathways (those driving spread within regions after initial introduction). Understanding pathways helps researchers, managers, and policymakers identify intervention points and design effective strategies to manage biological invasions (Hulme et al. 2008; Britton et al. 2011; Essl et al. 2015). For instance, preventing introductions to new regions through pre-border or at-border management often provides the most cost-effective and efficient way to manage biological invasions (Leung et al. 2004, Roy et al. 2024). Consequently, introduction pathways have garnered attention, not only in invasion science but also in management and policy frameworks for preserving biodiversity. Under Target 6 of the Kunming-Montreal Global Biodiversity Framework, signatories to the Convention on Biological Diversity are required to reduce the rate of non-native species introductions by 50% by 2030, in part by identifying and managing introduction pathways (CBD 2022).

To support such efforts, several pathway classification schemes have been developed, grouping pathways into well-defined categories (Essl et al. 2015; Faulkner et al. 2020). Initially, these schemes were broad, focusing on intentional and unintentional introductions that transported non-native species across regions (Saul et al. 2017). Hulme et al. (2008) formalized a more systematic approach, introducing a framework that categorized pathways into six key groups (i.e., release, escape, contaminant, stowaway, corridor, and unaided) explicitly linked to management and policy needs. This system was later refined with the addition of 44 subcategories and proposed as a global standard by the Convention on Biological Diversity (CBD 2014a). The standard global pathway classification scheme was developed primarily to categorize introduction pathways and does not explicitly distinguish between primary and secondary pathway types (Faulkner et al. 2020; but see Pergl et al. 2020). While some frameworks acknowledge spread as a stage of the invasion process (e.g., Blackburn et al. 2011; Faulkner et al. 2024), no consistent or universally adopted framework treats introduction and post-introduction spread as operationally distinct pathway categories requiring different management approaches, a significant conceptual gap highlighted by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES 2023). This lack of differentiation limits the ability to allocate management resources efficiently, particularly given that the majority of introduced species still occupy small portions of their potential range and are likely to spread further via secondary pathways (Robeck et al. 2024; Saul et al. 2017).

Recently, Faulkner et al. (2024) expanded the global framework to encompass all contemporary species movement types, including invasive species dispersal mechanisms. The expanded scheme organizes pathways into three broad categories: active dispersal by humans, human-mediated natural dispersal (i.e., dispersal without direct human assistance but resulting from human activities), and natural dispersal. These divide further into ten general dispersal mechanisms, such as intentional release, unintentional transport with commodities, movement along human-built corridors, and dispersal by natural abiotic vectors. The expanded scheme more adequately captures natural dispersal and thus is suitable for classifying both primary and secondary pathways.

Despite these framework developments, legal and regulatory pathway definitions remain inconsistent and often fail to distinguish between primary and secondary pathways. For instance, the United States Executive Order 13751 defines "pathway" as "the mechanisms and processes by which non-native species are moved, intentionally or unintentionally, into a new ecosystem" (E.O. 2016). This definition leaves geopolitical borders undefined, makes no distinction between primary and secondary pathways, and omits unaided dispersal. Similarly, the European Union defines pathways as "the routes and mechanisms of the introduction and spread of invasive alien species" under EU Regulation No. 1143/2014 (Trouwborst 2015). While both regulatory frameworks explicitly define policies to prevent invasive species introduction, establishment, and spread, neither provides clear guidance for addressing spread through secondary pathway management. This regulatory gap reflects a broader pattern in invasion science and management, where introduction and post-introduction spread are rarely treated as operationally distinct pathway types, leaving secondary pathways without clear management guidance. The challenges of documenting and tracking species movement via secondary pathways further compound this gap. Primary pathways often have better documentation due to their association with intentional or traceable human activities (Pergl et al. 2020). In contrast, secondary pathways, which include additional intentional, accidental, or unaided natural spread to new areas, prove harder to monitor and appear less frequently in primary literature, databases, and other information sources. Notably, unaided dispersal (i.e., natural spread following introduction) often plays an important role in post-introduction invasion phases (Padayachee et al. 2017; Pergl et al. 2020; Sandvik et al. 2022), yet most legal frameworks typically exclude or ambiguously address it (Gilroy et al. 2016).

While some argue that secondary pathway management need not be a priority introductions are prevented in the first place (Reynolds et al. 2015, 2017; Solarz et al. 2017), preventing all non-native species primary introductions is unlikely. The rate of new non-native species establishments continues to increase globally, with no signs of saturation despite existing and growing biosecurity measures (Seebens et al. 2025). Moreover, established non-native populations increasingly drive invasions as sources for further spread, whether through subsequent introductions to new regions (Bertelsmeier et al. 2018) or through secondary pathways within regions (Gherardi et al. 2011). Therefore, managing secondary pathways after primary introduction remains critical to containing and eradicating invasive species, as well as limiting their impacts.

Here we build on previous work to clarify primary and secondary pathway concepts for invasive non-native species, exploring how their explicit separation can support effective invasion management. Specifically, we aim to (1) develop clear, operational definitions for primary and secondary pathways, (2) document how these pathway types differ in their ecological, economic, and governance dimensions, and (3) evaluate the impact of secondary pathways in current classification and management frameworks. This analysis offers guidance for environmental managers and policymakers seeking to improve surveillance prioritization, efficient resource allocation, and effective intervention strategies for both primary and secondary pathways based on species characteristics, invasion stage, and available management options.

Defining primary and secondary pathways

Primary pathways refer to processes that facilitate species movement across a biogeographical or jurisdictional boundary (**Figure 1**). These pathways encompass vectors (how species are transported) and routes (the paths along which they travel) (Essl et al. 2015). Individuals transported via primary pathways may originate from populations of either native species or non-native species established in the source region. Thus, primary pathways include both initial introductions from native ranges and subsequent introductions from invaded regions, as long as they cross new jurisdictional or biogeographical boundaries. These pathways typically entail long-distance movements facilitated in some way by human activities [e.g., active dispersal by humans, *sensu* Faulkner et al. (2024)], because non-native species must cross significant barriers (e.g., oceans, deserts, continental divides, or land masses for aquatic species) that have greatly reduced the probability of natural movement across evolutionary time. These pathways may include international trade, travel, or transportation [for defined pathways see Hulme et al. 2008 and Faulkner et al. 2024]. Examples include transport for use as ornamental plants, pets, or biological control agents; stowaways in ship ballast water; hitchhikers in tourists' luggage and gear; and dispersal along human-built canals or with floating plastics. Once a species arrives in a new jurisdiction, it is classified as non-native, and subsequent movement within that jurisdiction or biogeographical region occurs via secondary pathways.

Secondary pathways refer to processes facilitating non-native species movement within jurisdictional or biogeographical boundaries after their initial introduction (**Figure 1**). These pathways operate post-border (however defined) and encompass both secondary intentional movement of captive or contained individuals within the region; and movement from free-living populations within the region (intentional and unintentional movement by humans, or natural dispersal). In practice, the relevant boundary type depends on context and objectives. Jurisdictional boundaries are often prioritized for regulatory purposes, biogeographical boundaries for ecological assessments, though factors such as funding mechanisms, management capacity, and stakeholder coordination also influence boundary selection. Secondary pathways can involve individual organisms, contained specimens, or established populations serving as propagule sources. While human activities can directly facilitate these movements (i.e., active dispersal by humans), they also frequently occur through natural dispersal mechanisms (i.e., human-mediated natural dispersal or unaided natural dispersal; Faulkner et al. 2024). Note that the use of 'primary' and 'secondary' refers to pathways across or within boundaries, not to primary and secondary dispersal mechanisms related to seed ecology (Rogers et al. 2019).

The Asian longhorned beetle (*Anoplophora glabripennis* or ALB) illustrates the distinction between primary and secondary pathways. It was initially introduced to North America and Europe from Asia in imported wooden packing materials (Smith and Wu 2008; Javal et al. 2019). After establishment in North America and Europe, some initial ALB infestations served as sources for secondary transport and spread, creating additional discrete infestations that made containment even more difficult. Secondary pathways for ALB included natural flight and human-mediated movement of infested materials, such as firewood, wooden pallets, and construction debris (Meurisse et al. 2019), which facilitated its spread within the United States, Canada, and European countries (noting that movement between EU countries could be classified as either primary or secondary depending on whether we consider national or EU-level boundaries; Javal et al. 2019; Solano et al. 2021). This pattern holds across taxonomic groups (**Table 1**).

Importantly, our distinction between primary and secondary pathways mostly aligns with the invasion process framework (see **Figure 1**; Blackburn et al. 2011), which underscores the central role of human activities in shaping species distributions (Essl et al. 2018). Specifically, primary pathways include both (1) the transport phase, where human activities intentionally or unintentionally move individuals or propagules beyond the barriers that define their natural range, and (2) the introduction phase, which marks a species' arrival at a new location outside its native range due to human intervention. Secondary pathways principally align with the spread stage, which includes individual or propagule dispersal within the new region. However, our framework extends beyond the traditional invasion process model by recognizing that secondary pathways also encompass the intentional transport of organisms by humans within jurisdictional boundaries, a process not captured by Blackburn et al. (2011), which is critical because extensive distribution can occur before population establishment. For example, 'Marimo moss balls' made of a green algae that were shipped from Ukraine to pet stores across the United States for sale in aquaria were found to be contaminated by zebra mussels (*Dreissena polymorpha*), an invasive species that causes ecological and economic harm when released into waterways (U.S. Fish and Wildlife Service 2021). With secondary transport, multiple introduction events may continue over time and space, overlapping with establishment and spread. This enhances establishment likelihood by increasing the probability that propagules will encounter favourable conditions or 'windows of opportunity' for invasion success (Johnstone 1986).

Our terminology follows the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) 2023 report, which distinguishes primary pathways as those responsible for introducing species to new regions and secondary pathways as those facilitating their subsequent spread within those regions. However, terminology varies across the literature. Some authors use terms such as "within-country dispersal pathways" (Zengeya and Wilson 2023) in ways that align the definition of secondary pathways used here, while others, such as Turbelin et al. (2022), use "secondary pathways" to describe less significant routes of movement rather than movement within boundaries, a definition that differs from the one applied here. This terminological inconsistency is widespread across the invasion science literature, with a range of terms used to describe both primary pathways (e.g., "cross-boundary introduction," "transboundary movement," "import pathway," "entry route," "cross-border transport") and secondary pathways (e.g., "post-introduction spread," "within-region spread," "domestic movement," "post-establishment spread") (**Figure 3**).

While we define primary and secondary pathways relative to jurisdictional or biogeographical boundaries, these two types of boundaries rarely align. Single island nations like Iceland or Cuba have aligned jurisdictional and biogeographical boundaries, making pathway classification straightforward. However, complexity arises in several scenarios: large countries with multiple biogeographical regions (e.g., Brazil, United States, Russia, South Africa), biogeographical provinces that span multiple countries (e.g., West Africa, Mediterranean region; Traveset et al. 2008), federal systems where both national and sub-national boundaries may be relevant (e.g., United States vs. individual states, EU vs. member countries), and archipelagos with complex biogeographical and legal boundary combinations (e.g., New Zealand, Hawaiian Islands). This misalignment means that what is considered a primary or secondary pathway can shift depending on the scale and context chosen for management. Moreover, the phenomenon of stratified dispersal, where species expand via jumps that then grow and coalesce, occurs across multiple spatial scales (Liebhold et al. 2020), meaning the distinction between primary and secondary pathways is not always clear-cut, nor is it always useful to make such a distinction. However, in many management contexts, explicitly considering whether movement crosses or occurs within operational boundaries provides a practical heuristic for identifying intervention points and allocating resources. In practice, these boundaries must be defined pragmatically: funding mechanisms, governance structures, and management capacity often dictate the relevant jurisdictional level. The framework is not intended to classify every instance of species movement but rather to provide a management heuristic that becomes increasingly useful as the boundary in question separates distinct regulatory or biosecurity regimes. Maintaining this flexibility in application is particularly important for secondary pathways, which often require coordination across multiple administrative levels.

Table 1. Examples of primary and secondary invasion pathways for select species. Pathway categories follow the CBD framework (CBD 2014): 1 release (dark green); 2 escape (yellow); 3 contaminant (blue); 4 stowaway (black); 5 corridor (green); 6 unaided (pink). Images via Wikimedia Commons: Common carp (D. Raver/USFWS); Red imported fire ant (AntWeb, CC BY 4.0); Lantana and Mesquite (F.M. Blanco, c. 1880–1883); Zebra mussel (S. Stukel/USFWS); Japanese knotweed (A. Barnard, 1880); Wakame (CSIRO, CC BY 3.0).

Species	Primary Pathway	Secondary Pathway
Invasive carp *(Cyprinus spp.)* 	**RELEASE** **ESCAPE** Intentionally introduced to the United States in the 1970s for aquaculture and aquatic vegetation control, subsequently escaping into natural waterways (Kolar et al. 2005)	**UNAIDED** Natural dispersal via Mississippi River system during major flooding events, enabling upstream movement past open dams (Chick et al. 2020); **CONTAINMENT** inadvertent release from bait buckets when young carp are mistaken for native baitfish (MDC 2024)
Red imported fire ant *(Solenopsis invicta)* 	**CONTAINMENT** Accidentally introduced from South America to the United States in the 1930s via contaminated soil accompanying agricultural shipments (Buren et al. 1974; Allen et al. 2004)	**UNAIDED** Flood-driven rafting of floating colony masses, dispersing to new locations during extreme weather events increasingly frequent under climate change (Ojen 2019); **CONTAINMENT** long-distance transport via infested hay bales (Wylie & Janssen-May 2017; Drees 2001)
Lantana *(Lantana camara)* 	**RELEASE** Intentionally introduced from the Americas to Africa and Asia through the horticultural trade as an ornamental plant (Vardien et al. 2012; Kannan et al. 2013)	**UNAIDED** Bird-mediated seed dispersal facilitating invasion of natural areas (Bhagwat et al. 2012); **CORRIDOR** road construction and maintenance activities transporting seeds and plant fragments while creating disturbed microsites suitable for germination (Ramaswami & Sukumar 2014)
Zebra mussel *(Dreissena polymorpha)* 	**STOWAWAY** Accidentally introduced from Europe to the North American Great Lakes in the 1980s via ballast water discharge from transatlantic shipping (Herbert et al. 1989)	**STOWAWAY** Recreational boat traffic spreading adults attached to hulls, motors, anchors, and trailers between inland water bodies (Johnson & Carlton 1996; Benson et al. 2015); **UNAIDED** waterfowl and fish serving as

		vectors for larval dispersal (Ricciardi & Hill 2023)
Japanese knotweed *(Reynoutria japonica)* 	① **RELEASE** Introduced to Europe and North America in the mid-1800s as an ornamental and fodder crop (Bailey & Conolly 2000)	⑥ **UNAIDED** Downstream dispersal of stem and rhizome fragments during flood events (Colleran & Goodall 2014); ⑤ **CORRIDOR** spread along roads and trails associated with human activity and disturbance (Rouifed et al. 2014)
Asian tiger mosquito *(Aedes albopictus)* 	③ **CONTAINMENT** Introduced globally through the used tire trade, with larvae surviving in rainwater collected in tire casings (Reiter & Sprenger 1987; Hawley et al. 1987)	③ **CONTAINMENT** Secondary spread via lucky bamboo and ornamental plant trade in standing water (Madon et al. 2002); ⑥ **UNAIDED** local dispersal and establishment in novel container habitats including cemetery vases, bird baths, and discarded plastics (Lounibos 2002)
Wakame *(Undaria pinnatifida)* 	④ **STOWAWAY** ③ **CONTAINMENT** Introduced from Asia to Europe, Australasia, and the Americas primarily through hull fouling of commercial shipping and accidental transport with aquaculture imports (Hay & Luckens 1987; Silva et al. 2002)	④ **STOWAWAY** Secondary spread via recreational vessel movements and aquaculture equipment transfers between ports and farms (Forrest & Hopkins 2013); ⑥ **UNAIDED** drift of fertile sporophytes establishing new populations in harbours and natural reefs (Russell et al. 2008)
Mesquite *(Prosopis sp.)* 	① **RELEASE** Deliberately introduced to Africa from the early 19th century for timber, fuel, charcoal, and to combat land degradation (Kamiri et al. 2024; Mungoche et al. 2025)	⑥ **UNAIDED** Spread from introduction sites along livestock and wildlife corridors as seeds pass through digestive systems and germinate from dung in new grazing areas (Mungoche et al. 2025); ③ **CONTAINMENT** additional spread via trading and transport of pods valued for fodder, traditional medicine, and brewing (Shackleton et al. 2014)

2. Distinguishing between primary and secondary pathways

Primary and secondary pathways differ in their economic, political, social, and ecological dimensions, with direct implications for how management approaches are designed and implemented (summarised in **Table 2**).

2.1. Differences in pathway characteristics

Primary pathways typically involve transport of organisms across significant barriers through specific entry points such as seaports and airports. These introduction events are typically episodic and infrequent, especially compared to the continuous movement that characterizes many secondary pathways. Though primary pathway routes are often well-defined, the species arriving through them can be highly unpredictable, as stowaways from global trade may include unexpected taxa from distant regions. These pathways often require organisms to survive long-distance transport, with the surviving individuals forming the genetic backbone for nascent populations. In contrast, secondary pathways are numerous, diffuse, and difficult to monitor. They include human-mediated transport (e.g., of contaminated materials like mulch or gravel) and natural processes such as flooding or animal-mediated dispersal (including zoochory; Hirsch et al. 2018). The diversity of secondary pathways makes them less predictable than primary pathways, even when the identity of spreading species is known. Secondary pathways generally involve shorter transport distances, often between ecologically similar regions. The combination of reduced transport stress and multiple introduction sites increases both survival and establishment success (Gippet et al. 2019). Multiple introduction events via secondary pathways also increase the probability that organisms will arrive at the right time (matching seasonal windows for establishment) and in the right place (suitable microsites).

Secondary pathways can involve varying levels of propagule pressure, defined as the number of individuals available to establish a new local population (Lockwood et al. 2005). When established populations serve as sources for natural dispersal, propagule pressure may be high and continuous. Alternatively, human-mediated secondary transport (such as the movement of pets or horticultural plants within a region) may involve fewer individuals, but repeated movement events increase opportunities for individuals to escape and establish across diverse locations and broad geographic areas (Lockwood et al. 2005). Over time, secondary pathways can shape the genetic structure of non-native populations by mixing individuals from multiple introduction events or source populations, potentially increasing genetic diversity and enhancing adaptive potential and establishment success (Wilson et al. 2009). This mixing can create novel genetic admixtures not found in the native range, leading to unpredictable phenotypes and potentially more aggressive hybrid forms that may exceed the invasive capabilities of either parent population (Meyerson et al. 2010).

2.2. Differences in management & intervention

Today's formalized boundaries and biosecurity systems make distinguishing primary and secondary pathways essential for categorizing actions into pre-border, at-border, and post-border interventions. These distinctions align with established biosecurity models, such as international treaties and national policies under frameworks like the Convention on Biological Diversity, the International Plant Protection Convention (IPPC), and the Kunming-Montreal Biodiversity Framework. Because primary pathways typically involve larger, well-defined boundaries (but see discussion on biogeographic boundaries above), such as international borders and distinct entry points like seaports and airports, limiting primary introductions relies on pre-border and at-border management strategies. These actions include leveraging international agreements and biosecurity protocols to intercept species at concentrated locations. Consequently, primary pathway interventions often use centralized management approaches.

Sub-national legislation, priorities, and capacities guide post-border interventions for secondary pathways, which operate at multiple spatial scales with a more fragmented governance structure. Instead of uniform, centralized policies, a mosaic of sub-national regulations including state, provincial, local and Indigenous management approaches shapes biosecurity actions. This decentralized arrangement must contend with species spreading through complex movement networks that cross administrative boundaries (e.g., crossing state borders, or from private to public land) and extend across ecologically connected but jurisdictionally fragmented areas (e.g., watersheds spanning multiple counties, continuous forest patches under mixed ownership). For example, managing the red imported fire ant (*Solenopsis invicta*) in the United States, the world's costliest invasive ant species (Angulo et al. 2022), illustrates ecological federalism, where federal agencies set overarching policies while states retain implementation authority (Sims et al. 2023). This division of responsibilities requires extensive coordination as secondary pathways cross jurisdictional boundaries. In the southern United States, these ants disperse via human-assisted activities (e.g., nursery plant trade, soil movement) and natural mechanisms (e.g., rafting during floods, flying queens establishing new colonies; **Figure 1a; Table 1**) across interstate boundaries (Callcott and Collins 1996; Shoemaker et al. 2006; Tschinkel 2006). Federal agencies, such as the United States Department of Agriculture's Animal and Plant Health Inspection Service (USDA-APHIS), establish quarantines and regulate interstate shipments, while state and local authorities conduct inspections, coordinate treatments, and work with outreach programs to detect and report new infestations (Drees and Gold 2003; Morrison et al. 2004; USDA-APHIS 2023). Although this governance landscape demands extensive communication and collaboration between state/provincial and federal agencies to be effective, it also creates opportunities for regionally tailored actions and community initiatives.

Managing secondary pathways involves ongoing containment, suppression, and mitigation efforts, which may need to persist for decades. Because secondary pathways include numerous, sometimes unexpected movement modes, they often pose unique management challenges. For example, human-mediated dispersal largely drives spotted lanternfly (*Lycorma delicatula*) spread in the United States, particularly through cryptic egg masses laid on outdoor objects, including trucks, trains, firewood, outdoor furniture, and pallets, allowing the species to cross administrative boundaries rapidly and evade containment measures (Figure 1. Ladin et al. 2023). Cryptic invasions, whether morphologically similar species or cryptic genotypes of known invaders, present additional challenges as they can spread undetected via secondary pathways and complicate control efforts, including biological control options (Morais and Reichard 2018; Jarić et al. 2019; Canavan et al. 2020). Secondary pathways also operate through informal channels that are difficult to regulate, including hobbyist trading networks, online marketplaces, movement of recreational equipment, and travel to seasonal properties near ecologically sensitive areas (Seekamp et al. 2016; Novoa et al. 2020). Such diverse and spatially and temporally diffuse pathways necessitate continuous, flexible management strategies that integrate public awareness campaigns, regulatory measures, and cross-sector collaboration. This sustained commitment to monitoring, outreach, and rapid response substantially contributes to secondary pathway management's resource-intensive nature (**Table 2).**

Table 2. Generalized differences in the characteristics of primary and secondary pathways and the corresponding management approaches most likely to reduce propagule pressure. These differences illustrate how treating introduction and post-introduction spread as operationally distinct pathway types can support effective management.

		Primary Pathways	Secondary Pathways
Differences in pathway characteristics			
	Pathway complexity	Fewer, well-defined, often predictable entry points. Tends not to include natural dispersal.	More diverse routes, diffuse. Includes natural dispersal once established.
	Geographic scale	Generally large-scale, international or national.	Variable in scale, from localized movements to international distribution networks.
	Boundaries	Clear, established, often international boundaries (e.g., borders) or significant biogeographic barriers that have separated landscapes or seascapes for millennia.	Less defined, fragmented boundaries (e.g., sub-national jurisdictions, land ownership).
	Ecological considerations	Species must survive long-distance transport and introduction bottlenecks. Both singular introductions and multiple repeated introductions are possible.	Shorter distances with multiple introduction points, leading to higher propagule pressure and admixture. Shorter distances can correspond to more similar ecological conditions between source and recipient communities, promoting establishment.
Differences in management and intervention			
	Management focus	Primarily preventative, pre- and at-border measures to avert initial introductions. Implementation is less complex due to predictability of entry points and the established, often international nature of relevant boundaries.	Primarily focused on containment and mitigation of impacts after species introduction. Prevention is difficult due to the complexity of pathways and the diffuse nature of entry points.
	Stakeholder involvement/ governance structure	Comparatively more centralized (e.g., federal agencies, treaties, international bodies, trade/industry groups).	Management involves multiple jurisdictions and diverse stakeholders, including local governments, communities, NGOs, industries, and landowners, requiring coordinated multi-level governance across fragmented institutional boundaries.
	Management costs	High initial investment in infrastructure and biosecurity, yielding long-term benefits by preventing costly, often irreversible biological invasions.	Ongoing costs for containment, but also opportunities for pathway-level interventions (e.g., boat inspection stations, boot brush stations) that can prevent simultaneous spread of multiple species. Cost-benefit balance of management often shifts over time for any given species.

Political/economic Barriers	Broadly applicable treaties and other policies (e.g., import/export regulations) have variable enforcement at both source and destination; effectiveness is subject to larger-scale political and economic interests.	Fragmented responsibility across multiple jurisdictions, requiring cooperative management and alignment of local policies in often ad hoc scenarios.
Public awareness	Generally lower, as the public may have limited direct interaction with primary introduction pathways. Prohibitions of movements of large pets and fresh fruits and meats are notable exceptions.	Despite outreach campaigns, awareness remains highly variable. The public is more directly involved in and affected by this category, creating opportunities for targeted outreach and education.
Research and data Needs	Data typically enable risk assessments and inspections, but legal and logistical barriers to obtaining trade and transport data are serious ongoing impediments.	Finer, detailed abundance and movement data largely lacking; local ecological knowledge and adaptive management strategies needed.

3. Why distinguishing primary and secondary pathways matters for invasion management

3.1. Secondary pathways often determine the scale and speed of invasion

While primary pathways are crucial for initial introductions, they do not always determine invasion extent or speed, as many species transported through them fail to establish. Many invasions exhibit stratified dispersal patterns, where long-distance jumps create satellite populations that subsequently expand and coalesce, dramatically accelerating spread beyond what simple diffusion models predict (Shigesada and Kawasaki 1997). Therefore, human-mediated secondary pathways play a significant role in determining the realized range of an invasive species at a given time since introduction, because species relying solely on natural dispersal often take many years to expand to their climate and biotic limits (Robeck et al. 2024). Even when propagule pressure through primary pathways is high, species may fail to establish and spread if key secondary pathways are absent. The spongy (*Lymantria dispar*) in North America illustrates the importance of human-mediated secondary spread (Liebold et al. 1992). Via natural dispersal alone, this species spreads approximately 2.5 km per year through larval ballooning (wind dispersal of larvae on silk threads). However, human-assisted movement of egg masses on vehicles, outdoor equipment, and firewood can accelerate spread rates beyond 20 km per year, an 8-fold or greater increase that has facilitated its expansion across the continent despite ongoing containment efforts (Liebold et al. 1992 ; Bigsby et al. 2011).

Secondary pathways can also restructure invasion dynamics, favouring some species over others. For example, some invasive species create new secondary pathways for other non-native species (e.g., when invasive ants become seed dispersers) by reshaping ecological interactions (Faulkner et al. 2024). In southeastern Australia, for example, displacement of native ants by the invasive Argentine ant (*Linepithema humile*) shifted seed dispersal toward the invasive shrub *Polygala myrtifolia* and away from native *Acacia retinodes*, contributing to invasion meltdown and enabling the spread of the invasive shrub (Human & Gordon 1997; Rowles & O'Dowd 2009; Ricciardi and Simberloff 2025; Simberloff & Von Holle 1999).

3.2. Secondary pathways may require culturally conscious intervention strategies

Cultural and social practices can serve as distinct secondary pathways. Some invasive species become deeply integrated into local cultures while others are universally reviled (Nuñez et al. 2019). While species may be initially introduced for one purpose, cultural integration can create new pathways for secondary spread through region-specific practices, also complicating management by reducing public support for control measures (Jarić et al. 2025). In South Africa, for example, non-native medicinal plants often introduced originally through botanical gardens or ornamental trade now spread through traditional healing networks, with 41% harvested locally (Williams et al. 2021; Yessoufou et al. 2021, 2022). Traditional knowledge systems and community demand, rather than commercial markets, drive such internal trade networks. Similarly, modelling of the non-native perennial Plectranthus barbatus in the southern Cape of South Africa showed that without human-mediated long-distance dispersal related to local cultural practices, its population would decline to only 30% of its current size (Botella et al. 2022).

Release practices, whether religious or based on perceived ethics, can rapidly create multiple disjunct populations across a landscape. In China, the religious practice of releasing turtles, fishes, and birds (prayer animal release) contributes to invasion risk, with 63% of high-intensity release sites overlapping with suitable habitat for the released species (Magellan 2019; Wasserman et al. 2019; Du et al. 2024). The belief that releasing unwanted pets is humane has similarly led to widespread establishments, including red-eared slider turtles across North America, Burmese pythons in Florida, and raccoons across Japan (Spear 2018; Willson et al. 2011; Ikeda et al. 2004). Garden plant sharing and informal plant collecting represent additional culturally embedded secondary pathways in Europe and North America. These culturally driven pathways involve deeply held beliefs and social norms, requiring management approaches that engage communities through education and value-based dialogue rather than through enforcement alone (Jarić et al. 2025).

3.3. Multiple secondary pathways increase invasion risk and impact

Multiple secondary pathways for the same species can amplify invasion risk because each additional pathway provides further opportunities for dispersal and evasion of population control. While causality may be bidirectional so that impactful species may access more pathways, and species using more pathways may cause greater impacts, evidence shows that species using multiple pathways tend to have higher ecological impacts (Pergl et al. 2017; Saul et al. 2017; Foxcroft et al. 2019).

Several studies demonstrate this pattern. In risk assessments, Ponto-Caspian aquatic species in Great Britain that used more secondary pathways (e.g., inland boating, unintentional stocking, and incidental transport by recreational activities) received higher cumulative risk scores, indicating a greater likelihood of both entering the region and spreading once initially introduced (Godard et al. 2012). Similarly, in North America's Great Lakes, recreational boating facilitates invasive species transport with an estimated 11 million boat trips per year, collectively generating substantial cumulative risk (Drake et al. 2021). Research in South Africa's national parks demonstrated a direct correlation: the number of secondary pathways invasive plants exploit, significantly predicted their ecological impact diversity and extent (Foxcroft et al. 2019).

These findings suggest that species with multiple dispersal routes colonize a broader range of suitable habitats and cause more varied environmental disturbances. From a management perspective, the number of secondary pathways a species uses provides a useful metric for estimating invasion risk and prioritizing control efforts.

3.4. Under-recorded and under-valued secondary pathways can hamper management efforts

The informal nature of most secondary pathways creates significant documentation and management challenges. Domestic movement of people and goods lacks the systematic tracking applied to international transport, making it difficult to assess risks associated with domestic commerce, informal exchanges, online marketplaces, and recreational activities (Pergl et al. 2020). Assumptions that natural dispersal dominates post-introduction spread may lead to undervaluing human-mediated dispersal, when human-assisted movement may actually be the more important secondary pathway (Beaury et al. 2021). For example, anglers seeking to establish sport fisheries may make unauthorized fish introductions through intentional releases, with human-assisted dispersal accounting for the majority of secondary introductions in freshwater systems (Rahel and Smith 2018; Cambray 2003). These documentation gaps mean that secondary spread rarely appears in invasion records, limiting the ability to assess pathway importance or target interventions. Social media trends can similarly trigger rapid surges in demand, as seen when ornamental plants like pampas grass experience viral popularity, creating sudden pulses of secondary spread through online sales and informal sharing networks (Canavan et al., in press). Addressing these interconnected challenges requires systematic sampling of secondary transport mechanisms, such as surveying trucks at weighing stations, railway cars at depots, or containers at domestic destinations, to quantify spread patterns and assess intervention efficacy.

4. Research gaps

Despite progress in understanding non-native species pathways, critical gaps remain, particularly concerning secondary pathways and the operational distinction between primary and secondary pathway types. Most fundamentally, the specific secondary pathways that drive or contribute the most to species spread are rarely known, as research relies on indirect proxy indicators (like trade volume or traffic patterns) rather than on direct observation of organism movement. This limits understanding of how secondary pathways function and how pathway diversity contributes to spreading species. Another critical gap is mapping where pathways actually occur on the landscape. While conceptual categories like 'firewood movement' or 'recreational boating' exist, the specific roads, water bodies, or trails that pose the highest risk are rarely identified. Creating spatially explicit representations of actual invasion routes could help target interventions more effectively.

Data are also lacking on propagule pressure and establishment success comparing primary versus secondary pathways and among different secondary pathways (but see Gippet et al. 2019 for insects). Without these data, identifying drivers of invasion risk and prioritizing interventions remains challenging. Many secondary pathways, such as human-mediated natural dispersal or abiotic mechanisms like flooding and hurricanes, remain under-researched (Pergl et al. 2020). While tools like the U.S. Geological Survey (USGS) Nonindigenous Aquatic Species Flood and Storm Tracker (FaST) help predict aquatic species spread during flood events, such predictive capabilities remain rare for most secondary pathways (Pfingsten et al. 2024). Shifting environmental conditions and an increase in climate-related disturbances may activate new pathways or alter the effectiveness of existing ones (Lieurance et al. 2025).

Understanding of how multiple secondary pathways interact to create synergistic or antagonistic effects is also limited, but this dynamic is central to invasion syndromes where predictable suites of factors drive invasion success (Foxcroft et al. 2019; Novoa et al. 2020). For instance, hurricanes can transform the pet trade pathway when storms destroy pet stores and release exotic species, or flooding events can activate aquaculture as an invasion pathway when farmed fish escape inundated ponds. These synergistic effects can also activate “sleeper pathways”. Kowarik and Lippe (2011) demonstrated that urban infrastructure significantly influences wind dispersal of tree-of-heaven (*Ailanthus altissima*) samaras, with smooth pavements facilitating long-distance movement whereas cobblestones hinder dispersal. Conversely, certain pathways may counteract each other, where natural barriers or containment measures mitigate human-facilitated spread. Assessing, or guarding against, such interactions are areas for future invasion pathways research.

Beyond ecological knowledge gaps, we also lack evidence-based communication strategies that effectively motivate secondary pathway management. While some studies have tested messaging approaches for specific pathways (e.g., Wallen & Kyle 2018; Shaw et al. 2021 for recreational boating), comprehensive evaluation of outreach effectiveness remains limited. Similarly, while invasive species economic impacts are well-documented, specific costs attributable to secondary pathways versus primary introductions remain largely unquantified. Available economic analyses may be biased toward pathways with easily documented costs, such as agricultural contaminants, while underestimating pathways with diffuse or indirect impacts (Turbelin et al. 2022). This limits the ability to demonstrate management benefits to stakeholders.

The potential misalignment of jurisdictional and biogeographical boundaries, discussed above, also creates practical challenges for pathway data collection and governance. Differences in boundary definitions across regions can create silos in pathway management responsibilities, and these governance challenges span international, national, and local scales, each requiring distinct coordination approaches. Cross-jurisdictional collaboration and systematic pathway monitoring can help address these challenges, strengthening the ability to distinguish and manage primary and secondary pathways effectively across scales.

Conclusion

In this paper, we clarified the distinction between primary and secondary pathways and highlighted how separating these concepts can support effective invasive species management. While the classification of pathways depends on how boundaries are defined, this distinction remains valuable because the ecological, economic, and governance challenges associated with primary and secondary pathways often differ substantially. While centralized border controls and international agreements can typically facilitate the management of primary pathways, secondary pathways usually require coordinated efforts across multiple jurisdictions, diverse stakeholders, and varied cultural contexts. Secondary pathways are often neglected in both the academic literature and in biosecurity planning, but they determine the ultimate scale and speed of invasions and present unique management challenges that current frameworks inadequately address. Explicitly distinguishing between primary and secondary pathways provides a practical foundation for pathway-based management that can adapt to local contexts while maintaining strategic focus. Future efforts can help to fill critical knowledge gaps: identifying which secondary pathways drive species spread, quantifying propagule pressure across different pathway types, and understanding pathway interactions. As climate change and global connectivity continue to evolve, secondary pathway management can help to prevent established species from becoming tomorrow's widespread invaders. Addressing both primary and secondary pathways can support building resilient ecosystems and achieving global biodiversity goals.

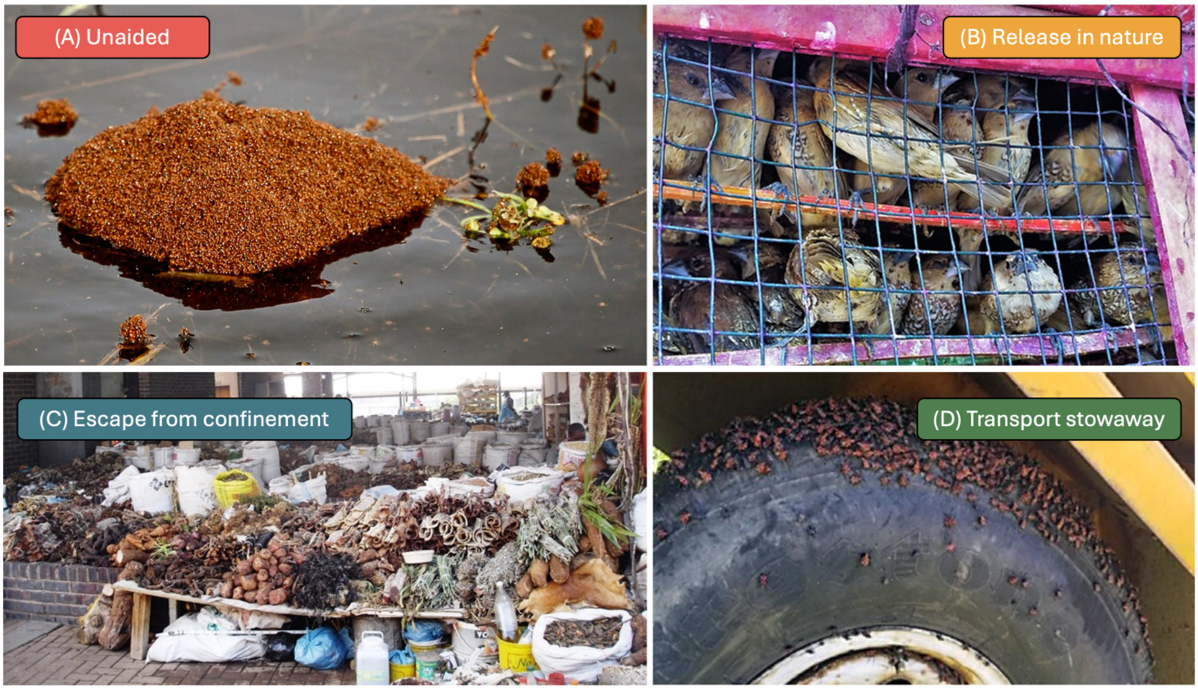

Figure 1. Examples of secondary pathways facilitating spread of invasive species within regions. (A) Fire ants (*Solenopsis invicta*) dispersing through natural rafting behavior during flood events, enabling colonies to survive and colonize new areas across the southern United States without human assistance (photo credit: Doris Ratchford/Flickr/CC BY 2.0). (B) Caged birds awaiting release in Jakarta, Indonesia, for prayer animal release ceremonies. This cultural practice of intentional release has been linked to the establishment of non-native turtles, fish, and birds. (Photo: Mike W/Creative Commons) (C) Non-native medicinal plants for sale, escaping confinement through the South African "muti" trade, contributing to their regional spread through traditional healing networks (Photo: Vivienne L. Williams). (D) Spotted lanternfly (*Lycorma delicatula*) egg nymphs on a vehicle, dispersing as a stowaway; these cryptic egg masses on cars, trucks, and trains have accelerated the species' spread throughout the northeastern United States (Photo: PA Department of Agriculture). Each pathway represents different management challenges, from natural processes that cannot be prevented to cultural practices that can be addressed through community engagement rather than regulatory enforcement.

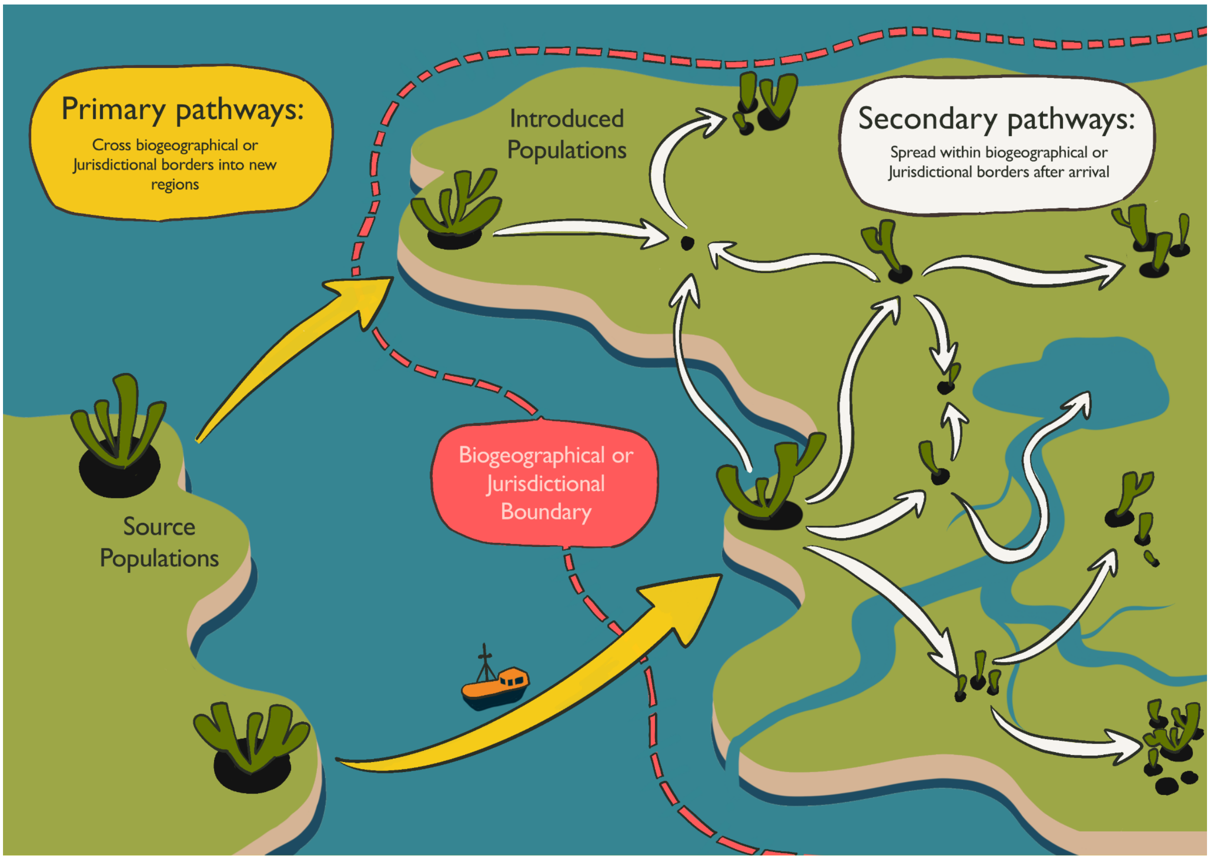

Figure 2. Conceptual diagram illustrating the distinction between primary and secondary pathways of non-native species movement. Yellow arrows crossing the pink dashed line (representing biogeographical or jurisdictional boundaries) show primary pathways, which move individuals from source populations across boundaries into new regions. White arrows represent secondary pathways, depicting the spread of non-native species within regions through networks of human-mediated or natural dispersal processes. Green plants indicate a hypothetical non-native species, with black circles representing individual populations established through these pathway processes.

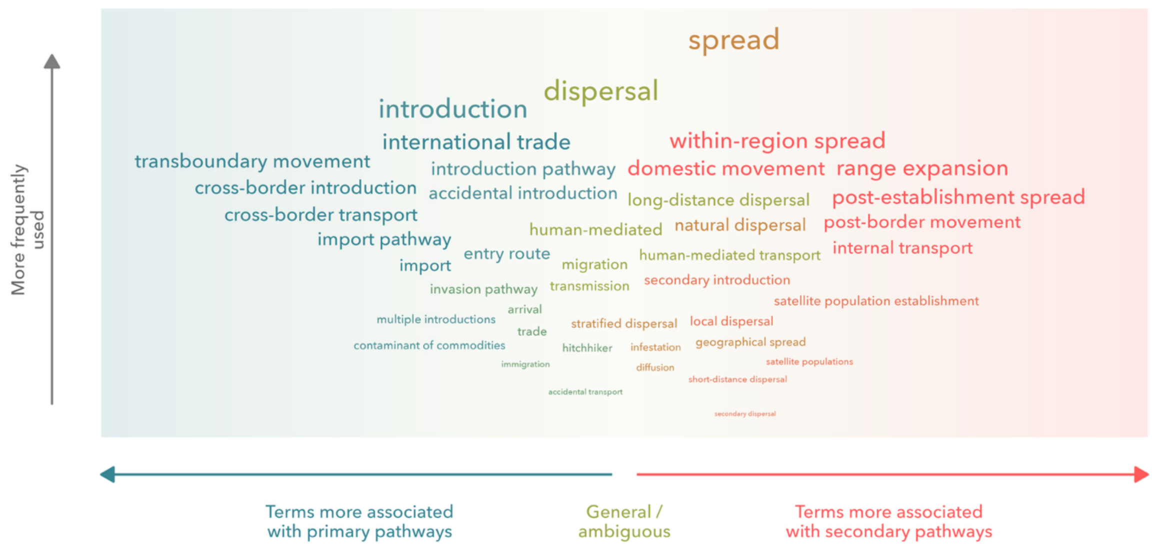

Figure 3. Illustrative semantic gradient of pathway terminology. The invasion science literature uses a wide variety of terms to describe how non-native species move into and within new regions. Some terms are more commonly associated with primary pathways (left), others with secondary pathways (right), while many are used in both contexts (centre). Terms were loosely assigned along this gradient for illustrative purposes; their position is not definitive, as most terms could apply to either pathway type depending on context. This gradient, based on terminology extracted from 2,706 research papers on forest pest invasions, illustrates the lack of consistent, operationally distinct language for distinguishing between these pathway types. Vertical position and text size reflect relative frequency of use.

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