Dark invasions as cryptic components of biological invasions

Jingrui Sun[1,2,3*], Teun Everts[4,5], Ronaldo Sousa[6], Ismael Soto[7,8], Philip E. Hulme[9], J. Robert Britton[10], Phillip J. Haubrock[7,10,11]

[1.] *Yunnan Key Laboratory of International Rivers and Transboundary Eco-Security, Institute of International Rivers and Eco-Security, Yunnan University, Kunming 650091, China*

[2.] *State Key Laboratory for Vegetation Structure, Function and Construction (VegLab), Kunming, China*

[3.] *Ministry of Education Key Laboratory for Transboundary Eco-Security of Southwest China, Yunnan University, Kunming, 650091, China*

[4.] *Genetic Diversity, Research Institute for Nature and Forest (INBO), Geraardsbergen, Belgium*

[5.] *Biology Department, KU Leuven, Heverlee, Belgium*

[6.] *CBMA – Centre for Molecular and Environmental Biology/ARNET-Aquatic Research Network/ IB-S, Institute of Science and Innovation for Bio-Sustainability, Department of Biology, University of Minho, Campus Gualtar, 4710-057 Braga, Portugal*

[7.] *Faculty of Fisheries and Protection of Waters, University of South Bohemia in České Budějovice, Czech Republic*

[8.] *Department of Conservation Biology and Global Change, Doñana Biological Station (CSIC), Seville, Spain*

[9.] *Bioprotection Aotearoa, Department of Pest-Management and Conservation, Lincoln University, PO Box 85084, Lincoln 7647, Christchurch, New Zealand*

[10.] *School of Life and Environmental Sciences, Faculty of Health, Environment and Medical Sciences, Bournemouth University, Poole, Dorset, The United Kingdom*

[11.] *Gulf University for Science and Technology, Department of Mathematics and Natural Sciences, Kuwait*

*Correspondence; jingrui.sun@ynu.edu.cn

Abstract

Understanding and managing biological invasions typically requires knowledge of species records, known impacts, recognized pathways and definitions of non-native status, yet this information is rarely complete or without uncertainties. We develop the concept of dark invasions to describe a suite of hidden or underacknowledged aspects of biological invasions that are rarely quantified because species, pathways, distributions, spread dynamics or impacts are undetected, misidentified, biogeographically unresolved, temporally delayed, poorly attributed or excluded by regulation. We characterize dark invasions as resulting from six interacting components of uncertainty: taxonomic, biogeographic, temporal, detection, impact, and regulatory. We describe how each component of dark invasions can cause invasion risks to be underestimated across monitoring, research, management, and policy activities. Dark invasions complement and integrate existing concepts, such as cryptic invasions, lag phases, invasion debt, and impact debt within an overarching concept centralized around the mismatch between recorded invasion data and realized invasion risk. We argue that some components of dark invasions can at least partially be mitigated through emerging technological approaches, and that the dark invasion concept can guide detection-based, uncertainty-based and inference-based assessments, while promoting more proactive, ecologically grounded biosecurity. Recognizing dark invasions can contribute to shifts in research, management and policy, moving from a reactive approach addressing well-known invaders towards a proactive and anticipatory approach that acknowledges uncertainties and addresses hidden invasion risks before they become detectable.

1. Introduction

Biological invasions jeopardize global biodiversity by affecting native species, ecosystem functions, and services (Haubrock, Everts, et al., 2026; IPBES, 2023). Invasion science (the field that studies the causes and consequences of biological invasions; Richardson, 2010) aims to understand how non-native species are transported, introduced, establish, spread, and cause impacts (Haubrock, Everts, et al., 2026; Haubrock, Tarkan, et al., 2026). The tools developed by invasion scientists, including risk assessment, impact classification, and national or regional non-native species checklists, have substantially advanced invasion management (Perrings et al., 2009; Peyton et al., 2026). However, these tools remain biased towards "known knowns" and thus what is already visible through scientific research, policy frameworks, and monitoring efforts (Hulme, 2012; Pyšek et al., 2008).

Traditional assessments of invasion risk (Leung et al., 2012) or impact (Blackburn et al., 2014) generally focus on species that are already known to be invasive somewhere, possess traits that were previously linked to high-impact, and have well understood global distributions (to assist with predicting pathways and climate matches). Conversely, species that are difficult to detect or identify, rarely targeted in systematic monitoring programmes, whose non-native status is uncertain, and/or for which there is no regulatory requirement for management, are usually overlooked despite their often pose substantial invasion risk (Davies et al., 2013; Morais & Reichard, 2018; Spear et al., 2021; Verloove, 2010). Moreover, molecular tools increasingly highlight the complexity of identifying what is or what is not a non-native species. For example, the pathogen *Phytophthora agathidicida* causes dramatic dieback of the endemic kauri *Agathis australis* in New Zealand and was initially believed to be a recent non-native introduction until phylogenetic data suggested a much earlier arrival pre-dating European settlement (Winkworth et al., 2021). Similarly, the spread of the non-native common reedgrass (*Phragmites australis*) in North America was long obscured because the invader belonged to the same nominal species as native lineages, making the invasion visible only after genetic evidence clarified its origin and identity (Saltonstall, 2002). Environmental DNA surveys are capable of detecting species that were previously thought absent from a region, such as for Asian carp (*Hypophthalmichthys* spp.) in the Chicago-area waterways, revealing an invasion risk that conventional capture-based surveys missed, demonstrating that recorded absence by capture methods does not necessarily indicate actual absence (Jerde et al., 2011).

These hidden aspects of biological invasions resemble the 'dark' concepts more widely used in ecology. Examples include 'dark diversity', which refers to species that are absent from a community despite belonging to the habitat-specific species pool (Pärtel et al., 2011); 'dark extinction' referring to extinctions that may have occurred before species were discovered, recorded, or assessed (Boehm & Cronk, 2021; Essl et al., 2026); 'dark taxa', denoting hyper-diverse groups of living things where less than 10% of the species are formally described (Page, 2016), ecological 'dark' matter, encompassing unseen microbial pathogens and parasites that shape food webs but are rarely accounted for in models (Roux et al., 2015); and 'Dark Ecology', which describes the paradoxical realisation that human civilization has inadvertently led to a global ecological collapse (Morton, 2016). A comparable set of 'dark' concepts may be extendable to the specific field of invasion science, where actual invasive species impacts, origins, as well as richness may be 'dark' (Paganeli et al., 2025; Zhang et al., 2026). These unknown, uncertain, or underrecognised components of biological invasions create a bias for scientists, land managers and policymakers, potentially leading to species being overlooked in terms of management. Because invasion management is most effective when actions are taken early (Britton et al., 2023; Leung et al., 2002), this can result in critical window of opportunity for effective eradication being missed. Many management strategies are based on formal lists of known harmful non-native species (Essl et al., 2011), leading to unlisted species often being ignored or overlooked in surveillance or management programmes. Effective management therefore requires anticipating risks before they are fully known (Crooks, 2005), addressing incomplete information on introduction pathways (Essl et al., 2015), broadening monitoring to understudied groups (Pyšek et al., 2008), and accounting for silent spread through domestic translocations (Robeck et al., 2024). Accordingly, management systems and policymaking must accommodate uncertainty and partial evidence to account for the components of biological invasions that remain hidden.

For this purpose, we present the concept of 'dark invasions'. It describes a wide range of hidden, uncertain, or unknown aspects of biological invasions, thereby combining, harmonizing, and extending the limited cases in which the concept is integrated into invasion science and management. Accounting for dark invasions offers a useful approach for identifying where current knowledge likely underestimates the true extent, timing, and consequences of invasions, while also providing a structured basis for identifying, estimating, and reducing associated uncertainties. By embracing the known unknowns in invasion science, management, and policy, the dark invasions concept can improve our understanding and management of the increasing number of non-native species that are establishing worldwide (Seebens et al., 2025).

2. Defining dark invasions

We define dark invasions as hidden components of biological invasions. These components can include unknown non-native species or hybrids (either non-native × non-native or non-native × native; (Brys et al., 2025; Pysek et al., 2013), unidentified or underrecognised invasion pathways (Haubrock, Tarkan, et al., 2026; Hulme, 2015), unresolved, or unknown biogeographical history, non-linear spread dynamics, and impacts that are unquantified (Haubrock, Everts, et al., 2026). The dark invasion concept builds on previous acknowledgement of the uncertainties inherent in studying biological invasions. It does not aim to replace existing specific concepts such as 'cryptic invasions' (Morais & Reichard, 2018), cryptogenic species, 'sleeper populations' (Everts, 2026; Spear et al., 2021), 'lag phases' (Aikio et al., 2010; Crooks, 2005), 'impact debt' (Rouget et al., 2016), or policy-driven exclusions of non-native species from invasion frameworks. Instead, it offers an overarching concept that links these phenomena as different manifestations of the same underlying gap between recorded status and realized risk.

Distinguishing recorded invasion data from actual risk matters because most governance and management decisions rely on species lists, which are shaped by survey effort, taxonomic expertise, legal definitions, and socio-economic factors rather than reflecting ecological reality (Faulkner et al., 2014; Kapitza et al., 2019; McGeoch et al., 2012). For instance, impact classification frameworks such as EICAT (Hawkins et al., 2015) or invasiveness screening tools like AS-ISK (Vilizzi et al., 2022) have improved the consistency of impact assessment but rely predominantly on expert-knowledge (Blackburn et al., 2014), with only a small fraction of all non-native species being quantitatively assessed (Bacher et al., 2025). These and many other phenomena where empirical evidence is absent or incomplete ultimately bias prioritization efforts towards prominent lists, whether these are non-binding (e.g. the IUCN list of *100 of the World's Worst Invasive Alien Species*) or regulatory (e.g. of the 114 invasive species of Union concern under the European Union Regulation 1143/2015 of Union concern).

3. Components of dark invasions

Dark invasions arise when multiple, interacting forms of uncertainty prevent the timely detection, correct identification, accurate ecological understanding, and effective management of non-native species. In the following, we outline six core components of uncertainty underpinning invasions: 'taxonomic', 'biogeographic', 'detection', 'temporal', 'impact', and 'regulatory'. Each represents a distinct mechanism through which invasions remain hidden from scientific scrutiny, on-the-ground action, and policy frameworks.

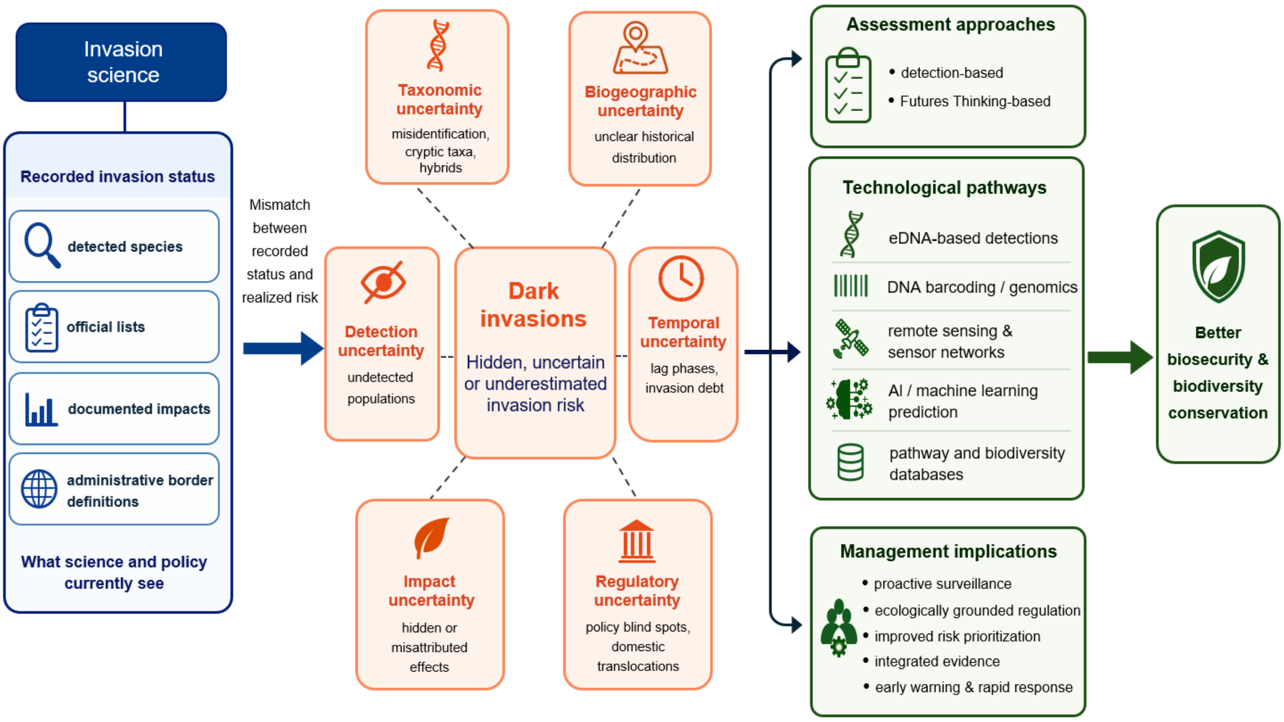

Figure 1. Overarching concept of dark invasions. Invasion science, invasive species management, and policy currently tend to focus on recorded invasion status, including detected species, official lists, documented impacts and national-border definitions. Dark invasions describe the mismatch between these visible records and realized invasion risk, which

may arise through detection, taxonomic, biogeographic, temporal, impact and regulatory uncertainties. These hidden risks can be identified and sometimes reduced through improved assessment approaches, technological tools and management actions, supporting a shift from reactive control to proactive biosecurity and biodiversity conservation.

3.1 Taxonomic uncertainty

Taxonomic uncertainty occurs when non-native species are present but misidentified, overlooked within species complexes, possibly confused with native taxa, or hidden by hybridization (Brys et al., 2025; Dufresnes et al., 2024; Meier et al., 2025; Morais & Reichard, 2018). It includes the concept of cryptic invasion, where an introduced taxon remains unrecognized because it is difficult to distinguish from native or previously established taxa. However, while cryptic invasions typically refer to cases of morphological similarity that obscure non-native status (Morais & Reichard, 2018), taxonomic uncertainty also includes situations where non-native status is obscured by unresolved taxonomy, incomplete genetic reference libraries, hybridization, introgression, or inconsistent nomenclature (Brys et al., 2025; Dufresnes et al., 2024). For example, non-native snails and slugs may remain unrecognized by some quarantine agencies due to the classification and distribution of the native fauna being poorly resolved, limited collections and literature, as well as scarce malacological expertise (Douglas et al., 2009). The continuous decline of taxonomic knowledge further exacerbates this trend (Drew, 2011; Forbes et al., 2025; Hopkins & Freckleton, 2002), since today's biological knowledge is built on the known global biodiversity, which only represents a fraction of what is currently extant on planet Earth (Kim & Byrne, 2006; Mora et al., 2011). The persistent taxonomic biases in invasion science (Pyšek et al., 2008), result in bacteria and fungi being systematically underrepresented while vertebrates and plants are overrepresented (Briski et al., 2024; Seebens et al., 2025).

3.2 Biogeographic uncertainty

Biogeographic uncertainty occurs when the historical and current distribution of a species is insufficiently understood and includes the concept of cryptogenic species whose true natural origins cannot be proven. It encompasses uncertainty about the origins, distributions, and historical baselines of species (Marcer et al., 2022) and arises when present-day distributions are poorly documented, historical records are sparse or unreliable, monitoring is non-comprehensive, or past human activities have reshuffled species distributions before systematic monitoring began (Carlton & Schwindt, 2024; Pergl et al., 2020). This is especially important in marine ecosystems, where centuries of shipping, ballast discharge, hull fouling, and aquaculture have redistributed species long before marine species distributions were fully mapped (Katsanevakis & Moustakas, 2018). Another example relates to plant species that were introduced to Europe before 1500AD (archaeophytes). In these cases, it is usually impossible to be certain about the history and geography of a species, resulting in plants labelled as non-native in one country being frequently treated as native just across the border (Ecseri & Honfi, 2020). In such cases, the historical native distribution becomes blurred, making it difficult to distinguish naturally occurring populations from those established through centuries of cultivation, releases, or accidental escapes. Consequently, some non-native species may be treated as native simply because they were recorded a long time ago, whereas other species remain cryptogenic because their original ranges can no longer be reconstructed. This form of uncertainty can lead to underestimated non-native richness, misclassified invasion status, and weak regulation of species moved beyond their natural ranges. It also contributes to shifting baselines, because present-day distributions may be accepted as natural even when they partly reflect past human-mediated dispersal (Clavero, 2014).

3.3 Detection uncertainty

'Detection uncertainty occurs when non-native species are established but remain undetected or unrecorded. This happens when monitoring is absent, infrequent or ineffective, or populations occur at too low a density to be recorded, occur in remote or inaccessible habitats or on private lands (Britton et al., 2011; McGeoch et al., 2012; Pergl et al., 2020). Consequently, regions with limited capacity to tackle biological invasions, either due to inadequate funding that restricts access to effective monitoring infrastructure, are particularly prone to miss non-native species (Bacher et al., 2026). This may be especially problematic in high-propagule-pressure environments with uneven surveillance (Reaser et al., 2008), including freshwater networks and small water bodies, urban soils, ports, and marinas, and aquaculture facilities (Pyšek et al., 2008). In aquatic systems, for instance, detection is particularly challenging because species are often rare, mobile, seasonally active, or difficult to observe and capture with standard methods (Britton et al., 2011, 2023). The longer non-native species remain undetected the window for successful eradication closes (Britton et al., 2011, 2023; Everts, van Doorn, et al., 2025).

3.4 Temporal uncertainty

Temporal uncertainty is comparable to the invasion debt concept (Rouget et al., 2016) and encompasses a broad range of uncertainties related to how invasion processes and their risk vary across temporal scales. It integrates similar forms of temporal uncertainty into a single measure, including phenomena such as lag phases (Crooks, 2005), secondary invasions (O'Loughlin & Green, 2017), and changing environments (Everts, 2026; Spear et al., 2021).When non-native species are introduced, many exhibit lag phases during which they remain at low population sizes or densities, limited geographic distributions, and often unobserved impacts before spreading (Crooks, 2005; Robeck et al., 2024). These delays can result from demographic stochasticity, low propagule pressure, unsuitable conditions, genetic constraints, or limited dispersal (Aikio et al., 2010). Recent work shows that successful non-native species can persist in lag phases while occupying only part of their potential niche, with spread often triggered once environmental or dispersal constraints are relaxed (Robeck et al., 2024; Soto et al., 2023). For instance, a species that appears harmless today may become invasive under changed environmental conditions (Jan et al., 2025) or increased human-mediated disturbance (Haubrock et al., 2024). Additionally, there is often a delay between a change in socioeconomic conditions and the response of non-native species that can be of the order of many decades (Essl et al., 2011). Collectively, these forms of temporal uncertainty highlight the non-stationary nature of biological invasions and the need to account for temporally varying abiotic and biotic conditions to accurately understand, manage, and govern invasions.

3.5 Impact uncertainty

Impact uncertainty generally occurs when the ecological, economic, or socio-cultural impacts of non-native species occur but are unquantified or incorrectly attributed. Many impacts are subtle, including changes in nutrient cycling, food-web structure, disease transmission, genetic integrity or ecosystem resilience (Haubrock, Everts, et al., 2026). Virtually all non-native species might affect recipient ecosystems by establishing novel biotic interactions, changing environmental conditions, using ecosystem resources, and occupying space. Nevertheless, only approximately 10% of non-native species have documented ecological impacts (Bacher et al., 2025), and the context dependence of these impacts precludes generalising findings from one region or ecosystem to another (Haubrock et al., 2024; Sapsford et al., 2020). The shortage of empirical impact data across species and geographics can at least partially be attributed to the fact that robustly detecting and quantifying such effects require long-term data, experimental evidence or before-after comparisons (Crystal-Ornelas & Lockwood, 2020), types of data that are difficult to obtain (Haubrock & Tarkan, 2026).

The economic impacts of biological invasions are also grossly underestimated (Diagne et al., 2021). While recent data compilations provided profound insights into the economic burden incurred by non-native species (Cuthbert et al., 2022; Soto et al., 2025), estimates suffer from substantial biases and unknowns. For instance, cost reporting differs notably among countries (Diagne et al., 2021; Haubrock, Turbelin, et al., 2021), taxonomic groups (see e.g. Cuthbert et al., 2021; Wang et al., 2023) and over time (Haubrock et al., 2022), with numerous costs attributed to genera or multiple species while likely also driven by inaccuracies in the underlying *InvaCost* database (Hulme et al., 2024) and discrepancies between non-native richness and cost reporting (Haubrock, Cuthbert, et al., 2021). Impact uncertainty also extends to socio-cultural dimensions, because invasion consequences can be perceived differently among stakeholders. A species may provide new economic or cultural benefits to some groups while simultaneously reducing native biodiversity or ecosystem services valued by others (Hossain et al., 2025). Such contrasting perceptions make it difficult to define a single measure of impact and can delay recognition of broader consequences.

3.6 Regulatory uncertainty

Regulatory uncertainty occurs when legal or management regulations fail to accurately target meaningful invasion risks due to an incomplete or biased knowledge base. One example is provided by policy-driven exclusions, whereby economically and socio-culturally important taxa are exempt from biosecurity legislation. For instance, the rainbow trout (*Oncorhynchus mykiss*) (Fausch, 2007) remains excluded from the scope of EU Regulation 1143 through Council Regulation (EC) No 708/2007 on the use of non-native and locally absent species in aquaculture, despite being capable of displacing native salmonid fishes (Hasegawa, 2020), including through hybridization (Carey et al., 2012). Another recent illustration is the American mink

(*Neogale vison*) and North American beaver (*Castor canadensis*), added to the Union list in 2025 (Commission Implementing Regulation (EU) 2025/1422) but with restrictions deferred until August 2027 to accommodate fur farming and management concerns.

Regulatory uncertainty is also problematic when a species' status as non-native is defined by administrative borders rather than ecological boundaries (Sun, 2025; Sun, Haubrock, Tarkan, et al., 2026). A species may be native to one part of a country but ecologically non-native if it is moved across drainage basins, ecoregions, or biogeographic limits (Sun, 2025; Sun, Haubrock, Tarkan, et al., 2026; Zamora-Marín et al., 2025). In policy terms, however, such species are often still treated as native because they occur within the same country. Freshwater ecosystems are particularly vulnerable to this problem (Dudgeon, 2019). River basins frequently function as distinct biogeographic units, yet species are routinely moved beyond their natural ranges through aquaculture, stocking, canal construction and recreational activities. This problem is evident in China's current regulatory framework, where the *Ecological and Environmental Code* defines invasive non-native species as species introduced from outside the national territory, which leave human-mediated translocations across internal ecological, hydrological, or biogeographic boundaries largely outside the formal non-native species management framework (Du & Cheng, 2026; Sun, Haubrock, Serhan Tarkan, et al., 2026).

Invasion pathways comprise another important component in regulatory uncertainty. While governance is already struggling with the regionally changing intensity of trade-related invasion pathways (Hulme, 2021), new potentially high-risk invasion pathways continue to emerge amid rapid global economic growth (Everts et al., 2026). The rise of e-commerce has proven to be an increasingly important gateway for non-native species introductions (Olden & Carvalho, 2024), where governance lags behind pathway installation (Chekunov et al., 2024). When done illegally, facilitated by anonymous platforms as those on the Dark Web, such pathways are particularly challenging, if not impossible, to regulate(Magalhães & São-Pedro, 2012). By providing new routes of entries and possibly enhancing existing trade-mediated non-native species introductions, these emerging pathways further pressure biosecurity systems. This potential regulatory dilution is particularly problematic in light of limited available resources, low enforcement capacity, and ever-increasing biological invasion rates (Seebens et al., 2025).

Table 1. Components of dark invasion and their definitions

Attribute of Dark Invasion	**Explanation**	**Reference / Example**
Taxonomic	Non-native species or their impacts remain hidden due to taxonomic uncertainty, cryptic invasions, hybridization, or misidentification of species, lineages, or genotypes.	(Zhang et al., 2026)
Biogeographic	Incomplete knowledge of current or historical species distributions obscures the classification of populations as native, non-native, cryptogenic, or translocated beyond their natural ranges.	(Carlton & Schwindt, 2024)
Detection	Non-native species are present in an area but remain unrecorded because monitoring is insufficient, populations are at low density, taxonomic expertise is limited, or habitats are difficult to survey.	(Lopes-Lima et al., 2025)
Temporal	Non-native species have already been introduced, but the reporting of their spread or impacts remain delayed in time because populations persist in lag phases before environmental change, disturbance or new dispersal pathways trigger rapid expansion.	(Robeck et al., 2024)
Impact	The ecological effects of non-native species are occurring but remain poorly measured, misattributed, or undetected because they are subtle, functional, or indirect (e.g., through pathogens or trophic changes).	(Scheele et al., 2019)
Regulatory	Ecologically meaningful invasion risks are not captured by legal or policy frameworks, particularly when species are moved within national borders but across ecological or biogeographic boundaries.	(Sun et al., 2026)

3.7 Interactions among dark invasion components

The six components of dark invasions are not independent sources of uncertainty, rather, they form an interconnected network with asymmetric relationships, where some components act as primary sources of uncertainty, whereas others represent downstream consequences of accumulated uncertainty. In particular, taxonomic, biogeographic and temporal uncertainties often act as upstream drivers of uncertainty, whereas detection and regulatory uncertainties represent intermediate processes through which dark invasions remain overlooked, and impact uncertainty represents a major downstream outcome where multiple uncertainties converge (Figure 2). They are more likely to reinforce than to nullify one another along the invasion process, from introduction and establishment to spread, impact recognition, and regulation.

Taxonomic uncertainty often sits at the start of these causal chains. It can lead to the underestimation of invasion frequency, introduction history, and ecological impact. Consequently, taxonomic uncertainty can increase detection uncertainty by reducing the ability to identify and record introduced populations, while simultaneously increasing impact uncertainty by obscuring the attribution of ecological effects. Biogeographic uncertainty represents another upstream driver by influencing both species detection and regulatory decisions.

When historical distributions and native ranges are unclear, populations may be incorrectly considered native or their introduction histories may remain unresolved. Temporal uncertainty connects upstream uncertainties with delayed recognition of invasion consequences. A species that is initially rare, cryptic, poorly identified, or legally exempt may remain in a lag phase while accumulating invasion- or impact-debt. By the time spread or impact becomes visible, earlier taxonomic, detection, biogeographic and regulatory uncertainties may have already narrowed the window for eradication or prevention (Simberloff, 2003).

Detection and impact uncertainties also interact. Low-density populations, highly mobile species, private or inaccessible habitats, and poorly monitored regions can keep an invader undetected, while subtle functional effects remain unattributed until long after establishment. This problem is particularly pronounced for bacteria, viruses, fungi and other pathogens because these groups are taxonomically understudied and their impacts are often expressed indirectly through disease-mediated community change (Briski et al., 2024; Nuñez et al., 2020; Roy et al., 2017). Thus, taxonomic uncertainty can hamper detection, detection uncertainty can delay impact assessment, and impact uncertainty can reduce the perceived need for management. Biogeographic uncertainty and regulatory failure interact when legal definitions of non-native status do not align with ecological boundaries. If regulation relies on administrative borders, within borders non-native species translocations may be treated as native and therefore fail to trigger risk assessment (Sun, Haubrock, Serhan Tarkan, et al., 2026). This regulatory uncertainty then feeds back into detection and impact uncertainties because unregulated species are less likely to be targeted by monitoring or included in impact databases. Ultimately, impact uncertainty represents the cumulative consequence of multiple interacting uncertainties: when species identity, origin, occurrence, timing or regulatory status remain unresolved, ecological impacts may be underestimated, misattributed, or recognized only after management feasibility has declined.

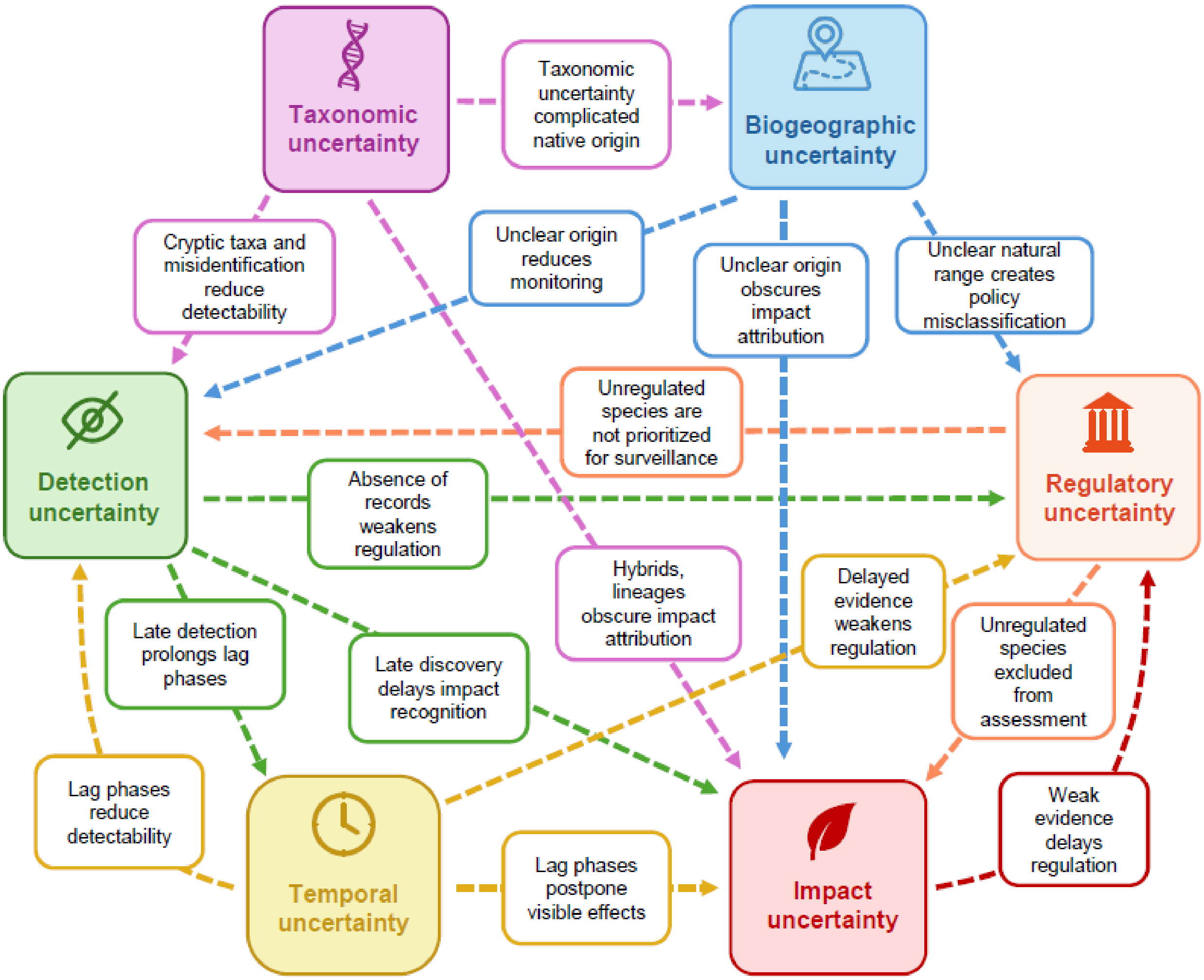

Figure 2. Possible interactions among six identified components of dark invasions.

4. Management implications

The concept of dark invasions has several practical implications for biosecurity and conservation. First, appreciating the complexity of dark invasions could contribute to a progressive shift from a predominantly reactive to proactive management. Instead of focusing mainly on high-profile invasive species, managers should also recognise the risks associated with species and pathways likely to be under-recorded, misidentified, or largely ignored by current policy definitions. Second, it calls for ecologically grounded regulation. Non-native status should be assessed relative to natural ranges and ecological boundaries rather than national borders alone (Haubrock, Everts, et al., 2026). Domestic translocations across ecoregions can create genuine invasion risks and should be assessed and monitored accordingly, regardless of whether the species is native in part of the region (Sun, Haubrock, Tarkan, et al., 2026). Third, consideration of this concept improves risk prioritization because regions with weak monitoring, exposed to high introduction and propagule pressure, and rapid environmental change warrant more effective surveillance. Fourth, it promotes integration of evidence because the implementation of dark invasions in broader frameworks connects occurrence records, pathway analysis, impact studies, and policy review by asking whether existing data capture realized invasion risk. Finally, dark invasions highlight that mapped, recorded, or administratively recognized patterns do not always reflect ecological reality. A good illustration of this is the hybridization between introduced mallards (*Anas platyrhynchos*) and native grey ducks (*Anas superciliosa*) in New Zealand. While native populations of the grey duck declined, the ability to assess the extent of hybridization and the difficulty in separating hybrids from native grey ducks hindered culling, making the resulting impact less visible than other types of invasive impact such as predation or habitat transformation (Quilodrán et al., 2018).

5. Assessing dark invasions

Assessing dark invasions requires approaches that account for components of the invasion process that remain hidden from standard monitoring, research, and policy. Unlike dark diversity or dark extinctions, dark invasions cannot be captured by a single metric and their assessment should not aim to produce a definitive global estimate. Instead, the concept should be used to identify where the gap between recorded invasion status and realized invasion is likely to be largest, how substantial the uncertainty may be, and what forms of evidence or emerging technologies would most effectively reduce that uncertainty. Two complementary strategies can shed light on dark invasions: (1) detection-based assessments to reveal hidden species and impacts, and (2) Futures Thinking-based assessments to evaluate conclusions under incomplete evidence. These strategies can be strengthened by technology-driven solutions to minimize uncertainty, and support informed decision-making across all phases of the invasion process.

5.1 Detection-based assessments

Detection-based assessments aim to reveal hidden non-native species, pathways, or impacts through improved data collection and analysis (see below sub-section 5.3). This includes targeted field surveys, environmental DNA (eDNA), molecular phylogenies, citizen science, trade and stocking records, port and market surveys, remote sensing, and long-term ecological monitoring (Fricke & Olden, 2023). Molecular tools, such as eDNA, are particularly effective for detecting low-density or cryptic aquatic invaders that conventional surveys often miss (Iacaruso et al., 2026). For example, eDNA techniques detected a previously unidentified early-stage population of the New Zealand mud snail (*Potamopyrgus antipodarum*) in rivers of central Pennsylvania, USA, illustrating their value for revealing overlooked aquatic invasions before they become widely established (Woodell et al., 2021). Citizen science has shown that official records often underestimate the first date of introduction of a non-native species to a country (González-Moreno et al., 2025), with such data being crucial for interpreting current and future temporal trends in biological invasions (Seebens et al., 2017, 2021) Historical records, museum specimens, and genetic analyses can show that an invasion began earlier than official records indicate (Everts, Deflem, et al., 2025). For example, museum records have substantially revised the inferred timing of several invasions, pushing back the apparent first records of *Asterocarpa humilis* in Chile by 103 years (Carlton & Schwindt, 2024). Similarly, screening of historical horticulture catalogues to integrate propagule pressure and plant traits can be used to identify cultivated non-native ornamental plant species likely to become established in the wild in the future (Dawes et al., 2025).

5.2 Futures Thinking-based assessment

When faced with high uncertainty of future risks, futures thinking approaches can guide researchers and policymakers to understand the limits of current knowledge and explore issues that require increased investment or caution to mitigate future threats (Hulme, 2025). While invasion scientists regularly use environmental scanning to forecast future invasive species (Peyton et al., 2026), these approaches are based on "known knowns" and fail to account for dark invasions. Alternatives such as horizon scanning can help identify "known unknowns" such as geopolitical, social or technological changes that will shape future invasions and provide opportunities to build resilience in biosecurity systems in relation to emerging pathways or shifting socioecological conditions (Hulme et al., 2023; Ricciardi et al., 2017). By identifying where management decisions are sensitive to uncertainty, this approach can support precautionary action even when current records are incomplete. More involved approaches use storylines to explore specific scenarios (Roura-Pascual et al., 2024) or megatrends (Hulme et al., 2026) to explore "unknown knowns" such as an ageing society or platform economies whose potential role in biological invasions have not been realized before. Nevertheless, despite the utility of these futures thinking approaches there are no tools capable of unpacking the "unknown unknowns" that capture truly unforeseen events that have no precedent in invasion science and epitomize dark invasions.

5.3 Technological pathways to unveil and reduce uncertainty

Emerging technologies offer concrete and increasingly powerful means to unveil dark invasions at least to some extent. While technology cannot resolve every form of uncertainty (particularly regulatory gaps) nor fully resolve a single component of uncertainty, emerging and near-future technologies may provide practical tools that can make invasions progressively more visible and actionable. Emerging eDNA methods using air, pollen, animal faeces, and other environmental substrates provide new opportunities to detect elusive species, reconstruct distributions, and identify hidden invasion risks across diverse ecosystems (Navarro et al., 2025; Sullivan et al., 2025). Portable sequencing devices and autonomous sampling platforms can increase the sensitivity, spatial coverage and turnover time of surveillance, allowing low-density or early-stage non-native populations to be detected in remote, poorly monitored or difficult-to-sample environments, opening the door for actionable measures (Heine et al., 2026). For taxonomic uncertainty, DNA barcoding, genomic tools, and AI-assisted taxonomic assignment can help distinguish cryptic species, introduced lineages, hybrids and misidentified taxa, especially in groups where morphology alone is insufficient for reliable identification (Dufresnes et al., 2024). However, these molecular approaches remain constrained by the availability and quality of reference databases, which are incomplete for many taxa and regions (Keck et al., 2023). Consequently, molecular and AI-based approaches may reduce but not fully eliminate taxonomic uncertainty, especially for poorly studied organisms lacking comprehensive genetic resources.

For temporal uncertainty, machine-learning models trained on multi-source data streams, including occurrence records, eDNA detections, climate projections, land-use change, and human activity data, can help forecast when and where lag-phase populations are likely to expand (Robeck et al., 2024). Such predictive tools could proactively identify non-native species that appear locally harmless at present but may spread rapidly once environmental conditions, disturbance regimes or dispersal pathways change. For impact uncertainty, satellite and drone-based remote sensing, sensor networks, food-web approaches and long-term automated monitoring can help detect functional ecosystem changes, such as shifts in primary productivity, habitat structure, water quality or community composition, in early stages. However, regulatory uncertainty cannot be resolved by technology alone. The most effective management response is to revise relevant biosecurity and conservation legislation so that the non-native status, when known, is defined not only by a specific regional or even origin, but also by whether a species has been moved beyond its natural ecological range through human activities (Sun, Haubrock, Tarkan, et al., 2026). In this sense, laws and risk-assessment frameworks should recognize anthropogenic spread across ecoregions, biogeographic regions, or other ecologically meaningful units as potential biological invasions. Integrating genetic assignment, pathway data, species distribution models and regional biodiversity databases could support such legal reform by providing evidence for more dynamic and ecologically grounded definitions of non-native status.

Looking ahead, technological advances will provide important opportunities to assess and reduce, but not eliminate, dark invasions. The greatest gains are likely to come from AI-supported early-warning systems that combine tools like eDNA, remote sensing, near real-time ecological monitoring, automated data mining, and pathway information into operational live platforms. Such systems could automatically flag ecological mismatches, such as unexplained native species declines or anomalous community shifts, and trigger targeted surveys or management responses. As some dimensions of dark invasions will likely remain unresolved, the goal should not be to eliminate uncertainty entirely, but to develop monitoring systems, decision frameworks, and management strategies that remain effective under uncertainty. Achieving this requires open data infrastructures, standardized protocols, computational capacity, and transdisciplinary and transnational collaboration (Pagad et al., 2018; Simpson et al., 2009). By combining improved detection with ecological resilience and adaptive governance, society can better anticipate, absorb, and respond to invasion risks that cannot be fully predicted or prevented.

6. Conclusions

Dark invasions describe the hidden components of biological invasions that remain unaccounted for in present day assessments. By distinguishing recorded invasion status from realized invasion risk, the concept links cryptic invasion, lag phases, invasion debt, hidden impacts, pathogen-mediated effects and within-country translocations within a single concept. Recognizing and addressing these hidden risks can help biosecurity systems become more preventive, ecologically realistic and responsive to rapid environmental change. Dark invasion is therefore both a conceptual framework and a practical reminder: the absence of evidence in invasion databases, official lists, or legal categories should not be interpreted as evidence of ecological safety in horizon scans, risk and impact assessments, and biosecurity practices.

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Author contribution statement

All authors (JS, TE, RS, IS, PEH, JRB, and PJH) contributed to the conceptualization of the study and discussions that shaped the content of the manuscript. JS led the writing and all authors contributed substantially to drafting and revising the manuscript. JS created the figures. All authors reviewed and edited the manuscript and approved the final version before submission.

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