



INVASION BIOLOGY: EVIDENCE, ASSUMPTIONS, AND CONSERVATIONISM

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Keywords

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Control

Abstract Although isolated records of nonindigenous species (i.e., species transported with the aid of human activities outside of their native geographic ranges) have been known for centuries, the first comprehensive work on these organisms and their impacts is the book by Charles Elton published in 1958. The rate of species introductions increased significantly since the middle XIX century, with recent estimates suggesting around 600 plant and animal species per year. Many of these introductions have been deliberate (crops and ornamental plants, domesticated and wild animals), but most were accidental, usually in association with the intra- and intercontinental transport, chiefly by sea, of people and merchandise. Some of these species have been very successful in colonizing the new habitats and became invasive, displacing native species and affecting resident communities and human interests. As a consequence of these high-profile invasions, in the last 30 years or so a new ecological discipline flourished - "Invasion Biology". Among its goals are attempts at establishing hypotheses or general rules aimed at explaining how and why some introduced species are so successful in the areas they colonized. However, empirical support for these hypotheses has been very uneven: each explains some cases, but fails to account for many others. Invasion Biology is presently moving on thin ice, unable to reach consensus on such elementary notions as differences between native, introduced, and invasive. Idiosyncratic conservation-related issues, as well as legitimate and personal interest-driven academic and social factors led to

the demonization of introduced species engendering a deep crevice in the field. A majority of the scholars in this young field adhered to the concept that geographic origin is of utmost importance: all introduced species are undesirable, and therefore guilty of negative impacts until proven innocent. In contrast, other researchers consider that geographic origin is of minor importance; like many indigenous species, most introduced organisms have negative impacts on some natives, positive on others, and mostly neutral impacts overall. The pristine state of ecosystems, free from introduced species, is a subjective human concept strongly influenced by emotional, ideological and cultural values fostered by conservationists. Both introduced and native species can have undesirable impacts on ecosystems and on human interests, and these impacts depend on multiple factors, especially the species concerned, but also many other conditions associated with functional roles, time, and space. When the overall impacts are clearly negative, both native and introduced species may require human intervention in the form of control or eradication actions, regardless of their geographic origin.

Palabras clave

Especies
introducidas
Especies
invasoras
Impacto
Origen
geográfico
Erradicación

Resumen La biología de las invasiones: evidencias, supuestos y conservacionismo. Si bien se conocen menciones de especies introducidas (insertadas por actividades humanas en sitios distantes de su área nativa) desde hace siglos, el primer tratado exhaustivo dedicado a estos organismos y sus impactos es el libro de Charles Elton publicado en 1958. El ritmo de crecimiento de estas introducciones se aceleró notablemente desde mediados del siglo XIX, y se estima que actualmente es de alrededor de 600 plantas y animales por año. Muchas de las introducciones han sido voluntarias (plantas cultivadas para sustento u ornamentales, animales domesticados y silvestres), pero la mayoría fueron accidentales, generalmente en asociación con el transporte intra- o intercontinental, principalmente marítimo, de personas y mercaderías. Algunos de estos organismos han sido muy exitosos en su colonización del nuevo ambiente, transformándose en invasores, desplazando a especies nativas y afectando hábitats e intereses humanos. Como consecuencia de estas invasiones espectaculares, en los últimos 30 años se afianzó una rama particular de la ecología, la “Biología de las Invasiones”. Uno de sus propósitos fue el intento de establecer hipótesis o reglas generales para explicar cómo y por qué las especies introducidas suelen ser tan exitosas en los ambientes invadidos. Sin embargo, el apoyo a estas hipótesis por parte de estudios puntuales fue muy heterogéneo: cada

una de ellas da cuenta de algunos casos, pero es rechazada en muchos otros. La Biología de las Invasiones se encuentra actualmente en terreno pantanoso, sin lograr consensos sobre aspectos tan básicos como la diferenciación entre especie nativa, vs. introducida vs. invasora. Cuestiones idiosincráticas relacionadas con el conservacionismo e intereses académicos y sociales (genuinos o no) contribuyeron a demonizar a las especies introducidas generando una división de criterios en la especialidad. Una fracción mayoritaria de los especialistas adhirieron al postulado que el origen es un factor determinante, todas las especies introducidas son indeseables y por lo tanto representan un riesgo hasta que se demuestre lo contrario. La otra fracción considera que el origen no es el factor definitivo del rol e impacto de las especies; al igual que las nativas, la gran mayoría de las introducidas tienen impactos negativos sobre algunos integrantes de las comunidades, positivos sobre otros, y mayormente neutros. El estado prístino de los ecosistemas, libres de especies introducidas, es una concepción humana subjetiva y con una fuerte carga emocional, ideológica y cultural que representa la base de la corriente conservacionista. Tanto especies introducidas como nativas pueden tener impactos indeseables sobre los ecosistemas y los intereses humanos, y estos impactos dependen de un sinnúmero de factores que varían en función de los organismos involucrados, el tiempo, y el espacio. Cuando los impactos son claramente negativos, ambas pueden requerir acciones de control o erradicación, independientemente de su origen.

1. Introduction

Each of the plant and animal species described on Planet Earth (around 1.5 million, although actual numbers are likely much higher, with some estimates reaching approximately 10 million; Mora et al. 2011) has a unique geographic origin. By definition, the same species could not have originated in two or more different locations. Each of these species is not a static entity, as it changes in time and space. Initially, its population normally expands its distribution, but eventually the range can shrink, move elsewhere, or disappear altogether. If **the same** species inhabits sites A and B, either contiguous or spatially separated, its origin may have been in one of them, and its presence at the other may be the result of the expansion of its geographic range (Fig. 1). In other words, the species can only first evolve in

one particular location, although that location may not be easy to determine. It is also possible that the species may have originated somewhere else, and then it may have expanded its range to another site, before becoming extinct in the initial site where it had originated. This is what often makes it hard to determine where species may have originated.

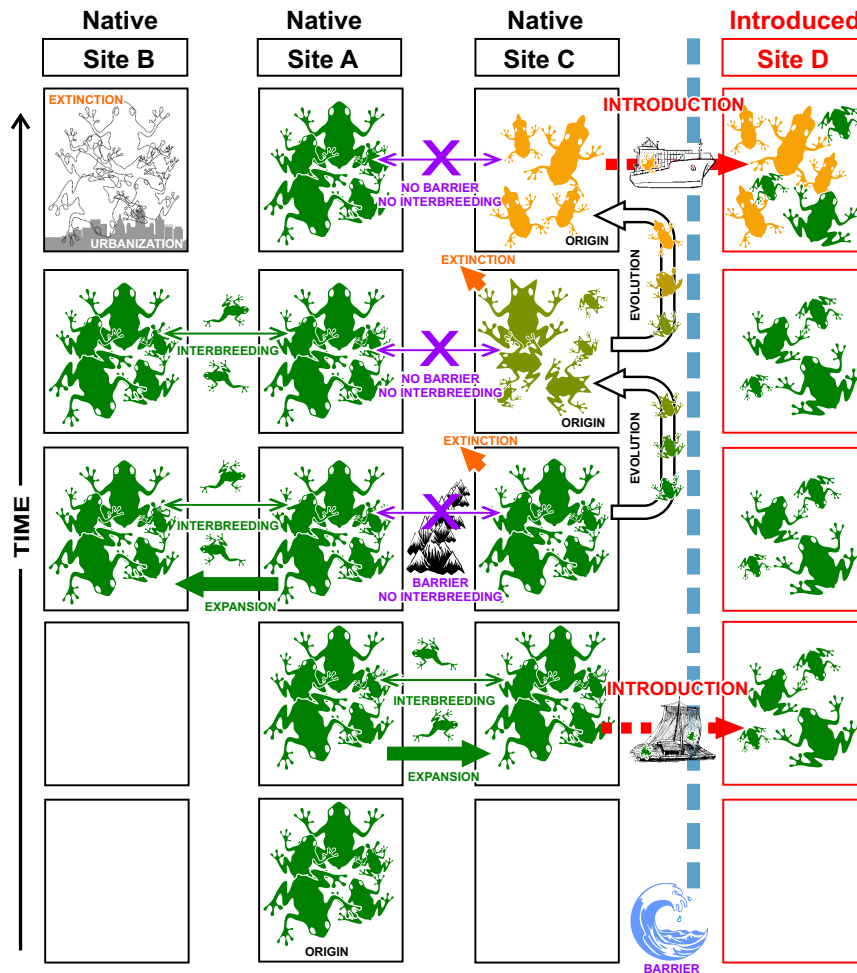


Fig. 1. Simplified scheme of the origin, dispersal, evolution, and introduction of a biological species.

Origination of new species can respond to numerous mechanisms, but the most common is geographic isolation which involves allopatric speciation (although sympatric speciation is also probably common: Dieckmann and Doebeli, 1999), which involves the emergence of a barrier (for example, a mountain chain) that splits a population (i.e., a group of individuals of the same species inhabiting the same area) so that members of the two sub-populations cannot come in contact and reproduce with those of the other. Over time (thousands to millions of years) both sub-populations evolve separately, and eventually even if the barrier disappears, they become unable to interbreed (Fig. 1).

During the geological history of our planet, major changes in the areas occupied by different species occurred many times. Range expansions were achieved using their own dispersal capabilities (flying, swimming, walking), through the action of natural phenomena (the wind that carries plant spores and seeds, river and ocean currents), or taking advantage of the dispersal capabilities of organisms they interacted with (for example, parasites, or seeds dispersed with the feces of animals that feed on them, plant seeds and small invertebrates which travel on the muddy feet of birds, etc.). On the other hand, changes in the geography and climate of the Earth (creation/disappearance or movements of continents and islands, sea-level changes, glaciations, orogenic and volcanic events, etc.) changed pre-existing boundaries and geographic connections (such as land bridges or links between oceans and seas) precluding or facilitating the dispersal of species (Stigall 2019), and engendering massive extinctions and compositional turnovers of plant and animal species (Barnosky et al. 2011).

In prehistoric times, humans contributed to these displacements by carrying around plants and animals used for fulfilling their needs (for instance, cultivated plants, domesticated animals, and wild animals kept as pets), as well as, involuntarily, many other organisms associated with humans and their belongings (parasites, commensals, plant seeds on clothing, pathogens, etc.). Because these human migrations were relatively slow, gradual and perhaps geographically more limited than in modern times, their effects on plant and animal range expansions were also thought to be rather limited. However, the effects of ancient human populations of hunters and gatherers on the distributions and associations of various other species are probably underestimated. For example, there is good evidence that humans played an important role in the extinction of the megafauna (large animals) on several continents – particularly in Australia and the Americas, as well as on the extinction of numerous island species, thousands of years ago, well before the arrival of the first European explorers (Martin 1984; Kirch 2002; Koch and Barnosky 2006; Ponting 2007). At the same time, prehistoric people had a significant impact in modifying environments previously believed to be “pristine”, such as the Amazon rainforest (Heckenberger et al. 2008), and were instrumental in changing the species compositions of these environments well before recorded history. Because these events occurred long ago, and were usually not documented, there may be a tendency to overlook, or minimize, the extent of the changes brought by prehistoric human populations to the distributions of various animals and plants around the world. The Polynesians, for example, colonized many islands in the Pacific Ocean, starting about 2,500 years ago, and brought with them several species of plants and animals, including the Polynesian or Pacific rat (*Rattus exulans*) – a species originally from Southeast Asia, which subsequently became established on some of these islands and contributed to major ecological changes there (Ponting 2007; Pascal 2011).



Fig. 2. Exchange of organisms (cultivated plants, domesticated animals, pathogens) between Eurasia and the Americas as a result of the European colonization of the New World.

Toward the XV century, technological advances allowed for larger and more frequent transoceanic voyages, especially between Eurasia and the Americas. With the European colonization of the Americas a large number of plants and animals used by humankind were transported across the ocean and introduced in territories which they could not have reached otherwise (Fig. 2). This process was called the “*Columbian Exchange*” (Nunn and Qian 2010), affecting both America and Eurasia. Cultivated plants, like potatoes, mandioca, peppers, sweet potatoes, corn, tomatoes, pineapples, natural rubber, tobacco, previously unknown in the Old World, were imported from the Americas. In exchange, from Eurasia colonizers brought to the Americas, a variety of commercially valuable plant species, including, among others, coffee, sugar cane, rice, wheat, barley, apples, citrus, grapes, bananas, and most domesticated animals, including horses, pigs, sheep, goats, chicken, and cattle (Fig. 2). These interchanges had positive effects for human welfare on both continents, but they also involved the exchange of pathogens previously absent on either side. From this perspective, American indigenous peoples suffered the most. European colonizers introduced many infectious diseases in the New World, including smallpox, measles, chickenpox, typhoid fever, malaria, bubonic plague and cholera, all of which decimated Native American populations severely (according to some estimates, up to 80-90% of the Native Americans were killed by these diseases) (Fig. 2). On the other hand, Eurasians received syphilis from the New World, but also the only known remedy for malaria at the time: quinine.

As opposed to species that migrated to new habitats using their own means or other processes unassociated with human activities, those transported by man are known as introduced species (IS). That is, species

that with the direct or indirect aid of humans succeeded in bridging otherwise presumably unsurmountable barriers (Fig. 3). It should be mentioned that this rather simple concept does not take into account the many definitions proposed for IS, many of which take other factors into account, such as the distance to the closest native site, or the requirement that in the introduced range the species can survive without human assistance, or the timing of the introduction, or the behavior of its prey, among others (Richardson et al. 2000; Carthey and Banks 2012; Essl et al. 2018).

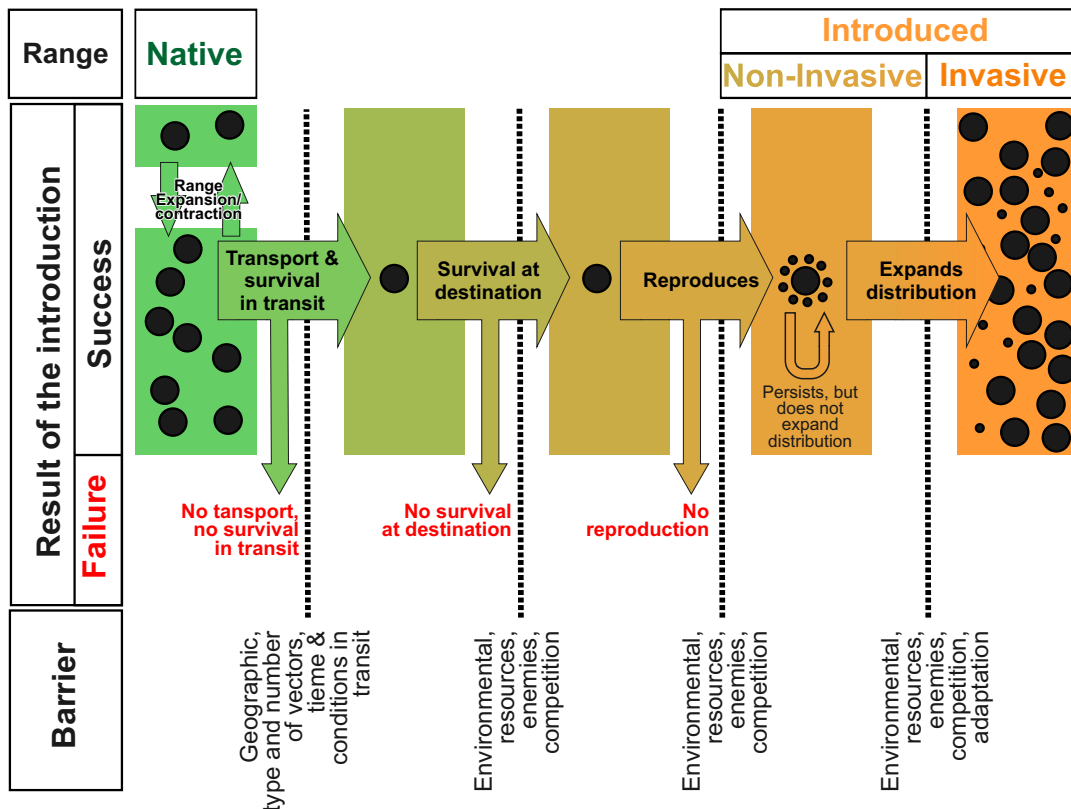


Fig. 3. Scheme of the phases of a biological introduction and the barriers involved in the process.

Concern about human-assisted species introductions and range expansions fostered the development of a discipline known as Invasion Biology. Its central goals are the investigation of species traits that favor their dispersal and establishment with the aid of man, the traits of communities and ecosystems that make them more receptive to IS, the mechanisms that explain the responses observed, the ways in which IS adjust to, and interact with, their new environments, and the impacts of biological introductions on the ecology of the invaded systems, and on human interests. All of the above, in turn, are linked to analyses of strategies related to the eradication and control of IS (Clout and Williams 2009; Keller et al. 2009; Wilcox and Turpin 2009).

2. The beginnings

Although the cornerstone of the studies of biological invasions is widely considered to be the book by the British ecologist Charles S. Elton, “*The ecology of invasions by animals and plants*”, published in London in 1958 (Elton 1958) (Fig. 4), there are many occasional published references to IS since at least the XVIII century. Some of these are related to the search for economically important species, such as the plants surveyed by Pehr Kalm, a disciple of Carl Linnaeus, in North America, where he recorded many plants and animals of European origin, including, for example, the common dandelion (*Taraxacum officinale*), which was growing abundantly in French Canada when Kalm visited the area in 1749 (Kalm 1771). Other such observations were reported by famous naturalists, such as Charles Darwin and Alexander von Humboldt, who recorded many redistributions of organisms by human activities around the world. Darwin, for instance, discussed plant species introduced by people in his seminal book “*On the origin of species*”, which was published in 1859 (Darwin 1859).

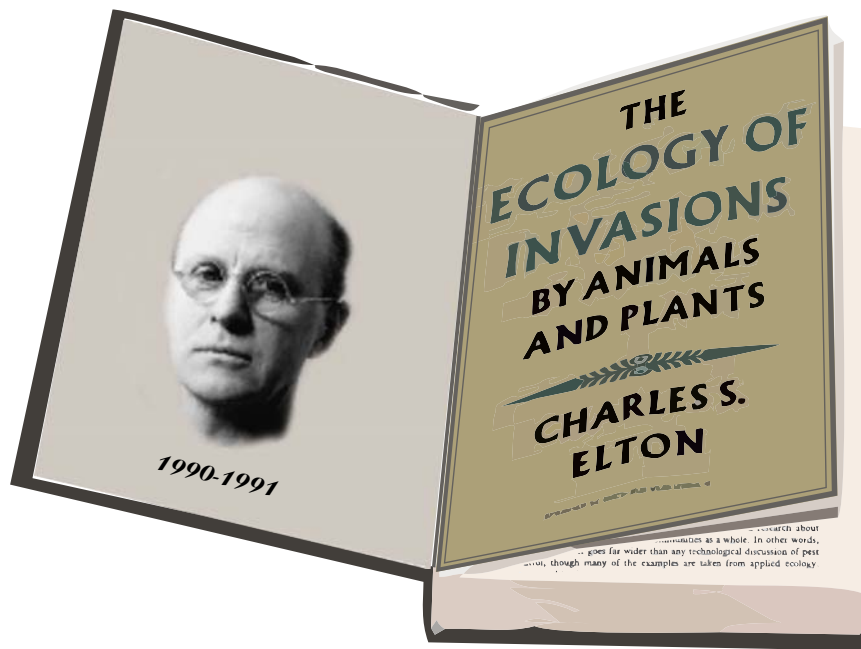


Fig. 4. Charles Sutherland Elton (1900–1991), the British ecologist that pioneered the study of biological invasions, and the cover of his seminal book, published in 1958.

However, it was Charles Elton (Fig. 4) who, for the first time, gathered in a single volume centered specifically on IS a large part of the existing knowledge on this phenomenon, and included his own observations and interpretations of the process of human-assisted species introductions itself and its consequences. His work includes many documented examples of biological introductions around the world, their impacts on nature and on

human welfare (almost exclusively focusing on the negative ones), and the strategies of prevention, mitigation and control attempted with and without success. The book also contains Elton's general thoughts about the need to maintain the pristine state of ecosystems, and anecdotal but illustrative remarks. For example, he describes how the entomologist J. G. Myers, in his 1929 voyage on the cargo ship *Rangoon*, from Trinidad to Manila, entertained himself recording the animals present on board, which totaled 41 stowaway species, including the red flour beetle (*Tribolium castaneum*), a worldwide pest of stored food grains. In his analyses of commercial marine transportation as a vector of introductions, Elton mentions the chart known as document B.R.84 in the archives of the British Admiralty. This chart (not included in the book), shows the positions of the 2314 British vessels on 7 March 1936 (Fig. 5). This figure is impressive for revealing the intensity of marine traffic almost a century ago.

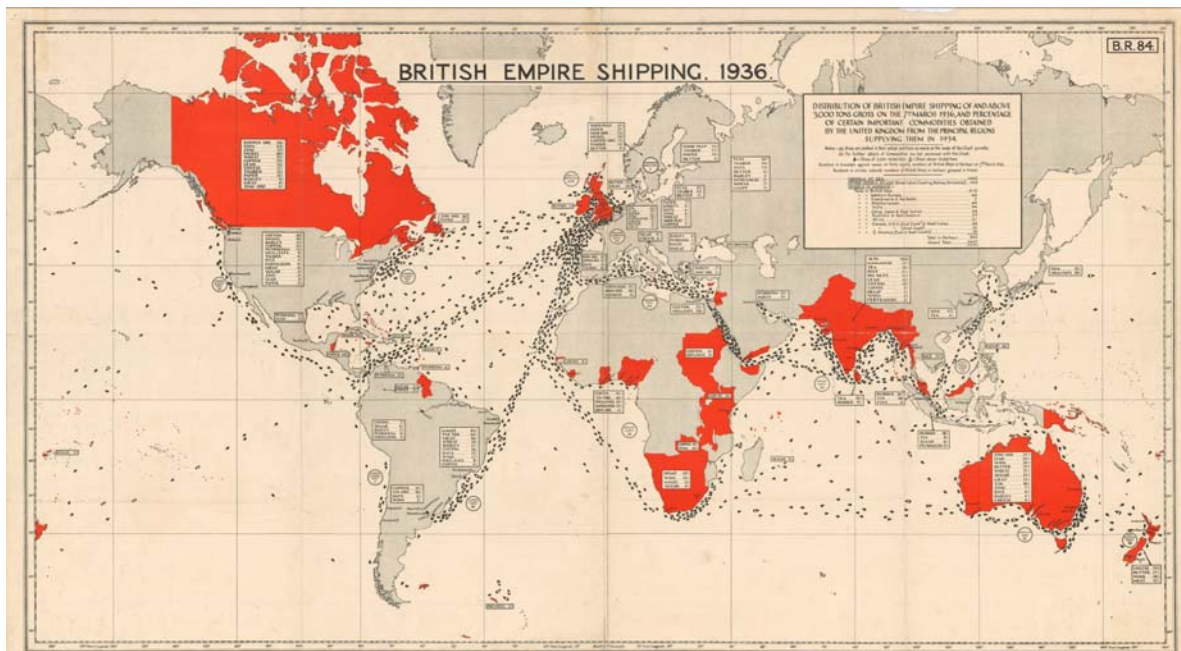


Fig. 5. Chart produced by the British Admiralty showing the position of the 2314 British ships over 3000 tons (852 of them in ports) on 7 March 1936. Red denotes British Empire possessions. At the time, British ships accounted for around 50% of the world total. Presently, the number of commercial vessels in the world is around 50 000. From Chew (2014).

Elton was strongly conservationist, and watched with dismay how the native flora and fauna were “contaminated”, in his opinion, with alien organisms. His views on human-mediated dispersals of species are vividly summarized in the phrase “*No one really knows how many species have been spreading from their natural homes, but it must be tens of thousands, and of these some thousands have made a noticeable impact on human life: that is, they have caused the loss of life, or made it more expensive to live.*” His opinion on introductions in insular areas, more isolated and presumably more vulnerable, was even more pessimistic: “*The fate of remote islands is rather*

melancholy... The reconstitution of their vegetation and fauna into a balanced network of species will take a great many years.”

Elton’s book, cited in thousands of publications (Fig. 6), is undoubtedly an influential work, but it is also clearly biased and tends to focus on the IS that turned out to be more successful, and often more harmful, in the world. The title he chose for this pioneering work is also partly responsible for the fact that the field focused on the ecology of IS is presently known as “Invasion Biology”, a name with clearly negative and militaristic connotations. Alternative names, such as SPRED (SPecies REDistribution) Ecology (Davis 2009), have been proposed in an attempt to avoid such *a priori* biases, but the catchy and now deeply entrenched “Invasion” term (sometimes more precise, but also often more convenient) turned out to be more appealing for most scholars in this field.

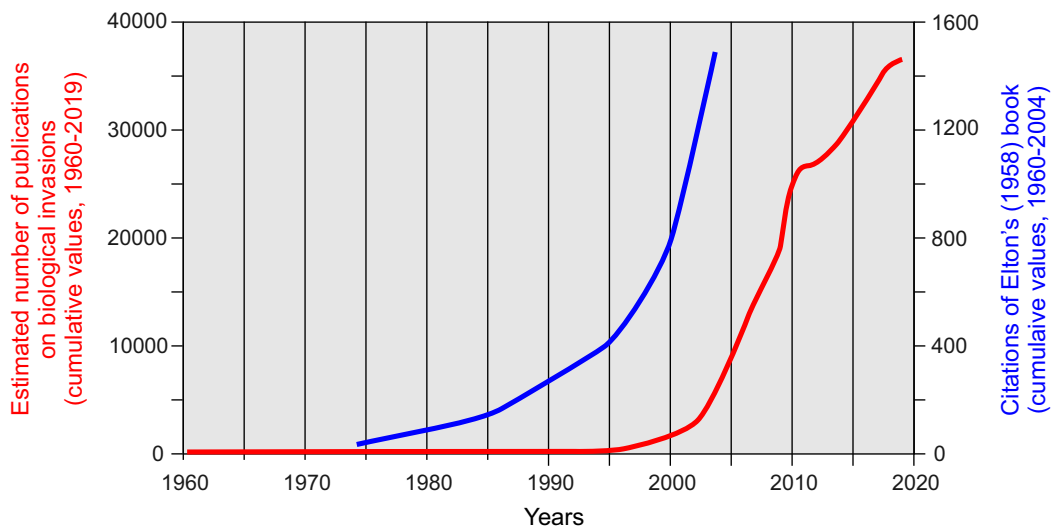


Fig. 6. Growth in the number of publications on biological invasions between 1960 and 2019, and number of citations to Elton’s (1958) book, between 1960 and 2004. Elton’s citations from Richardson and Pysek (2008).

Elton’s work had little impact until the 1990s, when interest in invasion biology started growing exponentially (Ricciardi and MacIsaac 2008; Richardson and Pysek 2008). This delay was due, at least in part, to the fact that some of the most spectacular and most damaging biological invasions were recorded in the 1980s and 1990s. Among these was the establishment of the Nile perch (*Lates niloticus*) in Lake Victoria (Africa), the alga *Caulerpa* spp. in the Mediterranean and elsewhere, and the Eurasian zebra mussel (*Dreissena polymorpha*) in North America (Rilov and Crooks 2009; Nalepa and Schloesser 2014; Canning-Clode 2015; Dudgeon 2020).

3. The pathways

The introduction vectors for IS are numerous, but two main different mechanisms can be identified: deliberate introductions and accidental introductions, although differences between the two are often imprecise and difficult to assess (Essl et al. 2018), and many species have been introduced both intentionally and accidentally (Turbelin et al. 2017). Among the deliberate or intentional ones of the last ~200 years are many of those carried out between the XIX and the middle XX centuries. The most frequent were ornamental plants, pets (mainly fishes, reptiles, birds, and mammals), as well as a number of wild animals released in various habitats.

Argentina hosts over 800 IS, with many examples of plants and animals introduced deliberately in the XIX and XX centuries. Many have adapted to the local conditions and are presently part of the local ecosystems and are interacting with native plants and animals over large areas. Several widespread plants were brought from Europe and Asia, including the silver poplar, thistle, privet, honeysuckle, nettle, white cedar, sweetbriar rose, Aleppo sorghum, blackberry, and many others. From North America several pine species were introduced, and the eucalyptus tree was brought from Australia. Among the introduced animals some of the most notorious are the common carp, red deer, wild boar, European hare, trout and salmon, mink, bees, etc. (Fig. 7; Correa and Boltovskoy 1998; Penchaszadeh 2005; Chebez and Rodríguez 2014; Schwindt et al. 2020).

Throughout the world, terrestrial plants used in horticulture are dominant among the deliberate introductions (Turbelin et al. 2017). Accidental introductions are associated with the movement of people, and the transport of live plants and animals, and goods and their packaging. Aquatic organisms are chiefly dispersed by ballast water and hull fouling. Ballast water is taken onboard in special compartments - the ballast water tanks, in order to compensate for the weight of cargo and fuel, enhance stability and maneuverability in transit, and mitigate vibrations. An unloaded ship typically compensates for its low weight by filling the ballast water tanks in the port of departure and emptying them in the port or ports where cargo is loaded (bulk, containers, liquids, etc.). Around 10 billion tons of ballast water per year are discharged in areas away from their origin, transporting ca. 40 thousand species per day (David and Gollasch 2015). Most of these species die during transport, and many cannot survive where released. Some, however, survive the voyage (either as adults, or in their larval or reproductive stages, like spores, seeds or cysts), and if the new site is favorable, get established (Fig. 3).

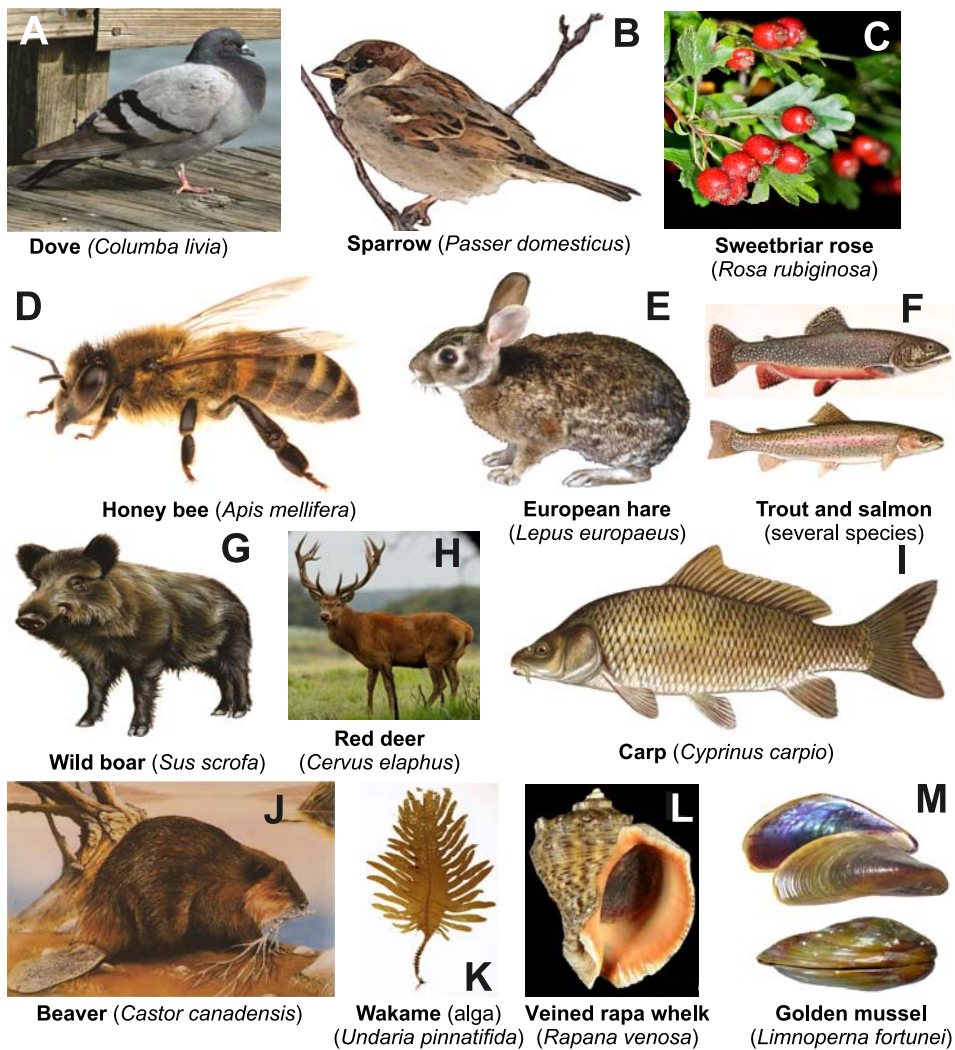


Fig. 7. Some species introduced in Argentina in the XIX and XX centuries. Most are deliberate introductions, except for the last three (wakame, veined rapa whelk, and golden mussel).

Sources: A: <https://allaves.ru/>; B: <https://www.pinterest.it/pin/253749760239560261/>; C: <https://zoom50.wordpress.com/2010/11/18/rosa-mosquetarosehip/>; D: <http://www.conap.coop.br/2016/01/15/agrotoxicos-estao-matando-as-abelhas/>; E: <https://commons.wikimedia.org/wiki/File:Liebre.png>; F: <https://www.mymotherlode.com/wp-content/uploads/2020/04/trout.jpg>; G: <http://www.farcaza.es/descargas>; H: <http://www.argentinahuntingandfishing.com/es/actividades.html>; I: <https://www.fishidy.com/resources/species/54e359a10d539d16d488ee44>; J: <https://hipwallpaper.com/view/vQBA67>; K: <https://doris.ffessm.fr/Especies/Undaria-pinnatifida-Wakame-1616>; L: http://www.gastropods.com/1/Shell_1631.shtml; http://www.gastropods.com/1/Shell_1631.shtml; M: Original.

4. Temporal evolution and geographic distribution of biological invasions

Cultivated plants and domesticated animals are but a few early examples of biological introductions. The rate of introductions has been

growing, especially since the middle XIX century, fostered by the increasing human mobility and commercial exchange. Recent estimates (Seebens et al. 2017) suggest that, in spite of the many regulations and management initiatives at the national, regional and international levels, the trend is far from decreasing, although patterns differ widely between organisms. For example, mammal introductions have dropped noticeably since the middle XIX century, but introductions of algae, insects, molluscs, crustaceans and other invertebrates keep rising (Fig. 8).

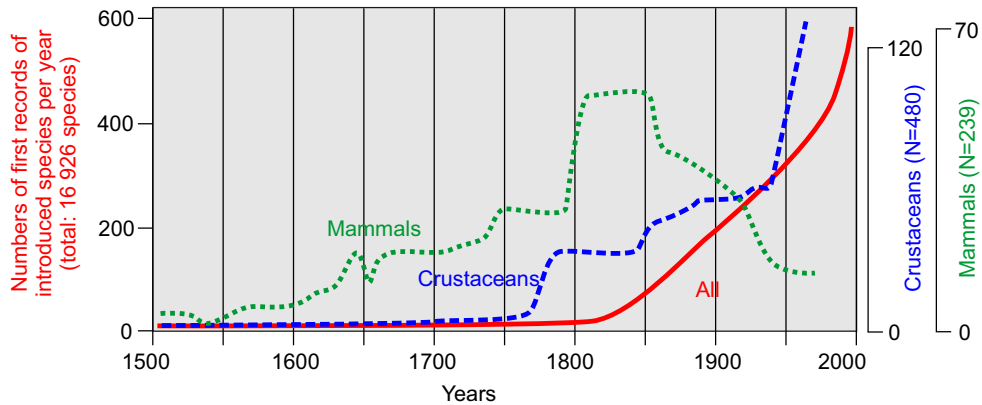


Fig. 8. Growth in the numbers of introduced species around the world between 1500 and ~2000, based on an overall total of 16926 species, and contrasts between some selected groups. From data in Seebens et al. (2016).

According to Turbelin et al. (2017), of the 1517 world IS recorded in the *Global Invasive Species Database* and the *CABI Invasive Species Compendium*, 39% were introduced intentionally only, 26% accidentally only, 22% both ways, and for 13% information is missing. Terrestrial plants account for over half of the introductions, followed by arthropods and other organisms (Fig. 9). The countries with the highest numbers of IS are the USA, Australia, New Zealand and South Africa. Argentina and Brazil have medium-high numbers, along with most of Europe, China and India. Lowest values are those in African and Arab countries, as well as some in Asia (Fig. 10). Of course, determining and comparing the numbers of species introductions in various regions are also dependent on the extent of the research efforts and resources spent looking for, and documenting, such introductions in different jurisdictions. Obviously, the more researchers are focusing on introduced species, the more such species they are likely to be found, so, to some extent, the growing number of species perceived as introduced may be a function of the rise of Invasion Biology.

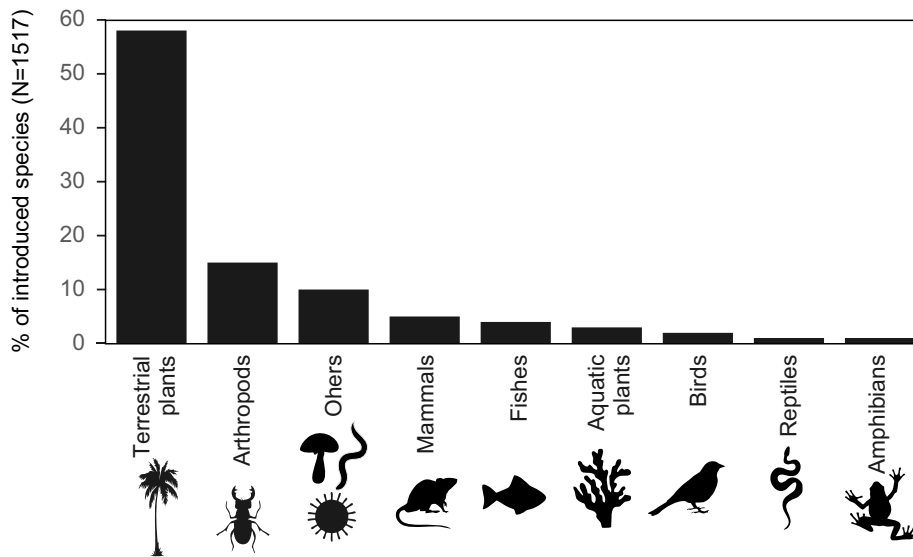


Fig. 9. Proportions of various introduced plant and animal groups worldwide, based on a total of 1517 introduced species recorded in the Global Invasive Species Database and the CABI Invasive Species Compendium, in the 143 countries included in the survey. “Others” includes algae, annelids, turbellarians, fungi, microorganisms (including virus), molluscs, nematodes, and parasites. Notice that the total number of introduced species is less than 10% of those identified by Seebens et al. (2016) (Fig. 8). From data in Turbelin et al. (2017).

An interesting outcome of this work (Turbelin et al. 2017) is the balance between the number of IS that each country spread to others and the number of IS it received. These numbers show that, again, the USA, Australia and New Zealand were affected the most, having received more IS than those they were donors of. At the other end are some Latin American countries, most of northern Africa and eastern Eurasia. Although these results are based on a small subset of species (less than 10% of the ~17 thousands identified by Seebens et al. (2017), they agree well with the magnitude of commerce and travel between countries in the world (Vilà and Pujadas 2001; Levine and D'Antonio 2003).

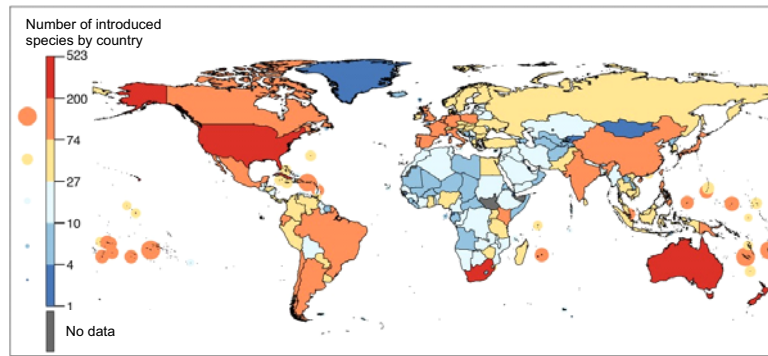


Fig. 10. Number of introduced species by country (based on a total of 1517 species recorded in the Global Invasive Species Database and the CABI Invasive Species Compendium). From Turbelin et al. (2017).

5. Competitive advantages of introduced species: the hypotheses

Invasion biology took off as a specific ecological discipline at the end of the 1980s, and since then the number of investigations grew exponentially. In 1990 the number of publications on IS was around 130. In 2019 it reached over 4000, accumulating an overall total (1962-2020) of over 40 thousand papers in research journals and several tens of books (Ricciardi and MacIsaac 2008; Richardson and Pysek 2008; Boltovskoy et al. 2018).

These efforts allowed detailed analyses of thousands of case studies and, as in other areas of science, fostered the search for general rules aimed at explaining how and why IS succeed in outcompeting the natives (when they do so), and attempts at quantifying their impacts in ecological and economic terms. As a result, many hypotheses were proposed, some conceptually interesting, some truistic, and many redundant, overlapping and even contradictory (Richardson and Pysek 2008). These hypotheses include both assessments of community traits that make them more receptive to IS, and species traits that contribute to their invasive success, as well as impacts of IS on resident communities (Jeschke and Heger 2018). Enders and Jeschke (2018) attempted a systematic summary of these hypotheses based on five categories of intervening factors: time since introduction, human disturbances, properties of the system invaded, biotic interactions, and traits of the IS. The most widely discussed are the following:

Propagule pressure. Successful introductions are a function of the number of transport and release events, as well as the number of individuals involved in each event. While this hypothesis was discussed in hundreds of publications (Cassey et al. 2018), conceptually it is a null hypothesis (Colautti et al. 2006b), insofar as its fulfillment is embedded in its premise, regardless of other conditions. Indeed, unless the introduction is absolutely unfeasible

(e.g., elephants in the Antarctic), it is obvious that large numbers of individuals and many attempts at introducing an alien species are more likely to end up in success than few attempts and few individuals. A single shot at the target has fewer chances of hitting the center than 100 shots.

Evolution of increased competitive ability (or EICA) posits that, after having been released from natural enemies, IS change genetically investing more energy in growth and/or reproduction, thus making them more competitive (Blossey and Nötzold 1995).

Enemy release. In the areas colonized, IS are free from the competition or predation pressure of the enemies they co-evolved with (Keane and Crawley 2002).

Prey naïveté. Due to lack of co-evolutionary history, native prey organisms do not recognize the introduced predator as dangerous, and are therefore more vulnerable (Cox and Lima 2006). However, the opposite - and contradictory - situation is as likely as the former: the introduced predator does not recognize native prey as a potential food resource (predator naïveté: Howard et al. 2017).

Vacant niche and biotic resistance (or diversity vs. invasibility) posits that in diverse communities ecological niches (or functional positions) are more saturated, vacant niches to accommodate new species are scarcer, and therefore they are less vulnerable to introductions than low-diversity communities (MacArthur 1970). However, it has also been argued that higher diversity is the result of more previous colonization events, and therefore might be associated with a higher receptivity to IS.

Invasional meltdown. The theory behind this catchy term is that past introductions favor subsequent ones (Simberloff and Von Holle 1999). Testing this hypothesis is equivocal, because high numbers of IS might effectively be due to invasional meltdown, or to the fact that the community under scrutiny is inherently more receptive to IS (Mizrahi et al. 2017).

Disturbance. IS are more successful in disturbed systems (e.g., pollution, urbanization, grazing by cattle, fire), than in intact ones (Elton 1958). However, the association of most disturbances with human presence complicates disentangling the effects of the disturbance itself from those of the enhancement of accidental or deliberate transport and release due to human presence.

Trophic relationships. Since trophic interactions are among the most important between organisms, it has been proposed that IS of low trophic levels (i.e., those that are consumed by others, like plants) should generally have positive effects because they broaden the spectrum of resources, whereas

consumer IS should generally have the opposite effect, decreasing the abundance and diversity of the natives (Thomsen et al. 2014).

These hypotheses are but a small sample, probably the most often discussed, of the 30-35 proposed in the last decades (Jeschke and Heger 2018; Crystal-Ornelas and Lockwood 2020a). Enders et al. (2018) carried out an interesting experiment through an online survey of 357 experts in invasion biology in order to assess the degree of knowledge, overlapping, and acceptance of 33 invasion biology hypotheses. Their conclusion was that the resulting network of similarities between hypotheses was random, indicating that specialists have little understanding of and consensus on of how these hypotheses are related to each other. On the other hand, there was a statistically significant coincidence in the support for four of the 33 hypotheses (enemy release, propagule pressure, disturbance, and vacant niche).

The growth in the number of surveys in all the fields of knowledge called for the need and allowed the implementation of reviews and meta-analyses. Meta-analyses consist in the extraction of results from different sources and their statistical evaluation based on a common indicator, usually the effect size (Gurevitch et al. 2018). In principle, meta-analyses have the advantage of avoiding the subjectivity that can bias the less methodologically strict approaches of narrative reviews.

A survey of 72 meta-analyses on biological invasions in aquatic and terrestrial habitats based on 4822 primary sources included an estimate of the support for several major hypotheses (Boltovskoy et al. 2020). The assumption that IS have or acquire superior competitive abilities (EICA) was confirmed by 4 meta-analyses, but rejected by 6, and 5 arrived at mixed or inconclusive results. The enemy release hypothesis was found to play a major role in 3 meta-analyses, but was rejected by 5, and 2 found inconclusive support. Prey naïveté was confirmed in one meta-analysis, and partially supported by one, but rejected by 2. The vacant niche hypothesis was supported by 3 meta-analyses, but rejected by 2. Invasional meltdown was confirmed by 2 meta-analyses, rejected by 2, and one arrived at mixed results. The assumption that IS of low trophic levels have positive effects on the residents was confirmed in 3 surveys, and 2 found mixed evidence. However, the ensuing conclusion that introduced plants have more positive (and less negative) effects on native animals than on native plants did not hold across studies. One of the most widely held notions is that the impacts of IS are significantly stronger on islands than in continents. Of the 4 meta-analyses that addressed this issue explicitly, only one supported it.

Among the 30+ hypotheses proposed some are likely “*zombie ideas*” (Fox 2011), that survive in spite of their lack of logic and empirical support due their apparent theoretical elegance and pervasive repetition. Others have

reasonable conceptual grounds and at least some empirical support. However, although one should not expect that any one explanation will fit all invasions (Catford et al. 2009; Ricciardi et al. 2013), these discrepancies with respect to basic tenets of the theory of biological invasions are discouraging (Moles et al. 2012). Most studies are at least as likely to reject as to support these popular invasion biology hypotheses. Moreover, support for these hypotheses has been declining over time (Jeschke et al. 2012), which may be partly explained by the underpublication of null results in the early years after a hypothesis is proposed (Mueck 2013), and especially by the fact that the growth of empirical knowledge leads to a growing recognition of complexity and ambiguity (Davis and Chew 2017), defying the strict bounds imposed by these attempts at establishing universal cause-effect relationships (Hulme et al. 2013; Boltovskoy et al. 2020).

6. Native, introduced or invasive?

Our concept of harm or benefit associated with biological introductions is tightly intertwined with personal outlooks on the issue of conservation which, in turn, are based on the value we assign to an ideal original or pristine state. However, this pristine state has many shades which often make it an equivocal notion (Hobbs et al. 2009; Pereyra 2016; Jernelöv 2017; Orth et al. 2020; Pereyra 2020). Cassini (2020) proposed an interesting discussion of the ethical and cultural implications of idealizing native species suggesting that, for many conservationists, native flora and fauna represent the natural, correct, acceptable and positive situation, and therefore are worth maintaining, as opposed to IS, which are unnatural and undesirable (Brown and Sax 2004; Davis et al. 2011; Wallach et al. 2020).

However, even the distinction between native and introduced species is ambiguous. For example, there is no consensus on the length of time after introduction during which a species remains alien, or whether there is a time limit at all. Humans have been moving species around since prehistoric times (50-60 thousand years); should those species still be considered introduced today? In the British Isles over 150 plants introduced between 500 and 6000 years ago have been identified (Preston et al. 2004); scientists still disagree on whether these species should be considered native or introduced (Willis and Birks 2006).

Many plants and animals evolved in an area, dispersed elsewhere, went extinct in their original range, and were re-inserted in it by man; are they introduced? What is the status of the species moved between America and Eurasia five centuries ago? Will they be considered introduced forever? (Jernelöv 2017). Native prey animals have been shown to evolve introduced predator-avoiding adaptations (Carthey and Banks 2012); thus

circumventing one of main hypotheses of invasion biology - the “Prey naïveté” principle (see above). Many plants and animals changed their distributional ranges (in terms of latitude and/or altitude) in response to (human-driven) climate changes (Sorte et al. 2010; Webber and Scott 2012; Lenoir and Svenning 2015); are they introduced in their new ranges? (Gilroy et al. 2016). Most studies that compared the effects of IS with those of these range shifters concluded that both have similar effects on the newly colonized areas (Sorte et al. 2010; Hoffmann and Courchamp 2016; Nackley et al. 2017). However, because range shifts in response to climate changes ensure the survival of the species involved, it has been suggested that they should not be labeled as undesirable (Davis and Watson 2018), and even that these displacements should be aided by man (Hoegh-Guldberg et al. 2008).

A pervasive problem, especially in areas with scarce information, is whether a newly recorded species is truly introduced, or if it was overlooked in earlier surveys due to the paucity of data or to the absence of historical information (Bortolus et al. 2015; Guiaşu and Labib 2021). Although these doubtful records are usually labeled as cryptogenic (uncertain origin), considering them as introduced is currently perceived as a more important finding and, therefore, with better chances of being published. The new record that 20 years ago could have been entitled “New record of *Protozoa sconosciutta* in...”, today appears under the title “The invasive species *Protozoa sconosciutta* and its potential impacts on...”.

With the aim of solving these problems and improving communication, several scholars tried to address these ambiguities and disagreements in the terminology used in the discipline by proposing a unified language (Richardson et al. 2000; Colautti and MacIsaac 2004; Davis 2009). However, their success has been very limited (Sagoff 2018), and they were strongly criticized (Larson 2007; Hodges 2008). Discrepancies are not restricted to the concepts of “native” vs. “introduced”. The terms “introduced” and “invasive”, which (as they suggest) should define different situations, are often used interchangeably. In spite of the fact that “invasive” is a value-laden term with clear negative connotations, it dominates not only scientific reports (Pereyra 2016), but also documents issued by international organizations that include the notion of harmful impact in their statements on IS (IUCN 2018; Soorae 2018).

7. Problems associated with biological invasions

There is no doubt that the impacts of some IS are extremely harmful for the environment, many native species, and for human interests. Many pests of cultivated and human and animal pathogens are clear examples of major damage. Introduced pathogens can parasitize humans and their vectors can

spread diseases, ruin crops, decimate domesticated animals, and strongly impact human resources (food, water, etc.; Sumner 2003; Davis 2009; Keller et al. 2009; Simberloff and Rejmanek 2011).

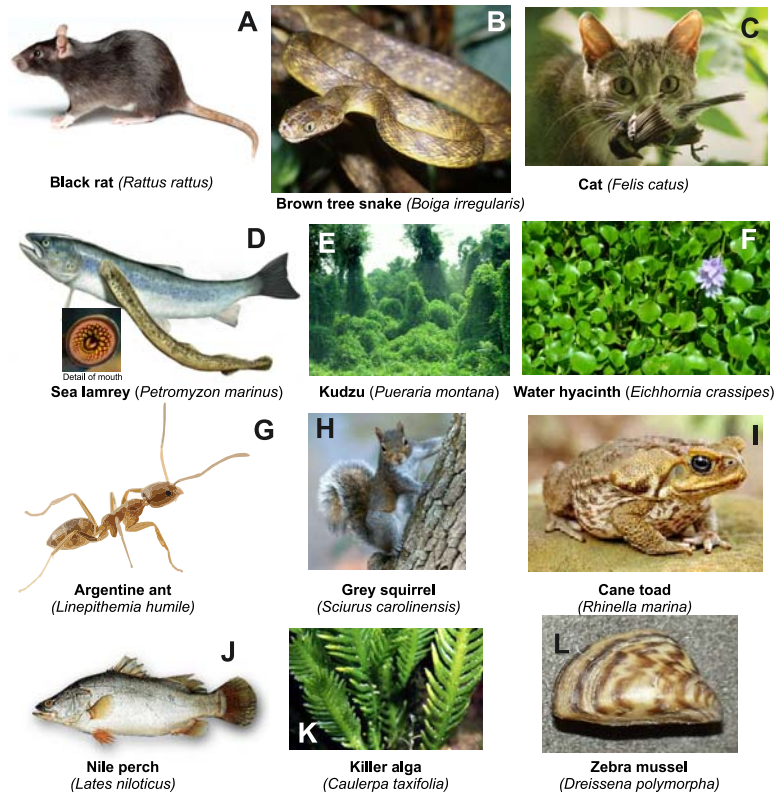


Fig. 11. Some iconic invasive species that had important impacts around the world. From various sources.

The black rat (*Rattus rattus*, Fig. 11A), a native of Southeast Asia, is one of the best known and frequently mentioned examples. Its worldwide dispersal started before the Roman Empire through shipping and overland trading and military campaigns, and presently the rodent is present in all continents. The rat transmits numerous infectious diseases, and is a pest of many human resources (Nentwig 2008). On some islands, rats (along with feral cats, dogs, and pigs) have extirpated many native species, in particular birds (Drake and Hunt 2009; Doherty et al. 2016).

The brown tree snake *Boiga irregularis* (Fig. 11B), a native of New Guinea, invaded the island of Guam around 1945-1950. Guam lacked animals large enough to feed on the snake, but had many native birds and mammals. Towards 1970, practically all native Guam birds and bats had been eliminated by the snake (Fritts and Rodda 1998). However, because the brown tree snake population on Guam has exceeded the carrying capacity of the island, its densities are currently declining as a result of depleted food resources, adult mortality, and/or suppressed reproduction (Mortensen and Dupont 2008).

Since the early XIX century, in order to allow sea-going merchant vessels to operate in the Great Lakes of North America (USA- Canada), a complex system of canals started being built linking the lakes with the North Atlantic Ocean. By bypassing the Niagara Falls, these canals provided an entry route to a parasitic fish, the sea lamprey *Petromyzon marinus* (Fig. 11D), which feeds on other fish. The lamprey thrived in the lakes decimating several local fishes of major economic value. By 1960, fish landings dropped by 98%, collapsing the local fishery. In subsequent years the fishery was restored, yet at the expense of several costly management actions which require permanent investment (Keller et al. 2015).

The vine kudzu (*Pueraria* sp., Fig. 11E) was deliberately introduced in the USA from Japan in 1876, primarily with the purpose of mitigating soil erosion. Although initially its cultivation was encouraged, and it effectively did mitigate erosion, as well as proved to serve as fodder, fertilizer, cosmetics, and some other uses, it dispersed uncontrollably covering 30 thousand km² throughout 12 states. In 1970 the US Department of Agriculture included kudzu in its list of weeds, and in 1977 in the list of noxious weeds. The vine climbs rapidly over grass, bushes and trees and smothers them by blocking sunlight, eventually killing them (Wilcox and Turpin 2009).

In Argentina, some IS have also had baneful impacts (Chebez and Rodríguez 2014; Schwindt et al. 2020) (Fig. 7), although not as devastating as the ones described above. In Patagonia, the sweetbriar rose outcompetes and displaces several native plants. The European hare and the red deer compete with cattle and sheep (which are also IS, of course) for food and favor soil erosion (as most introduced, economically valuable farm animals do). Trout and salmon impact native fish populations. The Asian carp feeds on native fish species and is a voracious omnivore that can deprive other freshwater organisms of food. In Tierra del Fuego, the beaver's dams flood large areas of native forest killing the trees (Lizarralde 2016). Negative impacts of some accidental introductions have also been reported. The marine macroalga wakame (*Undaria pinnatifida*) has been associated with a decrease in the abundance and diversity of native algae along the Patagonian coast (Casas et al. 2004), although subsequent studies noticed that it can significantly enhance the abundance and diversity of many invertebrates (Irigoyen et al. 2010). The veined rapa whelk (*Rapana venosa*) feeds on bivalves, including several commercially important species (Giberto et al. 2006). The golden mussel (*Limnoperna fortunei*) has mixed effects on the native biota (Fig. 12), but its impact on human activities is clearly negative, as its colonies clog water sieves and heat exchangers of industrial and power plants that use raw river, lake or reservoir water, as well as water-transfer canals and pipelines (Boltovskoy et al. 2015b).

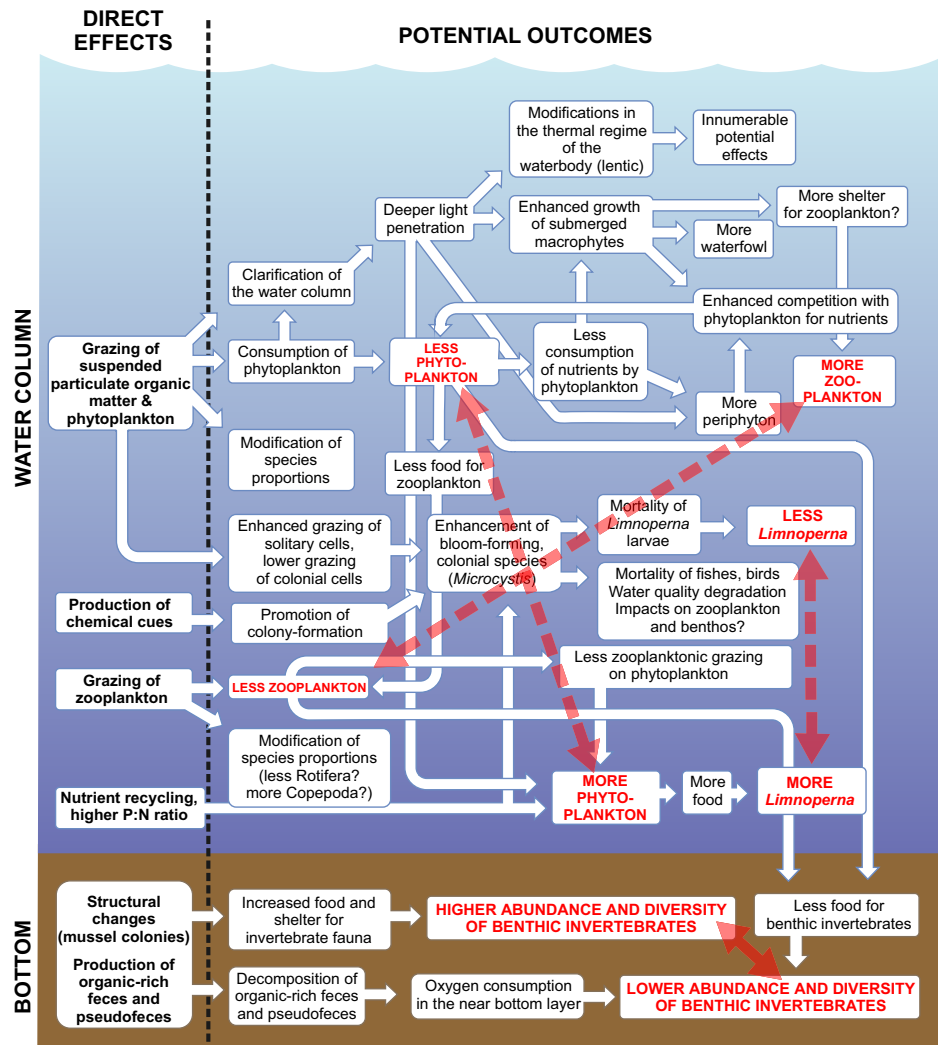


Fig. 12. Effects of *Limnoperna fortunei* on different freshwater communities and their potential outcomes. Red labels and the connecting dashed lines denote opposed impacts on the same component, which can occur simultaneously in the same waterbody, but their strength varies depending on the context. Modified from Boltovskoy et al. (2015a).

For introduced plants, most impacts are associated with the fact that they can outcompete native plants in the use of space, light, water and nutrients (Arceo-Gómez and Ashman 2016; Kuebbing and Nuñez 2016; Golivets and Wallin 2018). This effect can cascade to native phytophagous animals by reducing their food availability, as well as native predators, by reducing native phytophagous prey (van Hengstum et al. 2014; Yoon and Read 2016). For introduced animals, the most salient examples are those of predators that can strongly affect, and even extirpate, some native organisms (Salo et al. 2007). Total elimination of natives has been recorded in some islands and freshwater bodies, but it is uncommon on continents and in the ocean (Davis 2009; Doherty et al. 2016).

It is important to point out that in many cases impacts are subtle and take place through indirect pathways. For example, some introduced plants can promote fires, or favor allergic reactions in humans (Potgieter et al. 2017), or affect insects and birds that use them, rather than native plants, for reproductive activities, but with lower survival rates, or negatively affecting various mutualistic relationships (Davis 2009). Hybridization with natives can produce sterile or less fit offspring (Cox 2002), but native-introduced hybrids more fit than their parents have also been described (Lockwood et al. 2007). In mammals, IS can produce major changes in the sex ratio of native species (Barrientos 2015).

One of the widely held notions is that IS can negatively impact global biodiversity. At the local and regional scales IS can contribute to the roster of species increasing diversity (Peoples et al. 2020), but at global scales they can decrease diversity. For example, in the USA, the between-states similarity in fish species composition increased significantly after the European colonization, although this change was largely driven by the introduction of several important sport fishing species, rather than by the extinction of native fishes (Davis 2009). However, this process can also involve the extinction of natives and endemics (and the corresponding gene pools), particularly on islands (Vizentin-Bugoni et al. 2019), or changes in dominance relationships between the natives (Muthukrishnan and Larkin 2020). At the global scale, this can produce a structure with a few “winners” very efficient at colonizing new habitats, and many “losers” that are displaced by the former, with the consequent homogenization and reduction of the global species pool (McKinney and Lockwood 1999; Rahel 2007). Although IS have been identified as responsible for this process in several surveys, the overall outcome has been questioned (Rosenzweig 2001), and it has been noticed to change with the spatial scale employed (Daga et al. 2020). Further, this seems particularly noticeable in human-disturbed areas (urbanization, forestation-deforestation, agriculture and cattle raising, eutrophication, connectivity), which complicates interpretations insofar as it is hard to sort out the effects of the IS from those of these other human disturbances. This ambiguity led to the development of the “driver or passenger” notion, which questions whether disturbances (mostly caused by humans) are at the cause of biological invasions, or if biological invasions themselves are the driver of community or ecosystem changes (MacDougall and Turkington 2005; Bauer 2011; Gioria and Osborne 2014).

In short, practically all scholars agree that certain IS can have major negative impacts on the systems colonized, including deleterious effects on human interests, global biodiversity, and ecosystem services (landscape and recreational aspects, resources, etc.), and also admit that some have positive effects (chiefly cultivated plants and domesticated animals, but also IS which participate in mutualistic relationships with native species, for example). However, the large majority of studies on IS focus on the baneful aspects

(Boltovskoy et al. 2020; Vimercati et al. 2020). Many publications on IS start with boilerplate statements like “ecosystems are dominated by introduced species, leading to loss of biodiversity and ecosystem function” (Davis 2009; Thompson 2014; Warren et al. 2017; Sagoff 2018), fueling an apocalyptic vision of the impacts of invasions (David et al. 2017).

This perception of the impacts of IS is also partially due to methodological issues. The research designs can focus on two questions with subtle, but important differences. The first approach, used by most studies, compares habitats without vs. habitats with IS: does the presence of the IS change significantly the variables measured (resident abundance, diversity, etc.) in the two habitats? Or, alternatively, with respect to the same habitat before the species was introduced? The second approach involves more sophisticated, and much less frequently used designs, but conceptually more correct for searching the answers sought: are the impacts of IS larger than those of functionally similar native species? Or, alternatively, are the impacts of IS larger in their introduced ranges than in their home ranges? (Boltovskoy et al. 2020). The former strategy is simpler and more straightforward, but it involves the addition of a new element to the system, which inevitably has to have some effect on the residents, regardless of how it got there (Thomsen et al. 2015; Guiaşu 2016). Thus, it deals with a general ecological issue, rather than more specifically with the impact of a species added with human intervention. The second design is more specific because it effectively compares the impacts of an IS with those of a native (Leffler et al. 2014). In fact, several of the hypotheses reviewed above require explicit comparisons between native and invasive ranges (Hierro et al. 2005). These different approaches likely explain the fact that the number of significant IS-native differences is much larger when using the first design, than when using the second (Boltovskoy et al. 2020).

Obviously, negative impacts are not restricted to IS. For example, as Davis et al. (2011) pointed out, the mountain pine beetle (*Dendroctonus ponderosae*) is a native species which kills more trees in North America than any other insect. In Argentina, many native or cosmopolitan species have undesirable impacts on the environment, on other organisms, and on the economy. Toxic strains of the cosmopolitan (van Gremberghe et al. 2011) freshwater cyanobacteria *Microcystis aeruginosa* are responsible for blooms that cause massive fish and bird mortalities, and can severely affect human health (Carmichael 1994; Pizzolón et al. 1999; Merel et al. 2013; O'Farrell et al. 2019). The native predators puma (*Puma concolor*) and foxes (*Lycalopex culpaeus*, *L. gymnocercus*) are major threats for domesticated animals, particularly sheep, in many areas of the country (Elbroch and Wittmer 2013; Periago et al. 2017; Llanos and Travaini 2020). The guanaco (*Lama guanicoe*) competes with sheep for food and its grazing strongly affects southern beech (*Nothofagus* spp.) forests (Quinteros et al. 2017).

Positive impacts of IS are very common (Goodenough 2010; Rodriguez 2016; Collins 2017, Silknetter 2020, Albertson et al. 2021). Returning to the Argentine examples (Fig. 7), bees sustain the honey industry, and are of major importance for the pollination of a large number of plants. The dove, wild boar, hare, deer, and trout and salmon are targets of sports hunting and fishing. The sweetbriar rose is used for manufacturing jelly, infusions and cosmetics. The carp is a freshwater resource of some value, and its omnivorous habits can mitigate the growth of aquatic vegetation in freshwater bodies, including water transfer canals. In Tierra del Fuego, the beaver is used for the promotion of tourism and facilitates fishes. The alga wakame is cultivated and/or harvested for human consumption in several countries (Japan, Korea, France, Australia, New Zealand). The larvae and adults of the golden mussel are an important source of food for over 50 South American fish species (Cataldo 2015; Paolucci and Thuesen 2015), and also probably reptiles, birds and aquatic mammals (Sylvester et al. 2007).

Insofar as all organisms use resources to survive, both introduced and native species have negative impacts on some members of their communities and positive impacts on others (Fig. 12), and their impacts on human interests are very often mixed.

8. The two currents

During its brief history, the field of biological invasions attracted the attention of the most prominent ecologists of the last decades, both due to its interest as large-scale experiments of the interaction between species, and because of its cultural, emotional and economic implications. Interest went far beyond academia (biologists, sociologists, economists, philosophers), extending to popular science and news media, as well as the agendas of organizations involved in environmental policies and management. However, it was only in the 1980s when invasion biology started acquiring a major conservation dimension. Despite the strongly conservationist approach of Elton's book (published in 1958), his perspective was scarcely reflected in publications between the 1960s and the 1980s, which were centered on genetic, evolutionary and ecological theory aspects (Davis 2006). Neither did these early surveys make much use of terms with negative, militaristic, and xenophobic connotations such as "invasion", "pest", "plague", "alien" or "exotic", which became widespread after the establishment of the Society for Ecologic Restoration (in 1987). It was also in the 1980s when, inspired by the restoration ecology movement, a sharp distinction based on geographic origin started to occupy the center stage, with native species being desirable and non-natives being undesirable (Davis 2006; Goodenough 2010; Wallach et al. 2020). In the 1990s the discipline began growing vigorously (Fig. 6), and also aligned more sharply with conservation, a relationship that persists to this

day. At the same time, the divide separating two different currents of thought was gradually reinforced. Most scholars adhered to Elton's stand, advocating geographic origin as a major predictor of potential negative impacts. Simply put, this tenet claims that all IS are harmful by default, and therefore guilty until proven innocent (Guiasu 2016), a trend described as "guilt by association" by Guiasu and Tindale (2018). This viewpoint was adopted in the Rio Declaration on Environment and Development of 1992: "Where there are threats of serious or irreversible damage, lack of full scientific certainty shall not be used as a reason for postponing cost-effective measures to prevent environmental degradation." In relation to IS, this statement has two issues of interest. First, preventive measures should be undertaken even when the threat is not certain, thus endorsing the precautionary principle widely heralded in thousands of surveys. Second, the rather cryptic statement related to "cost-effective measures" seems to suggest that investment in these measures should be proportional to the damage expected. However, estimates of economic damage are almost invariably very debatable (see below) (Jernelöv 2017).

On the other hand, a smaller group of researchers adopted a less radical position, suggesting that the core of IS-related issues are the ecological processes that occur upon adding a new species to a community, rather than geographic origin, and that these processes vary widely depending on the species and habitats involved, among many other factors (Davis 2006; Thompson 2014; Guiasu 2016; Jernelöv 2017; Sagoff 2019). In other words, geographic origin is not an indicator of the likelihood of harm; every introduction is a particular event that can have more negative than positive impacts, or the other way around, and usually effects are mixed and highly variable between species and communities. One of the consequences of this stand is that the search for general rules (the hypotheses) is not a fruitful task because there are no general rules.

Although discussions around these issues emerged repeatedly in the literature, they were based on facts and stayed within the bounds of reasonable evidence-based academic arguments. However, in recent years debates became increasingly aggressive, and arguments switched from scientific data to personal accusations of ignorance and purposeful fabrication of results.

In June 2011, Mark Davis and 18 coworkers published a short note entitled "*Don't judge species by their origins*" (Davis et al. 2011), where they argued that conservationists should focus much more on the functions of species, and much less on where they originated (Brown and Sax 2005; van der Wal et al. 2015). Further, they questioned costly and unnecessary attempts at eradicating IS. A month later, Daniel Simberloff, with the endorsement of 141 colleagues, published in the same journal a rebuttal to M. Davis stating that geographic origin is of prime importance, and that

precluding introductions and eradicating/controlling IS are widely justified by the precautionary principle (Simberloff et al. 2011).

A few years later some conservation ecologists started producing papers centered on the same disagreement, but rather than supporting their arguments with scientific data, they resorted to accusations of ignorance, denialism of facts and scientific consensus, fabrication of results based on spurious motivations, and even urging journal editors to reconsider acceptance of “denialist” essays (Richardson and Ricciardi 2013; Russell and Blackburn 2017a; b; Ricciardi and Ryan 2018a; b; Cuthbert et al. 2020). These articles were rebutted by the scholars questioned, as well as by several others who strongly disapproved of the arguments used and the obvious manipulation of data in some of the claims (Briggs 2017; Crowley et al. 2017; Olenin 2017; Boltovskoy et al. 2018; Guiaşu and Tindale 2018; Sagoff 2018; Frank 2019; Guerin 2019; Munro et al. 2019; Davis 2020; Gbèdomon et al. 2020).

Thus, unexpectedly, far from fostering convergence and agreement, the growing volume of information fueled conflicting points of view. However, most regrettably, the discussions became belligerent and abandoned the bounds of reasonable scientific debate entering the swampy and sterile grounds of personal accusations and name calling, which warded off the possibilities of reaching a consensus even further. There are several reasons which can account for this situation.

The growing numbers of case studies with conflicting results confirmed the heterogeneity of the impacts of IS, questioning many key issues, from basic definitions (e.g., “native”, “introduced”, “invasive”, Fig. 3), to the hypotheses proposed, as well as the qualification of the impacts and the feasibility of discerning with reasonable confidence the negative ones, from the neutral and the positive (Jeschke et al. 2014; Kamenova et al. 2017). Support for the conservationists’ arguments is also partly explained by the fact that most studies focused on the highly visible IS, with major effects on the biota, rather than on a random selection of IS (Radville et al. 2014; Guerin et al. 2018; Boltovskoy et al. 2020).

Idiosyncratic and convenience-driven factors have also likely been important. The conservation-oriented education of most ecologists is probably a major reason for endorsing this current. This inclination can be traced in some studies where the conclusions of major IS impacts are not supported by the actual results presented (Montero-Castaño and Vilà 2012; Gallardo et al. 2016; Suárez-Jiménez et al. 2017; Ferlian et al. 2018). However, a key motive seems to be the intention and the need to underscore the importance and social relevance of the issue dealt with in a dissertation, manuscript submission or grant proposal. The chances of getting published or receiving a research grant are obviously higher if one succeeds in convincing editors or

granting agency committees that the introduction in question is a major threat to the environment and/or the economy, than if no significant problems or changes occurred or are expected (Thompson 2014). This bias has been noticed in published research, where significant results and important negative impacts are over-represented (Byers et al. 2002; Pysek et al. 2008; Warren et al. 2017; Vimercati et al. 2020).

9. More on problems associated with biological invasions: the other outlook

Since its beginnings, the discipline of biological invasions has strived to answer the question of what fraction of the IS are effectively harmful in ecologic, economic, and ecosystem service terms. In the mid-1980s, the “tens rule” was proposed: 10% of the IS succeed in establishing themselves upon release, and of these 10% end up being harmful (Williamson and Brown 1986). However, as many other heuristic rules, this one is very debatable, and although it was generally endorsed by some studies, many others rejected it (Davis 2009).

Several studies tried to quantify the economic losses due to IS. Most were surveys restricted in time and space, and often centered on one or a few species, including pathogens (Sumner 2003), and in restricted areas (Perrings et al. 2001; Colautti et al. 2006a; Keller et al. 2009; Walsh et al. 2016). The most ambitious and encompassing work is a series of articles edited by David Pimentel (Pimentel 2002) with estimates for several countries, revised some years later (Pimentel et al. 2005; Pimentel 2011). Pimentel concluded that the overall world economic losses due to IS amounts to 1.4 trillion US dollars per year, or 5% of the world GDP. Pimentel’s estimates had a major impact on the discipline, and were cited in thousands of publications, but although the economic losses due to many introduced pathogens and plagues are effectively huge, these estimates are clearly biased and very imprecise. For example, they ignore the economic benefits of most IS, the costs include control and eradication programs often of questionable need, harmful alien and native species are lumped together in some estimates, and for many IS the values given are highly speculative and poorly supported (Lockwood et al. 2007; Davis 2009; Pearce 2015; Guaiasu 2016; Sagoff 2019).

A more nuanced approach to the problem was provided by the comprehensive analysis of Vilà and Hulme (2017), who concluded that cost estimates are extremely complex and their net result can differ widely depending on the stakeholders involved. For example, in New Zealand the Monterey pine, *Pinus radiata*, has invaded natural areas, yet its value as a forestry crop amounts to more than US\$ 10 billion (Vilà and Hulme 2017). Even management costs may be viewed as benefits, as in the Working for

Water program in South Africa where the costs of labor required to remove non-native trees were seen as a social benefit because this task provided employment for marginalized sectors of society (Vilà and Hulme 2017).

Further, complications arise when the same IS has opposite effects on different ecosystem components, or losses associated with one IS are canceled out by another IS. For example, Walsh et al. (2016) assessed the costs of the decrease in water clarity due to the invasion of Lake Mendota (USA) by the predatory planktonic crustacean *Bythotrephes longimanus*. However, shortly afterwards the same lake was invaded by another IS, the Caspian Sea zebra mussel (*Dreissena polymorpha*), which was predicted to significantly enhance the water clarity of the lake (Reed-Andersen et al. 2000).

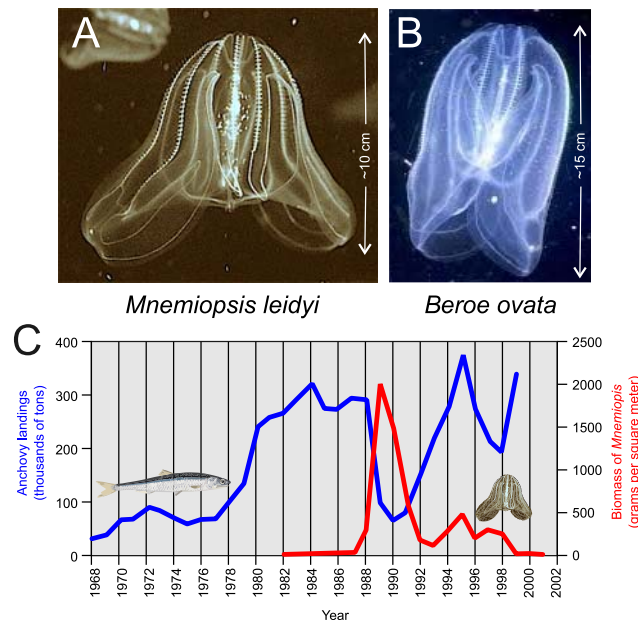


Fig. 13. The ctenophores *M. leidyi* and *B. ovata*, and changes in Black Sea anchovy landings between 1968 and 2002. A: from https://es.wikipedia.org/wiki/Mnemiopsis_leidy; B: from <http://www.sevin.ru/top100worst/priortargets/ctenophora/ovata.html>; C: modified from <http://www.biomareweb.org/3.3.html>.

A particularly interesting case is that of the ctenophore (a planktonic gelatinous marine invertebrate) *Mnemiopsis leidyi*, that accidentally invaded the Black Sea around 1982 (Fig. 13A). This animal is a voracious consumer of zooplankton, including fish larvae. By 1990, *Mnemiopsis* collapsed the fisheries of all bordering countries (Turkey, Romania, Bulgaria, Ukraine, Russia), particularly the anchovy, whose landings fell 90%. However, in the 1990s another ctenophore, *Beroe ovata*, was introduced (also accidentally) (Fig. 13B). *Beroe* feeds chiefly on *Mnemiopsis*; it rapidly decimated the populations of the first invader and, when its food declined, *Beroe*'s densities

also decreased, but kept the numbers of *Mnemiopsis* at levels compatible with a total recovery of fish stocks (Rilov and Crooks 2009) (Fig. 13C).

A widely used argument, embedded in several of the hypotheses reviewed above, is that IS have disrupting effects on resident communities because they affect interactions established during thousands to millions of years of co-existence. However, the rates at which communities can adjust to change are probably much faster than envisioned. The island of Oahu (Hawaii) is one of the most invaded sites on the planet (Anthony 2017). Many of its native plants and almost all vertebrates (including birds, responsible for the dispersal of most plants) have been replaced by IS. A thorough survey of the degree to which introduced birds have filled in the void left by the disappearance of native birds in seed dispersal of plants showed that the efficiency of the introduced birds is extremely high (Vizentin-Bugoni et al. 2019). These results suggest that highly complex interactive networks do not necessarily require long co-evolutionary periods, which contradicts the notion that long-term coexistence and co-evolution must contribute to more complex and mutually more beneficial relationships, and thus decrease competition pressures (Thompson 2005). In addition, these findings reinforce the assumption that IS do not only displace native species, but they can also replace them functionally, restoring ecological functions which had been lost due to historic displacements and local or global extinctions (Janzen 1981; Vizentin-Bugoni et al. 2019; Wallach et al. 2020; Zwerschke et al. 2020), but also due to the massive human- and climate-driven extinctions which took place since the Late Pliocene (Lundgren et al. 2020), supporting the idea that eradication of these IS can have unexpected negative impacts (Vizentin-Bugoni et al. 2019).

A common problem associated with estimates of environmental and economic impacts is that they are usually largely based on the negative effects. This bias, clearly exemplified by Pimentel's work, is widespread in case studies, but less pronounced in meta-analyses. A recent survey by Albertson et al. (2021), focused on the positive interactions among freshwater organisms, concluded that the strength of the positive effects of non-invasive species is ~26% lower than that of invasive species. In the survey by Boltovskoy et al. (2020), the incidence of negative IS effects was based, on one hand, on the overall conclusions of the 72 meta-analyses reviewed, and on the other hand, on the 1526 partial results (usually cumulative effect sizes) of the 72 surveys. For the overall conclusions, one third of the meta-analyses found chiefly negative impacts, but in other two thirds the results were mixed and inconclusive (44%), or non-significant (25%). The 1526 partial results (across meta-analyses) showed that non-significant outcomes (57%) are more common than significant outcomes. Two thirds indicated that IS-native species trait differences and IS impacts are mixed, but when results are significant, IS are usually more fit or have negative impacts. However, these

results are biased toward negative consequences for the natives by the fact that most studies were based on invasive IS with baneful impacts.

There are several other problems that complicate estimates of the magnitude and sign of the impacts.

Both case studies and the reviews and meta-analyses based on the former assess one or more traits of the organisms, populations, or communities, including abundance, biomass, production, growth, reproduction, diversity, competition, resource use efficiency, predation, physiological aspects, effects on the environment (nutrient recycling, organic matter, water turbidity, soil moisture, gas emissions, pH), etc. While the interpretation of some of these parameters is fairly straightforward (for example, if an IS decreases native diversity the outcome is negative), for others interpretation of the sign (type of impact) is more equivocal (Vimercati et al. 2020). As a rule of thumb, the decrease in the abundance of natives or residents in the presence of an IS is interpreted as a negative impact. However, this does not take into account whether the natives or residents affected are valuable organisms worth preserving, or if they are noxious and undesirable whose reduction is preferable. For example, in agreement with the above approach, the decrease of phytoplankton densities by the invasive zebra mussel *Dreissena polymorpha* (Higgins and Vander Zanden 2010) was categorized as a negative impact by Boltovskoy et al. (2020). However, in the waterbodies invaded this mussel can strongly reduce the densities of human waterborne pathogens (Conn et al. 2014) and cyanobacteria, including toxic strains of *Microcystis* sp. (Dionisio Pires et al. 2010; Higgins and Vander Zanden 2010), whose blooms have very strong negative impacts on aquatic animals and human interests (Carmichael 1994; Merel et al. 2013), and are the target of costly control programs worldwide (Huisman et al. 2005; Rastogi et al. 2015).

Caveats associated with bulk evaluations of impact and generalizations are not restricted to the above. Both introduced and native organisms interact in multiple and intricate ways, and our understanding of the mechanisms involved is very scant. Further, these interactions are highly dynamic, changing in response to multiple factors, both intrinsic and external. All plants and animals have facilitating and detrimental effects on many other species, and IS are no exception: they favor some components of these extremely complex systems, and are baneful for others (DeVanna et al. 2011; Schlaepfer et al. 2011; Humair et al. 2014; Katsanevakis et al. 2014; Latombe et al. 2019; Vimercati et al. 2020). For example, in the mineral soil layer introduced earthworms increase bacterial biomass, but in the organic layer they decrease it (Ferlian et al. 2018). The golden mussel consumes phytoplankton and can enhance densities of toxic cyanobacteria (Cataldo et al. 2012; Boltovskoy and Correa 2015; Rojas Molina et al. 2015), but, in South America, its larvae and adults are a food resource for at least 50 fish species

(Cataldo 2015; Paolucci and Thuesen 2015). Of the 49 meta-analyses that investigated the impacts of IS on native species and/or the environment (the other 23 compared competitive traits of introduced and native species; Boltovskoy et al. 2020), only 7 found exclusively negative impacts (although mostly based on 1-2 indicators or point estimates), and only 3 concluded that all interactions are non-significant. In contrast, 38 studies arrived at various combinations of neutral and negative impacts, and 13 found some positive effects of IS on the natives.

A salient result of this survey (Boltovskoy et al. 2020) is that more categorical overall conclusions (i.e., overall support, or the lack thereof, for the concept that IS are more fit, perform better, or have negative effects on the natives) were based on significantly lower numbers of estimates than conclusions supporting the concept that IS-native traits and the impacts of IS on natives are mixed and context-dependent. This result indicates that higher numbers of estimates are more likely to yield lower proportions of significant (positive or negative) outcomes. It also supports previous suggestions that as the number of analyses increases, so do the exceptions to the hypotheses proposed and the proportions of conflicting outcomes (Hulme et al. 2013; Crystal-Ornelas and Lockwood 2020a; b).

10. Concluding comments

Disagreements are common in all areas of human activities, and sciences are no exception. However, because sciences are essentially guided by inductive processes and abide by relatively strict rules, presumably less vulnerable to unsubstantiated and subjective perceptions, they have reached consensus on many issues that not long ago were a matter of debate. In fact, debate and discrepancies are a major contributor to these advances, but every new answer poses new questions. Ecology is not an exception. Even in topics devoid of the load of idiosyncratic and emotional components, and researched for centuries, discrepancies persist to this day.

An interesting example is the association between biotic diversity and latitude. In both terrestrial and aquatic environments, the number of species present increases from the poles to the equator. This trend has been analyzed in hundreds of investigations since the XIX century on the basis of millions of data; however, there still is no agreement not only on the drivers of this relationship, but even on its validity for all living creatures (Hillebrand 2004; Brayard et al. 2005; Tittensor et al. 2010; Tittensor and Worm 2016; Kinlock et al. 2018). The most likely explanation for these disagreements is that there is no unique trend and cause-effect relationship (Willig et al. 2003; Boltovskoy and Correa 2017; Grady et al. 2019).

Despite contradicting evidence, debatable issues are repeated time and again as firm facts in research papers, books, and the media. For example, the widespread notion that, on worldwide scales, global biodiversity is decreasing (Barnosky et al. 2011) was recently challenged by a study by Vellend et al. (2013). These authors compiled data on the plants present in 16 thousand continental and insular sites worldwide. They concluded that, for periods ranging between 5 and 261 years, this purported decrease does not differ significantly from zero. Because the harmful impacts of IS make up the mainstream of invasion biology, it is also conceivable that the conversion of hypothesis into fact through citation alone (Greenberg 2009) permeates much of the literature.

Even ignoring its highly value-laden character, the discipline of biological invasions is also likely unable to find general rules because each biological introduction is a particular case, whose influence on resident species and on the environment depends on factors which are specific to that particular introduction. The aforementioned survey (Boltovskoy et al. 2020) included an estimate of the number of cases where the outcome of an assessment changed in response to the settings of the experiments or field observations involved. These settings covered 12 different categories (e.g., trophic or functional levels, climatic or biogeographic areas, plant growth form - herbs, vines, bushes, trees, different habitats, etc.). In about 40% of the 306 assessments, the result of the comparison changed when the settings varied (usually from significant to non-significant, or vice versa).

Several scholars voiced their concerns that invasion biology is evolving as a discipline independent from ecology in general (Davis and Thompson 2002; Thompson and Davis 2011). Their argument is that all ecosystems have numerically and functionally dominant species (native or introduced) due to intrinsic factors, and that these intrinsic factors are neither static nor universal, but dependent on numerous historical, evolutionary and environmental conditions that modulate the ability of these species to compete successfully. Although there indeed are some mechanisms that can favor IS selectively (for example, the absence of co-evolved enemies), these mechanisms are circumstantial and ephemeral (Hawkes 2007; Carlsson and Strayer 2009; Diez et al. 2010; Gioria and Osborne 2014; Anton et al. 2020). In the long run, it is the species' attributes and their interactions that define their success or their failure, rather than geographic origin. Invasion ecology has been labeled as a pseudo-discipline, largely based on, and maintained by the use of a specific jargon. In academia, funding agencies and in the media, this resulted in the perception that the introduction, and occasionally the spectacular success, of IS is a unique process requiring special hypotheses and methods, different from those of ecology in general. However, rather than contributing to our understanding, this divorce between ecology and invasion biology hindered advances in the interpretation of the processes involved in

the introduction of new species (Davis and Thompson 2002; Valéry et al. 2013).

Current knowledge of the impacts of IS leave little doubt that some can be devastating, but also that a large number have no noticeable effects, and usually effects are mixed, with some negative, many non-significant, and some positive. This suggests that management strategies, which are usually costly and complicated, should consider two different situations.

One of them refers to potential IS, but that have not yet been introduced, which has been the subject of numerous modelling assessments (Levine and D'Antonio 2003; Broennimann and Guisan 2008; Jiménez-Valverde et al. 2011; Snyder et al. 2014; Karatayev et al. 2015; Mellin et al. 2016; Kramer et al. 2017; Mackie and Brinsmead 2017; Rinella and Sheley 2017; Tingley et al. 2017; Barbet-Massin et al. 2018; Kvistad et al. 2019; Petsch et al. 2020). The many examples of harmful introductions seem to justify the precautionary principle: avoid introduction, if possible. The fact that by 2015 244 countries subscribed one or more of the 48 international treaties on IS (Turbelin et al. 2017) suggests that, globally, this concern is not absent from the political agendas, even if subsequent compliance actions are often not as efficient as they should (Boltovskoy et al. 2011). However, species introductions can be highly unpredictable. In many cases, it is obviously not easy to predict which species may be successfully introduced at various locations, and when, especially if these introductions are accidental. Furthermore, sometimes IS that, in theory, should thrive in certain new environments fail to establish themselves there. Occasionally, IS are introduced several times unsuccessfully, before becoming successfully established, for reasons unknown. On the other hand, IS can sometimes adjust in surprising ways to seemingly unsuitable environments (Guaşu 2016).

One of the widely held arguments supporting these control measures is that they are cheaper and easier to implement than programs aimed at mitigating the damage due to some IS (Simberloff 2020). However, this line of thought is not without pitfalls. If one agrees that infectious diseases, such as the SARS-CoV-2 pandemic, should be included in the roster of IS (Nuñez et al. 2020), it is still unclear whether the financial burdens associated with our attempts to stop its dispersal are lower than the impacts of the virus itself (Sarcodie and Owusu 2020). This is obviously an extreme example because it involves human lives, but it illustrates clearly that precautionary measures are not cheap (Tait and Larson 2018). Ballast water-related introductions, originally fought using relatively inexpensive methods (i.e., the exchange of ballast water in the open ocean and the assessment of compliance through salinity measurements), are being replaced by much more expensive options (installation onboard of ballast water treatment plants and assessment of compliance evaluating the densities of viable organisms left after the

treatment; procedures D1 and D2 of the International Maritime Organization, enforced since 2017).

The second situation is that of already present IS. In this case, the precautionary principle might suggest their eradication, or at least stopping further spread. However, even if eradication were feasible (and often it is not, especially in marine environments: Simberloff 2020), the resources needed are usually very high, programs are often unsuccessful (except on islands and when aimed at large organisms; Cassini 2020) and, because chances that negative impacts will be large are low, these actions are often unnecessary (Stromberg et al. 2009). Further, if the introduction is tens to hundreds of years old, the IS might already be tightly inter-connected with the natives or with other IS, and its elimination can cause unexpected negative consequences (Bergstrom et al. 2009; Hanna and Cardillo 2014; Guiaşu 2016; Vizentin-Bugoni et al. 2019; Cassini 2020). In these cases, attempting an assessment of potential negative impact seems the best first option. Unfortunately, such assessments are complicated by the fact that impacts are highly context-dependent, implying that previous information, when available, is of dubious usefulness. Further, the magnitude of the prediction of environmental and socio-economic impacts of invasive species is proportional to their cost, and may often require international research collaborations and capacity building with scientists from high income areas (Measey 2020). The option of doing nothing in the case of a recent introduction is questioned because some IS have a time lag before their populations start growing exponentially, and because introductions that seemed initially harmless showed damage in the long term (Simberloff 2020) (although both the decrease of negative impacts with time since introduction and no change have also been observed; Parker et al. 2013; Závorka et al. 2018). However, these arguments do not seem to suffice for undertaking control or eradication programs for each of the ~600 IS that pop-up each year worldwide (Seebens et al. 2017). Thus, the argument in favor of control measures should probably be inverted, undertaking them (and bearing the costs involved) only when impacts are doubtless and, obviously, more costly than coexisting with the problem. Mitigation methods include total eradication and maintenance management, aimed at keeping the IS at abundance levels compatible with the minimization of damage (Simberloff 2020). Both are usually expensive, but in addition to the initial investment, maintenance management requires permanent costs in order to keep the IS under check. In both cases, these costs are ultimately supported by the society.

As with the human perception of a pristine state of nature, which is subjective and strongly influenced by emotional, ideological, and cultural aspects, eradication also poses ethical problems associated with the extermination of living creatures. From this perspective, killing plants or animals in order to get rid of an IS can engender major social conflicts (Wallach et al. 2018; Cassini 2020; Wallach et al. 2020). Such conflicts are

unlikely if the IS is a pathogen, or a low-visibility species such as most microorganisms, many inconspicuous plants, and most invertebrates. However, with vertebrates, in particular amphibians, reptiles, and most birds and mammals, the situation can be very different. An interesting example is that of the attempts at eradicating, in Italy, the grey squirrel (*Sciurus carolinensis*), introduced in 1948 from the USA, and which strongly impacted the native red squirrel (*Sciurus vulgaris*), as well as native trees. The eradication program, started in 1997, had to be halted due to strong opposition by animal rights groups. After 3 years of legal struggles the program was finally abandoned (Genovesi and Bertolino 2001). Further problems are posed by species that were driven to extinction in their native range or parts of it, but were reintroduced using specimens taken elsewhere previously and bred in captivity or in the wild, like the Chinese Père David's deer (*Elaphurus davidianus*; Zheng et al. 2013; Chebez and Rodríguez 2014), or from populations that survived elsewhere, like the European beaver (*Castor fiber*) (Gaywood et al. 2008), and many others (https://en.wikipedia.org/wiki/Species_reintroduction). De-extinction of globally extinct species, such as possibly bringing back the woolly mammoth, which goes a major step beyond re-introduction of a living species, is yet another highly debatable issue which does not fit the simple native-alien dichotomy (Novak 2018).

A more holistic and more inclusive view of the disagreements on IS would probably offer better chances of reaching consensus and implementing more fruitful strategies for the interpretation of their effects and finding less costly methods for their management, when deemed necessary (Schlaepfer et al. 2011; Orion 2015; Büscher and Fletcher 2020; Vimercati et al. 2020). In this context, there are two concepts that should be given closer attention.

One of them is that each biological introduction is a unique phenomenon, and so are its consequences. These consequences, in turn, are different for different native species, environments, and human interests (Hattingh 2011; Boltovskoy et al. 2020; Vimercati et al. 2020; Albertson et al. 2021). Generalizations usually contribute little to the adequate understanding of the subject. The impacts of the golden mussel are a case in point of the variety of outcomes brought about by an IS. These impacts can be widely different depending on the native species, community, or process considered (Fig. 12). Further, these effects change in space and time, such that their overall impact is hardly definable, let alone predictable. Human interventions responsible for some of the most dramatic impacts of IS, like the connection of the North Atlantic and the Great Lakes, that allowed the entry of the sea lamprey (along with 187 other IS) in the latter (Sturtevant et al. 2019), have had an enormous positive impact on the economy of Canada and the USA (Martin Associates 2018). In highly invaded New Zealand (Mooney and Hobbs 2000), more than 95% of export earnings are derived from alien species (Ewel et al. 1999). The expansion of the Nile perch population in Lake Victoria boosted fish exports

of Uganda, Kenya, and Tanzania from ~25 million US dollars in 1992 to >300 million in 2005-2008 (overfishing eroded these revenues subsequently; Aloo et al. 2017).

The second issue is the recognition that Earth's nature is highly dynamic, permanently changing, and many (or most) IS are as much a part of the world's ecosystems as the natives, rather than just a baneful and destabilizing component that has to be eliminated by all means (Orion 2015; Pearce 2015; Cassini 2020). It is impractical, and mostly unfeasible, to try to restore ecosystems to some "rightful" historical state (Davis et al. 2011). Furthermore, this is obviously a highly subjective exercise. How far back in time should we go when attempting to reconstruct past environments and why? Comparison of the impacts by IS with those due to other human actions, in particular global warming, deforestation, pollution, over-exploitation, habitat fragmentation, and urbanization is tempting (Vitousek et al. 1997; Goudie and Viles 2003), but misguided. Although all these involve environmental changes and changing living conditions, their impacts are much less debatable and generally more directional than those of IS. Faunal replacements in Oahu (see above) are a clear example of the resilience and adaptation capabilities of the biota to IS (Hubbell 2001; Vizentin-Bugoni et al. 2019). We are not suggesting that efforts to mitigate major problems caused by some introduced species should not be made. As many native species, including crop weeds, parasites or animals whose population growth puts other organisms or human welfare at risk (Goodrich and Buskirk 1995; Hill et al. 2007), harmful IS, in particular those involved in endangering human health (Mazza et al. 2013), should be the object of eradication or control actions. Several viral (smallpox, measles, mumps, rubella, polio, rinderpest) and non-viral (dracunculiasis, filariasis, onchocerciasis) infectious diseases have been almost totally extirpated worldwide, regardless of their geographic origin, and without objections concerning the elimination of species or gene pools.

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