



Review

Cryptic invasions: A review



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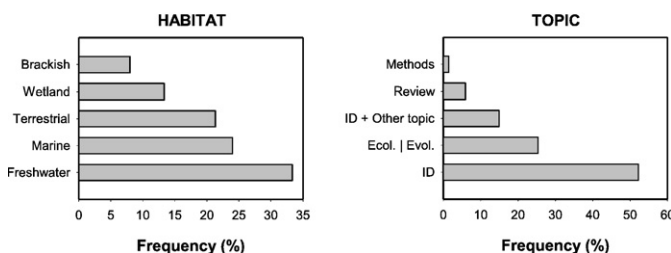
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HIGHLIGHTS

- Sources, causes, mechanisms and consequences of cryptic invasions are examined.
- Cryptic invasions are much more common than currently acknowledged.
- We suggest a framework to manage intraspecific cryptic invasions.

GRAPHICAL ABSTRACT

Cryptic Invasions



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ABSTRACT

Cryptic invasions are defined as the introduction and spread of non-native lineages within the species' native range (intra-specific cryptic invasion) or the invasion of non-native species that goes unnoticed due to misidentification as a native or another invasive species (inter-specific cryptic invasion). While population-specific attributes are acknowledged to play a critical role in the success and impact of biological invasions in general, our knowledge of the causes and consequences of cryptic invasions is largely neglected. Cryptic invasions are inherently difficult to recognize and, despite being likely widespread, often go undetected. In this review, we analyse the sources, mechanisms, and consequences of cryptic invasions. Using a bibliometric survey, we first quantify the relative proportion of study questions, taxa, and geographic regions. We then highlight the value of comparative information from archived specimens in uncovering the occurrence and timing of cryptic invasions. We examine the mechanisms of cryptic invasions and emphasise the role of anthropogenic environmental changes on the arrival of cryptic invaders. We then discuss the role of interspecific biological interactions in the success of cryptic invasions and the role of hybridization between native and non-native lineages in cryptic invasions. We examine the competitive advantage of some invasive lineages in key physiological, ecological or sexually-selected traits. We argue that cryptic invasions, often undetected, may trigger subsequent rapid range expansions. We suggest that cryptic invasions are much more common than currently acknowledged. We highlight the role of coevolved associations (host-parasite, mutualism, herbivory), inherently population-specific, in the impacts of cryptic invasions on local communities. Finally, we outline a framework to manage intraspecific cryptic invasions.

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## 1. Introduction

Cryptic invasions were originally defined as “the occurrence of a species or genotype that was not previously recognized as alien in origin or not distinguished from other aliens” (Novak, 2011). This definition includes two separate circumstances. *Interspecific cryptic invasion* refers to the invasion of non-native species that goes unnoticed due to misidentification as a native or another non-indigenous species, often closely related. *Intraspecific cryptic invasion* refers to the invasion of another lineage of a species into the area where a distinct local lineage of the same species already exists. Given the variations in taxonomic approaches and variations in the concepts to define a species, these apparently separate cases rather represent a continuum and should be studied within the same framework. Indeed, many cases of intraspecific cryptic invasions were later reconsidered as being interspecific and vice versa.

Population-specific attributes are now acknowledged to play a critical role in governing the success and impact of biological invasions. Yet our knowledge of cryptic invasions, their frequency, and impacts is seriously neglected. Cryptic invasions form a minor part of current research on biological invasions, despite their potential to affect native species and impact native communities and ecosystems at the same rate as standard biological invasions. Cryptic invasions are difficult to recognize due to the morphological similarities between the invasive and native species or genotypes. We think that many cases of abrupt range expansion or local increases in population abundance may be driven by unrecognized cryptic invasions. At present, such cases are typically explained as species responses to environmental changes (e.g. climate change, response to alterations in community structure, habitat modification). While this may hold true in many cases, cryptic invasions may be involved, with consequent changes in range and population dynamics. Therefore, we argue that cryptic invasions are likely widespread, but often remain undetected.

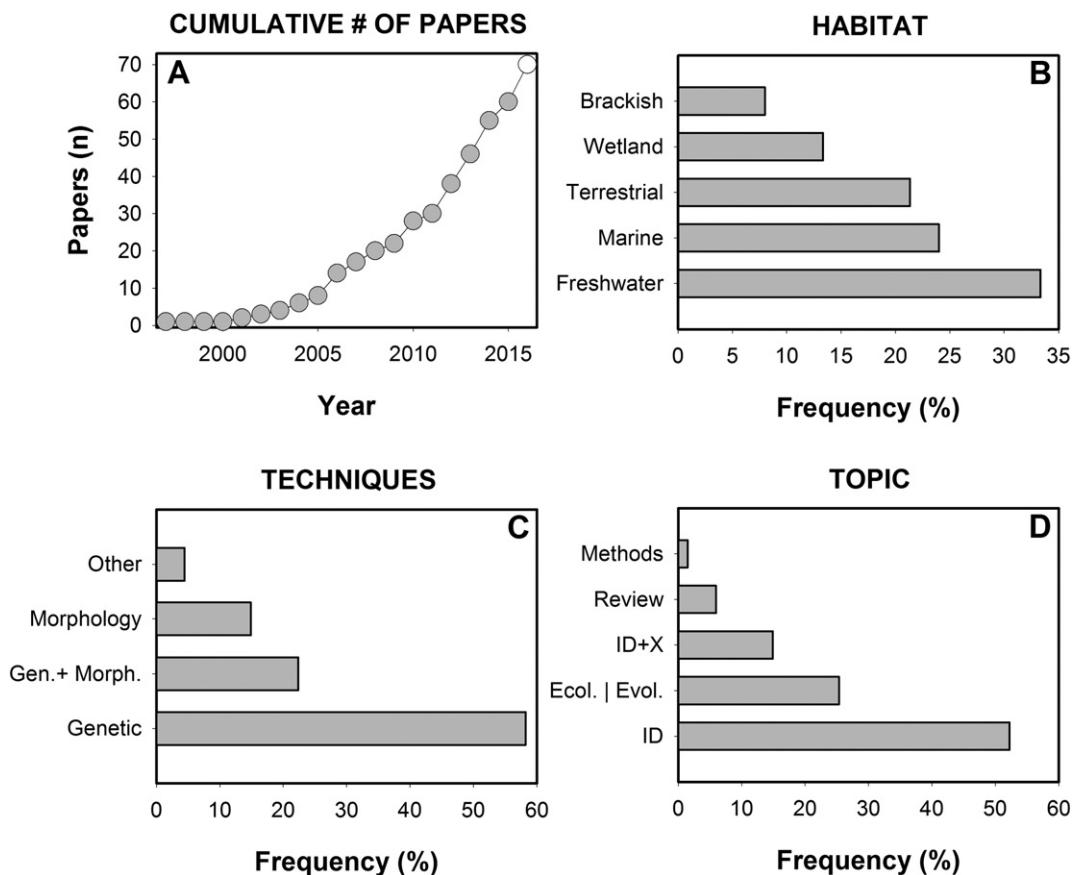
In this review, we analyse the sources, mechanisms, and consequences of cryptic invasions at both interspecific and intraspecific levels. We quantify the key characteristics of published studies on cryptic invasions, especially taxonomic, environmental and geographic patterns and biases. We then highlight the benefit of comparative information from archived specimens in detecting and analysing cryptic invasions. Focusing on sources and mechanisms of cryptic invasions, we stress the role of human-mediated environmental changes in the frequency and success of cryptic invasions. Given a lack of reproductive barriers between native and non-native lineages, we discuss the role of hybridization between native and non-native lineages in the success and impact of cryptic invasions. We argue that cryptic invasions, often undetected, may trigger subsequent rapid range expansions. We then summarize the consequences of cryptic invasions and highlight the intricate complexity of success of non-native lineages and the role of coevolved adaptations that are often population-specific. We conclude by suggesting a

framework for the management of cryptic invasions. While there is no dichotomy between standard and cryptic invasions, we highlight the specific features where cryptic invasions differ in the mechanisms and consequences and may require different management practice.

## 2. Insights from bibliometric survey

Bibliometric surveys provide baseline quantitative information about a discipline's history and current state, namely how well particular study questions, taxa or geographic regions are covered. A search for the general term “biological invasions” in the title, keywords and abstract in Scopus and subsequent classification of retrieved information revealed that studies on cryptic invasions represented less than 0.6% of the studies on biological invasions (Scopus, 2016). The first paper on cryptic invasions listed by Scopus dates back to 1997 (Geller et al., 1997). However, some studies clearly addressed cryptic invasions but were not explicitly labeled as such (e.g. Kawamura et al., 2001; Martínková et al., 2007, 2013), and some papers were even published before 1997 (e.g. Taylor and Hebert, 1993). Indeed, as early as 1993, Carlton and Geller (1993) drew attention to the presence of putative cryptic invasions in aquatic ecosystems introduced via ballast water, and stated that “unrecognized historical transport may have led to false conclusions of cosmopolitanism”. For the data compiled up to 2016, we retrieved 70 papers on cryptic invasions, with a maximum of nine in any given year (Fig. 1A). We acknowledge that some studies may not have been located by our search terms due to discipline-specific terms used in the original papers. A summary of the studies is listed in Table 1.

We classified these papers into several categories to quantify patterns and biases towards study questions, taxa, geographic regions and environmentally relevant locations. We searched the Scopus and Google Scholar databases using the keywords “cryptic invasion”, “cryptic invader”, “intraspecific invasion” and “interspecific invasion” for the period between 1 Jan 1997 and 30 Nov 2016. The resulting set of papers on cryptic invasions was purged from misclassifications (3 papers) and repetitions (1 paper), and restricted to research articles and reviews. Most papers were published by researchers affiliated with US institutions (31%). This is similar to the percentage of US-affiliated papers published on a sample of geographically neutral research topics from the field of biology over the same period; “fish migration” (26%,  $n = 741$ ), “senescence + wild” (39%,  $n = 2163$ ) and “disturbance + senescence + mammal” (31%,  $n = 132$ ) (retrieved using particular keywords in Scopus). The papers with UK, French, Japanese, Belgian, Canadian, New Zealand, Russian, and Spanish affiliated authors represented 3–8% published on cryptic invasions. This is also comparable to the same control set of papers. The journal “Biological Invasions” published the highest proportion of papers, although it accounted for only 15% of the total, followed by Molecular Ecology (12%). Other journals published less than 6% of the papers on cryptic



**Fig. 1.** Summary of papers on cryptic invasions published between 1 Jan 1997 and 30 Nov 2016. The cumulative number of papers published (including papers *in press* for 2016/2017) (A), habitats where cryptic invasions were identified ( $n = 70$ ) (B), techniques used ( $n = 67$ ) (C) and papers' subject topic (ID: identifying a cryptic invasion, Ecol.-Evol: ecological and evolutionary mechanisms and consequences of a cryptic invasion, ID + X: combining identification with other aspects;  $n = 67$ ) (D).

invasions. Aquatic environments, and particularly freshwater (33%) and marine (24%) ecosystems, were the most commonly studied (Fig. 1B). Animals (63%) were studied more often than plants (36%), with only 1% studies combining plant and animal taxa. Interestingly, this contrasts with the field of invasion biology in general where studies are biased towards terrestrial ecosystems and plants (Pyšek et al., 2008; Jeschke et al., 2012). The use of archived specimens (including museum, herbarium, voucher and archaeological samples) was relatively uncommon (21%), but studies that made use of these specimens provided the strongest insights (e.g. Saltonstall, 2002; Genner et al., 2004; Roman, 2006; Martínková et al., 2007, 2013; Väinölä and Strelkov, 2011; Beauclerc et al., 2013; Conroy et al., 2013). The comparison of techniques used by researchers exposed the difficulty of assessing the presence of cryptic invasions; most studies relied on genetic analyses (genetic analyses: 58%; genetic and morphological analyses: 22%) and solely morphology-based studies were used only in 15% of the papers. This perhaps illustrates why more studies concentrated merely on the identification of a cryptic invasion (52%) than on the mechanisms and consequences of such invasions from an ecological or evolutionary point of view (25%; Fig. 1C). Slightly more studies investigated intraspecific cryptic invasions (58%) than interspecific cryptic invasions (42%).

The most often cited keywords reflected the necessity of using molecular techniques to determine cryptic invasions (mitochondrial DNA, haplotype, DNA sequence, population genetics). The relative use of keywords highlighted the most commonly studied ecosystems (freshwater ecosystems, Mediterranean Sea, Pacific Ocean), countries or regions (North America, United States, Japan, Europe, California), and taxa (*Phragmites australis*, *Codium* sp., *Carcinus* sp., Gastropoda, bivalve, Ancyliidae) (Scopus, 2016). The common reed *Phragmites australis* (Poaceae) is by far the most widely investigated taxon for intraspecific

cryptic invasions (Table S1), with studies covering the history of the invasion (Saltonstall, 2002), population genetics (e.g. Paul et al., 2010; Kettenring and Mock, 2012) and several ecological traits (Vasquez et al., 2005; Holdredge et al., 2010; Caplan et al., 2014; Price et al., 2014; Allen et al., 2015).

### 3. Detecting cryptic invasions: the advantage of archived voucher specimens and insights from biogeography

The intrinsic difficulty with identifying cryptic invasions is that they are, by definition, cryptic. However, to fully reveal and understand the causes and consequences of cryptic invasions, their correct recognition is crucial. At the interspecific level it is difficult to distinguish the invasive solitary sea squirt *Ciona savignyi* (Ascidiacea) from other sea squirts (*Ciona intestinalis*, *Ciona* spp.) (Smith et al., 2010), the invasive *Hediste diadroma* from the native *Hediste limnicola* (Polychaeta) (Nishizawa et al., 2014), and the invasive *Myriophyllum spicatum* from the native *Myriophyllum sibiricum* (Haloragaceae) (Zuellig and Thum, 2012). Within species, non-indigenous and native genotypes are phenotypically indistinguishable in *Bactrocera depressa* (Diptera) (Mun et al., 2003) or *Melanoides tuberculata* (Gastropoda) (Genner et al., 2004; van Bocxlaer et al., 2015). Other examples are listed in Table S1. Problems with the identification of cryptic invasions are even more apparent in taxa with unresolved taxonomy, such as *Glyceria declinata* (Poaceae) (Gerlach et al., 2009), *Ciona intestinalis* (Ascidiacea) (Zhan et al., 2010), *Ferrissia* spp. (Gastropoda) (Marrone et al., 2011, 2014), *Pyura* spp. (Ascidiacea) (Teske et al., 2011), *Philine* spp. (Gastropoda) (Krug et al., 2012), and *Bemisia tabaci* (Hemiptera) (Pan et al., 2015), or with unresolved biogeographic origin (in Bryozoa and Entoprocta: Hamelin et al., 2016; *Cardiospermum* spp.: Gildenhuis et al., 2015). For these

**Table 1**

The issues (detection, consequences, mechanisms, management) evaluated for each species in intraspecific cryptic invasion studies.

Systematics	Detection	Consequences	Mechanisms	Management	References	
Plants and algae	Asteraceae	<i>Chondrilla juncea</i> (rush skeletonweed)	•		Gaskin et al., 2013	
	Haloragaceae	<i>Myriophyllum heterophyllum</i> (variable-leaf watermilfoil)	•	•	Tavalire et al., 2012	
	Phrymaceae	<i>Mimulus guttatus</i> (common yellow monkeyflower)		•	van Kleunen et al., 2015	
	Poaceae	<i>Ammophila arenaria</i> (European marram grass) <i>Phalaris arundinacea</i> (reed canary grass) <i>Phragmites australis</i> (common reed)	• • •	• • •	Vandegheuchte et al., 2012 Spyreas et al., 2010 Saltonstall, 2002; Vasquez et al., 2005; Holdredge et al., 2010; Paul et al., 2010; Kettenring and Mock, 2012; Caplan et al., 2014; Price et al., 2014	
Arthropoda	Primulaceae	<i>Primula sieboldii</i> (Japanese primrose)	•		Honjo et al., 2008	
	Rhodophyta	<i>Eucheuma denticulatum</i> <i>Gracilaria vermiculophylla</i>	• •	• •	Tano et al., 2015 Thomsen et al., 2006a, 2006b	
	Acari	<i>Tetranychus evansi</i> (red tomato spider mite)	•		Boubou et al., 2010	
	Diptera	<i>Bactrocera depressa</i> (pumpkin fruit fly)	•		Mun et al., 2003	
	Hemiptera	<i>Bemisia tabaci</i> (silverleaf whitefly)		•	Chu et al., 2010; Pan et al., 2015	
	Amphipoda	<i>Grandidierella japonica</i> (Japanese amphipod)	•		Pilgrim et al., 2013	
	Cladocera	<i>Bythotrephes longimanus</i> (spiny waterflea) <i>Daphnia galeata mendotae</i> (waterflea, native); <i>Daphnia galeata galeata</i> (waterflea, invasive) <i>Daphnia pulex</i> (waterflea)	• • •	• • •	Berg et al., 2002 Taylor and Hebert, 1993	
	Decapoda	<i>Carcinus maenas</i> (European green crab)	•	•	Mergeay et al., 2005 Roman, 2006	
	Other aquatic invertebrates	Ascidacea	<i>Ciona savignyi</i> (solitary sea squirt)	•		Smith et al., 2012
		Bivalvia	<i>Mytilopsis leucophaeata</i> (dark false mussel)	•		Therriault et al., 2004
Gastropoda		<i>Ferrissia fragilis</i> (freshwater limpet)	•		Son, 2007; Marrone et al., 2011, 2014; de Lacerda et al., 2015	
		<i>Melanoides tuberculata</i> (red-rim melania)	•		Genner et al., 2004, van Bocxlaer et al., 2015	
		<i>Theodoxus fluviatilis</i> (river nerite)	•		Gergs et al., 2015	
Hydrozoa		<i>Gonionemus vertens</i>	•		Govindarajan and Carman, 2016	
Nemertea		<i>Cephalothrix cf. simula</i> (ribbon worm)	•		Fernández-Álvarez and Machordom, 2013	
Vertebrates		Platyhelminthes	<i>Ligula intestinalis</i> (tapeworm)	•	•	Bouzig et al., 2013
		Amphibia	<i>Rana pipiens</i> (northern leopard frog)	•	•	O'Donnell et al., 2017
		Aves	<i>Sialia sialis bermudensis</i> (eastern bluebirds)	•		Avery et al., 2013
	Carnivora	<i>Mustela erminea</i> (stoat)	•	•	Martínková et al., 2007	
	Cyprinidae	<i>Cyprinella lutrensis</i> (red shiner)	•		Glottzbecker et al., 2016	
		<i>Cyprinus carpio</i> (common carp)	•		Mabuchi et al., 2008, Uchii et al., 2016	
		<i>Rhodeus ocellatus kurumeus</i> (Japanese rosy bitterling, native); <i>Rhodeus ocellatus ocellatus</i> (rosy bitterling, invasive)	•	•	Kawamura et al., 2001	
		<i>Zacco platypus</i> (pale chub)	•	•	Takamura and Nakahara, 2015	
	Gasterosteidae	<i>Gasterosteus aculeatus</i> (three-spined stickleback)	•	•	Lucek, 2016	
	Mustelidae	<i>Neovison vison</i> (American mink)	•	•	Beaucherc et al., 2013	
Rodentia	<i>Microtus arvalis</i> (common vole) <i>Rattus rattus</i> (roof rats)	• •	• •	Martínková et al., 2013 Conroy et al., 2013		

reasons, we think that cryptic invasions might be much more widespread than commonly assumed (Carlton, 1996), and their proper assessment has to rely on molecular techniques (Roman and Darling, 2007).

Archived specimens provide robust material from which to infer putative invasiveness and the evolutionary consequences of intraspecific

invasions. Kettenring and Mock (2012) used historical herbarium collections to revisit the original sites of native populations of *Phragmites australis* to compare their contemporary genetic diversity and phenotypic traits with the invasive non-indigenous lineage of the same species. Museum specimens can be directly targeted as a source of genetic data. The underlying reason for the range expansion of the

European green crab *Carcinus maenas* (Decapoda) in the Northwest Atlantic (Roman, 2006) and the long-term contribution of domesticated American mink *Neovison vison* (Mustelidae) to feral populations (Beauchlerc et al., 2013) were resolved by comparing contemporary and historical samples from museum collections. Changes in phenotypic traits can be directly compared between archived museum specimens and recent populations. Both genetic and phenotypic shifts were recorded in Swiss populations of the threespined stickleback *Gasterosteus aculeatus* (Gasterosteidae). Native and non-indigenous stickleback lineages hybridize, with a marked increase in the number of lateral plates in contemporary populations compared to historical museum samples from the same sites (Lucek, 2016). In other cases, archived specimens provided a solid confirmation of the occurrence and dynamics of interspecific (Geller, 1999; Audzijonyte et al., 2006; Gerlach et al., 2009; Väinölä and Strelkov, 2011; Grabowski et al., 2012; Krug et al., 2012; Wolf et al., 2012; Grosser et al., 2016) or intraspecific cryptic invasions (Saltonstall, 2002; Genner et al., 2004; Martínková et al., 2007, 2013; Gergs et al., 2015).

Another approach to identifying cryptic invasions is from phylogeographic studies, despite a lack of historical samples (Gildenhuis et al., 2015). Phylogeographic studies document the contemporary distribution of intraspecific lineages, often including lineages of several closely related species. Their current distribution can be explained by historical processes, and instances of unexpected contemporary distribution may be signs of recent or historic cryptic invasions. Combining standard phylogeographic tools (e.g. mitochondrial markers to reconstruct the distribution of maternal lineages) with the tools of population genetics (e.g. nDNA microsatellite markers) and their statistical apparatus (e.g. Approximate Bayesian Computation) can provide insight into the demographic history of lineages and populations. This approach has been used to study historical cases of cryptic invasions (e.g. Martínková et al., 2007, 2013) and recent cases of standard and cryptic invasions (Konečný et al., 2013; Gildenhuis et al., 2015).

#### 4. Mechanisms of cryptic invasions

The process of invasion can be divided into (i) introduction, (ii) establishment and persistence, (iii) spatial spread and increase in local abundance. All aspects are well studied in standard biological invasions (Davis, 2009; Lockwood et al., 2013) and many outcomes can be generalized to the mechanisms driving cryptic invasions. Rather than providing an overview of general patterns, we concentrate on specific features of cryptic invasions.

##### 4.1. Sources of introduction

The introduction of cryptic non-indigenous lineages includes all major introduction vectors identified for common biological invasions and depends on the connection between its original and invaded range. Human-mediated transport related to cargo and passenger transport is the most likely cause of dispersal in many cryptic invasions, including ballast water (spiny waterflea *Bythotrephes longimanus* (Cladocera) (Berg et al., 2002)), ballast sediment (common reed *Phragmites australis* (Poaceae) (Saltonstall, 2002)) and hull fouling (solitary sea squirt *Ciona savignyi* (Ascidiacea) (Smith et al., 2012)). Navigation canals have enabled the cryptic introduction of mysid shrimps *Limnomysis benedeni* and *Paramysis lacustris* (Mysidacea) (Audzijonyte et al., 2006) and human-mediated land-use changes have likely driven the rapid historical lineage replacement of the common vole *Microtus arvalis* across the European continent (Martínková et al., 2013). Aquaculture (e.g. red algae *Eucheuma denticulatum* (Rhodophyta) (Tano et al., 2015)), crop plants (e.g. whitefly *Bemisia tabaci* (Hemiptera) (Chu et al., 2010; Pan et al., 2015)), and the ornamental species trade (e.g. rosy bitterling *Rhodeus ocellatus ocellatus* (Cyprinidae) (Kawamura et al., 2001)) are also important introduction vectors. Finally, breeding facilities (e.g. American mink *Neovison vison* (Mustelidae) (Beauchlerc et

al., 2013)) and angling (e.g. red shiner *Cyprinella lutrensis* (Cyprinidae) (Glottzbecker et al., 2016)) are sources of intentional and accidental introductions of non-native intraspecific lineages, reflecting the patterns of spatial distribution of their putative sources (Glottzbecker et al., 2016).

Cryptic invasions may often be triggered by the elimination of barriers between lineages. Species ranges may, naturally or as a consequence of environmental deterioration, be composed of isolated subunits (Gaston, 2003). Their ancient separation leads to intraspecific diversification and a contemporary breakdown of the barrier would enable one lineage to spread outside its original range. While this may be a natural process, many dispersals over former barriers in recent decades are due to anthropogenic effects. In freshwater ecosystems, the connection of naturally separated river basins by navigation canals has triggered numerous aquatic invasions (Ricciardi et al., 2013), including cryptic invasion such as the spread of non-indigenous stickleback lineage into Central Europe (Lucek et al., 2010). In other regions, stocked brown trout *Salmo trutta* (Salmonidae) have hybridized with local resident populations (Hansen et al., 2010). Such cases have only become apparent in species that are harvested and of commercial value (e.g. brown trout), when cryptic invasion results in obvious phenotypic change (e.g. stickleback) or when it dramatically alters species abundance, distribution, community structure or ecosystem functioning as in the case of common reed *Phragmites australis* (Poaceae) (Price et al., 2014), reed canary grass *Phalaris arundinacea* (Poaceae), (Spyreas et al., 2010) and European green crab *Carcinus maenas* (Decapoda) (Roman, 2006). We hypothesize that dispersal related to human alteration of natural barriers is a widespread source of range expansion and colonisation by non-native lineages that may sometimes result in cryptic invasions and loss of geographic variation.

##### 4.2. Establishment and persistence

Propagule pressure is an important mechanism of the establishment success and invasive potential of standard invasions (Duncan, 2011). How propagule pressure contributes to cryptic invasions is difficult to study but genetic markers provide indirect estimates. In European green crabs *Carcinus maenas* (Decapoda), continuous arrival of new propagules can be inferred from temporal increases in genetic diversity (Roman, 2006). The Eurasian spiny water flea *Bythotrephes longimanus* (Cladocera) established successfully in the Great Lakes despite apparently low rates of propagule pressure in terms of propagule abundance (Gertzen et al., 2011; Yan et al., 2011), but propagules continued to arrive over time (Berg et al., 2002).

Propagule pressure likely interacts with other mechanisms in the establishment and persistence of cryptic invasions. Altered environmental conditions, disturbance, and divergent phenotypic traits that increase the success of a non-indigenous genotype under new conditions may facilitate the long-term survival of a non-native lineage in a new environment. The predatory behaviour of *Bythotrephes longimanus*, a cryptic invader of the Great Lakes may be the primary reason for its successful establishment (Yan et al., 2002; Barbiero and Tuchman, 2004; Pangle and Peacor, 2009; Bunnell et al., 2011). At the intraspecific level, different sensitivity to pesticide treatment has enabled the persistence of the Q biotype of whitefly *Bemisia tabaci* (Hemiptera) in China (Pan et al., 2015) where it replaced previously common, pesticide-sensitive B biotype. Hybridization with native lineages is a form of persistence of a particular genotype outside its former range (Petit, 2004) – we discuss this in Sections 4.3.2 and 5.1 in relation to the impact of cryptic invasions on native populations.

##### 4.3. Population spread and increase in abundance

Cryptic invasions are ultimately realized by the spatial spread and increase in local abundance of a non-indigenous population or cryptic

species (Davis, 2009; Lockwood et al., 2013). Many features that contribute to the persistence of cryptic invaders facilitate their spatial spread and demographic success – the predatory behaviour of Eurasian spiny water fleas *Bythotrephes longimanus* being an example. Invasiveness may arise through new opportunities (enemy release, heterosis) or competitive advantage arising from unique physiological traits or adaptation to altered environmental conditions.

#### 4.3.1. Enemy release and parasite co-introduction

Release from a natural enemy in a novel range (Blossey, 2011) can contribute to the invasiveness of non-native lineages. The enemy release hypothesis refers to a decrease in biotic population regulation by predators, parasites and other natural enemies of the invading species, resulting in its rapid increase in distribution and abundance (Keane and Crawley, 2002 but see Heger and Jeschke, 2014). Given that populations of a species are genetically and phenotypically variable across their range, they likely possess population-specific abilities to coexist and interact in local communities. Therefore, the establishment (as well as temporal dynamics and impacts) of non-indigenous lineages can be driven by population-specific attributes of resistance, tolerance and mutual relationships between closely interacting species. These relationships can have either positive or negative effects on invading lineages, or on the native species involved in partnerships with the new lineages.

Host-parasite relationships are characterized by coevolutionary dynamics that are inherently fluctuating; an adaptation in one partner matches a corresponding adaptation in a second partner. This generates diverse geographic mosaics of coevolutionary states (Thompson, 1999; Bhattarai et al., 2017). The translocation of populations into non-indigenous areas of the species range can disrupt locally coevolved adaptations, exposing both non-native and local partner populations to novel interactions (Douda et al., 2014; Prior et al., 2015; Reichard et al., 2015) that may dramatically affect the outcome of their relationship (Reichard et al., 2012). For example, the native North American genotype of the common reed is more vulnerable both to native herbivores (Bhattarai et al., 2017) and to herbivores co-introduced with the non-indigenous European lineage (larvae of *Lipara* spp. flies, Diptera) (Allen et al., 2015). Hence, the release of the non-indigenous lineage from some natural enemies, coupled with higher vulnerability of the native lineage to co-introduced and native herbivores, may skew the competitive outcome in favour of the non-indigenous lineage (Allen et al., 2015; Bhattarai et al., 2017). This may contribute to the success of the non-indigenous common reed genotype, together with benefits conferred by other advantageous traits (see Section 4.3.3).

#### 4.3.2. Heterosis and hybrid vigour

Heterosis is a hybrid vigour achieved by hybridization, mediated by increased heterozygosity. At the interspecific level, heterosis is known to enhance invasiveness in several examples of cryptic invasions (Ellstrand and Schierenbeck, 2000; Vilà et al., 2000), either when a non-native species hybridizes with a native species (e.g. *Myriophyllum heterophyllum* × *Myriophyllum laxum* (Tavalire et al., 2012), *Mytilus trossulus* × *Mytilus edulis* (Väinölä and Strelkov, 2011)) or when two non-native species hybridize (e.g. salt cedar *Tamarix chinensis* × *Tamarix ramosissima* (Gaskin and Schaal, 2002; Whitcraft et al., 2007), green crabs *Carcinus maenas* × *Carcinus aestuarii* (Darling, 2011)) (Table S1).

At the intraspecific level, hybridization (admixture) between non-native and native lineages may enhance invasiveness via the same process (Ellstrand and Schierenbeck, 2000). Purple viper's-bugloss *Echium plantagineum* (Boraginaceae) is a highly invasive annual herb in Australia where its genetic diversity is higher than in native populations (Burdon and Brown, 1986). Similarly, North American populations of cheatgrass *Bromus tectorum* (Poaceae) also possess increased intra-population genetic variability compared to its native populations (Novak and Mack, 1993). It is likely that intraspecific hybridization between lineages introduced from several regions has triggered evolutionary changes leading to increased invasive potential (Ellstrand and

Schierenbeck, 2000). In both cases, the hybridization occurred between two lineages outside their native range and hence cannot be qualified as cryptic invasions.

The current evidence for the role of intraspecific hybridization in triggering the expansion of hybrid lineages as a consequence of cryptic invasions is inconclusive. The hybrid clones of two water flea subspecies, the native *Daphnia galeata mendotae* and the non-native *Daphnia galeata galeata* (Cladocera), were able to establish in the Great Lakes (North America), in contrast to the non-hybridized *D. galeata galeata*. Hybridization occurred through genetic introgression; the hybrids showed a morphological cline along the invaded sites and genetic distance increased from the putative initial site of invasion in Lake Erie (Taylor and Hebert, 1993). It should be noted that the taxonomic status of these subspecies is not consensual (e.g. Taylor and Hebert, 1993; Yorks et al., 2014; Todorova et al., 2015) and this case study might alternatively be considered an example of interspecific cryptic invasion and hybridization.

Experimental results demonstrate that genetic admixture may contribute to the invasiveness of the common yellow monkeyflower *Mimulus guttatus* (Phrymaceae). In a greenhouse experiment with controlled conditions, non-native populations overcame the effects of inbreeding depression better than native populations, particularly when crossed with native individuals. Heterosis was clearly displayed with regard to asexual and sexual reproduction and growth (van Kleunen et al., 2015).

In the wild, non-indigenous lineages frequently hybridize with native lineages, but a clear effect on invasiveness has not been unambiguously detected. In the common reed *Phragmites australis* (Poaceae), native and invasive lineages can produce fertile hybrids and backcross, but this happens rarely (Paul et al., 2010). The intraspecific hybridization of variable-leaf watermilfoil *Myriophyllum heterophyllum* does not increase invasiveness directly, although it has the potential to increase certain invasiveness traits (e.g. biomass, size, branching) (Tavalire et al., 2012).

In animals, admixture between native and non-indigenous lineages also does not appear to directly promote invasiveness. The invasion of the fully-plated lineage of the threespine stickleback *Gasterosteus aculeatus* (Gasterosteidae) in Switzerland clearly involves hybridization, but it is not clear whether admixture contributes to the invasion success (Lucek et al., 2010). In other freshwater fishes, hybrid lineages between native and non-native populations are readily formed (Takamura and Nakahara, 2015), but invasiveness is promoted by the expansion of non-native lineage rather than as a consequence of hybrid vigour (Kawamura et al., 2001). Individuals of American mink *Neovison vison* (Mustelidae) that escaped from fur farms in Ontario (Canada) do interbreed with the wild mink population. However, no significant effect on native mink populations has been detected, probably due to maladaptation or inbreeding depression of escapees and hybrids (Beaucherc et al., 2013). It is possible that admixture between divergent lineages may lead to the loss of local adaptation and problems associated with the expression of intermediate phenotypes (Nosil, 2012).

The expansion of a species range, or a rapid increase in a species abundance at locations where it is already present, can also occur after an increase in genetic diversity via hybridization. Declining native populations of Northern leopard frog, *Lithobates pipiens* (Ranidae), that hybridized with non-indigenous individuals have stabilized or even reversed their long-term demographic decreases (O'Donnell et al., 2017). Ostensibly, admixed populations thrive well compared to declining native populations (O'Donnell et al., 2017).

#### 4.3.3. Competitive advantage and advantageous traits

The invasiveness of a non-indigenous lineage often stems from its competitive advantage over the native genotype in key traits related to physiology and ecology. In the common reed *Phragmites australis* (Poaceae), increased tolerance to salinity enabled the invasive lineage to colonize available habitats (Vasquez et al., 2005). In addition, more efficient use of nutrients supports faster production of above-ground biomass (Holdredge et al., 2010; Caplan et al., 2014; Price et al., 2014).

The native common reed appears to be able to coexist and compete under nutrient-limited conditions due to its root architecture and to its symbiotic relationship with mycorrhiza (Holdredge et al., 2010). However, while Holdredge et al. (2010) listed eutrophication as a factor significantly contributing to the invasiveness of the non-native genotype, Price et al. (2014) demonstrated that it was not associated with more eutrophic habitats. Hence, the competitive advantage of the non-native common reed lineage in eutrophic environments requires more work to be resolved.

The Asian lineage of a freshwater gastropod, red-rim melania *Melanoides tuberculata* (Gastropoda), has invaded several African regions (Genner et al., 2004), primarily becoming established in areas with high human population densities where it replaces endemic native lineages (van Bocxlaer et al., 2015). Eutrophication and pollution, and a consequent increase in the availability of soft substrates, have been implicated as ecological opportunity driving the invasiveness of non-indigenous *M. tuberculata* lineages. Yet, caution is needed when identifying eutrophication as the key factor driving the invasion success, as eutrophic sites near major human settlements are also most likely the primary points of introduction. Over-representation of invasive lineages near cities may therefore reflect propagule pressure rather than competitive advantage in human-affected environments (van Bocxlaer et al., 2015).

The northward expansion of the European green crab *Carcinus maenas* (Decapoda) in the northwest Atlantic, established since the early 19th century, was likely triggered by the introduction of new lineages adapted to colder water rather than the thermal adaptation of established non-indigenous populations (Roman, 2006). The predatory behaviour of the spiny waterflea *Bythotrephes longimanus* (Cladocera), given above as an example of a determining factor in successful persistence, certainly also conferred a competitive advantage (Yan et al., 2002; Barbiero and Tuchman, 2004; Pangle and Peacor, 2009; Bunnell et al., 2011).

The success of the non-native rosy bitterling *Rhodeus ocellatus* (Cyprinidae) appears to be related to sexual selection. Males of the non-native lineage are preferred over males of the native Japanese rosy bitterling *Rhodeus ocellatus kurumeus* by females from both lineages (Kawamura et al., 2001). The polygynandrous mating system of bitterling fishes results in considerable reproductive skew among males (Casalini et al., 2009). Hence, rare non-native males may obtain a disproportionately high reproductive success which certainly accelerates the replacement of the native lineage by non-native invaders.

## 5. Impacts

The consequences of cryptic invasions are not well documented. A new lineage can compromise the persistence of native lineage(s) via hybridization. Hybridization may promote consequent evolutionary change via recombination and the emergence of novel genotypes and phenotypes. Invasive lineages may replace native lineages and take new roles in biotic interactions, with potential impact on community structure and ecosystem functioning. Below, we provide an overview of current evidence or an indication of potential impacts of cryptic invasions.

### 5.1. Hybridization and consequent evolutionary change

Hybridization between native and non-indigenous invasive lineages may cause homogenization of genetic diversity and loss of potentially unique endemic genotypes. This happens when hybrids spread rapidly and replace native genotypes, as observed in the Japanese rosy bitterling (Kawamura et al., 2001). In most cases, however, there is no evidence that hybridization leads to native lineage extinction. Native and non-indigenous common reeds coexist and hybridization is uncommon (Paul et al., 2010). Introgression of feral mink into natural populations does not appear to constitute a major problem, perhaps because escapees

of domestic mink are poorly adapted to natural conditions (Beauclerc et al., 2013). Introgression (Hansen et al., 2010; Lucek, 2016) and admixture (Takamura and Nakahara, 2015) is evident in Swiss sticklebacks, Danish brown trout and Japanese pale chub (*Zacco platypus*, Cyprinidae), but there is no information on consequences beyond genetic homogenization.

We hypothesize that cryptic invasions might also promote invasiveness through rapid evolutionary change. Increased genetic diversity due to introgression might enhance the adaptive potential of a population/species (Ellstrand and Schierenbeck, 2000; Kettenring and Mock, 2012) and thus contribute to the establishment, expansion, and impact of non-indigenous species (Thompson, 1991; Darling, 2011). However, there is insufficient evidence for this hypothesis, largely due to the paucity of research on the subject. The emergence of hybridogenic invasive plants such as *Spartina anglica*, a hybrid between native and invasive *Spartina* species, colonizing British salt marshes (Thompson, 1991), illustrates that the hypothesis is plausible. Similarly, the intraspecific admixture of two non-native lineages of purple viper's-bugloss *Echium plantagineum* (Boraginaceae) in Australia and cheatgrass *Bromus tectorum* (Poaceae) in North America triggered their invasive potential (Ellstrand and Schierenbeck, 2000) and demonstrates the potential of this process. The concept of biological invasions at the gene level (Petit, 2004) highlights that introgression typically results in hybrid swarms rather than new stable hybrid taxa and argues that invasions may be considered at the level of individual genes. Hence, translocations of individuals within a species' range should be recognized as an important (though cryptic) component of biological invasions (Petit, 2004).

### 5.2. Replacement

During cryptic invasions, replacement may occur through introgression (e.g. Japanese rosy bitterling (Kawamura et al., 2001); northern leopard frog (O'Donnell et al., 2017)) or via the ecologically-driven replacement of the native lineage by a lineage that possesses superior adaptation (Tano et al., 2015; van Bocxlaer et al., 2015). The clearest example of this is the whitefly *Bemisia tabaci* (Hemiptera), a viral vector of the tomato yellow leaf curl virus. The invasive Q biotype is more resistant to pesticide treatment, conferring a competitive advantage over previously common B biotype, and leads to its replacement in Chinese croplands (Pan et al., 2015) and to its spread throughout China (Chu et al., 2010; Pan et al., 2015).

At least local replacement is expected in cases when a new lineage invades altered habitats to which a native lineage is not adapted. Asian lineages of red-rim melania *Melanoides tuberculata* (Gastropoda) in Africa are candidates for such environmentally driven replacement, although data from natural populations do not indicate that this has happened (van Bocxlaer et al., 2015). Seaweed farming causes the introduction of non-indigenous seaweed species and genotypes. South-east Asian genotypes of red algae *Euclima denticulatum* (Rhodophyta) have been cultured across East Africa, including Zanzibar. The non-indigenous genotypes have widely replaced the native lineage of *E. denticulatum*, and are now present in sites where the Asian lineage has never been farmed (Tano et al., 2015).

### 5.3. Novel roles in biotic interactions, communities and ecosystem roles

A series of cascading impacts frequently follows intraspecific cryptic invasions, as has been well described for standard biological invasions (Ricciardi et al., 2013). The expansion of the invasive red alga *Gracilaria vermiculophylla* (Rhodophyta) distribution in Virginia (USA) has led to an increase of native diversity of epiphytic algae (Thomsen et al., 2006b) and provided new substrates for native gastropods to lay their eggs (Guidone et al., 2014). So, the new *G. vermiculophylla* lineage has arguably acted as an ecosystem engineer.

Other complex interactions in ecosystem functioning have followed the expansion of non-indigenous haplotypes of angiosperm plant

species. For example, the diversity of plant communities was found to be lower in areas dominated by non-native common reed compared to native common reed stands, and comprised tolerant and generalist plant species (Price et al., 2014). Similarly, the expansion of the reed canary grass *Phalaris arundinacea* (Poaceae) distribution range in Illinois (USA) has negative impact on plant diversity and floristic quality, arthropod abundance and diversity, and communities of small mammals (Spyreas et al., 2010). The diversity of invertebrates associated with the non-indigenous haplotypes of the European marram grass *Ammophila arenaria* (Poaceae) has also decreased, even when the source of the non-native population was geographically close (~270 km away) (Vandegheuchte et al., 2012). This suggests the presence of tight links between native genotypes within a community.

Affiliated species (directly depending on the presence of another species) represent a threatened part of local communities (Dunn et al., 2009). Their inherent fragility stems from the existence of complex coevolved relationships. Any rapid disturbance of those relationships, such as invasion of a novel intraspecific lineage that is at a different state of coevolutionary dynamics, may affect local fine-tuned associations. The host-compatibility between native freshwater mussel glochidia and their fish hosts differs between sites within a fragmented river system, suggesting intricate population-level interactions (Douda et al., 2014). Different populations of thick-shelled river mussel *Unio crassus* (Bivalvia), an endangered European freshwater mussel, vary in their sensitivity to different fish host species and populations of the most commonly used species of host fish (Douda et al., 2014). With widespread translocations of European freshwater fishes as a result of the stocking of natural freshwater systems with hatchery-reared fish by angling associations throughout Europe (Copp et al., 2005), non-native host fish populations are abundant (Douda et al., 2013; Stanković et al., 2016) and may have significantly contributed to the extensive decline of European unionids. The lack of locally adapted hosts may severely limit the developmental success of parasitic mussel larvae (Douda et al., 2014).

## 6. Management

Managing and eradicating invasive species is a complex and expensive endeavour, whose success often depends on early detection (Westbrooks and Eplee, 2011) and correct identification (Pyšek et al., 2013). This can be particularly challenging in the cases of cryptic invasive species (Zuellig and Thum, 2012; O'Donnell et al., 2017) and even more difficult for invasive populations. Management of intraspecific cryptic invasions must rely on acknowledging their existence (Zuellig and Thum, 2012; Conroy et al., 2013; O'Donnell et al., 2017), and the context of their existence. The disjunct distribution of red shiner *Cyprinella lutrensis* (Cyprinidae) in the Western US results from multiple and independent introductions, making localized management actions effective (Glottzbecker et al., 2016). The development of easy-to-use methods to detect (Japanese primrose *Primula sieboldii* (Primulaceae) (Honjo et al., 2008)) and quantify native and invasive haplotypes is also crucial for effective management actions (common carp *Cyprinus carpio* (Cyprinidae): Uchii et al., 2016). Indeed, the development of such methods should be a management priority. Managing intraspecific cryptic invasions also has to be lineage-specific, and managed in the same way as a standard invasion when a non-indigenous lineage is recognized as a distinct biological entity. This point of view is well illustrated by the example of the whitefly cryptic invasion in China (see Section 4.2) (Chu et al., 2010; Pan et al., 2015).

One potential approach to detecting cryptic invasions at an early stage includes the use of environmental DNA (eDNA) assays. The eDNA is based on detection of trace DNA present in air, water, soil or biological samples (honey, saliva, blood, faeces; Bohmann et al., 2014) and has been successfully used in metabarcoding trials across taxa and environments (Taberlet et al., 2012). This could serve as an efficient

early detection method for invasive species that are otherwise difficult to record (Dejean et al., 2012; Bohmann et al., 2014; Rees et al., 2014; Darling, 2015), including cryptic invasions. For example, in aquatic environments, the sensitivity of eDNA surveys enables the detection of non-indigenous invertebrates, including planktonic species, and vertebrates, such as fish and birds (Lin et al., 2012; Rees et al., 2014; Uchii et al., 2016). In controlled trials, a positive relationship was found between the quantity of native and invasive DNA present in PCR products and their biomass ratio in the experimental units (Uchii et al., 2016). In natural habitats, an eDNA survey completed to detect and quantify the presence of the American bullfrog *Lithobates catesbeianus* (Amphibia) was more efficient than traditional field methods by a factor of 5.4 (Dejean et al., 2012).

Despite its obvious advantages, eDNA surveys should only be part of a systematic approach to detecting and assessing invasive species (Januchowski-Hartley et al., 2011), because species-specific early-detection surveys should never be excluded from such an approach (Økland et al., 2010). At present, eDNA assays are not widespread and prone to classification errors (Ricciardi et al., 2017). However, the cost of genotyping is decreasing rapidly while its efficiency is increasing and the use of previously expensive or laborious methods will likely become easily accessible in the near future. In the particular context of cryptic invasions, the development of lineage-specific libraries is essential for this approach to become a common practice, and to diminish the cost of analyses.

Specific steps are required prior to the use of eDNA monitoring, such as compilation of a reference library, a list of potentially invading species and lineages within a species, initially targeted towards the most problematic taxa. Recognizing potentially invasive lineages should lead to the development of specific libraries for the most problematic species and lineages. Groups to be targeted likely include agricultural pests resistant to locally used pesticides and the most common passengers of ballast water or cargo traffic that have potential medical consequences, such as particular lineages of mosquito species that may carry infectious diseases. We think that such analyses may become routine management practice in the near future, namely with rapid progress in the speed and accessibility of high-throughput genetic and genomic analyses, together with a decrease in cost, and increasing recognition of the risk of emerging diseases.

Intraspecific hybridization, and consequent admixture, poses additional management problems because the new entity compromises the integrity of pre-established ecological relationships between the native lineage and other ecosystem components. Therefore, native lineages should ideally be identified within the native range to be used as source populations in recolonization programs, once – if desired – hybrid lineages are removed (O'Donnell et al., 2017). However, if native lineages suffer from inbreeding depression, the use of lineages that are expanding elsewhere might be considered. This means that intraspecific invasions might be seen as “genetic arks” (Martínková et al., 2013) with the potential to be used in conservation programs devoted to restoring lost native diversity (Waters and Grosser, 2016), as suggested for common vole conservation in continental Europe (Martínková et al., 2013). However, a very modest approach is recommended, always contingent upon the particular problem, because such decisions are likely to have long-term consequences.

The dilemma of the introgressed populations of highly endangered species can be exemplified by an iconic species of Japanese freshwater fish conservation – the Tokyo bitterling *Pseudorhodeus tanago* (Cyprinidae). This species, endemic to Tokyo-Yokohama region, is critically endangered due to the destruction of its habitat and a captive breeding programme has been established to save it from extinction (Kubota et al., 2010). Recently, new wild populations were discovered but genetic analysis revealed that they are composed of introgressed individuals, posing a question of how to approach this population from the perspective of endangered species management (Saitoh et al., 2017).



## 7. Conclusions

Cryptic invasions often arise through intrinsic competitive advantage over native lineages or through hybridization and subsequent hybrid vigour. The introduction of new lineages adapted to other abiotic conditions can also promote the range expansion of non-native species, as well as the disruption of competitive hierarchies through anthropogenic mediation, co-introduction of other non-native species or release from natural enemies during the invasion. These mechanisms are certainly only a glimpse of the complexity involved in cryptic invasions. However, the current lack of recognition of the existence of cryptic invasions precludes their potential role in providing insights to both invasion biology and ecology in general. Therefore, we urge invasion biologists to consider cryptic invasions while developing their research agenda.

Intrinsically, managing and eradicating cryptic invasive species and lineages faces an additional problem compared with standard invasions - the difficulty of their identification. Museum voucher specimens should be used whenever they are available. In addition, eDNA surveys may be used to detect some cryptic invasions at an early stage. Overall, the initial approach to an intraspecific invasion should be made with caution, as if it were a distinct biological entity, i.e. a distinct species, until ecological and genetic profiling is completed.

While the most visible invasions tend to receive the greatest attention, they may bias our understanding of the impacts of invasions (Strayer, 2012). We argue that cryptic invasions may have a high impact on local communities, and these are often precipitated via a complex network of population-specific relationships between closely interacting species (Douda et al., 2014). In addition to the need to recognize cryptic invasions and mitigate their effects if necessary and feasible, studies on novel combinations of population-specific interactions offer an opportunity to test evolutionary and ecological hypotheses.

There are clearly several mechanisms mediating cryptic invasions, similar to those promoting the invasiveness of a “common” non-indigenous species. It is not yet possible, however, to determine the relative importance of particular mechanisms. More case studies need to be completed to gain a better insight. We think that future studies should consider the prevalence of a given mechanism taking into account reports from distinct populations. The population-specific rather than species-specific impacts of biological invasions have recently been suggested as a relevant measure of impact (Reichard et al., 2015). This paradigm shift postulates the existence of an intricate complexity of success of non-native lineages and the role of local adaptations that are often population-specific. We believe that a population-specific approach to invasions, in general, can increase our understanding of the successes, mechanisms and impacts of invasions.

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