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Opinion

Crypticity in Biological Invasions

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Ecological effects of alien species can be dramatic, but management and prevention of negative impacts are often hindered by crypticity of the species or their ecological functions. Ecological functions can change dramatically over time, or manifest after long periods of an innocuous presence. Such cryptic processes may lead to an underestimation of long-term impacts and constrain management effectiveness. Here, we present a conceptual framework of crypticity in biological invasions. We identify the underlying mechanisms, provide evidence of their importance, and illustrate this phenomenon with case studies. This framework has potential to improve the recognition of the full risks and impacts of invasive species.

Crypticity in Biological Invasions: A Conceptual Framework

Invasive alien species (IAS) (see Glossary) can have large-scale effects on the environment, including alterations to nutrient cycling, changes in disturbance regimes, and modifications to physical structures [1]. However, **ecological functions**, and consequently the direction and magnitude of IAS impacts, can change dramatically over time [2], or appear after long periods of an innocuous presence of the invader [3]. As a result, IAS impacts are difficult to predict, and many interactions with other biota remain unnoticed or lead to unexpected consequences [4]. The full potential of an invader to affect native biota through different functions is often only understood in retrospect, when the impacts have already become evident, and long after the control measures would have been effective.

Whether we can detect **alien species** and the manifestations of their ecological functions or whether they remain cryptic depends on ecological properties of the alien species, its new environment, and the circumstances of its invasion. Crypticity in IAS may lead to underestimation and reduced predictability of long-term impacts and constrain timeliness and effectiveness of IAS management.

Similarly, a sudden partial or complete loss of an invader's critical ecological function can remain undetected. In this situation, the resulting reduction in negative impacts of managed IAS may not be recognized and may lead to unwarranted and costly management measures.

Here, we propose a conceptual framework to untangle different sources of crypticity of alien species and their functions (Figure 1 and Table 1). In particular, we highlight the role of three key issues potentially leading to crypticity in biological invasions: (i) **crypticity of species**, (ii) **crypticity of functions**, and (iii) spatio-temporal crypticity (Figure 1 and Table 1). An additional, overarching factor is the 'observer' problem, a lack of knowledge and understanding of relevant processes and mechanisms that constrains identification of key ecological functions [5,6].

Highlights

Crypticity of biological invasions may blur invasion impacts and reduce their predictability.

The impacts are often only detected in retrospect, and understood with delay, long after control measures would have been effective.

Crypticity of biological invasions can be driven by inherent crypticity of alien species and their ecological functions and by time lags, spatio-temporal variability, and anthropogenic impacts.

Considering crypticity in biological invasions would strongly enhance efficiency of monitoring and management planning.

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Crypticity of Species

Current and potential future impacts of alien species are hard to detect and predict if the alien species themselves are cryptic. This includes undescribed species, taxonomically difficult and unresolved species complexes, **pseudoindigenous** and **cryptogenic species**, and undetected species [6–13]. While crypticity of species is often represented by morphological crypticity, it can also be driven by other factors such as species rarity and occurrence in less accessible areas, or habitats. In invasion science, crypticity of species may lead to underestimation of introduction and invasion rates, as well as of resulting impacts [14].

With only a minority of the world's species described so far, it is likely that the actual number of invasions is greater than currently recorded and will further increase. For alien species yet unknown to science, any function they perform in their introduced range remains unobserved or poorly understood. Smaller-bodied taxa and those occurring in less accessible habitats, such as aquatic or terrestrial below-ground environments, are more likely to stay cryptic [10,15]. For example, many pathogens now recognized as invasive were either unknown or scarcely known before their introduction [11,16]. A pathogen can be native at the species level, but one or more of its lineages can be invasive, as is the case for the chytrid *Batrachochytrium dendrobatidis* affecting amphibians (Box 1) [17]. Crypticity is also an important issue for other types of novel organisms, such as synthetic and genetically modified organisms [18]. Species can remain unobserved in their novel range until detected by chance or after targeted search efforts have been initiated. For example, the presence and dominance of the highly invasive freshwater snail *Physa acuta* in northern and central Chile, with multiple introductions of different lineages, was detected only after detailed morphological and genetic studies, partly because of its morphological similarity with native congeners [14].

Crypticity of alien species is also relevant in taxonomically difficult **cryptic species complexes** comprising both native and alien taxa, or alien taxa only, as well as their hybrids. Molecular analyses revealed that the moon-jellyfish (*Aurelia* sp.) is in fact a complex of 13 species, with one of them globally distributed by multiple introductions [8]. Common reed (*Phragmites australis*) populations in North America consist of both native and introduced European subspecies, with the latter being highly invasive and comprising three distinct lineages and hybrids, forming a complex and evolving patchwork of genotypes (Figure 2A) [19]. Such taxa can differ in their potential impacts on the environment, based on the specific functions they perform [9].

Finally, alien species might remain undetected if they establish viable populations without attaining visible abundances (e.g., because they are camouflaged, or rare), occupy uncommon or undersampled habitats, or belong to understudied and overlooked species groups. Rare alien species can however still be functionally significant, with obvious examples that include pathogens, pathogen hosts, and toxic aliens.

Crypticity of Functions

Some ecological functions are inherently difficult to observe and may remain unnoticed for long periods after IAS introduction and establishment. Crypticity of functions can be represented either by functions that are undetected or by those that are novel and thus hard to predict beforehand, although they might be highly detectable after their effects are manifested. The difference between these two modes of functional crypticity can have relevant management implications. Although unpredictable, novel functions may become apparent soon after the invasion if they lead to high impacts, while some undetected functions may never yield a high impact and remain cryptic.

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The problem of crypticity of IAS functions could be more efficiently addressed through a proper classification system of ecological functions. While no such system has been proposed to date, the Environmental Impact Classification for Alien Taxa [20,21] represents a promising basis for this purpose. It comprises **environmental impact** mechanisms that can be grouped into the following four broader categories: trophic interactions (predation, parasitism, grazing, herbivory, and browsing), non-trophic interactions (competition, hybridization, disease transmission), abiotic effects (chemical, physical, or structural impacts on ecosystems), and welfare impacts (poisoning, toxicity, bio-fouling), which correspond well to functional roles alien species can fulfill.

The Mediterranean mussel (*Mytilus galloprovincialis*) invasion in South Africa is a prime example for a case in which an unknown ecological function performed by an alien species led to unexpected (and, according to the authors [22], completely unpredictable) effects. Although most impacts of this species were successfully predicted, mussel attachment to the eyestalks and mouthparts of the crab *Ovalipes trimaculatus* were not and led to massive mortalities in this crab species (Figure 2B) [22]. The novel, initially cryptic effects of the Mediterranean mussel were ultimately detected, but only long after the impacts were manifested and the opportunity for timely management measures missed. Novel functions of IAS tend to be cryptic, because they are inherently hard to predict. Novelty of traits and/or taxa has been advocated as a predictor of high impacts [23]. However, while the presence of novelty may be used to predict high-risk IAS, clear understanding of the way impacts will unfold may be missing. Novel functions may be indirect or subtle, thus initially overlooked or ignored [20,24], as was the predation by a giant African slug (*Achatina fulica*) on a native veronicellid slug (*Veronicella cubensis*) in Hawaii that had gone undetected for more than 5 decades [4]. Since this species was previously known only as a herbivore and scavenger, its predatory feeding represented a novel, and consequently, a cryptic function [4]. Furthermore, some ecological functions are more likely to be inconspicuous; for example, specific novel weapons such as allelopathy, novel behavior, provision of transformed substrates and habitats by alien plants, carrion subsidies and resource pulses, novel vectors, and phoresis (Table 1) [25–28]. Emergence of novel ecological functions brought about by alien species is especially likely on islands, characterized by endemic and unbalanced biota [29].

The effects of alien parasites and pathogens also tend to be cryptic [11]. Pathogens are able to quickly evolve, adapt, shift to novel hosts, hybridize, and exchange genes with native species, which can even lead to the evolution of new pathogens [11,16,18,30,31]. As a result, many alien pathogens with severe impacts were not recognized as threats before their establishment in new hosts [11]. Novel interactions with native organisms may further increase their pathogenic potential, or they might have no effect on host fitness until the host establishes interactions with another species [16,31,32].

Apparently innocuous alien species can have critical ecological functions as vectors of diseases or parasites, or through phoresis or zoochory [10,26]. Such ecological roles may emerge long after initial introduction and establishment, for example, when the parasites are transmitted later than the vectors [33]. Lagged parasite or pathogen transmission can be caused by critical population densities required for transmission, by multiple introduction events from different sources, or by a specific set of spatiotemporal conditions required for transmission [32]. Similarly to pathogen transmission, phoresis can remain largely unnoticed and result in cryptogenic invasions, due to the small size of carried species [26].

Indirect functions of aliens are especially unpredictable and likely to remain unobserved, often occurring through altered behavioral patterns of the invading species. Complexity of

Glossary

Alien species: an organism occurring outside its natural range after crossing biogeographical barriers due to direct or indirect human agency [6].

Crypticity of functions: a function that is either not perceived, unexpected, or not easily identified. Novel functions are very likely to be cryptic, because they are inherently hard to predict.

Crypticity of functional change: undetected or unexpected post-introduction change in an ecological function.

Crypticity of species: species are not identified, or not detected in their non-native range, so their functions also remain unobserved.

Cryptic species complexes: taxonomically difficult species complexes, with two or more distinct taxa erroneously classified (and hidden) under one species name [9].

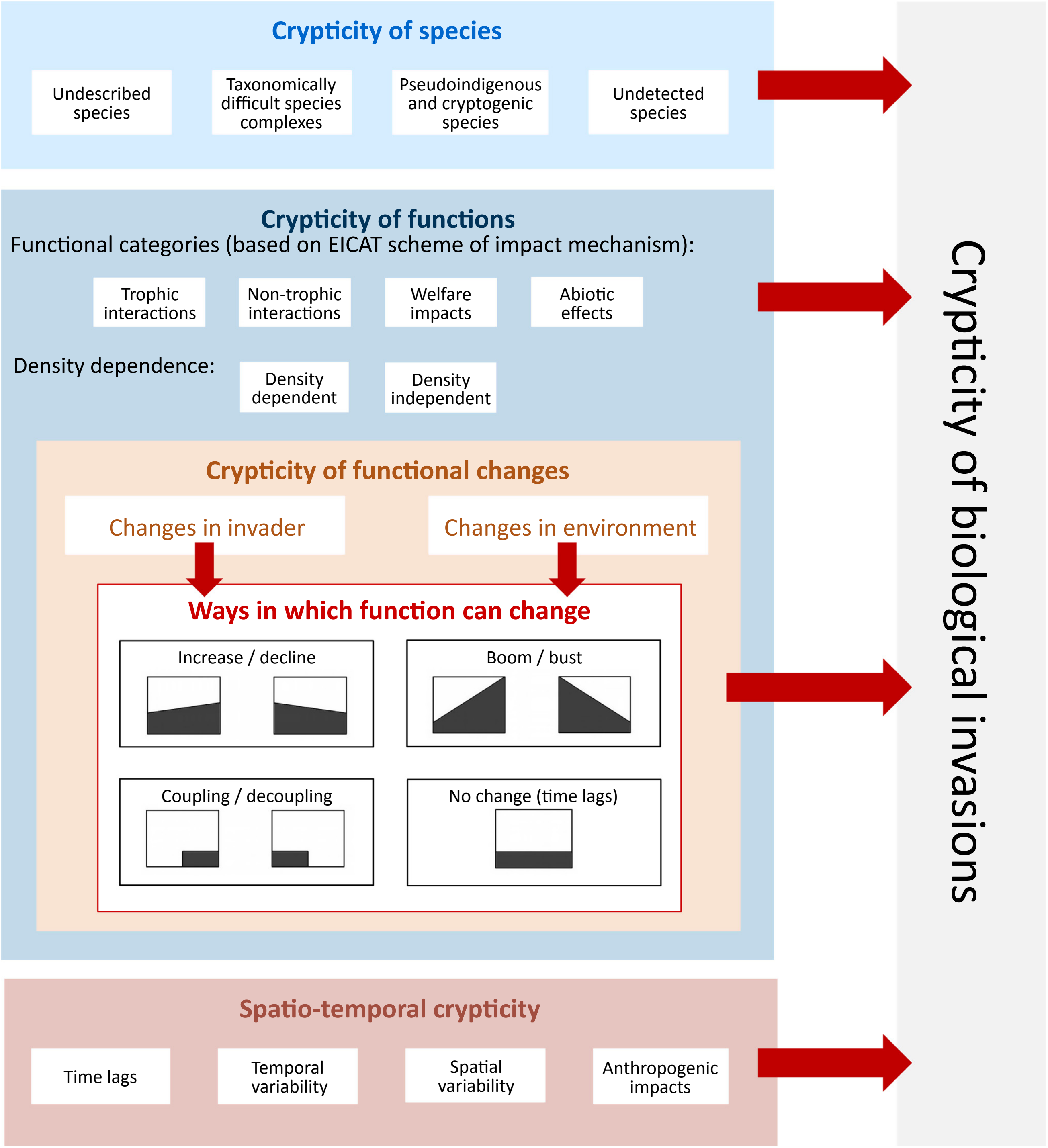
Cryptogenic species: taxa of unknown biogeographic origin, which results in an uncertain alien status [7].

Ecological function: a role that an alien species performs in habitats within its novel range.

Environmental impact: measurable change to the properties of an ecosystem caused by alien species [20].

Invasive alien species (IAS): established alien species that are rapidly extending their range in the new region [76].

Pseudoindigenous species: alien species erroneously considered to be native.



Trends in Ecology & Evolution

Figure 1. Conceptual Framework of Crypticity in Biological Invasions. A lack of knowledge on the impact of an alien species can be driven by crypticity of species, crypticity of functions or functional changes, and spatio-temporal crypticity. Functional changes can be driven either by changes in the invader or its environment; black-and-white panels represent different modes of functional change, such as increase or decline in the ecological function, stronger changes that correspond to boom or bust dynamics, functional coupling or decoupling, and no apparent change that may occur due to time lags. EICAT, Environmental Impact Classification for Alien Taxa.

Table 1. Role of Ecological Properties in Facilitating the Occurrence of Different Categories of Crypticity and Useful Methods for Studying and Identifying Different Categories of Crypticity

Category and description	Facilitating ecological properties	Methods for reducing the lack of knowledge and increasing detectability	Refs
Crypticity of species: species that are not identified, or not detected in their non-native range, so their functions also remain unobserved	Small body size, less-accessible habitat (e.g., aquatic or below-ground environments), endoparasitism, camouflage, systematically complex and/or poorly studied species group, interspecific morphological homogeneity, taxonomic instability	Environmental DNA, DNA barcoding, metagenomics, automated species identification, camera traps, bioacoustics, citizen science initiatives	[65,66,68–73]
Crypticity of functions: functions that are not perceived, not expected, or not easily identified	Novelty of a species for the recipient community, novel behavioral patterns, pathogenicity, parasitism, or provision of novel substrates, habitats, carrion subsidies, resource pulses, novel pathogen or parasite vectors or reservoirs, phoresis or zoochory	Targeted field studies and experiments, continuous ecosystem monitoring	[28,37,73]
Crypticity of functional change: functions change in a way that is hard to observe or predict (i.e., nonlinearly), or the drivers or resulting effects are inconspicuous	Exposure to density-independent factors, fast life history, ability for rapid evolutionary and epigenetic changes, ability to hybridize, phenotypic plasticity, phenological and demographic susceptibility to environmental factors, climate change and anthropogenic disturbances	Field studies, experiments (i.e., microcosm and mesocosm), simulation models, improved risk assessment tools	[35,43,47, 48,74,75]
Spatio-temporal crypticity: delayed effects of functional changes, spatio-temporal variation and other factors that reduce detectability of species and their functions	Species potential to exhibit long-term accumulation or depletion of slow pools in an ecosystem, spatio-temporal variability, slow life history, function likely related to evolutionary processes or cascading effects, exposure to anthropogenic impacts	Improved use of available long-term data (historic records, herbaria, chronosequences), long-term ecosystem research projects, continuous ecosystem monitoring, surveys along environmental and anthropogenic disturbance gradients, microcosm experiments, models	[40,57,60]

behavioral responses and interactions contributes to the crypticity of behavior-based functions [34,35]. Besides their direct role as parasite vectors, alien species can also act as reservoirs and thus support parasite species that could otherwise disappear from the invaded region [32]. Introduced pheasants (*Phasianus colchicus*) in the UK were identified as reservoirs for the caecal nematode *Heterakis gallinarum*. While the nematode did not affect pheasant populations, it caused population declines in the native grey partridge (*Perdix perdix*; Figure 2H) [32].

Box 1. Multifaceted Crypticity of the Amphibian Chytrid Parasite *Batrachochytrium dendrobatidis*

The link between infection by the chytrid parasite *B. dendrobatidis* and amphibian declines in Central America and Australia was not detected until 1998, when the parasite had already spread throughout the world. Museum specimens and recent molecular analyses suggest that this parasite was present globally for decades before its detection [77]. Another challenge is that *B. dendrobatidis* has several strains that vary in virulence, which has only recently been discovered [17].

Crypticity in *B. dendrobatidis* invasion has additional layers, as it also includes amphibian hosts that are difficult to identify: the gray tree frog (*Hyla versicolor*) and Cope’s gray tree frog (*Hyla chrysoscelis*), for example, are virtually identical (Figure I). Even when infection has been detected, it is difficult to ascertain which species is being affected [78]. The confusion on species identity goes further, as taxonomy of amphibian groups changes, sometimes splitting a species into two and thus making it challenging to determine the species to which previous work refers. Such is the case of the Rio Grande leopard frog (*Lithobates berlandieri*), an invasive organism whose taxonomy changed, dividing the species into two, *Rana berlandieri* and *Rana brownorum*. It is now difficult to ascertain which species was reported as invasive or susceptible to chytrid infection (e.g., [79]), and for that matter which was the strain of chytrid infecting the sampled amphibians.

Figure I. Tree Frog Hosts of *Batrachochytrium dendrobatidis*. Gray tree frog (right) and Cope's gray tree frog (left), two chytrid hosts indistinguishable based on external morphology (photo by James Harding).

Similarly, alien species can represent exotic and alternative food resources that subsidize native consumers, with unpredictable and potentially large indirect impacts on native communities [36,37]. The red swamp crayfish (*Procambarus clarkii*) invasion in Doñana, southwestern Spain, resulted in novel and unforeseen dispersal pathways of native and alien plants and invertebrates through interaction with their waterfowl predators (Figure 2D) [38].

Alien species can also indirectly alter interactions among native species and lead to a cascade of ecological effects [24]. Introduced beech scale (*Cryptococcus fagisuga*; Hemiptera), for example, does not cause discernible effects on North American beech trees directly but makes them predisposed to attacks by the fungus *Neonectria faginata*, which damages the tree and causes cascade effects (Figure 2E) [24]. Indirect functions are especially difficult to detect if they manifest over large distances. For example, pollen from the plantations of alien Monterey pine (*Pinus radiata*) in New Zealand was found in Southwest Pacific trenches at depths of up to 10 800 m, where it represents a novel food resource for deep-sea benthic organisms (Figure 2G) [39].

Crypticity of Functional Change

Ecological functions of IAS can be identified and well understood at one point in time, but they may subsequently change in quality or magnitude, resulting in considerable changes in their impact. Post-introduction changes in functional roles performed by alien species differ in both direction and magnitude, depending on drivers and the type of ecological function. Functional changes can become apparent in divergent ways such as increasing or decreasing function, dramatic changes due to boom or bust dynamics [40], and functional coupling or decoupling processes with novel functions being established, or existing functions being lost (Figure 1). However, certain types of functional changes tend to be cryptic, even though they may cause

Trends in Ecology & Evolution

Figure 2. Examples of Different Forms of Crypticity in Invasive Alien Species. (A) Common reed (*Phragmites australis*) populations in North America form a complex and evolving patchwork of native and introduced subspecies and their hybrids [19] (photo by Petr Pyšek). (B) Mediterranean mussel (*Mytilus galloprovincialis*) attachment to the eyestalks and mouthparts of the crab *Ovalipes trimaculatus* leads to massive mortalities in this crab species [22] (photo by George M. Branch). (C) red quinine tree (*Cinchona pubescens*) introduction on the Galápagos Islands resulting in unforeseen and changing characteristics and effects [41] (photo by Carolina Carrion). (D) Red swamp crayfish (*Procambarus clarkii*) invasion in Doñana producing novel and unforeseen dispersal pathways of native and alien plants and invertebrates through interactions with their predators [38] (photo by Andy J. Green). (E) Introduced beech scale (*Cryptococcus fagisuga*) does not produce direct effects on North American beech trees, but it predisposes them to attack by the fungus *Neonectria faginata* [24] (photo by Chris Malumphy). (F) Decline of larger specimens in zebra mussel (*Dreissena polymorpha*) populations in the Hudson River alters its filter-feeding impact on zooplankton [52] (photo by Heather M. Malcom). (G) Pollen from the plantations of alien Monterey pine (*Pinus radiata*) in New Zealand was found in Southwest Pacific trenches, where it represents a novel food resource for deep-sea benthic organisms [39]; photomicrograph shows a gromiid specimen from the Tonga Trench (10 811-m water depth) with ingested *P. radiata* pollen (photo by Daniel Leduc, NIWA). (H) Introduced pheasants (*Phasianus colchicus*) in the UK acting as reservoirs for caecal nematodes *Heterakis gallinarum* that caused population declines in the native grey partridge (*Perdix perdix*) [32] (photo by Lars Petersson). A, crypticity of species; B–H, crypticity of function and/or functional change.

relevant changes in IAS impacts. The introduced red quinine tree (*Cinchona pubescens*) had strongly transformed ecosystems of formerly treeless highlands on the Galápagos Islands (Figure 2C) [41], but these effects are declining along with an unexpected decrease in canopy cover of the invader due to yet unknown reasons [42]. While strong ecosystem transformation effects of red quinine tree invasion were expected, the unforeseen changes in invader characteristics will likely modify previous impact patterns.

Examples of **cryptic functional changes** include evolutionary and epigenetic changes; hybridization; shifts in demographic structure; and changes in interspecific interactions, environmental factors, and phenology [16,32,43]. Such mechanisms do not follow the standard relationship established by Parker *et al*. [44], where IAS impacts are based on per capita effects multiplied with species abundance; instead, such mechanisms have density-independent effects.

The introduction of an alien species to a novel environment can lead to its rapid evolution. While often highly unpredictable and mostly inconspicuous, evolutionary changes have had a role in some of the most damaging invasions worldwide, and they are expected to be further stimulated by habitat degradation, climate change, and genetic admixture due to multiple introductions [16,45,46]. Rapid post-introduction evolutionary changes can lead to functional changes while simultaneously remaining undetected. Post-introduction admixtures of previously isolated lineages from different source populations might also induce rapid evolution and lead to changes in genome size and structure, associated with stronger IAS impacts [19,47,48].

The importance of epigenetic changes for biological invasions is poorly understood [16], but recent findings indicate that they can affect invasion success more strongly than genetic changes [49]. Epigenetic changes can alter gene regulation and modify physiological, morphological, life-history, and behavioral traits [16]. Their ability to produce strong and rapid adaptive shifts, without genetic changes and even at low levels of genetic variability, contributes to the crypticity of such processes [16,49].

Hybridization is an important mechanism underlying biological invasions, creating new genotypes with often differing ecological functions [25,50], which makes it a likely driver of crypticity. An example of functional novelty in plants can be found in knotweeds (genus *Fallopia*), where the hybrid *Fallopia* × *bohemica* resulting from crossing of two Asian parents in their invaded European range spreads comparatively faster, grows more vigorously, is more competitive, and is able to occupy a wider range of habitats [51]. Microbial taxa are especially prone to fast evolutionary changes due to natural selection or horizontal gene transfer, which may lead to the emergence of novel abilities or new pathogen strains [16].

Demographic structure of alien species can undergo substantial and abrupt shifts even in stable populations, such as changes in age or stage class, or particular sex ratio that was essential for their function in the ecosystem. Such changes tend to be cryptic, as the resulting change in impact is not density dependent. For example, reduction in the abundance of larger specimens of the invasive zebra mussel (*Dreissena polymorpha*) in the Hudson River altered the filter-feeding impact of this species on zooplankton and allowed recovery of zooplankton community, even though the overall mussel population remained at the essentially same level of abundance (Figure 2F) [52].

Biological invasions bring together alien species from various biogeographical regions, habitats, climates, and life histories, resulting in novel, unpredictable, and often cryptic interactions among the introduced taxa [30]. Native species in the recipient community are also able to modify ecological functions of the alien species. Parasites are especially likely to produce complex alterations in the physiology and behavior of hosts, which will mediate other interspecific interactions and functional roles of the host, such as competition and predation, in a way that can be highly cryptic [31,32]. For example, infection of the amphipod *Gammarus pulex* by the acanthocephalan fish parasite *Echinorhynchus truttae* led both to reduced predation and change in target prey size classes [53].

Functional responses in alien species will be most unpredictable and cryptic when they are mediated by multiple stressors with non-additive, synergistic, or antagonistic interactions [43]. Ecological functions can be affected and modified simultaneously by various environmental factors such as temperature, water salinity, CO_2, and moisture as well as by climate change, ecosystem changes, and changes in habitat structure, resource distribution, and nonstructural conditions, such as noise and light levels [34,43].

Phenological shifts can produce cryptic functional changes in apparently stable populations when they disrupt temporal matching between species or processes, such as plants and nectarivores, or between the peak abundances or emergence of key life stages (e.g., egg laying, hatching, metamorphosis, end of dormancy) in a prey species and its predator [54]. Climate change is a widely documented driver of phenological shifts in alien species [30,55,56].

Spatio-temporal Crypticity

Besides the mechanisms described above that may cause crypticity in species or their functions, crypticity may arise due to four mechanisms that we summarize under 'spatio-temporal crypticity': (i) time lags, (ii) temporal variability, (iii) spatial variability, and (iv) anthropogenic impacts.

Time lags in biological invasions are common and may occur at each stage of the invasion process, and IAS impacts consequently often become discernible or substantial after considerable delays [20,25,57]. Mechanisms that mediate delayed responses to environmental factors such as changes in biotic interactions are manifold and poorly understood, and their effects therefore tend to be underestimated [58]. Time lags in plant invasions can last well over a century [59]. They are expected to be longest and least predictable in cases of evolutionary change, either in alien or in related interacting native species [25], as well as in cases of long-term accumulation or depletion of slow pools in an ecosystem (e.g., soils or sediments). Time lags in invasions have a strong effect on functional change crypticity by masking true lag mechanisms and key functions and their changes [57].

Even if a species is detected in its alien range, and its ecological functions and their changes are not inherently cryptic, they can still remain undetected if the process is masked by temporal and spatial variability of the recipient community and anthropogenic impacts (e.g., seasonal, annual, or regional variation). Strong spatio-temporal variability in interspecific interactions will lead to both quantitatively and qualitatively different interactions between the alien and native species over space and time [60]. Ecosystem heterogeneity, characterized by complex environmental gradients that cause differing local conditions, will result in variable functional patterns and environmental impacts [10,35,61].

Functional changes and the emergence of novel ecological functions in alien species can be masked by anthropogenic impacts and other disturbances in the recipient community. For example, the role of invasive Japanese stiltgrass (*Microstegium vimineum*) in carbon and nitrogen cycling in forest ecosystems in Connecticut was masked by logging [2]. Such overlapping effects may fundamentally alter the observed direction and magnitude of interactions attributed to the alien species alone and can hamper our understanding of its ecological functions [2].

Concluding Remarks, Consequences for Science and Management, and Ways Forward

After decades of extensive research and despite impressive progress in invasion science, our understanding of how ecosystems may change over time is incomplete [2,60].

Knowledge of life histories and ecological characteristics of alien species is often based on studies in their native range [62], which limits their potential use for predictions of novel interactions in the alien range [4]. Low predictability of potential ecological interactions of alien species may further result from incomplete understanding of the recipient community. Even with further improvement of our predictive capabilities, there will be unexpected consequences of introductions, making the adoption of the precautionary principle crucial [22,63], especially given the ongoing high rate of emergence of new alien species [64]. Invasion scientists should also alert the public and policymakers about subtle or non-obvious effects of alien species [3].

Consideration of cryptic functional dynamics is particularly relevant when planning activities to monitor or manage invasions. It is necessary to improve our understanding of relevant mechanisms and dynamics during biological invasions and to develop appropriate sets of monitoring metrics that allow for capturing such processes. We present here a set of research methods and tools that can help to effectively tackle each of the crypticity categories (Table 1). Inclusion of promising novel approaches, such as environmental DNA combined with metabarcoding, automated species identification, and citizen science initiatives, would provide great benefits to the ongoing monitoring programs [65–67]. Here, to build links between the fields of functional ecology and invasion biology, interdisciplinary collaboration will be fruitful. Long-term monitoring programs will also be necessary to overcome confounding effects such as time lags, fluctuations, and transient changes. Furthermore, existing policy measures should be improved by specifically accounting for the different sources of crypticity, outlined within the conceptual framework. Since the crypticity makes impacts of biological invasions unpredictable to a large extent, policy measures should focus primarily on prevention, risk assessment, and adaptive management. One promising strategy, already introduced in the European Union regulation on IAS to prevent their further introductions and spread, is to develop measures that address the most common transportation pathways, instead of a focus on single species. Such measures would simultaneously affect cryptic species, if they are expected to use same pathways as known species.

The framework presented here highlights crypticity in its various forms and illustrates how crypticity can make IAS impacts hard to detect. It is intended to raise awareness; improve understanding of crypticity in biological invasions, its complexity, and the risks it poses to IAS management; and guide future research efforts (see Outstanding Questions).

Outstanding Questions

What is the proportion of cryptic invasive alien species (IAS), including undescribed and undetected species?

What is the frequency of occurrence of cryptic functions and functional changes in IAS?

Which taxonomic and functional species groups are most likely to exhibit crypticity?

Which ecosystem conditions and population characteristics increase the likelihood of crypticity in biological invasions?

Which traits are most suitable for screening IAS for risks of exhibiting cryptic functional dynamics?

How can invasion science and IAS management effectively tackle the problem of uncertainty and unpredictability in cryptic functional dynamics?

Which tools and methods are most promising for early detection of novel functions in invasive alien species?

Is it possible to develop an optimum set of policy measures that would adequately address the problem of crypticity in biological invasions?

What is the actual magnitude of economic and environmental impacts caused by crypticity in biological invasions?

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