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Opinion

Harnessing traits to predict economic impacts from biological invasions

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Biological invasions stand among the main anthropogenic threats to ecosystems globally while causing multitrillion-dollar impacts. Surprisingly, while trait-based frameworks have been designed to predict invasion success and invader ecological impacts, no such approaches exist to understand and predict economic impacts. We propose the first such framework by bridging the evolutionary biology of traits and the escalation of invasion costs. Previously acquired traits can benefit performance, and their rapid change could exacerbate impacts through adaptive and non-adaptive processes during invasion, such as natural selection, genetic drift, or phenotypic plasticity. Emerging evidence suggests that some organismal traits can determine economic impact magnitudes. We discuss new transdisciplinary avenues that can inform cost forecasting and management responses for current and future biological invasions.

Traits underpin impacts across biological invasion stages

Biological invasions (see Glossary) are drivers of biodiversity declines, degradations of social well-being, and trillion-dollar economic burdens globally. Biological invasion is a stage-based process comprising transport, introduction, establishment, and spread, with economic and environmental impacts possible at each of these stages [1]. Invasion rates are growing as global trade and transport networks intensify, precipitating rapid redistributions of Earth's biodiversity [2,3].

Most research on the consequences of biological invasions has focused on the **ecological impact** that invaders exert on native biodiversity and on ecosystem stability and function [4]. However, burgeoning evidence syntheses have revealed the trillion-dollar **economic impact** caused by non-native species (NNS) globally [5,6]. Cost analyses help to translate environmental impacts into tangible values, alerting the public and government bodies to the invasion issue. Invasion costs take many different forms, and, because they can be incurred across all stages of the invasion process, effective actions to address them need to consider the biological characteristics of invasions at each of these stages (Figure 1). At (pre-)transport and introduction stages, economic impacts can be incurred via targeted proactive biosecurity strategies such as **vector** management (e.g., ballast water treatment systems), where costs can be further incurred via transport infrastructure damage (e.g., fouling) and border checks at origin and recipient ports [6]. At later stages of establishment and spread, non-native populations can generate management costs through eradication, containment, or long-term control initiatives. They can also cause damage to a variety of economic sectors [7].

While evolutionary dynamics underpin all stages of the invasion process [8], their incorporation into economic impact assessments has been neglected. The importance of specific **traits** for NNS success can differ across invasion stages [9,10], but little is known about how traits or

Highlights

Understanding monetary cost drivers arising from biological invasions is critical for achieving effective impact mitigation and management responses. This includes global sustainability objectives around ecosystem services.

Frameworks in invasion science have identified taxon-specific trait profiles and macroecological patterns that promote establishment success, spread, and impact. Studies have also indicated that trait changes can occur rapidly during invasion, with implications for impact and management. However, the integration of economic impacts and the characteristics of recipient economies into these frameworks remain undeveloped.

Costs from biological invasions can be understood and predicted through an evolutionary framework by harnessing traits and trait changes during invasion to forecast impacts on different economic sectors. Our perspective provides a key step toward elucidating these mechanisms.

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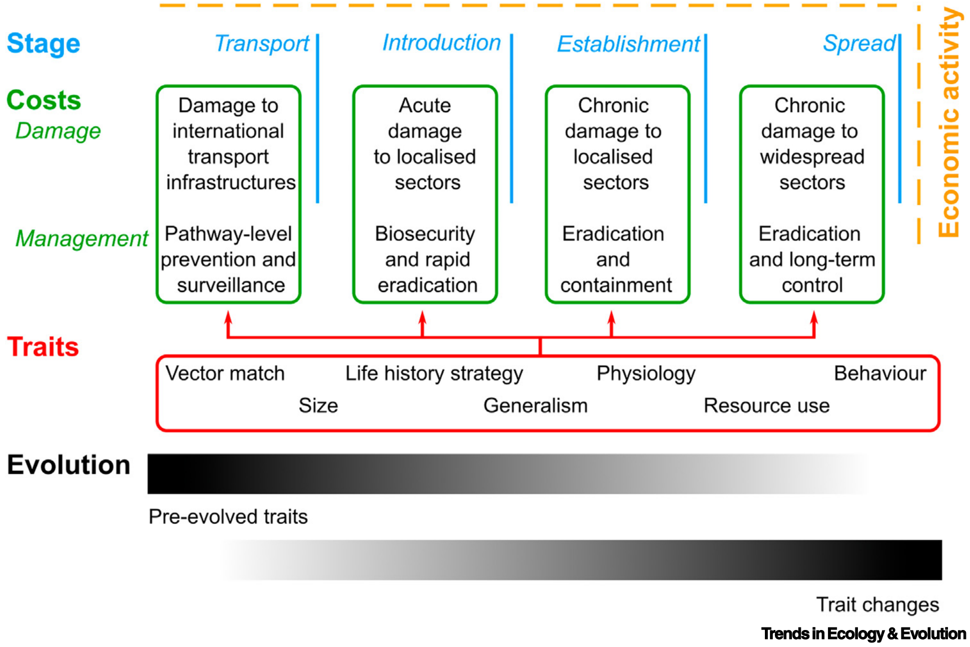

Figure 1. Schematic display of different traits that influence economic impact from biological invasions. Biological invasions follow a series of stages with discrete spatiotemporal damage and management costs within each stage. The nature and severity of economic costs ultimately depends on the economic activity sectors present, such as primary industries, as well as management decisions, which can be politically motivated. Non-native species traits can influence their impacts across all invasion stages. Examples of non-native species traits that can be important over these stages are shown, although note that these can be strongly species- and context-specific in their alignment. Initially, pre-evolved traits from the native or source range are of high importance, after which adaptive or non-adaptive changes during invasion become more prominent, as reflected by the color gradient.

their rapid changes during invasion link to impact. Understanding the trait-based determinants of costly invasions would help with management planning by identifying the characteristics of high-impact current and future NNS. In turn, this will permit quantitative assessments of how rapid changes in costly traits can exacerbate impacts, thereby linking evolutionary biology, invasion science, and economics.

To address this need, we suggest that the impacts of NNS can be predicted from (i) their traits and (ii) rapid changes to those traits during invasion. By studying and integrating both of these facets, we propose a framework to better understand how invasion costs are driven by traits over the whole invasion process.

Previous trait-based assessments

Species' traits have widely been used in **risk assessments** [11,12]. However, a general limitation of frameworks designed to forecast the consequences of biological invasions on the basis of species-level trait profiles is that the approach neglects different magnitudes of invasion success and impacts within and between populations of the same species, determined by the interaction between NNS and their new environment [13]. Moreover, while species traits have received attention within risk assessment frameworks, the integration of economic costs into trait-based frameworks remains unexplored. A major step forward would be to understand how trait characteristics and their rapid changes predict and explain variations in cost magnitudes [14].

A framework for economic impact forecasting can draw from established invasion frameworks, and particularly the concept of 'invasion syndromes.' These are based on **pathways**, traits, and recipient ecosystem characteristics that determine invasion dynamics and impacts and thus inform effective management response options [9,15]. Syndromes can also be used to identify high-risk species without an invasion history on the basis of organismal life history and ecological traits, as well as macroecological patterns such as species distribution [16]. Similar lessons can be learned from evaluations of species range shifts with climate change, whereby ecological traits such as movement capacity, population size, ecological generalism, climatic tolerance, and reproductive rates are informative [17].

Whereas species traits related to invasion success and range shift may putatively explain different economic costs, little research has explicitly investigated whether NNS traits and their rapid changes over the invasion process explain economic impacts [18,19]. Recent evidence using non-native tetrapods suggests that certain biological and biogeographic traits can explain monetary costs, including lifespan, invaded range size, non-native residence time, and habitat breadth in birds; fecundity and diet in mammals; and maturation time and diet in reptiles (Table S1 in the supplemental information online). While traits linked to costs are generally taxon-specific [19], as is the case for success across invasion stages [20–22], it is likely that the understanding of these emerging drivers can help advance management responses to mitigate impacts (Box 1).

Traits, invasion success, and impact

Traits can shape both NNS success and impact [8,23]. These traits can change over the course of invasions, driven by both **adaptive** and non-adaptive forces from three main mechanisms. First, **preadaptation** can facilitate invasion success of populations through environmental matching between native and invaded areas [8]. Second, **phenotypic plasticity** can allow organisms to rapidly respond morphologically, physiologically, or behaviorally to stressors at all stages of the invasion process [24,25]. Third, local selective pressures can rapidly contribute to the emergence of novel genotypes in the invaded environment – alongside trait changes through

Box 1. Traits, economic costs, and management of biological invasions

Understanding links between species traits and costs is critical for both proactive (i.e., predicting and preventing future impacts on the basis of trait profiles) and reactive (i.e., responses to observed impacts) management actions. Substantial monetary savings, as widely recognized in the invasion science literature [55,71,72], can be achieved through earlier, more efficient management, and we argue that trait-based profiling is a key step to achieve this goal. Identifying traits, within and across taxonomic groups, that heighten non-native species (NNS) impacts is expected to improve proactive prioritization efforts. This includes informing political and legal avenues, such as lists of high-risk species to be banned from trading or rapidly eradicated once detected (e.g., European Union Invasive Alien Species Regulation 1143/2014), thereby contributing to the design of biosecurity strategies [73]. Furthermore, by highlighting traits and macroecological factors that link to costs, species that do not yet have an invasion history (in either specific locations or timeframes) could be identified in preventative and prioritized efforts against novel invasions. An alternative to focusing on individual traits is identifying ecological functions linked to high NNS costs, from which specific traits serving as functional proxies could be pinpointed [74].

Quantification of rapid trait changes along spatial and temporal gradients during invasion could help direct efficient management by targeting the most impactful individuals, populations, and species [75]. This includes targeting individuals with certain phenotypes, such as high mobility at invasion fronts, certain dietary preferences, or particular life history strategies [75]. It could also inform timescales for effective management before traits in benign species potentially change to become costly [36]. Incorporating such information will help to avoid pitfalls associated with static cost assumptions in conservation management initiatives [76], ultimately supporting more robust and effective management initiatives.

It is important to stress that even in the absence of known economic impacts, there is an imperative to manage NNS because of their effects on numerous ecological processes and ecosystem services. These should not be ignored, despite the challenges in quantifying and/or monetizing such effects [71]. Therefore, an absence of documented economic costs for some NNS does not excuse a lack of management in the presence of severe environmental effects.

Glossary

Adaptive: pressures such as selection that create a bias in the reproduction of individuals with beneficial traits, by contrast to nonadaptive changes that are primarily random, owing to mutation or genetic drift.

Admixture: interbreeding of previously isolated populations of non-native species, resulting in a lineage that descended from multiple sources.

Biological invasions: the process of human-mediated introduction of species outside of their natural range. Successful biological invasions are characterized by population establishment and spread in the new environment.

Context dependence: biological or environmental characteristics that modify biological invasions and their impact on ecosystems or socioeconomies.

Ecological impact: a change in a biotic or abiotic ecosystem component caused by a biological invasion.

Economic impact: a monetary or nonmonetary cost incurred by a socioeconomic system as a result of biological invasion.

Extragenetic: processes driving nongenetic changes, including epigenetic inheritance, parental effects, microbiome transmission, and cultural inheritance.

Genetic drift: a random process that changes the frequency of a gene variant in a population, such as through genetic bottlenecks that reduce population size.

Hybridization: the mating of individuals from genetically distinct populations that produces offspring, with links to invasiveness and impact.

Invasion core: the central area of an invading population, often proximal to the point of introduction and characterized by high abundances of the non-native species and population stability.

Invasion front: the leading edge of an invading population as it expands, which often includes individuals adapted to spread effectively and lower abundances.

Invasiveness: the potential for a non-native species to successfully establish and spread in its new environment. Invasiveness can be considered as a gradient independent of impact.

Mutation: a change in the DNA sequence of an organism that can occur during the invasion process, which can be harmful, beneficial, or neutral.

genetic drift, **admixture**, **polyploidization**, **hybridization**, or **mutation** [10,24]. These processes are broadly appraised below.

Preadaptations that facilitate success in NNS are traits that have previously been acquired in the source population within the native range and facilitate success in the introduced range [22,25,26]. Stressors could confer beneficial adaptations within NNS, such as tolerances to harsh environmental conditions [27–29]. Selective filters for individuals displaying specific traits can bolster invasion success through accentuation of traits in founding populations, creating **propagules** that are more resilient to novel environments and predisposed to enter, survive, and exit the transport stage to then be introduced and established [25,28,30]. Management strategies targeting specific vectors could further select for resilient individuals and foster evolved resistance to stressors, such as that arising from long-term chemical control [28,31]. The outcome of these effects can have an overwhelming influence on the rate of establishment and spread postintroduction and potential future costs.

High phenotypic plasticity can bolster tolerance to changeable environmental conditions experienced through the invasion process. Plasticity can be particularly beneficial for populations with limited adaptive potential in the case of low founding genetic diversity. Phenotypic plasticity can differentially affect individual life history components and, in an economic cost context, could result in taxa that are primed to affect different economic sectors under various environmental conditions in the invaded range. However, plasticity can also evolve within populations, potentially exacerbating **invasiveness** by conferring greater 'plasticity potential' [24,32].

During invasion, rapid trait changes can occur because of nonrandom sorting of trait variants within populations in response to selective pressures [28,33]. These adaptive changes can influence the dynamics of invasion by modifying traits related to dispersal, reproduction, or resource use. For example, postintroduction, individual animals with trait variants that promote mobility likely advance to the **invasion front** from the **invasion core**, creating subpopulations characterized by distinct traits via environmentally or behaviorally assortative mating. These changes can include high levels of boldness, aggression, feeding, dispersal, or reproductive investment compared with the invasion core [33,34] but are subject to **context dependence** [35]. Regardless of their adaptive or non-adaptive drivers, rapid trait changes in NNS could exacerbate damages to various activity sectors [7,36]. Selective pressures caused by invaders on the fitness of resident species can shift native evolutionary trajectories, with the potential to disrupt ecological networks and communities, including by constraining available resources or moderating trophic interactions [10,37]. Rapid growth in invasive populations could also stifle management efforts, such as by overwhelming existing response protocols or containment areas, thereby requiring additional funding to mitigate threats to various industries and/or human health.

Similarly to NNS establishment and spread [20,22,38], initial research linking traits to monetary costs of NNS has revealed context dependency across taxa (Table S1 in the supplemental information online). Several invasion hypotheses provide fruitful grounds for future trait-based assessments of economic costs at different invasion stages, considering both traits and rapid trait changes (Table 1) [39].

Extragenetic inheritance of functional traits

Trait-based frameworks are nearly invariably based on the assumption of genetically inherited functional phenotypes [40]. However, over the last two decades, a stream of evidence has demonstrated that **extragenetic** inheritance – epigenetic inheritance, parental effects, microbiome transmission, and cultural inheritance – from parents to offspring, and even horizontally within

Pathways: the routes or mechanisms for the introduction and spread of non-native species.
Phenotypic plasticity: the ability of an organism to shift its physical characteristics (phenotype) in relation to environmental characteristics.
Polyploidization: a heritable condition arising from whole-genome duplication that results in an organism possessing more than two sets of chromosomes.
Preadaptation: the degree of environmental match between native and invaded ranges, which confers advantages during invasion.
Propagule: a biological unit that functions in propagating an invasive population, such as a seed, spore, or gravid individual. Propagule pressure refers to the number, frequency, and quality of individuals introduced to a new area.
Risk assessments: the evaluation, identification, and estimation of the level of threat associated with a potential non-native species. This is often a qualitative or semiquantitative assessment.
Traits: distinguishable qualities within or among organisms, such as physiological, behavioral, or morphological characteristics, which are influenced by the environment and/or genes. Whereas species can be distinguished by a unique set of traits or genetic material, intraspecific variation in trait values can be substantial and is best considered across a distribution.
Vector: a physical means or agent that transfers non-native species into a new area.

Table 1. Synthesis of the main hypotheses that predict a functional role for traits as causes for economic impacts in non-native species (NNS)

Organismal traits	Hypotheses and derived predictions
I. Genetic traits	
Genetic diversity hypothesis	Hypothesis: NNS populations with greater genetic diversity are more likely to cause severe economic impacts because of greater adaptive potential and resilience to natural enemies.
Polyploidy hypothesis	Hypothesis: NNS that are polyploid organisms are likely to have more severe economic costs through improved performance in the invaded range (e.g., reproductive flexibility and greater growth rates).
II. Demographic traits	
Bet-hedging hypothesis	Hypothesis: Populations that employ bet-hedging strategies over time and/or space, to negate negative stochastic events (such as by spreading reproductive output across their lifespan or different habitats), are more likely to incur substantial economic costs.
Fast life histories hypothesis	Hypothesis: Life history traits conferring rapid population growth, facilitating establishment, and spread, influence the severity of economic costs among NNS and their populations.
III. Ecological traits	
Ecological generalism hypothesis	Hypothesis: Populations with ecologically generalist niche breadths (e.g., in diet, microhabitat use, or temporal activity) are more likely to cause substantial economic impacts across a wide range of non-native environments, relative to more specialist populations.
Enemy release hypothesis	Hypothesis: Release from natural enemies in the invaded range exacerbates factors that promote economic impacts, such as population abundance and spread, under greater resource availability.
Habitat filtering hypothesis	Hypothesis: The economic costs of an NNS are more severe where they are preadapted to a region, based on the environmental and primary industry conditions in their native range.
Resource consumption hypothesis	Hypothesis: NNS associated with traits conferring high rates of resource use are associated with greater economic impacts, owing to greater interaction strengths with commercially valuable resources.
IV. Extragenetic inheritance	
Extragenetic phenotypic adaptation hypothesis	Hypothesis: Establishment of NNS in new environments is facilitated by rapid nongenetic adjustment of fitness-relevant phenotypic traits (i.e., phenotypic adaptation) to newly encountered environmental demands. These adjustments can involve mechanisms such as activation or silencing of gene expression mediated by DNA methylation or demethylation, microbiome acquisition, or cultural adaptation.
V. Phenotypic plasticity	
Phenotypic plasticity hypothesis	Hypothesis: Costs are more severe where NNS populations exhibit high phenotypic plasticity, which facilitates tolerance to environmental changes and potentially widespread effects.
VI. Biological novelty	
Biogeographic distinctiveness hypothesis	Hypothesis: NNS from a different biogeographic region are more likely to cause socioeconomic damage because of a greater risk of naiveté in the recipient biota.
Island susceptibility hypothesis	Hypothesis: NNS are more likely to become established and have major economic impacts on islands than on continents.
Novel weapons hypothesis	Hypothesis: NNS that carry parasites, pathogens, or toxins that are novel to the biota of a region are likely to pose a risk to one or more bioeconomic resources.
Relatedness hypothesis	Hypothesis: NNS that are closely related, phylogenetically and/or functionally, to native species are less likely to cause severe economic costs, because the activity sector may already manage similar impacts from native species.

The hypotheses are organized according to the type of trait (from genetic to biological novelty) involved in economic impacts. The rationale of the hypotheses is derived from common hypotheses in invasion biology [39]. We propose that many of these traits can rapidly change during the invasion process, providing a further dimension for predictions.

populations, plays a significant role in shaping rapid phenotypic (nongenetic) adaptation [41–45]. Just like in evolutionary adaptation of phenotypes, extragenetic adaptation results in phenotypes functionally adjusted (i.e., phenotypically adapted) to environmental pressures, which thus correlate with fitness [42]. Extragenetic phenotypic adaptation can occur rapidly and in response to drastic differences in the environmental demands around individuals (e.g., such as a newly entered non-native environment) [42,46,47], which makes these phenotypic responses potentially key components for the successful establishment of introduced species. As expected, the success of biological invasions has been shown to be facilitated by extragenetic inheritance via multiple mechanisms [48,49], sometimes translating into large-scale impacts [50]. Therefore, while the role of extragenetically inherited traits has rarely been linked to the success and impacts of biological invasions, we suggest that this is an avenue that will have to be incorporated to fully account for the mechanisms underlying the escalation of economic impacts across invasion stages.

Towards a framework linking traits and trait changes to costs

Traits influencing invasiveness often differ across invasion stages [10,17], and these differences can lead to distinct socioeconomic impacts. In this context, we focus on traits linked to economic impact, which may not always align with those driving invasiveness [51]. To help advance predictive frameworks, we identify two key areas of focus: (i) traits that link to costs and (ii) rapid changes to these traits that exacerbate costs. This distinction allows a more targeted analysis of how traits contribute to economic costs at different stages of invasion. As we develop the rationale of this framework, we highlight the unprecedented advantages of rapidly emerging approaches for trait data acquisition, processing, and analysis (Box 2), which provide opportunities to refine predictive models.

Traits and economic costs

Species have evolved traits in their native range that can predispose them to succeed across all invasion stages. Pre-evolved traits affect the entrance, survival, and exit from introduction vectors, including organism behavior, morphology, and life history [25]. This leads to sampling effects that influence propagule diversity and therefore genetic diversity in founding NNS populations that can go on to establish and spread [8]. These pre-evolved traits could in turn mediate the propensity of NNS to cause economic impacts in the environments (sectors) encountered during invasion.

In a similar way to invasion success, identifying life history and ecological traits linked to costs could be used to screen for risk from current and future invaders and to inform management

Box 2. Modern resources and the emergence of novel opportunities to record traits and link them to biological invasion costs

A growing number of open-access, global-scale trait databases are rapidly enabling unprecedented collation of functional, morphological, and physiological information across taxonomic groups (e.g., Open Traits Network). Currently, comprehensive resources exist for all tetrapods (i.e., birds, mammals, reptiles, and amphibians). These databases collate trait data both among and within species under relevant spatiotemporal and environmental gradients [77–80]. Complementary macroecological data are also available from growing numbers of biodiversity databases (e.g., Global Biodiversity Information Facility). These data sources and capabilities can be leveraged alongside existing invasion frameworks, which explicitly integrate evolutionary processes [8].

Gaps in trait data are, however, pervasive for many taxa and regions, and their collection requires substantial sampling and financial efforts. Museum specimens provide unique opportunities for development of large-scale geographically, taxonomically, and temporally comprehensive databases, particularly for morphological traits, across as many stages of data collection as required. Considering the widespread devastation caused by human activities on biodiversity globally, museum collections offer unique resources. Using such specimens, standardized time series of trait changes can be built rapidly through measurements of preserved biological materials, which could in turn be linked to biological invasion costs across world regions. Moreover, these efforts could identify environmental factors that influence the rate of change in traits, such as climate change and habitat alteration.

The unparalleled volume of data accessible from museum collections synergizes with the rapid development of machine learning technologies for analyses of increasingly complex sets of interactions. These can then be employed to achieve a range of goals, including predicting the potential economic impacts of species, even for those for which knowledge is limited. For example, the rapid progress in bioinformatic technologies and integrative interspecific phylogenetic modeling approaches provides opportunities to interrogate large databases to identify and impute traits that statistically link to monetary costs. This allows discrimination of the extent of impacts of NNS with increasing predictive accuracy. Furthermore, phylogenetic comparative methods can help quantify how strongly traits translate into impact and can in turn be used to derive phylogenetically informed predictions of impact for future invaders. Species distribution models integrated with economic information could highlight where significant impacts are likely to occur, helping direct proactive policies, management, and precautionary action in these locations [81–83].

prioritization toward the most impactful species across locations [52]. Traits such as rapid generation time, high fecundity, dietary generalism, rapid and efficient use of limited resources, functional novelty, and ability to transmit diseases or zoonotic spillover have been associated with strong ecological – and potentially economic – impacts [19,53,54]. Nevertheless, the effects of these traits are likely to differ because of context dependence, including the taxon, invasion stage, or nature of economic activity in recipient countries (Figure 1; Table S1 in the supplemental information online).

In recent years, there have been extensive efforts to document monetary costs of biological invasion and to synthesize them at a global level [5,55]. Moving forward, the use of trait-based profiling could identify population- or species-specific characteristics relevant at all scales to mitigate future adverse effects [19]. Specifically, once explanatory traits for monetary costs are identified statistically (e.g., using generalized additive models or phylogenetic comparative approaches) [19], they could be used to (i) extrapolate unknown costs for known NNS and (ii) identify and prioritize taxa that, even if not currently invasive, possess traits suggesting they could impose significant economic burdens [16].

Given the prevailing data gaps and biases in these areas of research [5], it is critical to expand collective efforts to collate data on the costs of NNS and species traits. This is essential for accurately distinguishing genuine differences in species' impacts from artefacts driven by uneven research efforts. Notwithstanding the available cost information for approximately 1000 NNS [56], economic cost data are available for only a proportion of known impactful NNS, and their documented monetary impacts vary over several orders of magnitude [57]. These data are currently richest for taxa such as mammals, fishes, and insects, and it may thus be most pertinent to initially focus on these groups when linking traits to NNS costs [19].

Rapid changes to costly traits

The traits that NNS bring into the invasion process can rapidly change across stages, with differences between or within populations potentially profound [13]. As discussed above, these changes can be genetic adaptations from heritable genetic variation mediated by natural selection or via extragenetic inheritance. The role that rapid changes in traits play in the success and longer-term impacts of invaders has been neglected, but we provide tentative links for a handful of NNS (Box 3).

Ecological and evolutionary studies are required to elucidate how traits of individual NNS change along spatiotemporal invasion and anthropogenic stress gradients (e.g., urbanization) [26,58]. This information can then be used to determine how trait changes scale with economic impacts at different stages of invasion. Currently, monetary costs are often reported at coarse spatiotemporal scales that can preclude robust understandings of impact drivers [5]. To advance this area, researchers could employ quantitative approaches to identify traits that are explanatory of monetary costs (i.e., statistically explain variations in impacts), complemented by empirical data tracking how these traits change over time and space within species. Simulation studies could then use these established trait–cost relationships to forecast how changes in those same traits magnify or dampen economic impacts for a given population or species. Such studies could be conducted within and then compared among taxa, given the potential idiosyncratic and context-dependent nature of cost outcomes.

Studies across multiple generations with quantitative genetic techniques and exploiting the enormous wealth of data that can be extracted from museum specimens (Box 2) could allow precise determination of evolutionary rates among invaded communities [59]. Lessons could be learned

Box 3. Examples of evolution of non-native species (NNS) traits that can link to invasion costs

Invasion front cane toads, *Rhinella marina*, exhibit superior dispersal capacity because of evolution in morphological (e.g., longer legs), behavioral (e.g., moving more often and straighter), and physiological (e.g., greater endurance) traits in Australia [33]. Assortative mating through environmental trait filtering has facilitated an up to ten-fold increase in spread rates at invasion fronts within a century [33,84]. The cane toad has the highest invasion costs of all amphibians globally, with over US$43 billion in observed impacts, mainly from management [85]. It is intuitive that faster spread rates would require commensurately higher management investments to span control and containment efforts over a larger area. Therefore, these trait changes have directly raised management expenditures across the invasion gradient (Figure I).

In non-native consumers, feeding rates can increase at the invasion front [34]. If such responses are a general feature of NNS, primary industry losses could worsen along similar spatiotemporal gradients, such as through intensified consumption efficiency of economically valuable resources (Figure I). For example, maximum feeding rates of European green crab, *Carcinus maenas*, on commercially important shellfish more than doubled between native and highly impacted invaded ranges in Canada [86]. This change in consumption rate will exacerbate costs generated by this species, which have already surpassed US$86 million in North America [87].

Mosquitoes are the costliest group of NNS globally because of their medical costs, recreational disruptions, and management actions. *Aedes* spp. have cost at least US$95 billion in invaded ranges since 1975 [88]. The Asian tiger mosquito *Aedes albopictus* is adapted to breed in natural microhabitats such as forest edge tree holes in its native range. By contrast, invasive populations of this species now effectively exploit artificial habitats, thereby exacerbating contact with humans and disease risk in urban environments [89] (Figure I).

Competitive effects on native taxa, or productivity, could change because of the alteration of traits in plants (Figure I) [90,91]. This pattern is seen in defensive compounds against herbivory, with evolution in chemical deterrent responses shown in plants with longer invasion histories [92]. In European invaded ranges, the ragweed *Ambrosia artemisiifolia* has evolved distinct defensive genes and lower pathogen rates than native populations [93]. These have probably exacerbated their multibillion-dollar economic health costs from allergic reactions on the continent [94].

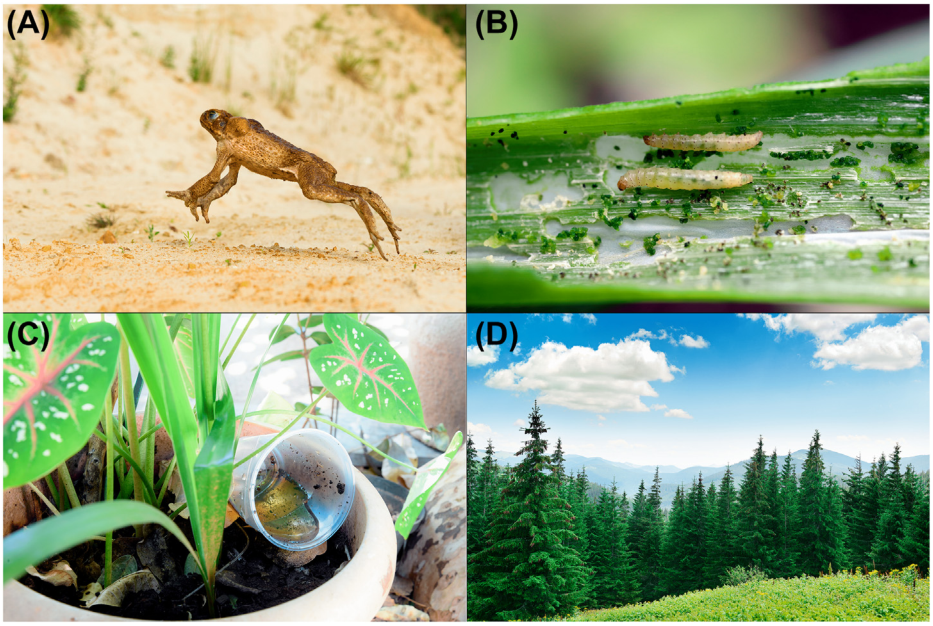

Figure I. Examples of non-native taxa evolving traits that promote impact. (A) Invasive cane toads can evolve traits that promote rapid dispersal, challenging management actions. (B) Invasive agricultural pests can exhibit greater feeding rates at invasion fronts. (C) Invasive mosquitoes can adapt to exploit human environments, increasing disease circulation and medical costs. (In the photograph, black resting eggs are shown above the water line in a plastic cup.) (D) Invasive trees can exhibit greater productivity at invasion fronts, requiring intensified management. Images sourced from Shutterstock.

from other fields, such as food science, where quantitative genetics have been used intensively to promote traits conducive to productivity in plants and livestock [60], albeit with trade-offs in terms of ecological resilience [61]. Common garden experiments that assess the roles of phenotypic plasticity can also be used to understand impacts under context dependencies in a similar way to assessments of invasion success [9,32]. Molecular genetics could be further used to reconstruct invasion histories and to analyze trait divergence between costly and uncostly invasions. A robust framework with the capabilities to develop quantitative predictions about the economic costs caused by NNS ultimately depends on the synergy between the traits that individuals bring into the invasion process and how these traits change during invasion.

Incorporating environmental change and socioeconomic context

Invader trait changes interact with and respond to major global climatic and land use changes, just as initial invasions can be triggered by such changes [62]. Indeed, some initially innocuous NNS incur conspicuous impacts following the arrival of novel genotypes, after the evolution of traits that enhance spread, or after being triggered by rapid environmental changes that favor enhanced reproduction or competitiveness [62,63]. These factors can create unexpected and rapidly escalating costs, potentially overwhelming key economic sectors. Integrating predicted responses to major environmental changes into trait-based species impact profiles can be expected to improve economic predictions, effect explanations, and societal outcomes. To achieve this, more fundamental studies are required to elucidate how traits conducive to impact change along relevant environmental gradients and then to link these trait data to the rapidly accruing economic costs [5].

Socioeconomic context means that impact prediction for monetary costs differs from existing frameworks for invasion success and ecological impact [57]. This is because the monetary impacts of NNS also depend on the characteristics, at the time of invasion, of the economic sectors in the locations considered. Therefore, the economic impact of an invasion ultimately results from the interactions between traits of the species with the recipient environmental and economic characteristics. For example, freshwater fouling bivalves cause substantial economic costs because of their short generation time, early maturity, high fecundity, and byssal attachment [64]. Likewise, industrial water supply system characteristics render them vulnerable to bivalve invasion success (e.g., easy entrainment of larvae in pipelines, abundance of complex artificial surfaces for colonization). Wood-boring insect impacts on forestry sectors are similarly bolstered in the presence of dense monospecific tree plantations, where they can rapidly spread and cause high costs per unit area [65]. Links between particular species' traits and economic impacts can thereby be described as a 'lock and key' mechanism, being contingent on the characteristics of the area invaded. A similar premise has been used to assess the likelihood of organism entry, survival, and exit considering the characteristics of anthropogenic vectors [25].

This mechanism conceptually parallels the importance of recipient ecosystem characteristics in the context of 'invasion syndromes' [9]. However, here we instead propose that the characteristics of the economy in the invaded region directly mediate impact susceptibility alongside NNS traits and environmental context. For example, countries that are reliant on a single activity sector, such as monospecific agriculture or forestry, could be strongly susceptible to impacts from a single invasion that generates specific impacts on those economically valuable organisms, especially in less developed countries [7]. Furthermore, different introduction pathways from various sources of origin also have a strong influence on the magnitude of invasion costs to recipient regions [66]. Countries with a higher gross domestic product (GDP) would generally be expected to incur greater absolute costs from NNS, owing to higher economic value of damages and greater spending capacities on management, as well as their global connectedness [67]. It is therefore likely that economic impact NNS syndromes could form from a nexus across (i) trait profiles, (ii) responses to environmental change, and (iii) recipient socioeconomic characteristics.

Concluding remarks

Transdisciplinary expertise, fostered through collaborations among biologists, epidemiologists, economists, and other scientists alongside practitioners, would facilitate implementation of our framework that will answer questions relating to trait linkages with economic impact predictions (see Outstanding questions). These collaborations could also help to resolve inconsistencies in terminology used across fields, jointly consider concepts in modeling and prediction of invasions, and enable the development of interdisciplinary tools and methods [68]. Furthermore, they can help to draw conceptual parallels among biological processes and economic impacts (e.g., between biological invasion and infectious disease impacts) [69]. These exciting possibilities for transdisciplinary work and collaborations should also consider future changes in socioeconomic activity patterns that can emerge rapidly on an evolutionary timescale [67,70]. Such changes could cause novel impacts from NNS to be realized as different economic sectors emerge and become susceptible. Rapid trait changes could therefore be a catalyst that amplifies or mitigates biological invasion costs over time. This dynamic has far-reaching implications across various socioeconomic sectors and introduction pathways in an increasingly globalized world.

Outstanding questions

Which evolved traits prior to invasion are linked to the highest economic costs, and which activity sectors are they strongly tied to?

How quickly do economic impacts manifest during invasion along spatiotemporal gradients, and to what extent do these economic impacts vary within and between invasive populations of the same species?

How effectively can environmental changes and shifting economic activity sectors amplify invasion costs through ‘lock and key’ mechanisms and the escalation of impactful traits?

How fast do species’ traits diverge from those displayed in native environments following invasion, and does this predict invasion costs?

What are the interlinkages and relative contributions between adaptive and non-adaptive processes in the escalation of invasion costs?

Can similar traits for ecological impacts be used to predict economic impacts from biological invasions?

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Declaration of interests

The authors have no interests to declare.

Supplemental information

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