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A synthesis of biological invasion hypotheses associated with the introduction–naturalisation–invasion continuum

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With the advent of the Anthropocene, biological invasions have reached an unprecedented level, and the number of species introductions is still increasing in an ever-changing world. Despite major advances in invasion science, significant debate and lack of clarity remain surrounding the determinants of success of introduced species, the magnitude and dimensions of their impact, and the mechanisms sustaining successful invasions. Empirical studies show divergent impacts of alien populations on ecosystems and contrasting effects of biotic and abiotic factors on the dynamics of alien populations, which hinders the creation of a unified theory of biological invasions. Compounding these issues is the plethora of hypotheses that aim to explain invasion success, which can be unclear and contradictory. We propose a synthesis that categorizes hypotheses along a timeline of invasion. We sorted invasion hypotheses along the invasion timeline, and considered population, community and ecosystem levels. This temporal sorting of invasion concepts shows that each is relevant at a specific stage of

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the invasion. Although concepts and empirical findings on alien species may appear contradictory, when mapped onto an invasion timeline, they may be combined in a complementary way. An overall scheme is proposed to summarise the theoretical dynamics of ecosystems subjected to invasions. For any given case study, this framework provides a guide through the maze of theories and should help choose the appropriate concepts according to the stage of invasion.

Keywords: alien populations, dispersal, geographic expansion, hypothesis, invasibility, invasion ecology, invasiveness, niche, phenotypic plasticity

Introduction

The frequency, magnitude and impacts of biological invasions are escalating globally (Seebens et al. 2017, Pyšek et al. 2020), and invasive species are now a major component of global change that can alter ecosystem functioning (Murphy and Romanuk 2014, Mollot et al. 2017, Lopez et al. 2022). The diversity of potential impacts, the complexity of biosecurity and management measures, and their use as model systems for testing ecological and evolutionary concepts (Westley 2011) have spurred great interest in biological invasions among the scientific community and other stakeholders. This has contributed to the emergence of diverse hypotheses aiming to explain the success or failure of biological invasions (Catford et al. 2009), the modifications that alien populations induce in native communities, and the evolutionary processes that facilitate establishment and range expansion (see Fig. 1 for an overview of invasion dynamics and associated factors). While these hypotheses have stimulated intense debates, and have opened novel research perspectives, some can appear redundant, contradictory or lacking clear empirical support (Enders et al. 2018). The large diversity of these hypotheses likely hinders their implementation in empirical research and their application to prevention and management strategies.

Assumptions about biological invasions can lose relevance when applied outside their original context, for example at different organizational, spatial and temporal scales (Catford et al. 2009, Jeschke and Heger 2018) or be ill-suited to complex natural environments (Betts et al. 2021). Generalization of hypotheses may also be hampered by the

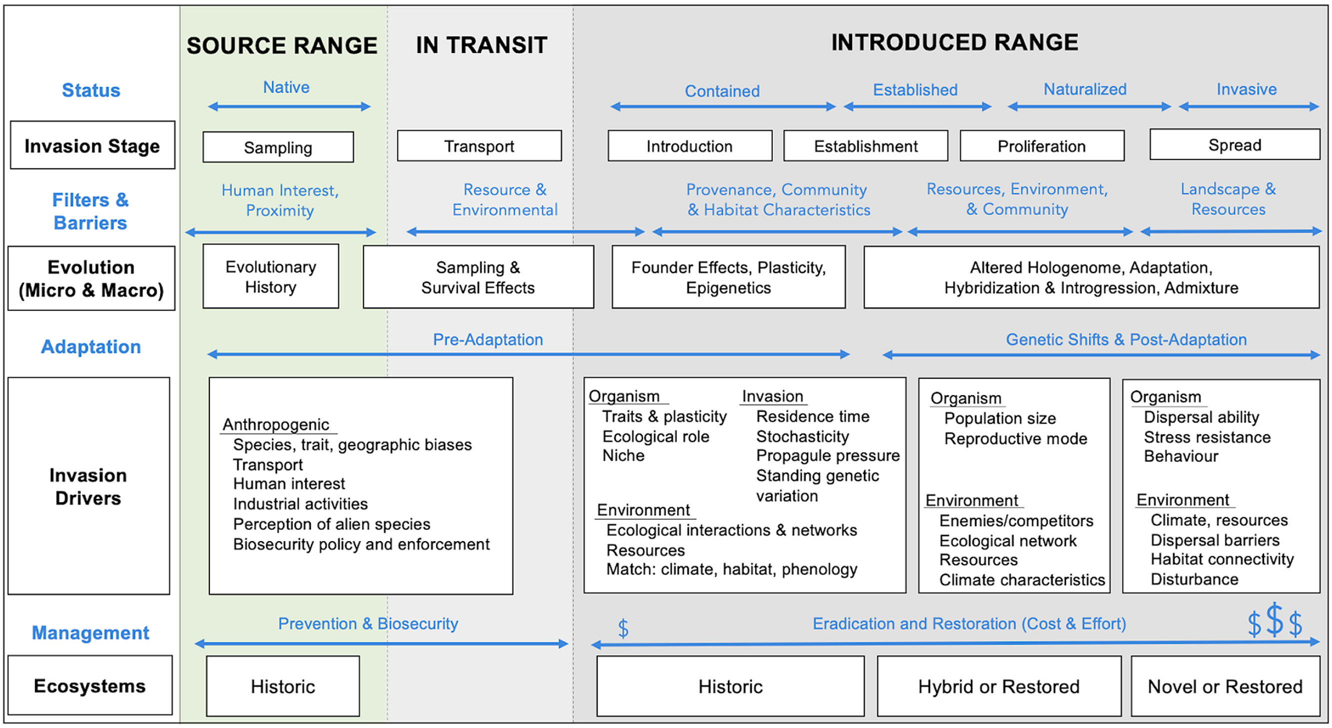

Figure 1. Overview of several perspectives of the phenomenon of biological invasions. The stages of the introduction–naturalisation–invasion continuum are presented. For each stage, the rows present the 1) different steps of the invasion process, 2) the factors that shape the evolution of organisms along the invasion process, 3) the main invasion drivers, and 4) the ecosystem transformation incurred by non-native species along the invasion process. The main invasion drivers list the direct and indirect human roles on the sampling and transport of the specimens, and reports the main organism, environmental or ecological (invasion) drivers assisting the establishment and invasion process. The arrows and associated text define the status of populations, the main filters and barriers, adaptation features assisting invasion, and management costs. This framework expands on that of Blackburn et al. (2011) to provide a higher resolution view of the process.

stage of the invasion process: some hypotheses may well explain the early stages of invasion but not the later stages (Fig. 1). As a result, our ability to either take advantage of these hypotheses for understanding biological invasion processes, make reliable predictions about invasion outcomes and communicate these findings may be diminished. We, however, acknowledge that scientists' ability to communicate clear messages to the public about prevention and management of these species has advanced significantly (Davis et al. 2018). Moreover, public and policymaker interest in biological invasions, accentuated by their economic and social costs (Haubrock et al. 2021, Renault et al. 2021, Moodley et al. 2022), has grown strongly along with scientific knowledge on the topic (Simberloff 2015, Pagad et al. 2018).

Progress must still be made as selecting hypotheses to test can be a daunting task, which can also lead to unnecessary duplication of work. This problem has been partially addressed by conceptual frameworks (Facon et al. 2006, Catford et al. 2009, Blackburn et al. 2011, Gurevitch et al. 2011, van Kleunen et al. 2018, Godoy 2019, Wilson et al. 2020), but confusion remains (Gurevitch et al. 2011, Gallien and Carboni 2017), as their application risks overgeneralisation and omission of potentially important details (Heger et al. 2021). In line with this idea, our aim is not to build a grand unified theory of biological invasions, but rather to move knowledge forward by organizing invasion biology theories and hypotheses in a systematic way.

First, we compile existing hypotheses in invasion biology, propose explicit definitions and provide illustrative examples. Beyond simply cataloguing these hypotheses, we organize and categorize them into three main groups based on whether they are related to the species (genetics, evolution and population), community (niches and species interactions) or ecosystem (environments and anthropogenic influence) levels. The hypotheses are thus better connected with their associated case studies. Second, we consider the dynamical nature inherent to invasion phenomena by splitting invasion into its main stages (transport, establishment, expansion), and build on the idea of hierarchical classification of invasion theories proposed by Jeschke and Heger (2018) and Enders et al. (2020). We do this by illustrating feedback and interactions between different hypotheses. By plotting hypotheses along an invasion timeline, we examine how the relevance of different hypotheses changes during the invasion process as well as the proximity or, in some cases, redundancy of invasion hypotheses. Finally, we discuss the crucial importance of conceptual clarity for invasion science and management of invasive species.

Compilation of hypotheses

The compilation of invasion hypotheses was conducted from 2020 to 2022. First, reviews (Catford et al. 2009, Jeschke and Heger 2018, Enders et al. 2020) and textbooks (Hui and Richardson 2017) on biological invasion were mined to create an initial list of invasion hypotheses. Following this, the initial list was updated with other hypotheses found by searching on SCOPUS and Web of Science using the following keywords: 'invasion', 'alien', 'invasive', 'non-native', 'exogenous', 'allochthonous', 'native', 'concept', 'hypothesis', 'theory', 'hierarchy of hypothesis' or 'conceptual map'. The extended list was then refined to exclude redundancies (hypotheses that have different names, but are conceptually identical) and listings that had been incorrectly labeled as hypotheses in the literature, but that do not fit the definition (for example, trends, concepts, etc.). We also have chosen to include hypotheses that have fallen out of use, unlike many other reviews, to reduce the chance of such hypotheses being 're-invented'.

We used this refined list as the basis for our table of hypotheses (Table 1), which includes the primary historical reference for the theories included, as well as any conceptually key supplemental references. When possible, we also included two examples (one plant, and one animal) that illustrate each hypothesis. In this table, we prioritized recent and highly cited references to serve as a 'jumping off point' or brief introduction for each hypothesis. In many cases, additional references were also included when they nicely complemented the illustration of the hypothesis by providing examples from other biological models or habitats. We also used this refined list as the basis for our timeline of hypotheses (Fig. 2). Here, we agreed on 'families' of hypotheses, i.e. groupings of hypotheses that overlap conceptually. We depicted connections between those hypothesis families that can interact, or feed back, during the different stages of the invasion continuum (Fig. 2).

Invasion timeline and related hypotheses

Pre-introduction: traits, evolutionary history, invasiveness and transport

The initial invasion stages occur before an individual has been introduced to a novel region. The behaviour, traits and evolutionary history of individuals in their native range are significant determinants of the invasive trajectory. The environment of origin also affects a population's chance of being sampled and introduced to, as well as being competitive within, the novel range (Fig. 1).

Pre-introduction: the often-neglected importance of individual and population characteristics

The successful integration of alien species in a novel region depends on their intrinsic characteristics that have evolved in their native range (Renault et al. 2018). These traits define species invasiveness (species invasiveness; SINV, as described in Table 1) (Richardson and Pyšek 2006). Although the evolutionary history of a species certainly contributes to invasion success (Fig. 1), the search for general traits related to invasiveness has achieved limited success to date, most likely because traits related to invasiveness vary with time and invasion stages (Mack et al. 2000, Catford et al. 2019). Typically,

Table 1. Exhaustive listing of invasion hypotheses. For each hypothesis, a description, key references and illustrative examples are provided. Indented entries are a sub-hypothesis of, or otherwise related to, the previous non-indented entry. Examples refer to main hypotheses.

Species: genetics, evolution and populations

Hypothesis description and key references	Illustrative examples
SINV – *Species invasiveness*, the propensity of a non-native species to become invasive, is determined by the performance, originality, and/or plasticity of traits (Elton 1958, Rejmánek and Richardson 1996, Alpert et al. 2000, van Kleunen et al. 2010) – see also 'Ideal weed'.	Plant traits such as reproductive ability, growth form, seed morphology, and dispersal ability can all influence invasiveness (Richardson and Pyšek 2006). Invasive fruit fly *Drosphila suzukii* has a unique ovipositor amongst fruit flies that allows it to colonize live fruit, thus filling a niche with no competition from other fruit flies (Atallah et al. 2014).
PLAST – Invasive species have greater *phenotypic plasticity* in ecologically important traits than non-invasive ones, and populations of invasive species are expected to evolve greater plasticity in their invasive range compared to populations within the native range, which facilitate invasion (Richards et al. 2006, Torchyk and Jeschke 2018).	Invasive populations of *Acer negundo* expressed greater plasticity for diameter growth and phenological sensitivity (Lamarque et al. 2015).
EIH – An *evolutionary imbalance* in competitive ability between non-native species from areas with diverse lineages and native species from less diverse areas should increase their relative invasiveness (Fridley and Sax 2014).	Founder diversity consistently increases establishment success and reduces chance of local extinction (Forsman 2013). This pattern holds for invasive animals, such as *Daphnia magna*, and plants, such as *Spartina alterniflora* (Wang et al. 2012, Robinson et al. 2013).
PREAD – Traits evolved in the native range can facilitate the invasion of non-native species into novel environments through *preadaptation* (Mack 2003).	Invasive ant *Linepithema humile* and native aphid *Chaitophorus populicola* form mutualistic association potentially because of exaptation of features for cross-species communication (Mondor and Addicott 2007). Vegetative traits evolved in invasive Himalayan balsam's *Impatiens glandulifera* native range contributed to its invasion success (Elst et al. 2016).
GBOT – Small founding populations can cause a *genetic bottleneck* of incipient invasion leading to high inbreeding levels in introduced populations (Willi et al. 2006). **INBRE –** *Inbreeding* in introduced populations can lead to inbreeding depression, potentially inhibiting long term establishment and expansion (Willi et al. 2006). **PURG –** Lethal mutations and part of the mutation load can be *purged* in small populations (Glémin 2003), such as founding populations of introduced species (Willi et al. 2006). **ALLEE –** The *Allee effect*, a positive association between fitness and population size, can cause a lag between introduction of non-native species and establishment in abundant populations (Allee 1938, Petrovskii et al. 2005).	Genetic bottlenecks in introduced populations of ladybug *Harmonia axyridis* are thought to purge deleterious alleles as introduced populations tend not to experience the same inbreeding depression as native populations (Facon et al. 2011). Invasive pale swallow-wort *Vincetoxicum rossicum* populations more effectively suppress other plants when growing in large patches and experience a lag between introduction and attainment of 'pest' status, which may be due to the Allee affect (Cappuccino 2004).
PROP – High *propagule pressure*, the number of introduced individuals, species, and/or introduction events, is a major determinant of the establishment and further colonization success of invasive species (Simberloff 2009, Bulleri et al. 2019). **COLP –** *Colonization pressure*, the number of species introduced into an area, is positively related to the number of established non-native species (Lockwood et al. 2009).	Propagule pressures in the range of 10–100 individuals have a critical positive effect on invasion success for diverse invertebrates, trees, herbaceous plants, and both terrestrial and aquatic vertebrates (Cassey et al. 2018).
GENS – *Genetic shifts* take place in the novel range that facilitate invasion of non-native species (Elst et al. 2016). **SORT –** Mating between individuals with high dispersal ability at the leading edge of invasion may lead to natural selection and novel phenotypes due to *spatial sorting* (Shine et al. 2011, Phillips and Perkins 2019). **HYBR –** *Hybridization* of introduced species with native or non-native species can promote invasiveness in the novel range.	Experimental evidence with the bean beetle *Callosobruchus maculatus* shows that spatial sorting promotes evolution relating to dispersal distance, which increases invasion speed (Ochocki and Miller 2017). Japanese knotweed *Fallopia* × *bohemica* is more invasive than its non-native parents *Fallopia japonica* and *Fallopia sachalinensis* (Mandak et al. 2004).

Communities: niches and species interactions

Hypothesis description and key references	Illustrative examples
REL – Invasion success is influenced by the *relatedness* of non-native species to native species in the novel range. Relatedness may promote (Duncan and Williams 2002) or inhibit invasion (Darwin 1859, Daehler 2003) **NAIVE –** The impact of the invader is likely to be higher in *eco-evolutionary naive* communities, i.e. in communities where no phylogenetically or functionally similar species are present (Diamond and Case 1986, Carthey and Banks 2014).	Moose *Alces alces* populations that have been free from non-human predation for several decades quickly regain antipredator behaviour when its natural predators are reintroduced. Contrast this with Galapagos Island fauna, which when exposed to evolutionarily novel predators cannot adapt antipredator defenses (Carthey and Banks 2014). Functional trait overlap in forbs confers community resistance to invasion (Price and Pärtel 2012).

(Continued)

Table 1. Continued.

Communities: niches and species interactions	
Hypothesis description and key references	**Illustrative examples**
NICHE – Non-native species expand into new areas by filling an *empty niche* (Elton 1958) and non-native species will be unlikely to establish in a community dominated by functionally similar species because of greater niche overlap (MacArthur and Levins 1967, Abrams 1983, Stachowicz and Tilman 2005).	Phenological traits can allow non-native species to exploit a resource earlier (empty niche), and potentially longer, than native species. This has been observed in native vs. non-native members of family Torymidae in France (Gidoin et al. 2015) and with members of the genus *Acer* in North America (Paquette et al. 2012).
BIOR – A diversity–invasibility relationship known as *biotic resistance* exists such that highly biodiverse ecosystems are more resistant to biological invasion because more niches are already filled, thus providing more competition with non-native species (Elton 1958, Levine and D'Antonio 1999).	
NICHER – Non-native species similar to *residents* can become 'sleeper' invasives, waiting for disturbance to facilitate expansion, as similarity ensures habitat suitability (Hui et al. 2016). See also the concept of 'invasion debt'.	
ENICHE – Specialized interactions in ecological networks may leave niche space unoccupied by inhibiting co-evolution. The *empty niches* can be exploited by non-native species through ecological fitting (Hui and Richardson 2017).	
OW – The *opportunity window* for successful invasion fluctuates as niche availability varies spatiotemporally (Johnstone 1986). See also **NICHER** and **FLUC.**	Reductions in local graminoid populations due to drought can provide an opportunity window facilitating the establishment and expansion an exotic grass (Manea et al. 2016).
DYE – Non-native species establishment can depend on fluctuations in the *dynamic equilibrium* of recipient ecosystems that influence the competition of local species (Huston 1979).	
NINT – *Novel interactions* that occur in new combinations of native and non-native species influence the establishment and success of non-natives (Poyet et al. 2015). These novel interactions often occur through ecological fitting (Hui and Richardson 2017).	Numerous novel trophic interactions appear between native fleshy-fruited plants and the invasive fruit fly *Drosophila suzukii* (Poyet et al. 2015). Non-native plants can inhibit mycorrhizal growth and activity, which disrupts the mutualistic mycorrhizal-native plant relationship and indirectly inhibit native plant growth (Vogelsang and Bever 2009).
ENI – Due to differing conditions in the novel range, *enemy inversion* may occur whereby introduced enemies are less harmful for non-native species (Colautti et al. 2004).	
SPILL – Introduced species may carry parasites that go on to infect local species ('*spillover*') and may also catch and amplify a part of local parasites, then constituting reservoirs for parasite transmission and acting as hosts to ultimately release them into ecosystem ('*spillback*') (Daszak et al. 2000, Eppinga et al. 2006, Amsellem et al. 2017).	
BIE – Invasion success of non-native organisms is mediated by *biotic indirect effects* from native populations.	
EMH – Introduced species can benefit from novel or *enhanced mutualisms* with native species, which can increase their performance relative to native populations (Reinhart and Callaway 2006). See also host-jumping and new associations hypothesis (Hui and Richardson 2017).	
MDH – Invasive populations can *disrupt mutualistic interactions* between native species in their introduced ranges (Traveset and Richardson 2006). Disruptions may also take place at the community scale ('Keystone Mutualist Hypothesis' (Gilbert 1980)).	
MISS – The fitness of non-native species may be reduced in the novel range due to *missing mutualistic* interaction partners from the native range (Mitchell et al. 2006). Co-introduction of mutualists may be necessary for invasive success (Hui and Richardson 2017).	
BEHAV – Invasion may be inhibited when non-native species are *behaviourally constrained* and require adaptations before recognizing and readily consuming, evading, or outcompeting an introduced population (Lankau et al. 2004).	Both non-native shore crabs *Hemigrapsus sanguineus* and white campion (*Silene latifolia*) are more susceptible to parasitism than native counterparts in exotic USA range (Keogh et al. 2017, Wolfe et al. 2004).
INSUS – Invasion may be inhibited when non-native species are at *increased susceptibility* to consumption due to consumer preference and lack of effective defences (Colautti et al. 2004, Parker and Hay 2005).	Invasive plants, such as *Sapium sebiferum* in USA, benefit from lower herbivory rates due to behavioural avoidance despite it being a suitable host plant (Lankau et al. 2004).

(Continued)

Table 1. Continued.

Communities: niches and species interactions	
Hypothesis description and key references	**Illustrative examples**
ERH – Non-native species may rapidly increase in abundance and distribution due to *enemy release*: the absence, or reduction, of regulation by natural enemies (Keane and Crawley 2002).	Invasive rodents in Senegal have lower parasite loads than native rodents, which may partially explain their relative success (Diagne et al. 2016).
RERH – Fast growing species with weak defences against enemies benefit experience disproportionate success through the interaction of increased *resources and enemy release* in the novel range (Blumenthal 2005).	Noxious diffuse knapweed *Centaurea diffusa* is much better able to suppress surrounding plants from naive populations than from its native range due to their lack of evolved defense strategies (Callaway and Aschehoug 2000).
EICA – Introduced species can undergo *evolution of increased competitive ability* by reinvesting resources used for defense and in growth, biomass, reproduction, and competitiveness when they escape natural enemies in their invasive range (Blossey and Nötzold 1995).	
SDH – Under lower pressure by enemies in the invaded range, species can *shift defenses* against specialist predators to less costly defenses against generalists (Müller-Schärer 2004, Joshi and Vrieling 2005).	
SG – Non-native species are more successful in a new region if the local predators are *specialists* and local mutualists are *generalists* (Callaway et al. 2008).	
NWH – *Novel weapons*, such as chemical or biological defences, evolved in a species' native range may have a greater effect in its novel range where other species are naïve to them (Callaway and Ridenour 2004).	
MELT – Previously introduced species may facilitate the establishment of newly introduced species resulting in *invasional meltdown* (Simberloff and Von Holle 1999).	Invasive soil microbiota can change soil conditions such that they are less hospitable for native microbes than other non-native species, potentially causing in invasional meltdown (Zhang et al. 2020).
IMD – Eurasian species have better invasion success relative to other species because of coevolution with Europeans and their associated species, which were globally dispersed during European *imperialism* (Crosby 1986, Jeschke and Strayer 2005).	In North America's Great Lakes, many invasive species interactive positively with each other. For example, Eurasian macrophytes provide substrate to Asian bryozoans which may have facilitated their spread (Ricciardi 2001).
Ecosystems: environments and anthropogenic influence	
Hypothesis description and key references	**Illustrative examples**
EINV – The successful integration of non-native organisms in a new area depends on the characteristics, or *ecosystem invasibility*, of the recipient environment (Alpert et al. 2000, Richardson and Pyšek 2006).	Environmental heterogeneity promotes dispersal and range expansion of animals with density-dependent dispersal as populations outgrow their patches in heterogenous environments (O'Reilly-Nugent et al. 2016).
DIST – Invasion success is increased in *disturbed* ecosystems relative to undisturbed ecosystems (Elton 1958, Hobbs and Huenneke 1992). See also hypothesis of 'increased resource availability' from Sher and Hyatt (1999).	Sub-arctic ecosystems are not uniformly invasible. Plant invasion success in these ecosystems is influenced by community composition and disturbance level (Milbau et al. 2013).
EHET – *Environmental heterogeneity* promotes invasions by increasing both ecosystem invasibility and coexistence with native species (Melbourne et al. 2007). See also **FLUC**.	
FLUC – *Fluctuating resources* affect ecosystem invasibility, with unused resources facilitating invasion (Davis et al. 2000).	
BIOME – *Biomes* differ in their inherent invasibility because of biotic and abiotic differences (Hui and Richardson 2017).	
IS – *Island* ecosystems have higher *susceptibility* to ecological impacts from biological invasion than continents (Jeschke 2008).	
CLIM – *Climate change* facilitates invasion of non-native species adapted to the new environmental conditions and exacerbate their impacts. (Dukes and Mooney 1999, Hulme 2017).	Range expansion of invasive moth *Lymantria dispar*'s and invasive tree mallow *Malva arborea* range expansion in their novel ranges is linked to local warming (Tobin et al. 2014, van der Wal et al. 2008).
BIOA – *Biotic acceptance* is a diversity-invasibility relationship where that the richness of native and non-native species is positively related (Stohlgren et al. 2006).	The richness of non-native and native plants is often correlated, likely because favourable environments for native species are similarly favourable for non-native species (Souza et al. 2011, Bjarnason et al. 2017).
ANTR – The increasing global abundance of invasive species is related to *anthropogenic transportation* through inter- and intra-continental exchanges (Perrings et al. 2005, Seebens et al. 2017).	Population characteristics of invasive earthworms and plants are predicted by proximity to roads and their characteristics (Cameron and Bayne 2009, Paudel et al. 2016).
ANOP – Species associated with humans are more likely to become invasive because of their increased *opportunity* for *anthropogenic transport* (Hufbauer et al. 2012). See also **HCOM**.	Genetic evidence indicates that the abundance of invasive plants in the sub-Antarctic is a result of repeated introductions by human activities (Mairal et al. 2021).

(Continued)

Table 1. Continued.

Ecosystems: environments and anthropogenic influence	
Hypothesis description and key references	**Illustrative examples**
HREL – Non-native species establishment and expansion can be limited by land-management activities and cessation of these *human* activities can *release* non-native species, facilitating expansion (Zimmermann et al. 2014).	Abandonment of agricultural land, and related land management activities, in rural Hungary allowed the proliferation of previously suppressed invasive plants (Pándi et al. 2014).
HCOM – *Human commensalism* is positively related to invasion success (Jeschke and Strayer 2006).	Many rats have a commensal relationship with humans that have allowed them to spread and survive over much of the globe (Puckett et al. 2020).
AIAI – *Anthropogenically induced adaptation to invade* can facilitate invasion and invasiveness of an organism or population (Hufbauer et al. 2012). **URCM –** *Urban competition* may increase competitiveness of urban adapted species, which may facilitate their success as invaders (Borden and Flory 2021).	The ability of the Asian house gecko *Hemidactylus frenatus* to grip smooth surfaces is thought to have arisen due to urban evolution, as this trait allows the geckos to easily climb human-made materials (Petren and Case 1998). This species has become invasive in many areas, potentially aided by its superior ability to survive in urban areas (Borden and Flory 2021).
ANHO – Adaptation to *homogenized anthropogenic environments* can serve as a form of preadaptation of the organism to homogenous human-altered habitats globally (Hufbauer et al. 2012).	Fungal graminiod pathogen, *Mycosphaerella graminicola*, is thought to have adapted to wheat during its domestication (Stukenbrock et al. 2007). It is now the only of its congeners to be invasive (Hufbauer et al. 2012).
URCLM – Urban adapted species may be more likely to become invasive because they may be better adapted to future environments because of *urban climate* conditions (Borden and Flory 2021).	

invasion-facilitating traits are only relevant to a few taxonomic groups (Kolar and Lodge 2001) and are context-dependent (Leffler et al. 2014, Catford et al. 2019, 2022). Figure 2 shows how the role of alien species traits can change with the stage in invasion process and ecosystem transformation, which has thus far been poorly considered. When these useful traits originate in the species' native range, and assist in their novel range integration, it may be thought of as preadaptation (preadaptation; PREAD, Mack 2003, Rey et al. 2012) (Table 1). Preadaptation, sometimes referred to as preselection, includes repurposing a trait for a new function (exaptation) or the use of a trait which serves the same function in both environments (prior adaptation) (Hufbauer et al. 2012, Rey et al. 2012), however most known examples are of prior adaptation.

Some biological traits have been found to strongly support invasion success, and several lines of evidence suggest that traits that enable an alien population to become a successful invader (species invasiveness; SINV) are often life-history traits that promote rapid growth, efficient reproduction and dispersal to rapidly establish viable populations (Fig. 1, 2). For plants, those traits and characteristics are high ploidy level and asexual reproduction, and for plants and animals, high reproduction rate, high phenotypic plasticity, broad and flexible diet, reduced systemic inflammatory responses (Lee and Klasing 2004), and a broad ecological tolerance that allow establishment and subsequent potential spread (Rejmánek and Richardson 1996, Alpert et al. 2000, Kolar and Lodge 2001, Pyšek and Richardson 2007, Castillo et al. 2021). A meta-analysis by van Kleunen et al. (2010) established that invasive plant species generally have higher values of performance-related traits characterizing physiology, leaf-area and shoot allocation, growth rate and size, i.e. better values for many proxies of plant fitness, than non-invasive species do. However, contradictory results of several global analyses searching for important traits have been reported (Daehler 2003, Leffler et al. 2014). The 'ideal weed' is a perspective on invasiveness in plant ecology, which focuses on the traits of alien plant populations that enhance their establishment, spread and/or competitive abilities allowing to outcompete indigenous populations (Elton 1958). Among these traits is uniparental reproduction (Baker 1967), which has consistently been reported in invasive terrestrial plants as an important trait for both establishment and spread (Pannell et al. 2015) across biogeographic regions and taxa (van Kleunen and Johnson 2007, van Kleunen et al. 2008). Type of vegetative propagule could also influence the success of establishment of invasive plants (Spencer and Rejmánek 1989). For example, *Hydrilla verticillata* plants growing from turions were weaker competitors than plants growing from tubers. However, theoretical models on the evolution of dispersal and selfing in plants indicate that selfing in invasive species can only be expected under certain circumstances, not in general (Cheptou and Massol 2009, Massol and Cheptou 2011a, b).

One critical trait – or rather a syndrome of traits – is what could be viewed as a 'human-interest-related trait'. Many invasive species are first selected by humans based on different traits of interest. For plants, these include interest for use in forestry, horticulture and food production (Shackleton et al. 2011, Beaury et al. 2021) and for animals these predominantly include interest as a food source or as a companion animal (Lockwood et al. 2019, Hong et al. 2020). However, there may be as many motivations for moving around other species as there are incidences of this occurring. Alien species selected by humans for introduction (and those that may escape and become invasive afterwards) are selected based on a set of traits that may differ from those conferring an invasive advantage (Hui et al. 2011). Hence, a species has a much higher chance of becoming invasive if it possesses traits that confer advantages in the novel ecosystem, but also traits in its native ecosystem that favor its selection by humans for introduction (intentional or not). The personal and institutional behaviour surrounding the intentional importation of alien species deserves more research attention, especially for the purpose of reducing the release of alien species into novel regions.

Pre-introduction events in the community and ecosystem

Similar ecological niches and climatic environments occur in many parts of the world. In some instances, invasion may be facilitated by the introduction of organisms in regions displaying environmental characteristics, including climate, soil and disturbances, similar to those of their native range (Hufbauer et al. 2012). In this vein, an alien population would be preadapted to environmental conditions of the recipient ecosystem (preadaptation; PREAD) (Vermeij 1991, Mack 2003). Moreover, the never-ending anthropogenic alteration of terrestrial, freshwater and marine environments creates similarly disturbed habitats worldwide (Williams et al. 2020), which may drive invasion success of species adapted to these homogenized environments (adaptation to homogenized anthropogenic environments; ANHO). This is especially concerning when species selected by humans for these environments, and likely better adapted to contaminant exposure, are introduced to novel areas where they may more easily spread (Hufbauer et al. 2012, Bishop et al. 2017, Borden and Flory 2021). The predisposition of alien species to become successful invaders may also be increased when populations are imported from native areas hosting highly diverse evolutionary lineages, which are subsequently introduced into less diversified geographic regions (evolutionary imbalance hypothesis; EIH, Fridley and Sax 2014). This is postulated because species and populations from diverse areas are thought to have evolved enduring higher competitive pressure, thus improving their competitive ability relative to native species that evolved in a lower pressure environment.

The degree to which a species, or population, can be 'preadapted' to a novel environment depends not only on their evolutionary history, but also on any bias in sampling of individuals and their ability to survive during transport (Fig. 2). In this context, ecotypic variation in a species' native range must be considered, as sub-populations may be differentially invasive depending on characteristics of their source range. For example, the invasion of Israel by the tropical ant *Wasmannia auropunctata* likely occurred after the introduction of a particularly cold-tolerant population at the southern limit of its native range (Rey et al. 2012). The bridgehead effect is the high prevalence of alien organisms in human altered habitats, from which invasive populations can further spread (Lombaert et al. 2010, Bertelsmeier and Keller 2018). This effect may result from adaptation to resist factors typical of these habitats (such as pollutants, climatic conditions or availability of trophic resources), which evolved in their native range or as the population moved into human-altered environments (anthropogenically induced adaptation to invade; AIAI).

For a species to be considered invasive, by definition, it must be introduced to a novel environment via human activity. This can take place in a number of ways with levels of human involvement ranging from creation of dispersal corridors and invasion hubs increasing connectivity and spread of alien species (Morel-Journel et al. 2019), to intentional release (see Fig. 1 in Faulkner et al. 2020). The species most likely to be transported, whether advertently or not, are those commonly found in human-altered environments because they have more opportunities for anthropogenic transport (opportunity for anthropogenic transport; ANOP; Hufbauer et al. 2012). For this reason, human commensalism may be positively related to invasion success (human commensalism; HCOM; Jeschke and Strayer 2006). One decisive factor of invasion success is the match between species traits and the characteristics of the recipient ecosystem, i.e. the right traits in the right environment. The right time is also important. For example, a mismatch can occur between the phenology of invasive fruit flies and the fruiting period of their host plants, depending on their location along latitudinal gradients (Ulmer et al. 2022). Phenology and stochasticity are crucial to invasion success, but do not matter if the right species is never initially sampled for introduction (Fig. 2). Human activity and global movements are important drivers of the increasing abundance of invasive populations globally (anthropogenic transportation; ANTR; Perrings et al. 2005, Seebens et al. 2017). Populations can be introduced intentionally, such as through trade in pets or horticultural plants, and they are also transported unintentionally along commercial and touristic routes by aircraft, ships, cars or hikers. This is exemplified by the positive correlation between shipping trade and the number of marine alien species introduced in European seas (Nunes et al. 2014). This is also nicely illustrated by the invasion routes of the fruit fly *Drosophila suzukii*, which are closely related to fruit trade flows and pathways (Cini et al. 2014). Similarly, the invasion of European countries by the horse chestnut leafminer *Cameraria ohridella* was supported by flows of people, cars, trains and trucks (Gilbert et al. 2004). The invasion of the Great Lakes drainage basin by numerous Ponto-Caspian species, such as *Dreissena* mussels, has been ascribed to ballast waters (Ricciardi and MacIsaac 2000). A model based on observational data also showed that both shipping intensity and habitat match are good predictors of the risk of marine invasion (Seebens et al. 2016).

Introduction and establishment of alien species in recipient ecosystems

The initial contact phases of the invasion process comprise the introduction and establishment of founder populations in the novel range. Important considerations include the environmental and resource filters faced by alien species, as well as their characteristics and plasticity in the face of novel conditions (Fig. 1).

Introduction of alien individuals and establishment of founder populations

Alien species can fail to establish, partially establish in weakly persistent populations, or establish self-perpetuating

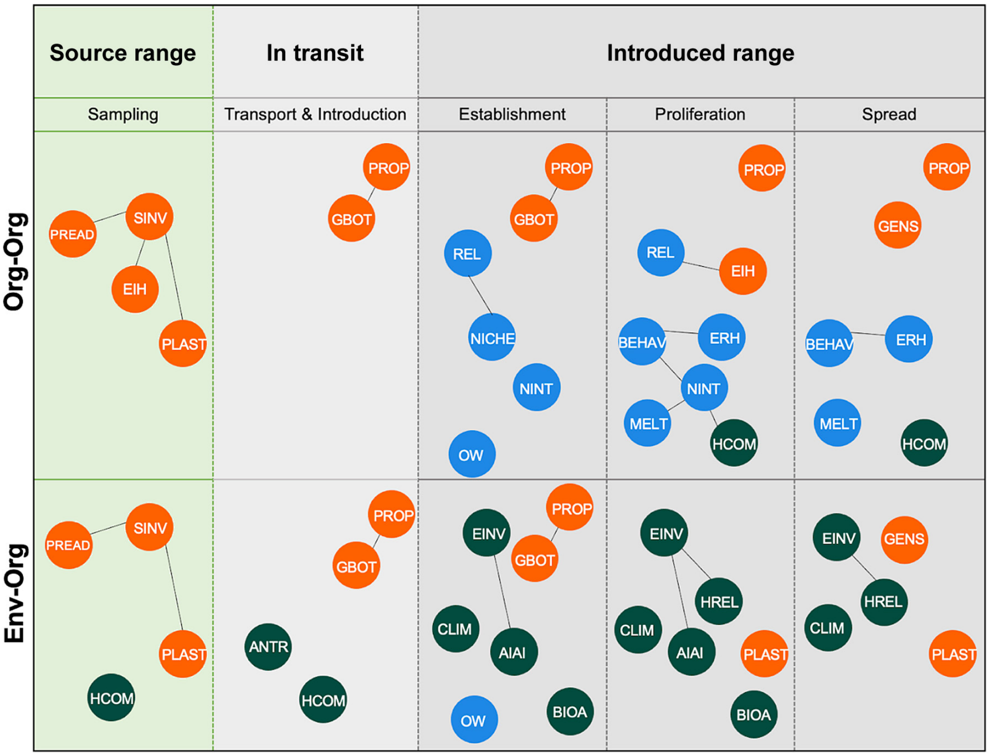

Figure 2. Invasion hypotheses presented with relevant stages in the invasion timeline and colour-coded by ecological level: species (orange), community (blue) and ecosystem (green). For each step, the main hypotheses, and their links, corresponding to interactions between organisms (org–org), and to interactions between organisms and their environment (org–env) are presented (see Table 1 for hypothesis definitions).

populations in the new range. A concept proposed by Williamson and Fitter (1996) focused on the proportion of imported species achieving different levels of invasion success: 1 in 10 imported plants or animals subsequently appear in the wild of recipient ecosystems. The same proportional rule was thought to hold between introduced and naturalised populations, and between naturalised and invasive populations. This was dubbed the 'tens rule' (Williamson 1996, 2006). Although subsequent tests of this rule failed to find support (Jeschke 2014), it remains a useful illustration of the relative rarity of invasion success and emphasizes the many filters and barriers that inhibit invasion or contribute to selecting specific phenotypes (Richardson and Pyšek 2006, Fig. 2).

There are many reasons for invasion failure (Zenni and Nuñez 2013). In most cases, characteristics of individuals do not match with biotic or abiotic characteristics of the area of introduction (species invasiveness; SINV, ecosystem invasibility; EINV and empty niche; NICHE), and populations are therefore unable to persist for long or remain undetectable (Fig. 2). However, propagule pressure (propagule pressure; PROP) is also important in the introduction stage of the invasion process (Zenni and Nuñez 2013, Cassey et al. 2018). Unbridled human-mediated species dispersal can lead to the repeated introduction of numerous individuals originating from multiple populations. This process increases propagule pressure and the probability of population establishment. The propagule pressure hypothesis (propagule pressure; PROP) (Simberloff 2009), also known as 'introduction effort' hypothesis (Blackburn and Duncan 2001), combines the number of propagules introduced and the number of introduction events. This hypothesis is often seen as the 'null model' determinant of invasion success (Colautti et al. 2006, Roman and Darling 2007). In combination with propagule composition (Bulleri et al. 2019), it is recognized as a major determinant (Cassey et al. 2018), yet not universal (Dressler 2018), of establishment and further colonization success of alien species. High propagule pressure increases the probability of persistence of the alien populations by counteracting negative effects associated with small populations (e.g. stochasticity), increasing genetic diversity and promoting admixture, and thus increasing adaptive potential of alien populations, and ultimately the probability of successful introduction (Bock et al. 2015, Rius et al. 2015). In the same vein, colonization pressure (colonization pressure; COLP) correlates the number of different species introduced to an area and the richness of invasive populations (Lockwood et al. 2009).

Adaptive phenotypic plasticity, which confers high performance in a broad range of environmental conditions (Richards et al. 2006), may also be key to species invasiveness and establishment success. This is because plasticity can allow an invader to thrive in environmental conditions that only partially match those of its native area (Renault et al. 2018). According to the phenotypic plasticity hypothesis (phenotypic plasticity; PLAST), invasive organisms may have a greater plasticity in ecologically important traits as compared with non-invasive ones (Manfredini et al. 2019, Castillo et al. 2021, Renault et al. 2022). In addition to this, populations of invasive species are expected to evolve greater plasticity in their invasive range compared to populations within the native range (Richards et al. 2006). Like many other invasion hypotheses, the phenotypic plasticity hypothesis has mixed support (Davidson et al. 2011, Palacio-López and Gianoli 2011); however, Torchyk and Jeschke (2018) suggested a relatively high level of support for this hypothesis compared to others. Discrepancies may be due to the absence of consideration of relevant functional traits (Castillo et al. 2021, Renault et al. 2022, Wang et al. 2022). Fewer studies have compared invasive and non-invasive populations, and most of these investigations have focused on plants. For plants, Lamarque et al. (2015) compared populations of *Acer* spp. from both their invasive and native ranges. They found that invasive populations of one, but not all, members of the genus expressed greater plasticity in the novel range. According to Lande (2015), the discrepancy in the observed tendency can be explained by several parameters, including the type of plasticity (reversible versus irreversible). Animal studies on phenotypic plasticity tend to focus instead on overall plasticity of the species and different expressions in the native and non-native ranges (reviewed by Manfredini et al. 2019).

Diverse degrees of trait plasticity do exist among alien species subjected to the same environmental pressures, as reported from plants exposed to windy conditions (Saiz et al. 2021). Plasticity should theoretically be highly beneficial at the early stages of invasion, because of the probable costs of maintaining plasticity (van Kleunen and Fischer 2005), and because it may allow for novel genetic variation to arise (Pigliucci et al. 2006). A trait may then lose its environmental sensitivity, and therefore become stable to environmental changes by genetic assimilation (Pigliucci et al. 2006). However, fluctuating environments are predicted to favour phenotypic plasticity, and this could explain the long-term persistence of plasticity in invaders of disturbed areas. The maintenance of adaptive plasticity could also be based on particular molecular genetic mechanisms, such as environmentally sensitive alleles, regulatory loci or epigenetic variation inducing environment-dependent expression patterns (Bock et al. 2015, Estoup et al. 2016, Gutekunst et al. 2018). Different forms of 'genomic shock' encountered by alien species may also lead to epigenetic changes increasing phenotypic variation, potentially resulting in novel phenotypes and increasing their fitness in the novel range (Mounger et al. 2021).

First responses of local communities to alien species introduction

The biotic resistance (biotic resistance; BIOR) of the recipient ecosystem can at least partly explain the failure of many invasion attempts. Some ecosystems are species-rich, stable and may hinder the infiltration and integration of new populations (Fig. 2). From Elton's empty niche hypothesis (empty niche; NICHE; Box 1) we know that species richness in a community partly explains its resistance to the integration of new populations, including alien ones (Elton 1958, Levine and D'Antonio 1999). In theory, at least two different mechanisms can explain this pattern: either resource availability and vacant niches decrease with species richness, or species-rich communities tend to comprise competitively superior species that resist invasions (Stachowicz and Tilman 2005). Some experimental tests seem to favour the former interpretation, i.e. that species-rich communities are protected against invasion through a saturation of niches and a decrease in resource (Tilman 1997, Stachowicz and Tilman 2005), although some field studies may mitigate these results (Stohlgren et al. 1999, 2006). Such a biotic resistance hypothesis assumes that the number of filled niches should be greater in a species-rich assemblage, which would also include a greater number of predators and competitors (Crawley et al. 1999). This is also one of the reasons why all types of islands (ecological and oceanic islands) are more susceptible to invasion than continents (island susceptibility; IS): they host fewer native species that all evolved in isolation. Both native plant species richness and functional group identity are important mediators of opportunities for the establishment success of an invasive population, as shown for the waterweed *Lagarosiphon major* (Petruzzella et al. 2018). The number of alien populations in an ecosystem accumulates over time, and may increase or decrease the biotic resistance of the historical ecosystem. Previous invasions can increase invasion resistance for functionally similar invaders by removing the populations more sensitive to invasion (Rodríguez 2001). This, or environmental differences, could also explain differential invasibility between biomes (BIOME).

Among the most important contributors of biotic resistance to invasions are the local native consumers (e.g. biotic resistance by predators in ports, Leclerc et al. 2019), but interactions with any species in the novel range may influence invasion success (novel interactions; NINT). Native consumers could prefer alien over native prey, and may consequently limit invasions (Parker and Hay 2005). Even if alien prey are not preferred, they may still be limited by native consumers if they are exceptionally susceptible to predation due to, for example, the absence of shared evolutionary history. The increased susceptibility hypothesis (increased susceptibility; INSUS; Colautti et al. 2004) posits that alien prey have not experienced selection from these consumers and therefore lack effective defences. Behavioural adaptations may be necessary for an alien species to evade, consume or compete with native species, including enemies (behaviourally constrained; BEHAV). If they lack such abilities, and are not able to adapt in a sufficiently short time span, the alien species population may fail to establish and proliferate (Fig. 2).

Alien populations may also escape predators, pathogens and parasites, which can be grouped under the general term 'enemies' (enemy release; ERH; Keane and Crawley 2002). This hypothesis predicts that a newly introduced invader establishes because of the lack of regulation by natural competitors and enemies (Williamson and Fitter 1996, Keane and Crawley 2002). For instance, using 26 host species of molluscs, crustaceans, fishes, birds, mammals, amphibians and reptiles, Torchin et al. (2003) found that introduced populations are less heavily parasitized than native ones. The behavioural constraint hypothesis (behaviourally constrained; BEHAV) posits that potential consumers and competitors need behavioural adaptations before recognizing and readily consuming or outcompeting an introduced population under natural conditions (Lankau et al. 2004). The absence of native 'ecosystem guards' capable of slowing the progression of alien populations may increase the establishment success and geographic expansion in the invaded area.

According to the empty niche hypothesis (empty niche; NICHE; Stachowicz and Tilman 2005), unsaturated ecological niches are poorly occupied because of their short evolutionary history (e.g. recent volcanic islands), their climatic (glaciation–deglaciation in northern systems), geologic and topographic (isolation of mountain or island ecosystems) histories, or their degree of anthropogenic alteration. The establishment of alien populations relies on the assumption of niche differentiation with native populations, involving either the exploitation of unused resources (empty niche), or enhanced competitive ability to access a shared resource (niche replacement). Niches may also be empty due to specialized interactions in ecological networks that inhibit co-evolution and leave niche space unoccupied (Hui and Richardson 2017). Neutral theory (Box 1; Hubbell 2001, Chave 2004) has also been applied to invasions with contrasted successes (Fargione et al. 2003, Herben et al. 2004, Tilman 2004, Chabrerie et al. 2008, Daleo et al. 2009).

The combination of the use of an empty niche and enemy-release opportunities (empty niche; NICHE and enemy release; ERH) is likely to facilitate the establishment of alien populations (Shea and Chesson 2002). Both the empty niche

Box 1. Ecological theory and biological invasion hypotheses

Multiple theories can be relevant for a given biological invasion timeline. This presents a challenge to the development and application of theory-based frameworks of invasion. Several of the most important theories in invasion ecology are presented here.

Niche and limiting similarity theory

Niche theory is based on Hutchinson's (1957) concepts of the realized and fundamental ecological niche. These concepts define the conditions for positive population growth of a species in the absence (fundamental niche) and presence of biotic interactions (realized niche). Niche theory states that ecological communities are made up of a limited number of niches, each of which can only be occupied by a single species, and that successful occupation of a niche depends on species fitness and interactions. Seen through an invasion lens, a species' ability to occupy a niche in its novel range determines its ability to establish, proliferate, and further spread. Examples of relevant hypotheses: NICHE, EIH, ENICHE. Limiting similarity theory is an extension of niche theory which states that in the absence of other factors, two species competing for an identical resource cannot coexist (MacArthur and Levins 1967). Applied to invasion ecology, this theory suggests that species should not be able to establish, proliferate, and spread in novel ranges that are home to species that are too similar to them (Jeschke and Heger 2018). Examples of relevant hypotheses: BIOR, REL, NAIVE, NICHER.

Unified neutral theory

Hubbell's unified neutral theory of biodiversity and biogeography states, as a null hypothesis, that differences between species have no impact on their success within an ecological community. Explicitly put, species are equivalent in their prospects of survival and reproduction (Hubbell 2001). Although the assumption of species equivalence in this theory is unrealistic in real systems, a weaker assumption of equivalent average fitness can be used in its place; both versions of this theory predict the same patterns as theories that allow for large differences between species (Chave 2004). This theory can be thought of as a null counterpart to niche theory. As such, many invasion hypotheses that are not based in niche theory can be thought of as stemming from neutral theory. Neutral theory is most relevant to hypotheses that address early invasion phases because they do not necessarily depend on differences in species interactions, niches, and genetics. Examples of relevant hypotheses: PROP, IRA, BIOA, ANTR, HREL.

Theory of fluctuating resources

The fluctuating resources theory of invasibility states that fluctuation in resource availability is a major determinant of ecosystem invasibility, with susceptibility to invasion increasing with the quantity of unused resources (Davis et al. 2000). Resources may be unused due to a drop in usage by native species or a resource pulse that cannot be fully, or quickly, exploited by resident species (Davis et al. 2000). Depending on the application of this theory, it is conceptually compatible with both neutral and niche theory. Examples of relevant hypotheses: OW, DYE, IRA, BIOA, NICHER, DIST.

and enemy release hypotheses invoke aspects of Charles Elton's hypothesis in seeking to explain the low biotic resistance of ecosystems. In this respect, insular ecosystems are particularly sensitive to the effects of invasion because they are often 'ecologically unsaturated', as depicted by the high number of alien populations generally recorded on islands (island susceptibility; IS; Patiño et al. 2017). The high level of endemicity of island communities, which, in many instances, evolved under lower biotic pressures and in relative isolation as compared with continental communities, can make them more easily invaded by alien species. A famous example is the brown tree snake *Boiga irregularis* which decimated the avian forest community on Guam that was naive to tree-climbing predators (Wiles et al. 2003). Similar case studies point to invasive populations accessing unused or under-utilized resources or to gain competitive advantage to exploit shared and limited resources, leading to significant community-level impacts (Fig. 2).

Several theoretical studies have assessed species invasiveness and ecosystem invasibility from a food-web perspective, mostly by using the niche model of Williams and Martinez (2000). Such work suggests that low-trophic level generalists are better invaders than specialists or higher-level consumers (Romanuk et al. 2009). Conversely, more densely connected food webs are more resistant to invasions (supporting Elton's hypothesis, but through the number of links rather than the number of species), but suffer larger extinction cascades when a successful non-native population invades (Romanuk et al. 2017). Food webs with more compartmentalization (where food webs are subdivided into groups of species that are more likely to interact with one another than with those outside the compartment) were also less susceptible to invasion (Krause et al. 2003). Finally, the theoretical study of Hui et al. (2016), based on the evolutionary food web model of Loeuille and Loreau (2005), indicates that the invasibility of recipient communities depends not only on their food-web architecture, but also on the ecological characteristics and properties of the invading individuals. The effects of invasive species can also be examined from the perspective of other types of ecological networks, including plant–pollinator and host–parasitoid, and social–ecological networks that can jointly consider both anthropogenic and ecological factors (Bodin et al. 2019). Changes in numerous network characteristics and structural properties have been associated with invasion in a variety of different ecological network types (see Table 1 in Frost et al. 2019 for summary). Much work remains in experimentally testing and explaining these patterns (Frost et al. 2019), but new network methods that can inform future research on biological invasions are constantly developing (Calizza et al. 2021).

Various degrees of ecosystem susceptibility to invasions

Several studies have examined whether invasive populations share biological traits (species invasiveness; SINV) and, in parallel, whether invaded habitats have similar features to ascertain which ones could be associated with ecosystem invasibility (ecosystem invasibility; EINV) (Lonsdale 1999, Kolar and Lodge 2001, Romanuk et al. 2017). Now, it is widely accepted that just as the success of alien species in novel regions depends on species invasiveness, so too does it depend on the characteristics of the recipient environment, i.e. ecosystem invasibility (ecosystem invasibility; EINV) (Alpert et al. 2000, Richardson and Pyšek 2006). EINV is determined by abiotic (physico-chemical factors) and biotic components (e.g. local community composition, ecological networks, biotic interactions). Invasiveness and invasibility tease apart the determinism of species invasions. When jointly considered, these concepts avoid dressing one-sided considerations that would assign the 'invasive' attribute to a species regardless of the characteristics of the invaded habitat, or conversely attribute the feature 'invasible' to an ecosystem regardless of the traits of potentially invasive organisms (Sol et al. 2008). Additionally, an ecosystem's invasibility may vary through time because of dynamic changes that affect interactions between native species (dynamic equilibrium; DYE; Huston 1979). This creates opportunity windows (opportunity window; OW; sensu Johnstone 1986) that can be exploited by alien populations for their establishment, proliferation or expansion.

The high invasibility of certain ecosystems is largely related to the use of niches neither exploited by local competitors nor defended by local enemies, such niches being more likely to occur in disturbed and heterogeneous sites. For this reason, the environments in which invasions proceed are often spatially and/or temporally heterogeneous in both their biotic and abiotic components. Environmental heterogeneity is likely to favour invasibility (environmental heterogeneity; EHET), possibly promoting coexistence mechanisms between native and alien populations and limiting the ecological impact of invaders (Melbourne et al. 2007). For instance, pulsed resources generate episodes of increased resource availability that can both increase niche opportunities and relax interspecific competition; this can favour the establishment of alien populations and the ability of native populations to persist in the presence of competitive invaders (Davis et al. 2000, Shea and Chesson 2002). The environmental heterogeneity hypothesis also encompasses the fluctuating resource hypothesis (fluctuating resources; FLUC) raised by Davis et al. (2000). This hypothesis assumes that invasion success is higher when some resources are not well used (unsaturated niche, low to absence of functional redundancy), or when there is a temporal or spatial increase in resource availability for an opportunistic invader (Thiébaut 2005). This can be due, for instance, to an increase in resource supply (e.g. eutrophication), or the local extinction of a competitor (Sher and Hyatt 1999, Davis et al. 2000). In many cases, this biotic and abiotic heterogeneity, which increases habitat invasibility, results from human-mediated disturbances.

Habitat disturbance (disturbed ecosystem; DIST) is globally recognized as an important feature of susceptibility to the installation and spread of alien populations (D'Antonio and Dudley 1995, Lozon and MacIsaac 1997, Chabrerie et al. 2008). Invasion frequency generally increases as levels of disturbance or ecosystem modification increase (Lonsdale 1999, Richardson and Pyšek 2006), as habitat disturbances affect native population abundance and diversity, in turn favouring alien populations (Didham et al. 2005). MacDougall and Turkington (2005) were among the first to empirically test the effects of habitat disturbance and invasive population abundance on native species declines using invasive grasses in fire-suppressed oak savanna of British Columbia. Another example is the intensive grazing which exacerbated the dominance of the invasive annual grass *Bromus tectorum* in the endangered *Artemisia tridentata* big sagebrush ecosystems of the Intermountain West, USA, by disrupting key resistance mechanisms associated with bunchgrass abundance and composition (Reisner et al. 2013).

The biotic acceptance hypothesis (biotic acceptance; BIOA), which positively relates native and alien species richness, is the counterpoint to biotic resistance. Stohlgren et al. (1999) showed that hot spots of plant diversity, and biodiversity in general, were successfully invaded by alien plant populations in many landscapes in the USA, with a probable link with the degree of resource availability in native plant communities (Sher and Hyatt 1999), independent of species richness. It was thus suggested that high species richness may not systematically support a complete use of all available resources, community stability or resistance to invasion; conversely, negative richness-invasibility correlations might not always be due to ecological processes but might instead be attributed to sampling effects (Wardle 2001). Levine et al. (2004) also suggested that biotic resistance may have a stronger influence on alien populations once established, rather than during their establishment, as seen with invaded fish communities in the USA (Carey and Wahl 2010). Similarly, microcosm experiments by Dukes (2001) suggested that functional diversity is a better proxy of resistance against invasion, whereas species diversity is a good proxy of resistance against negative effects of the invader on the ecosystem, once established.

When the characteristics of alien populations and recipient environments match only partially, newcomers face difficulties in fully ensuring their fundamental biological functions and in passing from the introduction and establishment stages to the proliferation stages of the invasion process. For instance, some alien plants are unable to reproduce sexually in their invasion range (Lambertini et al. 2010). Their proliferation is almost exclusively or totally ensured by clonal multiplication, at least in the early stages of the invasion process. Their sterility can be due to sub-suitable climatic conditions in recipient ecosystems (e.g. too cold to allow reproduction), to pollen sterility or auto-incompatibility. It may also be due to the absence of cross-fertilization because of low number of partners (allee effect; ALLEE; Allee 1938), dioecious species with only one sex introduced in the invasion range (Lambertini et al. 2010), or to the absence of associated pollinator mutualisms (missing mutualistic; MISS; Mitchell et al. 2006, Bufford and Daehler 2014). This apparent weakness (lack of sexual reproduction) may be converted into an advantage when vegetative reproduction is more efficient than sexual reproduction for invading recipient ecosystems such as aquatic ones (Lambertini et al. 2010).

Developments in the novel range: proliferation of individuals, expansion beyond introduction area and adaptive evolution

The main events characterizing the post-establishment stages of invasion are proliferation and expansion of alien populations. This process includes progressive adaptation to the environments encountered in their novel area and modification of assembly rules and interactions within the local community.

Developments in the novel range of individuals and populations

Invasive populations are generally thought to be founded locally by a small number of individuals (Dlugosch and Parker 2008) representing a reduced fraction of the genetic diversity of the source population (Nei et al. 1975, Barrett and Husband 1990). This genetic bottleneck (genetic bottleneck; GBOT) leads to high inbreeding levels (inbreeding; INBRE) in introduced populations (Willi et al. 2006). Furthermore, genetic diversity is considered an important basis for the ability of populations to adapt to new environmental conditions (Fisher 1930). From these two assumptions emerges the ‘genetic paradox of invasions’, which asks how invasive populations adapt to the novel selective pressures encountered in the introduced area despite presumed reduced genetic diversity (Sax and Brown 2000, Estoup et al. 2016). In this context, genetic investigations first focused on comparing levels of genetic diversity between native and introduced populations (Bossdorf et al. 2005, Wares et al. 2005, Dlugosch and Parker 2008, Rius et al. 2015). Many authors showed decreased levels of genetic diversity in the introduced populations compared with native ones (Filipova et al. 2011, Hagenblad et al. 2015). However, reduced genetic diversity is not the rule in every environment. In particular, twenty years of genetic studies of introduced marine and freshwater populations have consistently reported similar or higher genetic diversity in introduced populations compared to their native counterparts (e.g. in 76% of the European marine introduced species, Rius et al. 2015). High propagule pressure from repeated introductions from genetically diversified sources (propagule pressure; PROP) can explain this pattern (Rius et al. 2015, Viard et al. 2016).

Dlugosch et al. (2015) suggested that there is little explanatory power of the level of measured (and often neutral) genetic diversity on introduction success. This does not imply that genetic variation is not important to consider, because 1) admixture and hybridization processes may create evolutionary novelties (Rius and Darling 2014, Viard et al. 2020, Fournier and Aron 2021), 2) neutral genetic diversity may not correspond to adaptive variations on traits that are relevant for invasiveness (Dlugosch et al. 2015, Viard et al. 2016), 3) rapid adaptation can occur in genetically depauperate alien populations via few large-effects alleles, as shown in alien populations of the green crab (Tepolt et al. 2022) and maybe most importantly, 4) there remain several genetic mechanisms that must be investigated in the context of invasion (for instance: microRNA, exome-based functions and roles, degradome or genome-wide promoter interactome) in addition to mechanisms that are yet to be discovered.

Genetic bottlenecks do not seem to constrain invasion success (Sax et al. 2007), or even prevent rapid adaptive change (Prentis et al. 2008), as illustrated with the invasion case of *D. subobscura* in Chile (Huey et al. 2005). Severe genetic bottlenecks have been demonstrated for introduced populations worldwide. For example, the seaweed *Sargassum muticum*, for which 14 microsatellites failed to detect any genetic variation over > 1200 individuals sampled from 46 locations over its Pacific and Atlantic introduction ranges (Le Cam et al. 2019). In the same study, distinct introductions, but all accompanied by a severe genetic bottleneck, were confirmed with ddRad-Sequencing. As pointed out by Prentis et al. (2008), it is noteworthy that genetic bottlenecks can enable rapid adaptive change to occur through the conversion of epistatic variance to additive variance, for example, Whitlock et al. (1995) or a complex interaction between inbreeding depression and recipient environment (Schrieber and Lachmuth 2017). Alternative mechanisms such as phenotypic plasticity (phenotypic plasticity; PLAST) could play a major role in the rapid adaptation of invasive populations, as suggested for the parthenogenetic marbled crayfish (Gutekunst et al. 2018). Epigenetics may also increase the genetic and phenotypic diversity following the colonization of a new environment by alien species (genetic shift; GENS, Huang et al. 2017).

The genetic (and ecological) paradox between inbreeding depression and adaptive success of alien populations may also be resolved by understanding the evolution of the mutation load during the invasion process. The mutation load is defined as the proportion by which the population fitness, or any other attribute of interest, is altered by recurrent mutations (Kimura et al. 1963), and which constitutes a genetic burden. Consanguineous mating can purge a part of the mutation load and lethal mutations can also be purged in small populations (Glémin 2003). Thus, small populations of aliens, through the increase of consanguineous mating, may benefit from this purge of homozygous deleterious alleles (purged; PURG) reducing their mutation load and promoting invasion, as it has been shown for the invasive harlequin ladybird *Harmonia axyridis* (Facon et al. 2011). However, experimental evidence from this species shows that simulated bottlenecks fix deleterious alleles more often than they purge them (Laugier et al. 2016).

The intercontinental network of disturbed niches may facilitate the establishment of r-strategy alien populations (Davis 2005). These r-strategist populations or species are likely to be replaced by more competitive populations or species in later stages of the invasion (Facon et al. 2008). Pine species (*Pinus* spp.) that invade habitats undergoing strong disturbances, for example, were mainly characterized by three r-selected traits: short juvenile period, light seeds and short time intervals between breeding events (Rejmánek and Richardson 1996). On the contrary, secondary invasions should stem from K-strategist species with a set of life-history traits associated with competitive abilities, e.g. large size, late reproduction, low fecundity and long-life expectancy. Traits related to K-strategies will be favored in the subsequent stages of the invasion, when the invader enters into competitive interaction with the already invaded community in hybrid or novel ecosystems. Meanwhile, a meta-analysis in birds suggested that invasiveness cannot be solely explained by the r-K tradeoff (Sol et al. 2012). A bet-hedging life history, characterized by delayed reproduction and longer lifespan, could be the best invasive strategy, as it reduces the risk of reproductive failure associated with maladaptation to a novel environment and population fluctuations (Sol et al. 2012). This is also supported in experimental findings by Tayeh et al. (2015) in invasive *H. axyridis*, which highlights that life histories can evolve rapidly within alien populations, converging to a fine-tuned evolutionary match between the invader and the invaded environment.

Expansion beyond the introduction area often relies on dispersal ability, which determines the speed at which colonisation of new habitats will occur (Renault et al. 2018). Range expansion is often characterized by sequential founder events (Slatkin and Excoffier 2012), resulting from short (stepping stone) or long-distance jumps. Individuals colonizing new habitats, distant from the core population, can have direct fitness advantages like decreased intra-specific competition pressure (Travis and Dytham 2002, Burton et al. 2010). Moreover, founder individuals, theoretically characterized by a majority of individuals with good dispersal abilities (Renault et al. 2018), will share and transmit their genetic background at the invasion front (passive assortative mating). As this phenomenon repeats as the invasion front moves forward, dispersal traits should be enhanced at the leading edge of the range expansion (Renault 2020), generating phenotypic differentiation between front and core individuals (Laparie et al. 2013, Messager and Olden 2019), and possibly breaking genetic covariation between dispersal and other traits encountered in native populations (Brown et al. 2015). Behind the front wave and in core populations, higher population densities should favour competitive abilities of individuals, rather than biological traits enhancing their dispersal capacities (Burton et al. 2010).

The promotion of dispersal traits at the invasion front has been highlighted in the cane toad *Rhinella marina*, which is rapidly invading the north-east coast of Australia (Phillips et al. 2006, Phillips and Perkins 2019), leading to the theory of spatial sorting (spatial sorting; SORT; Shine et al. 2011). Using experimental evolution in replicated microcosm landscapes with different animal and plant models, several studies have sought to identify factors that mediate the evolution of increased dispersal during range expansion, and how this evolutionary shift may impact the ecological dynamics of invasion (Szűcs et al. 2017, Weiss-Lehman et al. 2017). These studies suggest that at least five different processes may impact the evolution of the dynamics of range expansions: 1) novel selection pressures in the new habitat, 2) spatial sorting, 3) lower density at the expansion edge, 4) gene surfing and 5) number and genetic background of the founders. The consequences of range expansion for population dynamics and the potential of invasive species to encompass rapid range expansion and adaptation are being extensively studied in theoretical and empirical works (Courant et al. 2019, Morris et al. 2019).

Some models show that the Allee effect can decrease invasion speed (Travis and Dytham 2002), to the point of counteracting spatial sorting (Shaw and Kokko 2015, Shaw et al. 2018). However, theoretical work on the dynamics of invasion waves has also shown that Allee effects might help maintain higher genetic diversity at invasion fronts (Roques et al. 2012), partly because decreased invasion speed lowers the intensity of genetic drift (inbreeding; INBRE) at the front. Despite such advances, our understanding of the processes generating phenotypic or genotypic variation in dispersal ability along the invasion gradient remains incomplete, especially under non-equilibrium conditions like range expansion and invasion (but see Phillips and Perkins 2019). Moreover, human-assisted dispersal events and multiple reintroductions impede our understanding of the actual expansion sequence.

Introduced populations may originate from different divergent lineages, which are spatially isolated in the native species range. These introduced individuals with distinct genetic backgrounds may come into contact and reproduce; the result of this interbreeding between two or more previously isolated genetic lineages (in the native or in the introduced ranges) is genetic admixture. Admixture increases the overall genetic variance, generates heterozygosity and heterosis, and increases species fitness (Handley et al. 2011, Keller et al. 2014). This can contribute to enhancing spread and can facilitate the adaptation of introduced populations, as suggested for the green crab *Carcinus maenas*, following the independent introduction and hybridization between cold- and warm-adapted ecotypes (Jeffery et al. 2018). The same process may, on the other hand, also contribute to outbreeding depression, i.e. a decrease in average fitness. The role of admixture in biological invasions remains an open question and deserves further work (Rius and Darling 2014).

Hybridization, and introgression (i.e. interspecific gene flow) is an extreme case of admixture that occurrs between accepted species. Secondary contacts between previously allopatric species are major outcomes of introductions. Human-mediated translocation of species thus promotes hybridization and introgression, which can facilitate the establishment of introduced species (hybridization; HYBR, Harrison and Larson 2014, McFarlane and Pemberton 2019, Viard et al. 2020). In cases where native and alien species are not fully reproductively isolated, inter-specific hybridization and introgression can occur with diverse outcomes from introgression swamping (asymmetric hybridization) and genome-wide admixture to semi-permeable barriers to gene flow (Brumfield 2010, Grabenstein and Taylor 2018). Hybridization between native and alien species has been documented over a large number of taxonomic groups, as shown in birds (Steeves et al. 2010), social insects (Fournier and Aron 2021), iguanas (Vuillaume et al. 2015), salamanders (Fitzpatrick et al. 2010), marine mussels (Saarman and Pogson 2015, Simon et al. 2020) and plants (Abbott 1992, Petit et al. 2004). It can occur even at a late speciation stage, as recently documented by the introgression of the European native tunicate *Ciona intestinalis* by its introduced congener *Ciona robusta*, native to Asia, which have diverged 4 millions years ago and display synonymous divergence rate of 15% (Le Moan et al. 2021). This latter case, which is presumably an adaptive introgression (Fraïsse et al. 2022), is rare, as in most cases, introgression is expected to occur in the reverse direction, i.e. from the native to the introduced species Viard et al. 2020).

While hybridization can threaten native populations (Todesco et al. 2016), it can also benefit the alien populations in several ways, such as through adaptive introgression (i.e. the introgression of adaptive alleles from native to alien populations) (Hedrick 2013). It can also protect alien species from Allee effects and thus facilitate invasions (Mesgaran et al. 2016). From a genomic standpoint, rearrangements like chromosomal inversions (Prevosti et al. 1988) and polyploidization have been reported in *Spartina* species where hybridization between native and alien taxa produced offspring with a wide range of chromosome numbers and fertility levels (Ainouche et al. 2009). In this context, the resulting complex evolution form, named 'reticulate evolution' (Linder and Rieseberg 2004, Trewick et al. 2004), can occur in species with relatively close common ancestors (species of the same or a closely related genus). Hybridization can also occur between two alien plant species. *Fallopia* × *bohemica* is reputed to be more invasive than the two alien parents *Fallopia japonica* and *Fallopia sachalinensis* (Mandak et al. 2004). In the long term, these complex forms of evolution may result in adaptive radiation of introduced populations confronted to contrasted environments in post-invasion events (Carroll and Dingle 1996). Finally, the selection resulting in evolutionary adaptations may lead to speciation in invasive species (Lee 2002, Abbott et al. 2013); thus, the invasive species of today may become the native species of tomorrow.

Development of invaded communities

At the onset of the invasion process, when the alien population has been recently introduced into a new ecosystem, its impacts on community composition and ecosystem processes are usually superficial or undetectable. This latency period (Hui and Richardson 2017) accompanying the initial invasion stages could partly explain why the consequences of invasive species for their host environment have been hotly debated (Gurevitch and Padilla 2004, Asner et al. 2008, Simberloff et al. 2013). Looking for impacts too early, i.e. before the population has time to proliferate, can lead to missing the impacts altogether. One potential mechanism behind this latency period could be the evolution of increased competition ability (evolution of increased competitive ability; EICA), first studied in plants (Blossey and Nötzold 1995) and modified by Joshi and Vrieling (2005). The premise behind this hypothesis, as well as enemy inversion (enemy inversion; ENI), human release (human release; HREL), enemy release (enemy release hypothesis; ERH) and sub-hypotheses (Table 1), is that species escape natural enemies in their invasive range. They can therefore save the energy formerly used for defence, and reinvest it in growth, biomass, reproduction and competitiveness. Following environmental filtering during the expansion stage, alien populations may rapidly increase in abundance due to this release from enemy pressure (Pyšek and Prach 1993). This could also explain and reinforce the differences in performance commonly observed between native and alien populations (Heberling and Fridley 2013), or between populations of alien species differing by the time since their introduction (Boiché et al. 2011). However, it is also important to consider that all introduced populations will lose at least some enemies in its novel range, however not all introduced populations will establish, proliferate and expand (Colautti et al. 2004). During the establishment, proliferation and expansion phases, novel interactions (novel interaction; NINT), including indirect interactions (biotic indirect effects; BIE), between alien species and other species begin to influence the dynamics of the invasion and community.

The magnitude of the impacts of alien species also depends on the evolutionary experiences of both the alien species and the invaded community and their relatedness (relatedness; REL; Darwin 1859, Duncan and Williams 2002). This imbalance of eco-evolutionary histories between the different parts of the world (evolutionary imbalance hypothesis; EIH) may be beneficial to alien species that experienced high, long-term selection pressure in environments diversified in evolutionary lineages. The impact of the invader will thus be higher in eco-evolutionarily naive communities (NAIVE; Diamond and Case 1986, Ricciardi and Atkinson 2004), i.e. in communities with shorter or lower evolutionary experience and where no phylogenetically or functionally similar species exists or has been produced. This eco-evolutionary naivety may also be one of the contributors facilitating the establishment of alien species by limiting their similarity with native competitors (Box 1). However, exclusionary similarity between species, and other niche related inhibitors of invasion, may take too long to act to be easily observable (Hess et al. 2019). In naive communities, alien species are more successful if local predators are specialists and mutualists are generalists (specialists generalists; SG, Callaway and Ridenour 2004). The 'novel weapons hypothesis' (novel weapons hypothesis; NWH; Callaway and Ridenour 2004, Vilcinskas 2015) is another explanation for the success of invasive populations. NWH posits that invasive populations may be equipped with new weaponry not detected or little used in the native range. In plants, numerous field and laboratory experiments have established the potential allelopathic effect of alien populations on seed germination and direct inhibition of native plants (Thorpe et al. 2009, Pinzone et al. 2018). NWH also covers various invasive plant phytochemical activities, including anti-herbivore functions, as well as anti-fungal and anti-microbial effects (Schaffner et al. 2011, Cipollini et al. 2012). As a consequence, allelopathic compounds can alter soil biota communities at different trophic levels from microbes to higher predators (Abgrall et al. 2018) with consequences on soil functions like nutrient cycling or pathogen control, and indirectly on native plant communities (Brousseau et al. 2021). The NWH can be 1) the result of changes of biological characteristics in the invasive population between its populations of origin and its host range or 2) existing traits related to negative interactions with its natural enemies in its native range against which native populations of its invasive range are not adapted (Callaway and Ridenour 2004, Yuan et al. 2013). In native plants, novel weapons of invaders are known to induce two responses: either 1) non-tolerance to the harmful allelochemicals due to the so-called 'naivety' observed with any antagonistic interactions (Schaffner et al. 2011, Carthey and Banks 2012) or 2) evolved tolerance to novel allelochemicals through natural selection (Callaway et al. 2005).

Although many of the ERH sub-hypotheses (Table 1) were developed from work on invasive plants (Zhao et al. 2020, Hartshorn et al. 2022), they are also relevant for invasive animals. Some invasive insects harbour new chemical weapons by using molecules naturally present in the local resources of invaded ecosystems. This is the case of the alien fruit fly *D. suzukii* which can use the toxic compounds of native plants present in its invasive range (Poyet et al. 2015). This fly lays its eggs preferentially in a toxic substrate (containing atropine, a compound naturally present in the fruits of the native plant *Atropa belladonna*) in the presence of parasitoids (Poyet et al. 2017). Interestingly, the presence of atropine in the developmental medium confers a better resistance of *Drosophila* offspring against parasitoids, thus revealing the existence of a form of transgenerational medication in this species. This new weapon may result from a shifting defence (shifting defenses hypothesis; SDH) mechanism, as the toxic plants used by the invasive insects are present in their invaded area but absent in their native area.

In contrast to native populations, some introduced plants can benefit from improved mutualisms with soil microorganisms (especially symbiotic fungi), which increases their performance (enhanced mutualism hypothesis; EMH; Marler et al. 1999, Reinhart and Callaway 2006). According to the EMH, mutualism may be relatively more beneficial in novel ranges because the invasive population has escaped from the negative effect of natural enemies that may attenuate the positive effect of mutualists (mainly bacteria and fungi). For example, neutral to negative impacts of soil biota were found for populations of *Triadiaca sebifera* in the species' native range (China) whereas positive effects of soil biota were reported in a North American non-native range of the species. These positive effects were linked to the higher levels of arbuscular mycorrhizal fungi colonization and to the greater net benefits to the invader in North America than in China (Yuan et al. 2013). Importantly, one needs to assess individual interactions between microbial species and alien macro-organisms to tease apart the importance of EMH from ERH. In contrast with the EMH, the mutualism disruption hypothesis (mutualism disruption hypothesis; MDH; Callaway et al. 2008) predicts that invasive populations can also suppress soil mutualists in introduced ranges more aggressively than mutualists in their native ranges.

Despite the loss of most of their enemies (enemy release hypothesis; ERH), alien populations may carry some of their parasites during the invasion process (Médoc et al. 2017). Parasites may spread into new environments and infect local species, which is defined as 'spillover' (spillover–spillback; SPILL; Daszak et al. 2000, Power and Mitchell 2004). Aliens may also catch and amplify a part of local parasites, then constituting reservoirs for parasite transmission and acting as hosts to ultimately release them into the ecosystem, which is defined as 'spillback' (spillover–spillback; SPILL; Kelly et al. 2009). Weinstein and Lafferty (2015) describe finding alien nematodes originating in domestic dogs, *Canis lupus familiaris*, in native species (spillover), and conversely finding native nematodes typically infecting red wolf, *Canis rufus*, within domestic dogs (spillback). Spillover and spillback processes (spillover–spillback; SPILL) have an effect on host–parasite dynamics and thus on ecosystem dynamics (Kelly et al. 2009, Lymbery et al. 2014, Amsellem et al. 2017). In some cases, invaders may act as poor hosts for native parasites and create a 'dilution effect', by reducing the density of parasites and thus risk of infection (Kopp and Jokela 2007, Kelly et al. 2009). Chalkowski et al. (2018) propose two extensions of spillover–spillback dynamics. The first, suppressive spillover, occurs when parasite infection incurs harmful effects to alien species, in turn lowering its spreading capacities. The second, disease facilitation, consists of the amplification of parasite transmission by alien species acting as reservoirs or vectors. Disease facilitation can also be a result of habitat alteration that enhances parasite habitat, physical transfer or mechanical vectoring (Chalkowski et al. 2018).

Native and alien species diversity are often positively correlated in large-scale studies (biotic acceptance; BIOA, Stohlgren et al. 2006), but negatively correlated in small-scale studies (Sax 2002, Byers and Noonburg 2003). Indeed, the same factors (light, degree of human-mediated modification of habitats, etc.) can have a positive effect on both alien and native species, generating correlations between the diversity of the two groups of species, without the existence of strong causal relationships between native and alien species diversity. The simple correlation between dominance of alien populations and decline of native diversity does not constitute evidence that diversity changes are driven by non-native populations (Didham et al. 2005). Also, the relationship between the richness of alien species and that of native species could even be positive according to the spatial scale of observation (Sax 2002, Byers and Noonburg 2003) and the nature of the interactions between the native and the alien species. For example, the presence of the invasive water primrose can have a positive effect on local diversity and ecosystem processes since the plant may act as a 'magnet' species facilitating pollinator visits to the native species *Lythrum salicaria* (Stiers et al. 2014).

Development of invaded ecosystems

Established populations of alien species sometimes facilitate the establishment and proliferation of later arrivals to the ecosystem through changes to the community or ecosystem, in a process known as invasional meltdown (invasional meltdown; MELT, Simberloff and Von Holle 1999). For example, Ricciardi (2001) found that facilitative relationships were common among invasives in the Great Lakes, particularly due to the presence of the invasive bivalve *Dreissena polymorpha*. A variation on this theme called the 'imperialism dogma' (imperialism dogma; IMD, Jeschke and Strayer 2005) posits that Eurasian species are more likely to establish in novel areas because imperialist activities previously facilitated the establishment of other Eurasian species in those regions. The presence of species with which the newly introduced Eurasian species coevolved was posited to increase the invasibility of the ecosystem, however no evidence for this hypothesis has been found (Jeschke and Strayer 2005). From a theoretical viewpoint, invasional meltdowns have been modelled in food webs, following the classic niche model, to assess the effect of alien species coexistence (before the 'impacting' stage of invasion) on final invasion success (Pantel et al. 2017): while coexistence of non-native populations is not necessary to obtain an increasing probability of invasion success with the number of species introductions, introductions of populations that have previously coexisted elsewhere increase the slope linking the number of introductions to the fraction of successful invasions and thus make invasional meltdown more intense (Pantel et al. 2017).

Alien populations can go from the status of 'passengers' (MacDougall and Turkington 2005, see also 'opportunist model' from Chabrerie et al. 2008) to the status of 'drivers' of environmental changes. The prevalence of invaders well described by the 'passenger' models may be low, however, as recent evidence suggests that global environmental changes interact antagonistically with invaders more often than they do synergistically (Lopez et al. 2022). In the driver model (MacDougall and Turkington 2005, Chabrerie et al. 2008, White et al. 2013), invasive populations affect local diversity by using ecosystem resources and space more effectively than native ones (Parker et al. 1999). A recent alternative to these models, called the 'backseat driver' model, describes the case where alien species both benefit from existing ecological disruptions and drive further changes (Bauer 2012). Dominant invaders subordinate native populations, which are thus limited or excluded by competition (MacDougall and Turkington 2005). In some cases, great transformations imposed by invaders to ecosystems, results in the designation of alien species as 'invasive engineers' (Cuddington and Hastings 2004), drawing on the concept of ecosystem engineers proposed by Jones et al. (1994). Invasive engineers (or habitat modifiers, habitat formers or bio-constructors) are among the most ecologically influential forms of biological invaders. Such populations create, destroy or transform the invaded habitats, thereby affecting native organisms (Guy-Haim et al. 2017). Some studies show that the impacts of invasive ecosystem engineers depend on their density, and that at low density their effects can be positive (e.g. for soil microorganisms in Straube et al. 2009).

Future considerations in invaded ecosystems: invasion debt and climate change

The term ‘invasion debt’ describes the time-delayed invasion of populations that are already present in a region (Seabloom et al. 2006, Essl et al. 2011). In areas with invasion debt, even if no new individuals are introduced, populations of alien species occurring at low abundance may be waiting for an opportunity to proliferate and expand (opportunity window; OW). For example, alien species that are too similar to native species to invade may persist in small numbers until a population crash of their native counterparts, at which point they have the opportunity to proliferate and expand (resident niche; NICHER; Hui et al. 2016). This means that prevention of future introductions is not enough on its own to maintain ecosystem integrity, as debt already incurred will have to be paid in the future even if new introductions cease (Essl et al. 2012). This concept also provides a valuable metric that can be used to quantify dimensions of future threats (Rouget et al. 2016). By separating the invasion into components corresponding to different stages in the invasion process (introduction, establishment, spread and impact debts), Rouget et al. (2016) worked with 58 Australian *Acacia* species introduced to South-Africa. The spread of debt over a 20-year period varied from 0 (species unlikely to extend any further) to 10 000 km^2 for species with a large potential range. This corresponds to a current impact debt of $174 million USD per species, which could increase to $500 million USD in two decades if left unmanaged. In Europe, Haeuser et al. (2018) estimated the invasion debt of ornamental plant species by considering climate change. Modelling the effect of climate and species characteristics on naturalisation risk together with climate projections such as this allows the forecasting of future threats and the implementation of proactive management of non-native populations.

Climate change (climate change; CLIM) can facilitate invasion in a myriad of ways, but perhaps most basically by allowing for the establishment of non-native populations that would otherwise not be able to establish. For example, changing climatic conditions can alter the reproductive strategies of alien plants by promoting a shift from clonal spread to greater sexual reproduction (Holm et al. 2018) and facilitate sexual reproduction by increasing germination rate and seed dispersal (Gillard et al. 2017). Such aliens may encounter conditions more suitable for breeding and spread in the future, as with the tree *Schinus molle* in South Africa (Richardson et al. 2010). Contrastingly, increasing temperature can also have indirect negative effects on alien species. For example, warming could reduce the fruit production of native plants on which the invasive fruit fly *D. suzukii* feeds and reproduces (Ulmer et al. 2022). Alien species adapted to urban areas may have an advantage as the global climate changes (urban climate; URCLM, Borden and Flory 2021) because urban areas tend to be warmer and drier than surrounding regions, so populations adapted to these areas may be more able to establish in novel environments because of preadaptation (preadaptation; PREAD). Urban-adapted populations may also have other competitive advantages over rural populations (urban competition; URCM, Borden and Flory 2021), such as unique traits developed in urban environments that can increase their invasiveness (species invasiveness; SINV). Global development may also facilitate the transport and arrival of new non-native populations (Gillard et al. 2017), and can homogenize anthropogenic landscapes thus facilitating the invasion of organisms adapted to these ecosystems (anthropogenic homogenization; ANHO, Hufbauer et al. 2012). A review by Juroszek and von Tiedemann (2015) established that disease risk is projected to remain unchanged or to be reduced in the future, mainly due to supra-optimal temperature conditions for the development of some pathogens during the growing season and/or reduced rainfall and leaf wetness, respectively. Climate change can exacerbate the impact of invasive populations on ecosystems through the disruption of the local species-interaction networks, potentially leading to phenological mismatches between plants and pollinators, predators and prey, and parasites and hosts.

The current and future effects of climate change, considered with the problems of invasion debt and continued anthropogenic disturbance, make actions inhibiting future introductions, managing contained populations of alien species, and mitigating the effects of established aliens, crucial (Fig. 1). Despite this, in recent years there have been misguided calls for the end of invasion biology within the research community and some growing discontent with the removal of invasive species by the public (Simberloff and Vitule 2014). Effective action to mitigate invasion impacts requires both significant support from stakeholders, which can only be achieved with clearer communication and conceptual understanding from invasion researchers. Effective communication with such stakeholders is a key aspect in the management of invasive species and should not be understated, as many of the barriers to biosecurity are not technical, but rather social and economic (Simberloff 2015).

Conclusion

Our review has explored and defined existing hypotheses relating to biological invasions, and elucidates how they divide into three main groups, depending on whether they relate to the species, community or ecosystem levels. We also provided illustrative examples covering a large range of animal and plant taxa and ecological situations, to aid understanding of individual case studies in a broader conceptual framework. The large-scale visualisation of the hypotheses and their potential links along an invasion timeline, from establishment to expansion and then evolution of invasive populations, may facilitate their use in future studies (Fig. 1). For further harmonization across contexts, we suggest that invasion hypotheses could benefit greatly from a functional perspective, and thus invite the community to consider incorporating functional traits in future studies. This could pave the way for a better perspective of the determinants of invasion success through elucidation of the actual roles of species, e.g. based on the consideration of the functional and ecological originality of the organisms, including species diet. Future studies should also combine ecological, physiological, immunological, chemical and microbiological measurements, when possible, to elucidate the key drivers of the different hypotheses and steps along the invasion timeline. Consistent use of properly organised and defined invasion hypotheses is particularly helpful for communication between researchers, which can only help when engaging with the public, managers and decision-makers.

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Author contributions

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Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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