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Four priority areas to advance invasion science in the face of rapid environmental change

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Abstract: Unprecedented rates of introduction and spread of non-native species pose burgeoning challenges to biodiversity, natural resource management, regional economies, and human health. Current biosecurity efforts are failing to keep pace with globalization, revealing critical gaps in our understanding and response to invasions. Here, we identify four priority areas to advance invasion science in the face of rapid global environmental change. First, invasion science should strive to develop a more comprehensive framework for predicting how the behavior, abundance, and interspecific interactions of non-native species vary in relation to conditions in receiving environments and how these factors govern the ecological impacts of invasion. A second priority is to understand the potential synergistic effects of multiple co-occurring stressors—particularly involving climate change—on the establishment and impact of non-native species. Climate adaptation and mitigation strategies will need to consider the possible consequences of promoting non-native species, and appropriate management responses to non-native species will need to be developed. The third priority is to address the taxonomic impediment. The ability to detect and evaluate invasion risks is compromised by a growing deficit in taxonomic expertise, which cannot be adequately compensated by new molecular technologies alone. Management of biosecurity risks will become increasingly challenging unless academia, industry, and governments train and employ new personnel in taxonomy and systematics. Fourth, we recommend that internationally cooperative biosecurity strategies consider the bridgehead effects of global dispersal networks, in which organisms tend to invade new regions from locations where they have already established. Cooperation among countries to eradicate or control species established in bridgehead regions should yield greater benefit than independent attempts by individual countries to exclude these species from arriving and establishing.

Key words: biosecurity, climate change, ecological impact, invasive species, management, risk assessment.

Résumé : Les taux sans précédent d'introduction et de propagation d'espèces non indigènes posent des défis croissants à la biodiversité, à la gestion des ressources naturelles, aux économies régionales et à la santé humaine. Les efforts actuels en

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matière de biosécurité ne parviennent pas à suivre le rythme de la mondialisation, révélant des lacunes critiques dans notre compréhension et notre réponse face aux invasions. Les auteurs identifient ici quatre domaines prioritaires permettant de faire progresser la science des invasions face aux changements environnementaux mondiaux rapides. Premièrement, la science des invasions devrait s'efforcer de développer un cadre plus complet pour prédire comment le comportement, l'abondance et les interactions interspécifiques des espèces non indigènes varient en fonction des conditions des environnements récepteurs et comment ces facteurs régissent les impacts écologiques des invasions. Une deuxième priorité consiste à comprendre les effets synergiques potentiels de multiples facteurs de stress concomitants—notamment les changements climatiques—sur l'établissement et l'impact des espèces non indigènes. Les stratégies d'adaptation au climat et d'atténuation devront tenir compte des conséquences possibles de la promotion des espèces non indigènes, et des réponses de gestion appropriées aux espèces non indigènes devront être élaborées. La troisième priorité est de s'attaquer à l'obstacle taxonomique. La capacité à détecter et à évaluer les risques d'invasion est compromise par un déficit croissant de compétences taxonomiques, qui ne peut être compensé de manière adéquate par les nouvelles technologies moléculaires seules. La gestion des risques de biosécurité deviendra de plus en plus difficile à moins que les universités, l'industrie et les gouvernements forment et emploient du nouveau personnel dans les domaines de la taxonomie et de la systématique. Quatrièmement, nous recommandons que les stratégies de coopération internationale en matière de biosécurité tiennent compte des effets de tête de pont des réseaux de dispersion mondiaux, dans lesquels des organismes ont tendance à envahir de nouvelles régions à partir d'endroits où ils sont déjà établis. La coopération entre les pays pour éradiquer ou contrôler les espèces établies dans les régions de tête de pont devrait donner de meilleurs résultats que les tentatives indépendantes de chaque pays pour empêcher ces espèces d'arriver et de s'établir. [Traduit par la Rédaction]

Mots-clés : biosécurité, changements climatiques, impact écologique, espèces envahissantes, gestion, évaluation des risques.

1. Introduction

Invasion science—the systematic investigation of the causes and consequences of biological invasions—is a rapidly evolving interdisciplinary field. Its explosive growth over the past few decades mirrors societal concern over the upsurge in the global rate of invasions (Seebens et al. 2017, 2021; Pyšek et al. 2020) and reflects the fundamental and applied importance of understanding how species spread into new regions, why some ecosystems are more vulnerable to invasions, and what factors govern the impacts of non-native species. To date, research addressing these issues has yielded valuable insights into the forces that structure ecological communities, the relationship between diversity and stability, mechanisms of adaptation and rapid evolution, causes of extinction and biotic homogenization, and the connectedness between socioeconomic and ecological systems, among other phenomena (Lockwood et al. 2013; Hui and Richardson 2019). More remains to be done to sharpen and integrate these insights into predictive frameworks. In addition, pressure is increasing for invasion science to adapt to emerging issues such as rapid advances in biotechnology, accelerating global change, expanding transportation networks, abrupt landscape transformations, and infectious disease emergence (Ricciardi et al. 2017; Nuñez et al. 2020). Invasion science is a relatively young discipline (Ricciardi and MacIsaac 2008) that has embraced diverse domains in ecology and related fields (e.g., population biology, biogeography, evolutionary biology, paleoecology, physiology) and has formed linkages with disciplines related to biosecurity—such as epidemiology, risk analysis, resource economics, and vector science (Vaz et al. 2017). This multidisciplinary expansion reflects the increasing complexity of biological invasions and their impacts (Richardson 2011; Pyšek et al. 2020).

Here, we consider how invasion science should adapt to the Anthropocene—an era of burgeoning human influence, novel stressors, and rapid environmental change (Steffen et al. 2015; Waters et al. 2016). We are an international team of ecologists, with diverse and extensive experience in biological invasions in many parts of the world. Our team gathered in September 2018 to consider emerging scientific, technological, and sociological issues that, if addressed, should ensure that invasion science can more successfully contend with rapid global change. Through consensus (see Supplemental Material[1]), we arrived at four overarching issues that are relevant to a broad range of taxa, environments, and geographic regions and that encompass some of the most important challenges facing our field today (Fig. 1).

2. Predicting ecological impacts of invasions under rapid environmental change

2.1. The need for greater predictive power: major advances and ongoing challenges

2.1.1. Environmental context-dependency of impacts

While invasion science has made substantial progress in understanding how non-native species arrive in new locations and establish self-sustaining populations (Catford et al. 2009; Jeschke and Heger 2018), it has been less successful in forecasting when and where such species will substantially affect their recipient environments (Ricciardi et al. 2013; Simberloff et al. 2013; Kumschick et al. 2015). Non-native species can affect ecological, economic, cultural, and human health in diverse ways (Jeschke et al. 2014; Shackleton et al. 2018), but in this section we focus on ecological impacts. Here, "impact" is defined broadly as a measurable change to the environment attributable directly or indirectly to the presence of a non-native species (Ricciardi et al. 2013), and includes their effects on individual performance, population size and composition of ecological communities of native species, which in some cases may be irreversible (IUCN 2020).

Impact prediction is a long-standing, complex challenge. While rates of non-native species introductions are increasing across regions (Seebens et al. 2017, 2021), impacts have been recorded for only a small fraction of these species and the sites they invade (Ruiz et al. 1999; Ricciardi and Kipp 2007; Vilà et al. 2011; Hulme et al. 2013; Simberloff et al. 2013; Evans et al. 2018*b*). It is generally assumed that most invasions have negligible environmental consequences (Williamson and Fitter 1996), whereas a small proportion has significant and sometimes enormous effects – an inverse magnitude–frequency distribution similar to that associated with natural disasters (Ricciardi et al. 2011). However, uncertainty exists concerning which cases truly reflect an absence of impact rather than a lack of study (Latombe et al. 2019). Even well-known impacts exhibit substantial variation over time and space; invaders may remain innocuous for years or even decades prior to becoming disruptive when, for example, environmental change triggers a new impact (Crooks 2005; Coutts et al. 2018). The impacts of any given invader can vary greatly among

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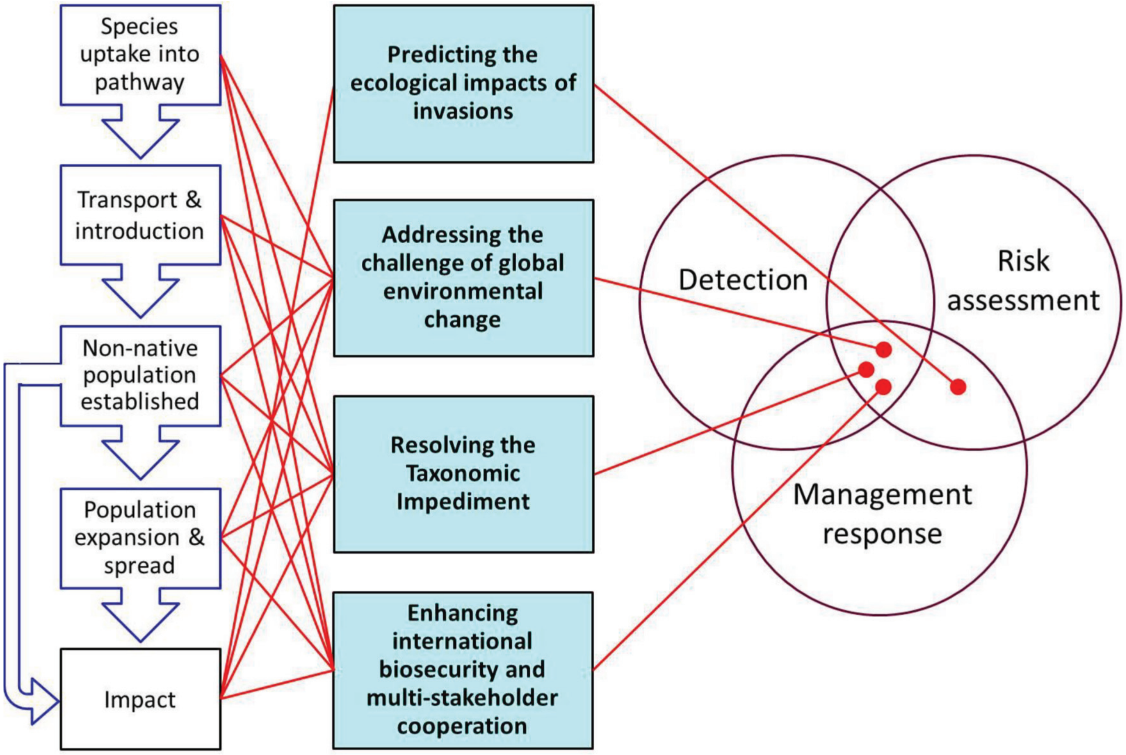
Fig. 1. Four priority issues (center column) that must be addressed by invasion science to meet burgeoning challenges in an era of rapid environmental change. Through multiple connections, each issue is implicated in one or more stages of the invasion process (left column), as well as in the impact of the invader (which can occur at any stage from introduction to establishment to spread) and in the detection, risk assessment, and management response of invasion threats. For example, scientific understanding of the processes that control the diversity, abundance, distribution, and impacts of non-native species ultimately depends on the quality of taxonomic data; therefore, resolving the "taxonomic impediment" (the erosion of our capacity to recognize biodiversity and distinguish non-native from native species accurately) would enhance our ability to detect non-native species, assess their impacts, and respond to new invasion threats.



ecosystems (Strayer 2020) and across environmental gradients within ecosystems (Kestrup and Ricciardi 2009; Stritar et al. 2010; Hulme et al. 2013; Sapsford et al. 2020). Context-dependencies of invasion—that is, interactions among propagule pressure, the traits of the invader, the composition of the recipient community, and the physicochemical environment—have hardly been addressed by any formal body of theory, but some overarching frameworks are now being explored (e.g., Cronin et al. 2015; Iacarella et al. 2015*a*; Dickey et al. 2020; Sapsford et al. 2020).

Coupled with the challenge of context-dependency is the sheer complexity of mechanisms by which non-native species can interact with their environment (Ricciardi et al. 2013; Kumschick et al. 2015). Synergistic interactions, nonlinearities, time lags, threshold effects, regime shifts, and indirect effects of non-native species are difficult to predict (Ricciardi et al. 2013; Essl et al. 2015*b*; Kumschick et al. 2015; Aagaard and Lockwood 2016; Hui and Richardson 2017; Strayer et al. 2017). Consequently, accurate risk assessment tools for sound management decisions are still lacking.

2.1.2. *Temporal variation and time lags of impacts*

Factors affecting temporal variation in impact remain a major research gap, in large part because the vast majority of impact studies are conducted over very short time scales (Strayer et al. 2006; Stricker et al. 2015). Time-since-invasion has been found to be an important correlate of the ecological impacts of non-native species (Iacarella et al. 2015*b*; Evans et al. 2018*a*; Zavorka et al. 2018), but time lags between establishment and peak impact have thus far evaded prediction and are increasingly recognized as hindering risk assessment (e.g., Coutts et al. 2018). Predictions of spatiotemporal variation in impact direction and magnitude could be improved through experimental and theoretical investigations of the relationship between an invader's per capita effect and its abundance (Yokomizo et al. 2009; Cronin et al. 2015; Sofaer et al. 2018; Bradley et al. 2019; Strayer 2020). We must also consider the influence of spatial scale on per capita effects or impacts measured in small plots and mesocosms; attempts to extrapolate these effects up to landscape scales relevant to management (e.g., by calculating the product of the per capita effect, local abundance, and range size of an invader) might not adequately capture changes to biodiversity, biotic interactions, and ecosystem function, and thus might underestimate some large-scale consequences of invasion (Hawkins et al. 2015; Bernard-Verdier and Hulme 2019; but see Dick et al. 2017*b*). Greater effort is required to test factors that mediate indirect and multi-scale effects, particularly where an invader's impact is transmitted across a suite of interacting species (Feit et al. 2018).

Conservation interventions and ecosystem management must contend with significant time lags between the onset of the environmental stressors and the expression of invader impacts, and forecasting such phenomena is plagued by context dependencies and nonlinearities (Essl et al. 2015*b*, 2015*c*; Coutts et al. 2018). An understudied issue is how to recognize and manage the interactive and cumulative effects of time lags in ecological responses to invasion. Delayed biodiversity responses (e.g., dominance shifts, species turnover, metapopulation dynamics, extinction debt) to anthropogenic stressors such as invasion can lead to abrupt shifts in ecosystem functioning (Essl et al. 2015*b*) and underestimation of rates of contemporary biodiversity change (Essl et al. 2015*c*). Given the management implications of this phenomenon, ecological responses to compounded and cumulative stressors are becoming an increasing focus of theory, experiments, and time series analyses (Foster et al. 2016; Candolin et al. 2018; Kleinman et al. 2019; Shinoda and Akasaka 2020).

2.1.3. Impacts on ecosystem processes

Demand is growing for reliable assessments and predictions of the ecosystem-level impacts of non-native species, especially those impacts that affect the provision of ecosystem services in rapidly changing environments (Vilà and Hulme 2017). This need reflects the larger challenge of understanding how ecosystem function is altered by the combined effects of species gains (invasion, range expansion) and losses (extinction, range contraction), which are simultaneously consequences and drivers of global change. With few exceptions (e.g., Mascaro et al. 2012; Kuebbing et al. 2015), work on how these two forces affect ecosystem functioning has developed largely in isolation (Wardle et al. 2011). Owing to this disconnect, ecologists are unable to predict over the coming decades the net ecosystem consequence of these two opposing forces—specifically, whether or not species that are gained at local scales through invasion will affect ecosystem process rates in a comparable way to those native species that are lost. Moreover, despite the many ecosystem impacts revealed thus far (Ehrenfeld 2010; Vilà et al. 2011; Simberloff et al. 2013), few types of ecosystems and invaders have been studied relative to those that exist (Crystal-Ornelas and Lockwood 2020). It is likely that an enormous number of non-native species have affected individual performance, population sizes, and community structure, through direct and indirect effects on native species (e.g., via competition, herbivory, predation, hybridization, and as diseases or their vectors), or by changing the physical, chemical, or structural characteristics of the environment (Blackburn et al. 2014; IUCN 2020) in ways that have not been documented (Carlton 2009; Simberloff 2011). Ecosystem-level impacts must remain a major focus, with researchers taking advantage of available technological tools (e.g., Asner et al. 2008). Further, research on how biodiversity loss affects ecosystem functioning must be evaluated alongside effects of non-native species additions, to better understand how human-driven species change will affect ecosystem processes across scales. For example, given that community composition can influence biosphere–atmosphere exchange of greenhouse gases (Metcalfe et al. 2011), how non-native species influence processes that underpin this exchange relative to native species extirpations can have significant, currently unrecognized consequences for climate change.

2.2. New and future challenges

2.2.1. Impacts of interventions for restoring ecosystem function

Co-occurring environmental stressors are increasing pressures to use non-native species for restoring ecosystem functions eroded by native species loss (Mascaro et al. 2012; Castro-Díez et al. 2019). The notion of restoring ecosystems that have lost important species by substituting non-native species to perform key functions traces back at least to the 1980s (Atkinson 1988) and has seen growing interest in recent years (Seddon et al. 2014*a*; Galetti et al. 2017; Pires 2017). Of particular interest are proposals and ongoing projects to establish species to replace seed dispersers of plant species that have lost their ancestral native mutualisms (Seddon et al. 2014*a*; Galetti et al. 2017), and large herbivores and carnivores to fulfill lost trophic linkages (Svenning et al. 2016). These efforts are often listed under the rubric of "rewilding" (Lorimer et al. 2015; Svenning et al. 2016). Calls for active rewilding to restore ecological processes (Perino et al. 2019) have primarily focused on the reintroduction of native species, but some practitioners have advocated a "flexible" approach to restoration that entails using non-native species (Ewel and Putz 2004; but see Sotka and Byers 2019) as well as the reintroduction of species into parts of their native range from which they have been absent for various lengths of time.

As with translocation to accommodate climate change (see section 3.2.3), proposals for translocations to restore ecosystem functions (e.g., IUCN 2013; Aslan et al. 2014) have been the subject of substantial discussion of potential risks and benefits (Nogués-Bravo et al. 2016; Rubenstein and Rubenstein 2016; Fernández et al. 2017; Pettorelli et al. 2018; Perino et al. 2019). Lunt et al. (2013) have compared possible risks and benefits of translocations to restore ecosystem functions and translocations to address climate change, pointing to the possibility of addressing both goals simultaneously. To employ proposed decision tools and adhere to the International Union for Conservation of Nature (IUCN) guidelines, both advocates and critics increasingly agree that progress is required on more accurate risk assessments and on characterization, categorization, and quantification of the environmental impacts of translocations (Jeschke et al. 2014), as has occurred with the Environmental Impact Classification for Alien Taxa (EICAT) framework (Blackburn et al. 2014; Hawkins et al. 2015; Evans et al. 2016), which has been adopted as an IUCN standard (IUCN 2020), and similarly for socioeconomic impacts, as has begun under the socio-economic impact classification of alien taxa (SEICAT) framework (Bacher et al. 2018).

Conversely, other efforts to conserve native species or restore ecosystems involve non-native species eradication. Such interventions should be preceded by a predictive risk assessment of the indirect effects of invader removal (Bergstrom et al. 2009; Caut et al. 2009; Ruscoe et al. 2011; Lindenmayer et al. 2017) and the legacy effects of invasion (Corbin and D'Antonio 2012; Grove et al. 2015; Reynolds et al. 2017; Pickett et al. 2019). Eradication has demonstrably benefited biodiversity (Baider and Florens 2011; Monks et al. 2014; Jones et al. 2016), but targeting the removal of a single invasive species within an ecosystem that contains several non-native species can be counterproductive. A predictive framework must consider the topology of species interactions, both trophic and nontrophic, to determine when single-species management may lead to unintended consequences (Glen et al. 2013; Ballari et al. 2016; Hui and Richardson 2019).

2.2.2. Burgeoning novel organisms

Escalating risks are associated with the intentional and unintentional release of novel organisms (those with no analogue in the natural environment) through biotechnological advances that create transgenic or genetically engineered organisms. For example, some proposals for rewilding entail "de-extinction"—i.e., creation of various sorts of proxies of extinct species for release to the wild. Versions of de-extinction are expected to become increasingly feasible (Stokstad 2015; Shapiro 2017). The process involves either backbreeding (Stokstad 2015) or the reconstruction of the genome of an extinct species from recovered strands of DNA, which can then be used either to modify or to replace the genome of a suitable living relative or to genetically engineer embryos that can be implanted in a compatible host. Some conservationists will advocate for such proxy species to be reintroduced to a suitable former geographic environment (Seddon et al. 2014*b*), and perceived ecosystem management benefits may arise from doing so (Church 2013). Environmental differences between contemporary and historic habitats (Peers et al. 2016) might encourage further genetic manipulation to create better adapted species. Depending on the length of time the proxy species has been extinct and the method used to produce the proxy, introducing such entities to the wild is tantamount to introducing a non-native species (IUCN 2013; IUCN/SSC 2016; Genovesi and Simberloff 2020), an action that in the absence of predictive knowledge increases the likelihood of unintended ecological consequences.

Advances in biotechnology will also facilitate the creation of self-replicating synthetic cells designed for novel tasks such as contaminant remediation, carbon sequestration, and the production of biofuels (Menetrez 2012; Azad et al. 2014; Singh et al. 2016; Dvořák et al. 2017). As synthetic and transgenic organisms will contain combinations of ecological traits that are unlikely to be encountered naturally, recipient communities will be evolutionarily naïve to these organisms and could be predisposed to being altered by them (Saul and Jeschke 2015). Such impacts could be subtle, but far-reaching, as has been demonstrated for macroscopic transgenic species (Post and Parry 2011; Vacher et al. 2011; Oke et al. 2013). Among the larger risks is the capacity for such organisms to evolve in the wild and to exchange genes with other organisms (Dana et al. 2012). Given the exponential growth of molecular technology, the rate of development of such organisms could outpace progress in developing effective risk assessments of their ecological effects. This issue emphasizes a need for greater integration of evolutionary and microbial biology into invasion science, and for developing impact theory and risk assessment methods that explicitly consider evolutionary change in both the invader and interacting species.

2.3. The way forward: a theoretical framework and tools for impact management

2.3.1. Developing and expanding a theoretical framework of impact

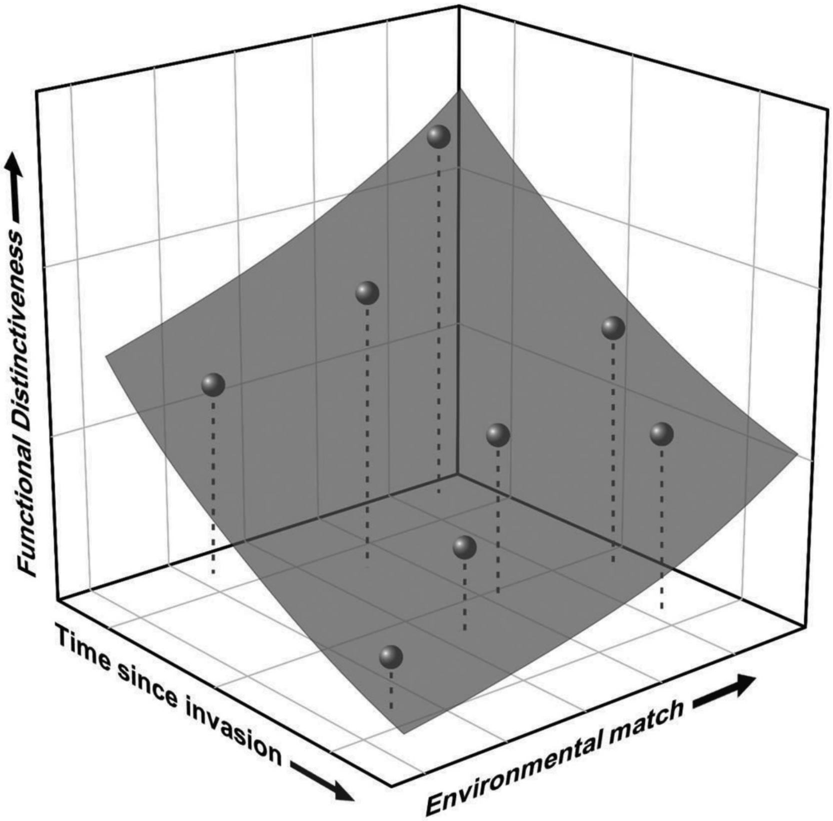
To meet societal demands, invasion science must continue to build a body of theory for understanding and predicting impacts from the level of populations to ecosystems (Ricciardi et al. 2013; Blackburn et al. 2014; Bacher et al. 2018). Progress toward this goal requires that hypotheses explicitly integrate abiotic and biotic context-dependencies, including biotic and abiotic drivers of spatiotemporal variation in impact. This integration parallels and perhaps can be informed by studies of how species loss affects ecosystem functioning in different environmental contexts (Ratcliffe et al. 2017; Baert et al. 2018; Kardol et al. 2018). One example of an integrative hypothesis is the Environmental Matching Hypothesis (Ricciardi et al. 2013), which posits that the per capita effects of an invader vary along environmental gradients such that they are maximal where abiotic conditions more closely match the physiological optimum of the invader (Kestrup and Ricciardi 2009; Iacarella et al. 2015*a*; Iacarella and Ricciardi 2015).

A second example that integrates context-dependence is the the Ecological (or Functional) Distinctiveness Hypothesis (Diamond and Case 1986; Vitousek 1990; Ricciardi and Atkinson 2004), which predicts that impact is most severe in communities missing species functionally similar to the invader. This hypothesis is derived from two observed patterns with strong empirical support. One such pattern is that a community's lack of eco-evolutionary experience, or ecological naïveté, determines its vulnerability to non-native consumers, parasites, pathogens, and competitors (Sih et al. 2010; Saul and Jeschke 2015; Davis et al. 2019; Nunes et al. 2019; Anton et al. 2020). The second empirically supported pattern is that the largest community-level and ecosystem-level impacts are generated by invaders that use key resources differently or more efficiently than natives do and that can alter disturbance regimes, habitat structure, or food web configurations (Vitousek 1990; Funk and Vitousek 2007; Morrison and Hay 2011). Given that more closely related species tend to be ecologically similar (Burns and Strauss 2011), it follows that phylogenetic distance, or simple taxonomic relatedness, is a proxy for functional distinctiveness. Thus, an allied hypothesis predicts that invaders representing novel taxa, once established in the community, are more likely to affect native populations negatively than invaders that are taxonomically similar to natives in the recipient community (Ricciardi and Atkinson 2004; Strauss et al. 2006; Davis et al. 2019). Despite longstanding recognition of eco-evolutionary experience as a driver of impact, most risk assessments do not consider evolutionary context. The consequences of the contemporary evolution of non-native species (e.g., Bertelsmeier and Keller 2018), and the effects of invaders on the evolution of native species, are underexploited, but promising areas of research (Saul and Jeschke 2015; van Kleunen et al. 2018) that point to the importance of integrating evolutionary biology in ways that enhance the predictive power of invasion science.

Several distinct, and over a dozen overlapping, hypotheses explain invader impact (Ricciardi et al. 2013), and additional hypotheses addressing invasion establishment success could potentially be extended to understanding impact (Catford et al. 2009; Jeschke and Heger 2018). These hypotheses could be organized into a coherent body of impact theory by eliminating redundancies and identifying commonalities (e.g., through consensus mapping of hypothesis networks; Enders et al. 2020). We can envision a general predictive framework built upon multiple axes that consider, among other things: (*i*) abiotic and biotic environmental context; (*ii*) functional distinctiveness between native and non-native species; and (*iii*) time-since-invasion (Fig. 2). The generality of hypotheses needs to be tested within various ecological and evolutionary contexts using, for example, spatially distributed experiments such as those employed to examine plant responses to nutrient enrichment and exclosure of mammalian herbivores (Borer et al. 2014). Experimental and survey designs that incorporate eco-evolutionary context have rarely been applied to the study of non-native species (but see Wardle et al. 2001; Colautti et al. 2014; Grimm et al. 2020). To address this gap, we advocate comparisons of conspecific populations across invaded and native ranges, recognizing that invasions and impact outcomes are population-level phenomena. Such experiments could be coordinated by collaborative global networks (Packer et al. 2017), which are a potentially powerful approach to understand the factors that govern large-scale variation in invader impact across climatic gradients, disturbance gradients, biogeographic realms, and boundaries of evolutionary significance.

Moreover, scientists would profit by looking to other areas of ecology and evolution, disease biology, and the social sciences, for theory that could potentially explain many components of impact and seeking to integrate these approaches into invasion science. Several classical ecological hypotheses, metrics, and concepts that have been tested in various contexts relevant to invasions (e.g., theories addressing biological control, island biogeography, metabolic scaling, resource utilization, competition) have arguably been underexploited by invasion scientists. Experimental approaches that have sought to incorporate principles of trophic ecology have revealed important patterns (Dick et al. 2017*a*, 2017*b*; Cuthbert et al. 2018, 2020). For example, prey switching (frequency-dependent predation) is a classical concept that has until recently been virtually ignored by invasion science (Cuthbert et al. 2018, 2019). In recent years, the classical functional response—the relationship between per capita consumption and resource density (Solomon 1949; Holling 1959)—has been adapted and applied to forecasting and explaining non-native species impacts through multi-species comparisons (Dick et al. 2017*a*; 2017*b*; Dickey et al. 2018; Faria et al. 2019). The rationale for exploring these experimental approaches is that invasion success and impact are often mediated by resource acquisition, a concept at the foundation of many hypotheses in invasion science (Catford et al. 2009; Ricciardi et al. 2013; Jeschke and Heger 2018) and that is relevant for both animals and plants (Rossiter-Racher et al. 2009; Ehrenfeld 2010). Indeed, several high-impact invaders have been found to be more efficient at using limiting resources than their native and non-invasive counterparts (Rehage et al. 2005; Funk and Vitousek 2007; Morrison and Hay 2011; Dick et al. 2017*a*; DeRoy et al. 2020).

Fig. 2. An example of integration of impact hypotheses. The three-dimensional plot represents the predicted variation in an invader's ecological impact in relation to three factors, shown as axes: (1) the functional (or phylogenetic) distinctiveness of the invader among resident species; (2) the degree of environmental match—i.e., the inverse of the distance between mean abiotic conditions in the invaded environment and the invader's physiological optimum; and (3) time since invasion. Functionally novel invaders, especially those that exploit key resources, are predicted to have greater impacts on the invaded ecosystem (Functional Distinctiveness Hypothesis). Invaders that are more physiologically matched to abiotic conditions in the invaded environment should have greater per capita effects (Environmental Matching Hypothesis). Further, in this example, impact is hypothesized to attenuate over time, based largely on the premise that given suitable time resident species (predators, prey, parasites, competitors) will adapt to the invader and dampen its influence. These factors are shown here to be mutually independent, but interactions are possible (e.g., physiological match may interact with time since invasion, owing to local adaptation or directional shifts in abiotic conditions).



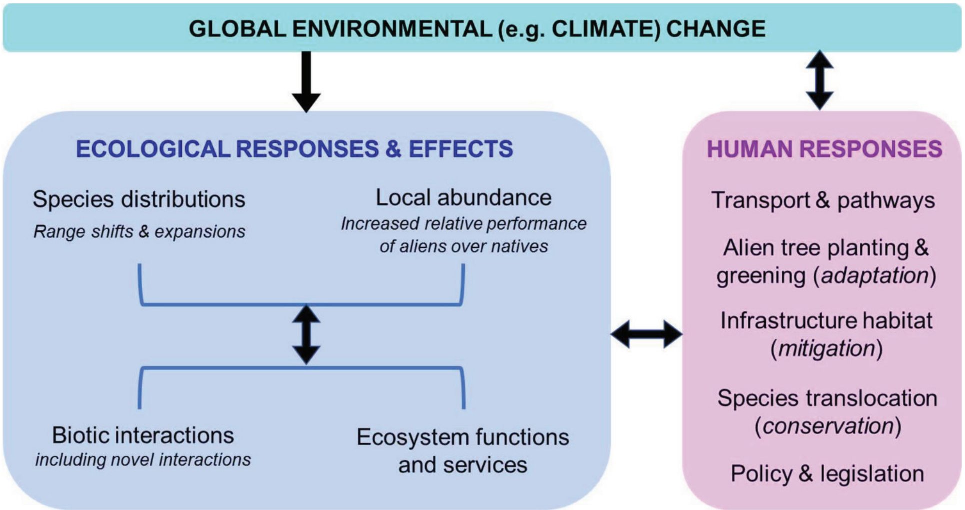
Broadening analyses to a more comprehensive community context could also help predict impacts in different environmental contexts (Smith-Ramesh 2017). An underexploited approach is to treat invaded communities as complex adaptive networks (Lurgi et al. 2014; Valdovinos et al. 2018; Hui and Richardson 2019). Predictive information could potentially be gained from modeling the dynamic responses of an ecological network, after developing appropriate metrics of interaction strength, and thus identifying resident species that are either facilitated or suppressed by the invasion (Hui and Richardson 2019).

2.3.2. Toward more comprehensive quantifications of invader impact

There is growing interest in quantifying impacts beyond traditional ecological and economic measures by using an ecosystem services framework that can capture information on provisioning (e.g., food, timber, fuel), regulating (e.g., climate, floods, nutrient cycling), and cultural services (Perrings 2010; Simberloff et al. 2013). For example, in highly-degraded ecosystems some established non-native species may offer beneficial services to some stakeholders (McLaughlan and Aldridge 2013), although any benefits of local cultivation of such species must be weighed carefully against risks of further spread. Such accounting would also need to consider negative impacts, which are diverse and substantive, on ecosystem services (e.g., Walsh et al. 2016; Vilà and Hulme 2017; Milanović et al. 2020). However, at present we know remarkably little about how even the most high-profile non-native species affect ecosystem services (Vilà et al. 2010; McLaughlan et al. 2014), a problem related to the challenges of evaluating ecosystem-level impacts (Simberloff 2011; Ricciardi et al. 2013). More reliable quantification of potential ecosystem services of invasive species, coupled with a deeper understanding of context-dependencies, would allow a more informed and comprehensive impact assessment. To this end, the Millennium Ecosystem Assessment and, more recently, the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES), which have examined how humans have altered ecosystems and these alterations have affected ecosystem services and human well-being (Millennium Ecosystem Assessment 2005; Díaz et al. 2019), could provide a suitable framework for developing protocols for risk assessment, perhaps informed by the EICAT and SEICAT classification schemes (Hawkins et al. 2015; Bacher et al. 2018).

Comprehensive impact quantification is challenged by knowledge gaps that may render risk assessments incomplete or misleading (Kumschick et al. 2015). One major gap is predictive knowledge of the role of species traits, combinations of traits, and trait–environment interactions in impacts, particularly at the ecosystem level. It is not clear under what situations the same species traits that confer an ecosystem service can also

Fig. 3. Global environmental change (in particular, climate change) directly and indirectly elicits ecological and human responses that promote invasions. Environmental change can trigger shifts in the distributions and abundances of native and non-native species, leading to novel biotic interactions and altered ecosystem functions and services, which can themselves prompt further ecological responses. Human responses include climate change adaptation and mitigation, as well as species conservation; many of the current human responses will likely facilitate invasions. These ecological and human responses also affect each other, compounding the direct impacts of environmental change.



damage an existing ecosystem service (Vilà and Hulme 2017) or contribute to an "ecosystem disservice"—properties or functions that are disadvantageous to humans (Milanović et al. 2020). Another major context-dependency that could distort risk assessment of a given invader is the presence of other invaders. Predictions, as well as post-hoc assessments, are potentially hampered by synergistic or antagonistic interactions between invaders, including those that can contribute to invasional meltdown—in which one invader facilitates another, leading to compounded impacts and potentially self-reinforcing effects (Simberloff and Von Holle 1999; Ricciardi 2001; Green et al. 2011). Disentangling the influence of various species involved in meltdowns requires detailed experimental planning (e.g., Braga et al. 2020), whereas invader interactions in multiple invaded ecosystems are generally poorly studied (Kuebbing et al. 2013). It therefore seems likely that most synergistic effects go unrecognized. Even where interactive effects do not occur, the cumulative effects of burgeoning numbers of low-impact invaders on ecosystems have been virtually ignored. Approaches toward quantifying and assessing the effects of multiple environmental stressors (Boyd et al. 2018; Hodgson and Halpern 2019; Hodgson et al. 2019) could potentially be adapted for multiple invading species and, furthermore, might be enhanced by efforts to collate experimentally validated invader interactions within global databases.

3. Addressing the challenge of global environmental change in invasion science

The second overarching issue is how invasion science can adapt to the onslaught of global environmental changes presently altering the rates, dynamics, and impacts of invasions through myriad drivers including climate change, overharvesting, extinction, pollution, landscape transformation, and shifting trade patterns. Ecosystems are likely to become more susceptible to invasions as these drivers degrade and modify food webs. For some native species, global changes create physiologically intolerable or suboptimal conditions that lower relative fitness (Catford et al. 2020) or provoke range shifts, further altering community composition and susceptibility to invader impacts (Gallardo and Aldridge 2013; Wallingford et al. 2020). Environmental change often affects native and non-native species differentially, modifying their interactions and selection pressures through shifting abiotic and biotic ecosystem conditions (Xiao et al. 2016; Meyerson et al. 2020; Stern and Lee 2020). This issue is well recognized and has been widely investigated for several years, yet the need for research and management solutions through the lens of invasion science is ongoing and increasing. Invasion science must continue to develop an understanding of key issues regarding global environmental change including interactions between invasions and other environmental stressors, climate adaptation and mitigation strategies, and evaluating and managing species range shifts and translocations. In this section, we primarily focus on climate change (Fig. 3), but note that many other forms of human-induced environmental change facilitate invasions and the relative dominance of non-native species (Catford et al. 2014; Seabloom et al. 2015; Liu et al. 2017; Essl et al. 2019).

3.1. Ecological synergies between invasions and climate change

3.1.1. Non-native species performance

Species distributions worldwide are mostly determined by climate, tectonic movements, and orographic barriers (Ficetola et al. 2017). Climate change will therefore have a major impact on species range and distributions irrespective of whether species are native or non-native to a particular region. However, differences in the magnitude of potential range shifts predicted for non-native and native species will be determined by differences in their biology, such as physiological tolerances and dispersal potential (Essl et al. 2019). The last decade has accordingly seen major efforts to investigate the role of climate change in the introduction, establishment, spread, and impact of non-native species (Hulme 2017).

Various meta-analyses have shown that non-native species often outperform and adjust better than native species to a rapidly changing climate (Sorte et al. 2013; Oduor et al. 2016; Liu et al. 2017). For example, hotter, drier environmental conditions enable non-native Asian tiger mosquitoes to outcompete native treehole mosquitoes in the United States (Smith et al. 2015), Eastern mosquitofish (*Gambusia holbrooki*) persist more successfully than native fish species in France (Cucherousset et al. 2007), and non-native Monterey pine (*Pinus radiata*) grow faster than native conifers in Spain (Godoy et al. 2011). Warmer temperatures in freshwater ecosystems will favor non-native species as these frequently have a greater heat tolerance than related native species (Bates et al. 2013); similarly, in the Mediterranean Sea, increases in temperature have facilitated the establishment of non-native tropical species (Raitsos et al. 2010).

A key element of climate change is an increase in the frequency and magnitude of extreme climatic events, which can have greater effects on invasion than changes in average conditions (Sheppard et al. 2012). Strong winds, floods, large waves, and storm surges can transport organisms into new regions (Diez et al. 2012), as discussed subsequently. Critically, extreme climatic events like heat waves, fires, severe storms, droughts, and floods act as major disturbances and will invariably destroy and damage resident native biota, reducing the uptake of resources, and can also increase resource supply (Catford and Jones 2019). Such disturbances are known to facilitate invasion (Davis et al. 2000), because many invasive species can take advantage of fluctuations in resource availability caused by disturbances (Catford et al. 2012; Singh et al. 2018). For example, European *Bromus* grasses that are highly invasive in North America can exploit available soil moisture more efficiently and thus recover more rapidly than native vegetation after drought (Harris 1967), enabling them to invade areas formerly dominated by native woody species (Kane et al. 2011). Similarly, a non-native freshwater phytoplankton species was able to invade and establish in a reservoir following the combined disturbance events of macrophyte removal and extreme drought (Crossetti et al. 2019).

3.1.2. Non-native species range shifts

Shifts in temperature and rainfall patterns attributed to climate change can increase the probability of establishment of non-native species that were previously constrained by climate (Walther et al. 2009; Hulme 2017) or climate-mediated interactions with native biota (Catford et al. 2020). Increasing evidence indicates that non-native species tend to respond faster than native species to climate change, with spread rates an order of magnitude higher than the velocity of climate change (Hulme 2012). For example, non-native plants have expanded upwards in the European Alps twice as fast as native species in response to warming (Dainese et al. 2017). Nevertheless, climate change can lead to both increases (Kriticos et al. 2003; Barbet-Massin et al. 2013; Gilioli et al. 2014) and declines (Bradley et al. 2009; Bellard et al. 2013; Xu et al. 2014) in the geographical range of non-native species. A general finding is that, as a result of climate change, the distribution range of non-native invertebrates and pathogens will expand, but range contractions are mostly expected for non-native plants and vertebrates (Bellard et al. 2018). For example, by the end of this century the suitable area worldwide for the red imported fire ant (*Solenopsis invicta*) is predicted to be 21% greater (Morrison et al. 2004), whereas for the velvet tree (*Miconia calvescens*) it is predicted that suitable habitat will be reduced in both its native and introduced ranges (González-Muñoz et al. 2015). However, trends may differ between terrestrial and aquatic environments. For instance, the warming of North American lakes is likely to increase thermal suitability for southern species of fishes that could expand their distribution poleward into non-native regions, potentially as far as the Arctic (Sharma et al. 2007; Della Venezia et al. 2018).

Besides overall change in temperature and precipitation, extreme climatic events can also help spread non-native species by overcoming dispersal barriers (Diez et al. 2012). For instance, hurricanes promoted dispersal of non-native cactus moth (*Cactoblastis cactorum*) across the Caribbean and into Mexico where it threatens native *Opuntia* species (Andraca-Gómez et al. 2015). Hurricane frequency was also positively correlated with the expansion of the non-native grass *Phragmites australis* across wetlands along the Gulf Coasts of the USA (Bhattarai and Cronin 2014). Likewise, flood events can increase pool connectivity and provide non-native freshwater species access to newly inundated areas (Vilizzi et al. 2014). For example, floods enabled the escape of cultured black carp (*Mylopharyngodon piceus*) in the Missouri River, US (Nico et al. 2005), and tilapia cichlids in southeast Asia (Canonico et al. 2005) and have facilitated the spread of zebra mussels (*Dreissena polymorpha*) in the Mississippi River catchment (Tucker 1996). Nevertheless, the natural variability of climate makes it difficult to attach high levels of confidence to some of the predicted changes, particularly those associated with extreme weather events (Bellard et al. 2013).

3.1.3. Novel interactions and per capita impacts

Climate change will, in many cases, increase the introduction rate, establishment probability, and spread rate of non-native species (Bellard et al. 2013), while simultaneously facilitating extensive range shifts of native species (Inderjit et al. 2017; Pecl et al. 2017; Essl et al. 2019), leading to novel ecological interactions and increased impacts. Range shifts are expected to contribute to widespread biotic homogenization (where more species are shared among communities) in some regions and the formation of novel communities in others (García-Molinos et al. 2015). Diverse novel biotic interactions and assemblages will arise from divergent responses of species and populations to climate change (Blois et al. 2013; Pecl et al. 2017). As discussed previously, new biotic interactions often result in high impacts when resident species have not co-evolved with newly arrived species (Ricciardi and Atkinson 2004; Cox and Lima 2006; Saul and Jeschke 2015). In some cases, range shifts of native species can cause impacts similar to those involving non-native species (Sorte et al. 2013; Inderjit et al. 2017), although impacts will be tempered by the eco-evolutionary experience of the resident species (sensu Saul and Jeschke 2015). Few studies have addressed range shifts of native and non-native species as a joint issue (Gallardo and Aldridge 2013; Sorte et al. 2013; Dainese et al. 2017; Inderjit et al. 2017; Singh et al. 2018).

While many studies have linked climate change to the spread of invasive species (detailed previously), the role of environmental factors in determining ecological impacts is understudied (Dickey et al. 2020). Climatic conditions that shift towards the physiological optimum of a non-native species could promote increased feeding rates, growth, or reproduction that amplifies its competitive or predatory effects (Hellmann et al. 2008; Iacarella et al. 2015*a*). For example, an invasive bryozoan is expected to have enhanced growth rates at warmer temperatures in the Northwest Atlantic, with greater modeled impacts on kelp beds under future climate conditions (Denley et al. 2019). Similarly, higher growth rates enable an invasive plant to outcompete a native plant in China at higher latitudes in the field and at warmer experimental temperatures (Wu et al. 2017). Predation rates of non-native species may also increase when warming temperatures are within the physiological optima of the invader (Iacarella et al. 2015*a*). For instance, the predatory response of an invasive freshwater amphipod increases when exposed to elevated temperatures and infected by a common parasite (Laverty et al.2017). Given that non-native species are expected often to outperform native species in response to environmental change, as discussed previously, their competitive and predatory impacts will likely also increase under these circumstances. A method has recently been developed that incorporates the per capita and abundance effects of non-native species under altered variables such as temperature, oxygen, salinity, and indeed any other variable in isolation or combination (Dickey et al. 2020). This predictive method crucially also factors in the climate response of the affected species (e.g., native prey), such that overall impact is holistically predictable. This method is in its infancy and ground-truthing is now limited only by data (Dickey et al. 2020).

3.1.4. *Changes to ecosystem services and human well-being*

Research on the interaction between invasions and global environmental change is essential to identify effects on ecosystem services and human well-being (Dukes and Mooney 1999; Walther et al. 2009; Pecl et al. 2017; Vilà and Hulme 2017). Although tools such as SEICAT (Bacher et al. 2018) and INSEAT ("INvasive Species Effects Assessment Tool"; Martinez-Cillero et al. 2019) have been developed to classify non-native species within a framework of ecosystem services and human well-being, these tools rely on expert elicitation as there are still surprisingly few quantitative data on the ecosystem services effects of even the most prolific invasive species. This is, in part, owing to the context-dependent impacts of invaders (see section 2) and because environmental change can alter the balance of positive and negative effects (McLaughlan et al. 2014). For instance, disturbed river banks and roadsides in Africa favor proliferation of the invasive tree, *Prosopis juliflora* (Shiferaw et al. 2019), which increases local income from wood sales, but reduces habitat suitable for livestock and results in lower income from cattle sales (Linders et al. 2020). The predicted future effect of interactions among climate, socioeconomic factors, and invasions on plant biodiversity hotspots constitutes the greatest threat in emerging economies located in megadiverse regions of the Southern Hemisphere (Seebens et al. 2015). Invasions and climate change also pose a combined threat to native species in protected areas and thus seriously compromise conservation of biodiversity and ecosystem services (Gallardo et al. 2017; Iacarella et al. 2020). Interactions between invasions and climate change will also affect human health; for instance, climate change models predict an increase in the life-cycle completion rate and extended periods suitable for development of the invasive mosquito *Aedes aegypti*, a vector of arboviruses including dengue, zika, and yellow fever, resulting in accelerated invasion in North America and China (Iwamura et al. 2020).

To investigate the effects of invasions on ecosystem services and human well-being, models should integrate interactions among several components of global change, not only climate change (Walther et al. 2009). Furthermore, studies should also explore these interactions in productive systems such as managed forests, agriculture, and aquaculture (Thomson et al. 2010; Ziska and Dukes 2014; Liebhold et al. 2017). A major concern for these resource sectors is that drought, warming, and elevated CO_2 will affect the performance of non-native species (i.e., pests, pathogens, and weeds) in complex and currently unpredictable ways. Research on their impacts requires, for example, quantifying not only how altered environmental conditions change weed and crop performance in isolation, but the magnitude of weed–crop competition on crop damage (Ramesh et al. 2017).

3.2. Human responses to climate change that favor non-native species

3.2.1. *Changes to invasion pathways*

Global change is also altering invasion risk by promoting new commercial trading routes and corridors. Shifting global economic forces (e.g., tariffs, manufacturing trends, recession, regional conflicts, climatic disasters) determine trade volume and thus the frequency with which aircraft or oceanic vessels travel between airports or seaports (Seebens et al. 2015). Such shifts drive temporal rates of species introduction and the range of taxa that invade (Levine and D'Antonio 2003; Hulme 2015; Bertelsmeier et al. 2018). For example, commercial shipping at polar latitudes of North America and Eurasia is either planned or already occurring, providing novel opportunities for introducing non-native species to Arctic waters (Miller and Ruiz 2014; Chan et al. 2019). The Southern Ocean is likewise becoming increasingly vulnerable to species introductions owing to increased propagule pressure from vessel traffic and reduced physical and physiological barriers (Aronson et al. 2015; Hughes and Ashton 2017; Smith et al. 2017; McCarthy et al. 2019; Cárdenas et al. 2020). Such human responses to climate change (Fig. 3) are altering the origins, taxonomic identity, and rate of introduction of non-native species in terrestrial, freshwater, and marine habitats worldwide (Seebens et al. 2015; Early et al. 2016; Della Venezia et al. 2018).

3.2.2. *Climate adaptation: planting non-native species and adding infrastructure*

As governments increasingly develop adaptive strategies to address climate change, many of these strategies are likely to entail using non-native species. Proposed interventions include initiatives to develop agricultural or aquacultural enterprises to deliver carbon-neutral energy sources (e.g., macroalgae and plants for biofuels) using known invasive non-native species (Barney and DiTomaso 2008). Pressure is also increasing to develop new varieties of pasture species that can better cope with changing climates, such as drought-tolerant and disease-resistant species, many of which are non-native in the countries in which they are sold and planted (Driscoll et al. 2014). Increased development of green roofs, vertical gardens, and water-saving horticulture to mitigate effects of climate change (Perini and Rosasco 2016) carry the risk of introducing non-native species by promoting drought-tolerant plants or breeding drought-resistant varieties, cultivars, or hybrids. Similarly, many large-scale tree-planting programs have not led to the replenishment of degraded forests with native tree species, but rather to afforestation of nonforest land, including biodiverse grasslands, with monocultures of non-native trees. Such efforts include massive tree-planting campaigns using non-native trees with the aim of mitigating the impacts of climate change and for poverty alleviation (Brundu et al. 2020). Such plantings might not help offset greenhouse gas emissions as much as expected, owing to unforeseen fluxes and complex system dynamics (Covey et al. 2012; Luyssaert et al. 2018; Popkin 2019). Indeed, inappropriate afforestation, especially in naturally treeless areas, can have serious consequences for sustainable development, biodiversity conservation, and ecosystem functioning (reviewed in Brundu et al. 2020). Furthermore, many species used in such programs are highly invasive, which means that their impacts extend beyond areas identified for afforestation (Brundu and Richardson 2016; Brundu et al. 2020).

Besides directly introducing species to sustain economic activities or to mitigate emissions, governments at all levels are responding to environmental change by developing new infrastructure. Strategies to combat sea-level rise have largely been addressed through engineered solutions (armoring, raising roadbeds, flood control structures). Each of these adaptation strategies presents an opportunity for existing non-native species to expand their range or impact and can create new suitable habitat for non-native species that arrive via ballast, hull-fouling, or the marine aquarium trade (Bulleri and Chapman 2010). Offshore wind farms also provide novel fouling habitats and "stepping stones" for invasions (Adams et al. 2014; De Mesel et al. 2015). Similarly, frequent droughts lead to efforts to provide secure water sources to urban populations, including construction of dams, canals, and other water-diverting mechanisms that can spread non-native species (Strayer 2010; Zhan et al. 2015; Gallardo and Aldridge 2018).

However, infrastructure developments can be designed to reduce their suitability as novel habitats or invasion routes for invasions by non-native species by minimizing environmental disturbances or emulating natural habitats (Dafforn et al. 2015).

3.2.3. *Species translocations for conservation*

Conservation scientists have introduced species to locations outside their native range for three main reasons: (*i*) to avoid extinction caused by an introduced species, often an introduced predator; (*ii*) to restore an ecological function (as detailed in section 2.2.1); or (*iii*) to allow species' ranges to keep up with climate change (Corlett 2016). Introductions to accommodate global climate change have increasingly attracted attention. As early as 1985, conservationists recognized that the climate of current species ranges will change so that locations with climate similar to that of today may be distant or separated by inhospitable habitat. They proposed several measures including direct human assistance in the form of translocation to suitable habitat unoccupied by the species of interest when adequate autonomous movement seemed unlikely (Peters and Darling 1985; Peters 1988, 1992; Davis 1989). This proposal received little interest for the next decade; a review of possible management responses to climate change listed only 13 mentions of translocations (Heller and Zavaleta 2009). None of these acknowledged possible negative effects of translocation. However, translocations had long been conducted in the name of conservation, notably of species threatened by introduced predators (Seddon et al. 2012, 2014*a*). For instance, endemic New Zealand birds threatened by non-native rats and mustelids had been translocated to predator-free islands since 1894, with many well-publicized projects (Clout and Craig 1995; Seddon et al. 2012); occasional concern about such efforts had been expressed on the grounds of potential unanticipated ecological impacts (e.g., IUCN 1987; Conant 1988; Atkinson 1990; Craig and Veitch 1990; Towns et al. 1990).

Translocation as a management response to climate change began to gain substantial attention with papers by McLachlan et al. (2007) and Hunter (2007), both raising the issue that this constitutes introducing a non-native species, which in turn might lead to a damaging invasion. Hoegh-Guldberg et al. (2008) produced the first decision tree for application of potential translocations in response to climate change, but they, and Hunter (2007), suggested that intercontinental introductions have proven far more likely to be damaging, whereas proposed translocations for climate change would be more restricted. A broader and more detailed criticism of climate change-motivated translocation (Ricciardi and Simberloff 2009*a*), based on the possibility of non-target impacts, elicited an exchange with several respondents (Ricciardi and Simberloff 2009*b*) and signaled a shift in the dialogue, with much more attention paid to the possibility of unintended consequences by virtue of introducing new species. Richardson et al. (2009) thus expanded the decision-tree approach into a heuristic decision tool with detailed considerations of both ecological and socioeconomic consequences of translocation or failure to translocate. The difficulty lies in estimating the probability of various potential outcomes (e.g., decline or loss of ecological functions in the recipient region) and quantifying other risks, both ecological and socioeconomic, to inform comparisons and decisions. In the last decade, translocation has received increasingly nuanced consideration of the relative risks and virtues owing to the rapidly growing understanding of the enormous conservation challenge posed by the scope and imminence of climate change and its likely effect on species ranges (Hewitt et al. 2011; Thomas 2011; Schwartz and Martin 2013; Williams and Dumroese 2013; Ricciardi and Simberloff 2014; Maier and Simberloff 2016; Simler et al. 2018).

The lines between translocation and biological invasion are becoming increasingly blurred. Both events involve species expanding beyond their historical biogeographic ranges, leading some authors to suggest that they differ only in public perception and value (Hoffmann and Courchamp 2016; but see Ricciardi 2007; Wilson et al. 2016). In addition, views on how to deal with the spectrum from "desirable" self-migrating species, to translocations undertaken for conservation (desirable to some, undesirable to others), to generally "undesirable" biological invasions are yet to be reconciled. Further, determination of "non-native", as defined by lack of co-evolution with the invaded community (Ricciardi 2012), and desirable or undesirable, as defined by valuations of impact (Jeschke et al. 2014), will become increasingly challenging as we seek to determine what to protect or manage in a shifting mosaic of species assemblages (Gilroy et al. 2017; Hill and Hadly 2018). The current framework for managing non-native species could yield protection of conservation-based translocated species despite potentially high impacts, compared to management and mitigation of high-impact species that spread via self-directed or direct, but accidental movement. Robust protocols for considering the entire range of possible impacts of facilitated range shifts, as well as those of self-migrating species, must be developed and integrated into policies and legislation with the engagement of stakeholders.

3.3. Government responses and global efforts

The global nature of biological invasions and their interactions with environmental change can strain the capabilities of governments to anticipate and respond to invasions now and into the future. As discussed in detail previously, the ecology of invasions under climate change is complicated. The directed asymmetrical movement of certain species poleward (Winter et al. 2014), and to higher elevations (Pyšek et al. 2011; Dainese et al. 2017), can point to systems requiring early-detection monitoring or intervention. Conversely, the effects of climate change could play out neatly along latitudinal or altitudinal gradients (Hanberry and Hansen 2015). A key unknown is the relative importance of introduction enhancement (e.g., colonization pressure, propagule pressure) from changing trade patterns versus the influence of climate change factors in facilitating species' range changes. Policies that address invasions could also be complicated by seemingly competing interests, including those associated with the economy and trade versus biodiversity and human health. Despite devastating new species invasions and pleas for a comprehensive approach to biosecurity, some countries, such as the United States, have even recently reduced coordinated federal leadership and investments to address invasions (Meyerson et al. 2019; Simberloff et al. 2020). Current coordinated global efforts to document invasions and impacts include the Global Register of Introduced and Invasive Species (GRIIS) and an invasive species assessment by the IPBES. These substantial undertakings will undoubtedly deepen our understanding of invasion trends, impacts, and management, but neither will result in policies to prevent species introductions that participating nations are obliged to adopt. Rather, it remains the role of national and local governments to identify, fund, implement, and enforce policies to manage invasions under changing conditions and, where possible, to coordinate with other nations.

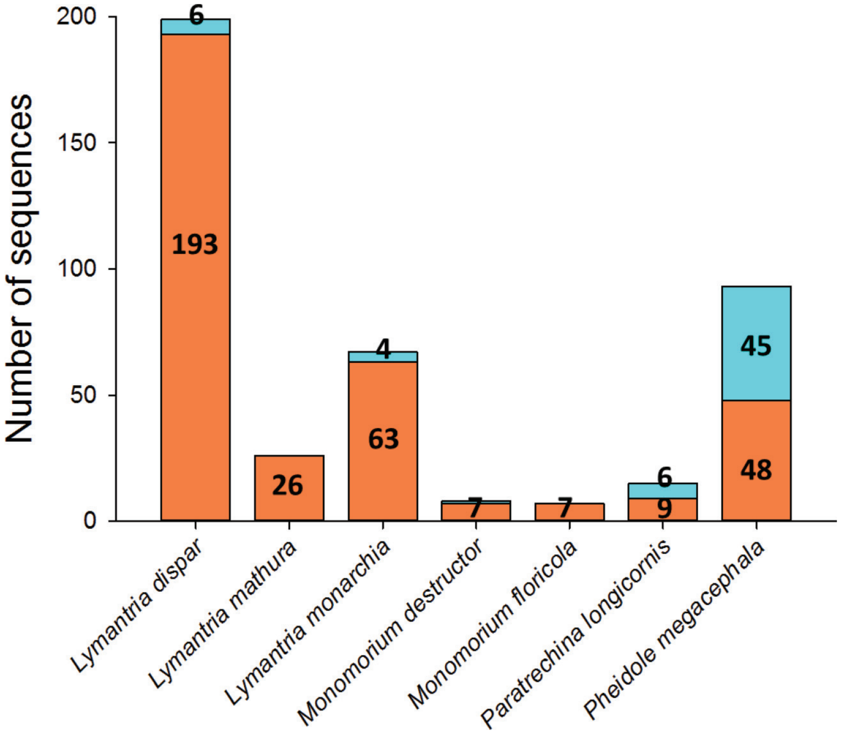
4. Resolving the taxonomic impediment

4.1. The enduring problem of taxonomic identification

The third overarching issue is our capacity to distinguish non-native from native species accurately. Scientific understanding of the processes that control the diversity, abundance, distribution, and impacts of non-native species ultimately depends on the quality of taxonomic data. The steady global erosion in training and expertise in systematics means that invasion science often lacks the taxonomic support to accurately identify many taxonomic groups in terrestrial, freshwater, and marine habitats (Godfray 2002). While this phenomenon exists across biomes and taxa, the largest gaps in taxonomic knowledge are associated with some of the most abundant species, including microorganisms and microfauna. Arguments (such as those of Costello et al. 2013) that the field of taxonomy is robust appear to be based on, among other fallacies, a misinterpretation that authorship inflation on taxonomic papers equates to an increasing number of taxonomists (Bebber et al. 2014; Daglio and Dawson 2019).

Molecular tools have made remarkable progress and offer great promise for illuminating the overlooked scale of biodiversity in all habitats (Hebert et al. 2003; Dincă et al. 2011). The application

Fig. 4. Examples of invasive insect species for which a discrepancy exists between the number of sequences available in GenBank v3.0 when using the two primary search query tools it provides: a taxonomy-based search of GenBank records (green) and a broader search using sequences or taxonomy of other publicly available data sources linked to GenBank (orange). Such discrepancies in search results across databases increase the risk that these species will be incorrectly classed as "unidentified" when metabarcoding approaches are used to identify non-native insects. Data from Boykin et al. (2012).



of modern sequencing techniques often reveals a vast array of unknown and often cryptic species. Srivathsan et al. (2019) report that of 7059 specimens of flies (Diptera, family Phoridae) collected in a single Malaise trap in Uganda over an 8-week period, MinION sequencing revealed more than 650 largely or entirely undescribed species, exceeding the total number of phorid taxa described for the entire Afrotropical region. Only one of these 650 species, however, has to date been formally described, based on morphological characters, as a new species. Molecular techniques combined with advanced culturing methods have revealed an enormous diversity of microbial taxa. Metagenomic sequencing of samples from only 68 ocean locations revealed over 35 000 microbial "species" (Sunagawa et al. 2015). Locey and Lennon (2016) predict that the Earth may support as many as a staggering 1 trillion (10^{12}) microbial species.

Nevertheless, the use of molecular technologies to identify taxa to the species level by genetic fingerprinting or "barcoding" has often proven to be an insufficient and unreliable response to the taxonomic impediment. The panacea that simply sequencing specimens and trusting that matching those sequences to databases will produce a reliable identification has proven not to compensate for the growing gap in taxonomic expertise. Two principal problems hinder molecular identifications: (*i*) accurate and complete barcoding of taxa across the taxonomic spectrum, and (*ii*) accurate and complete reference databases against which taxonomic assignments are made (Harris 2003).

These problems are hindering the compilation of inventories of non-native taxa, even in conspicuous and well-studied groups such as Australian *Acacia* species (Magona et al. 2018). Taxonomic biases may result from the markers used (Clarke et al. 2014), while many species for which sequences are obtained have no authenticated database reference (Briski et al. 2016). Further, all new sequence entries should (but do not) require that the sequenced taxon has been identified by a taxonomic expert based upon morphological evidence. Thus, a substantial fraction of the species in these databases can be misidentified, at times egregiously so, potentially producing erroneous matches that cannot be detected by nonspecialists (Fig. 4). For example, DNA barcoding sequence information is missing from either the Barcode of Life Database, GenBank, or both, for 60% of the 88 insect species listed in the Global Invasive Species Database; 41% of the 88 species could be misidentified as another species, owing to discrepancies between sequences and species identity (Boykin et al. 2012).

4.2. Taxonomic impediments lead to underestimations of invasion

Without changes to ensure the development of broad taxonomic expertise, invasion science will continue to underestimate, often substantially, the number (and also, therefore, the impacts) of non-native species across all habitats, regardless of the surveillance and detection program (e.g., De Barro et al. 2011). For example, Carlton and Fowler (2018) recently estimated that non-native species are under-reported globally for the majority of marine taxonomic groups, owing to a lack of widely available taxonomic expertise. Conversely, what has been initially viewed as an invasion by one widespread species is sometimes later discovered to be a group of similar species, some or all of which are restricted to their native ranges (Darling and Carlton 2018). More broadly, the inability to detect what could be the most common new invasions (by species and genotypes) across terrestrial, freshwater, and marine habitats undermines ecosystem management and biodiversity assessment, and our capacity to detect changes in ecosystem structure and function.

The deficit of taxonomic expertise associated with microorganisms is especially worrying. In general, species richness and density of organisms are inversely related to size. Not only do small-bodied creatures dominate the world, but the magnitude of non-native species transfers is often greatest for small organisms, many of which have life histories that facilitate colonization (e.g., asexual reproduction; resting stages) (Ruiz et al. 2000). While invasions of microorganisms are increasingly recorded (Seebens et al. 2017), the extent of these invasions and their impacts remain poorly described outside of forestry, agriculture, and aquaculture (Desprez-Loustau et al. 2007; Lohan et al. 2020).

Several marine disease outbreaks (such as those in oysters, sea urchins, and fishes) have been attributed to non-native pathogens. For example, MSX is an oyster disease caused by a protozoan (*Haplosporidium nelsoni*) that is native to Asia, but was detected on the Atlantic coast of North America in 1957. The native eastern oyster (*Crassostrea virginica*) proved highly susceptible to MSX, leaving local populations substantially depleted from Chesapeake Bay to Nova Scotia (Bushek and Ford 2016). The same is true for terrestrial and freshwater habitats where non-native pathogens cause diseases such as ash dieback, crayfish plague, chytridiomycosis, and sudden oak death (Skerratt et al. 2007; Grunwald et al. 2012; Roy et al. 2017). Many of these non-native pathogens spill-over, colonizing native host species in the invaded range, whereas non-native hosts may harbor native parasites that then spill-back to native hosts (Roy and Handley 2012; Blackburn and Ewen 2017). Both effects complicate parasite identification (Morand 2017). Given recent work on the role of microbial communities in ecosystem processes (Worden et al. 2015) and their importance in microbiomes, host–parasite interactions (Egan and Gardiner 2016), and plant mutualisms (Traveset and Richardson 2014), the potential importance of microorganism invasions is enormous. Thus, evaluation of microorganism biogeography is a high priority if we are to understand the full scope and impact of invasions in all ecosystems.

4.3. Lack of taxonomic expertise limits our ability to test and develop invasion theory

The taxonomic impediment also impairs our ability to evaluate and understand the spatiotemporal dynamics of invasions and their impacts. Much of the theory and current knowledge of invasion science has arisen from syntheses and analyses of secondary data drawn from regional checklists and distribution atlases of floras and faunas (van Kleunen et al. 2015, 2019; Dyer et al. 2017; Pyšek et al. 2017). However, such checklists and databases can be seriously compromised by the quality of species identifications (McGeoch et al. 2012). Identifying plant hybrids, in particular, requires professional taxonomic expertise and is crucial for management, given that hybridization often facilitates establishment (Yamaguchi et al. 2019) and stimulates invasiveness, where the new taxon is more vigorous than either parent (Ellstrand and Schierenbeck 2000; Vilà et al. 2000). An example is provided by *Fallopia* taxa (knotweeds) in the Czech Republic, for which redetermination of plants in the field revealed misidentifications for up to 16% of the records reported in the literature or deposited in herbaria for *Fallopia japonica* and *F. sachalinensis*, and 20% of records of the hybrid *Fallopia* × *bohemica*, (Pyšek et al. 2001). Only after the complicated patterns of increased ploidy variation and rapid post-invasion evolution in the invaded range of Europe were disentangled was it possible to conduct ecological studies that revealed the elevated invasiveness of the hybrid compared to that of the parents (Pyšek et al. 2003).

Other taxonomic challenges in plant invasion research include apomictic groups, karyologically variable complexes, genera with specific reproduction systems, or those for which horticulturalists have bred many cultivars and varieties (e.g., *Centaurea*, *Cotoneaster*, *Heracleum*, *Lupinus*, *Myriophyllum*, *Phragmites*, *Rhododendron*, *Rubus*, *Spartina*, and *Tamarix*). Some of those taxa are among the most widespread plant invaders, and ecological studies aimed at understanding their invasion have profited substantially from detailed taxonomic knowledge (Pyšek et al. 2013).

4.4. Lack of taxonomic expertise limits our ability to manage invasions

Taxonomic expertise is fundamental to management and policy efforts, from border control to early detection (and both encouraging and justifying rapid response based on expert identification) to post-invasion management. In several cases, misidentifications and failures to recognize cryptic species complexes have delayed the discovery and introduction of suitable biological control agents (Anderson and Wagner 2016). This is illustrated by biological control of Cactaceae in South Africa that was delayed because the wrong species of herbivorous insect was collected. After taxonomic problems were resolved and the appropriate insect was released, the population of the non-native cactus declined (Paterson et al. 2011). Similarly, a carnivorous beetle, *Laricobius naganoensis*, was inadvertently imported to eastern North America with a closely related species, *L. osakensis*, introduced from Japan to control an invasive insect—the hemlock woolly adelgid. The U.S. Department of Agriculture subsequently permitted further introduction of *L. naganoensis*, requiring no risk assessment or monitoring, simply because it was too difficult to distinguish it readily from its congener (Leppanen et al. 2019).

Food security is also compromised by taxonomic problems. Inability to determine species identity in imported live seafood can result in widespread substitution by cheaper species in many countries, some of which include invasive non-native species. For example, in South Africa several species of *Clarias* catfish are native to the continent and are used in aquaculture as a local food source. However, the walking catfish (*C. batrachus*)—a southeastern Asian species known to cause detrimental impacts where it has established—is prohibited for aquaculture. The walking catfish is difficult to distinguish from its African congeners based on morphology alone, making it an easy species to label inappropriately, import, grow, and sell (Grobler et al. 2015).

Equally worrisome is that, with the rapidity with which vectors and pathways are changing in today's globalized economy, we may be unaware of—and unprepared for—many future invasions. The widening gap between our desire to assess changing biodiversity and our ability to identify species implicates all taxa in all habitats and thus compromises our evaluation of the consequences of invasion. The need to narrow this gap through enhanced taxonomic expertise is crucial if we are to keep pace with the constantly expanding numbers of non-native animals and plants being introduced across the planet (Seebens et al. 2018, 2021).

4.5. The way forward: training the next generations of researchers to identify species

The way forward requires a new international emphasis on the value of taxonomy. The foundations of the scientific community's ability to recognize biodiversity, including the presence and impacts of non-native species, have been crumbling for decades. Rebuilding these foundations requires consensus that we need to do so, accompanied by agreement of the scale of restoration required, a plan to undertake renovation, and the commitment and capital to see it through. Each of these stages, except for commitment and capital, has been discussed exhaustively to little avail. The challenge of old and oft-repeated clarion calls is that they fall on deaf ears, or worse. And yet without this commitment, the global number of scientists who are trained in the basics of taxonomy (including expert field identification) and possess skills in measuring biodiversity will continue to diminish (Lücking 2020). Failures to identify organisms correctly will lead to spurious conclusions in ecological studies and ultimately to inappropriate and ineffective legislation, management, and policy (Pyšek et al. 2013). We note that recent championing of "taxonomic sufficiency" or the "higher taxon approach", which is designed to circumvent either the absence of, or the need for engaging, expert resources (de Oliveira et al. 2020; Gerwing et al. 2020), is inapplicable to invasion science—which requires the highest quality and accuracy of species-level identification.

Thousands of protist, animal, and plant phylogenies produced every year contain innumerable clades deprived of binomial nomenclature (Darling and Carlton 2018). Students engaged in such work should be trained, supported, and encouraged to provide taxonomic descriptions of clades as new species. The great satisfaction and pride of describing and publishing new species, including the honor of choosing a name, could inspire a measurable fraction of future generations of biologists and ecologists to become recognized taxonomic experts while at the same time remaining experts in other specialties. A key advance will be the dissolution of the enduring myth that simultaneously being an expert taxonomist and an expert ecologist (or neurobiologist or molecular biologist) is impossible. Building pride in contributing to global biodiversity knowledge is a critical step in addressing the taxonomic impediment in the 21st century. While we champion the rapidly growing concept of "integrative taxonomy" (Daglio and Dawson 2019; Zhang 2020)—what Boxshall (2020) describes as the "reciprocal illumination of morphological systematics and molecular sequence-based systematics"—we emphasize that no integration is possible if only one partner is on the stage. The central role of taxonomists in resource management, biodiversity conservation, and biosecurity must be affirmed (Hutchings 2020). The decline in funding and the startling erosion of taxonomic positions in museums and other institutions must be addressed through novel collaborations, underscoring societal significance.

5. Enhancing international biosecurity and multi-stakeholder cooperation

5.1. Shifting international trade and travel patterns mediate invasions

A final overarching issue is the need for invasion science to provide better guidance for biosecurity programs, at both national and international levels. The suite of species transferred between regions varies as global trade patterns wax and wane (Dyer et al. 2017; Seebens et al. 2018). An emerging example is the vast Chinese "Belt and Road" initiative, which can potentially elevate invasion risks greatly among the more than 120 countries through the development of a series of land-based economic corridors between core cities and key ports (Liu et al. 2019). Historically, changes to biosecurity policies that focus on specific pathways have been motivated by the impacts of species arriving via those pathways, but the effectiveness of such reactive approaches to policy development is hampered by long lags between the establishment of pathways and the onset of invasion. Novel, forward-looking approaches to pathway risk analysis are needed. For example, internet commerce of plants and animals is an expanding global pathway that can radically transform the composition and introduction routes of species in trade (Humair et al. 2015). Structural changes to the horticultural industry, such as the shift to offshore production, have major implications for plant health and trajectories of biological invasions (Dehnen-Schmutz et al. 2010). Another emerging pathway is ecotourism; well-meaning nature enthusiasts unwittingly introduce non-native species even to remote regions (e.g., Nash 2009). Research is needed to develop educational and social engineering tools that can be used to alter tourist behavior to reduce risks of future invasions.

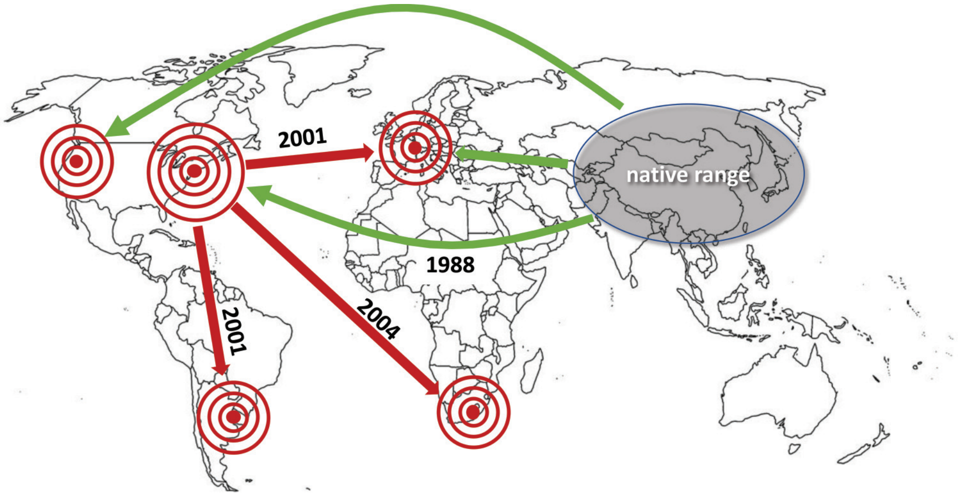
Contemporary problems with non-native species reflect economic, societal, and trade drivers and patterns that prevailed over the past few centuries (Essl et al. 2015*a*; Hulme 2015; Dyer et al. 2017; Zieritz et al. 2017). This means that interventions to regulate pathways and their effects on invasions are out of sync and that time horizons of decades must be considered in strategic planning. The time lags inherent in many biological invasions imply that many additional non-native species are destined to become established and cause problems in the coming decades, even if biosecurity measures are radically improved (Essl et al. 2011). The dimensions and implications of this invasion debt are yet to be clearly incorporated into strategic biosecurity planning anywhere in the world (Rouget et al. 2016). To this end, Wilson et al. (2018) included indicators pertaining to four components of invasion debt (introduction debt, establishment debt, spread debt, and impact debt) among 20 indicators for reporting on biological invasions at the national level. These indicators form the basis for regular reporting on the status of biological invasions developed for South Africa – the first country to have instituted such a comprehensive reporting protocol (van Wilgen et al. 2020). Uptake of such measures for all countries is a priority.

Trends observed in past invasions, most of which have played out over the last five decades, provide imperfect insights for planning of biosecurity interventions, since many aspects of future invasions (e.g., taxa involved, pathways, drivers of progression along the introduction-establishment-spread continuum, interactions between drivers) will differ from those of previous invasions. Invasion science must develop more detailed understanding of how international trade and travel are altered by national and international socioeconomic changes, and how these changes in turn influence invasion trends (Hulme 2015). Such insights can greatly enhance the development of scenarios and allow for improved risk categorization. A major priority for invasion science is thus to advance beyond pattern recognition to embrace mechanistic socio-ecological models; for example, the Global Trade Analysis Project model was used to assess the economic and trade impacts of required phytosanitary treatments of wood packaging (Strutt et al. 2013), and it was later applied to estimate the ultimate economic benefits of this policy (Leung et al. 2014). An improved understanding of the links between global socioeconomic trends and invasions will ensure more effective targeting of national and international biosecurity efforts. Such knowledge is also needed to inform the development of incentives and educational tools to alter the behavior of importers, travelers, and others whose activities pose significant invasion risks (Colton and Alpert 1998; Perry and Farmer 2011; Springborn et al. 2016).

5.2. Global cooperation among national biosecurity programs

Most countries operate biosecurity programs that are designed to prevent the arrival, establishment, and spread of non-native species inside their national borders (Meyerson and Reaser 2002; Hulme 2011). In some cases, unexpected prioritization of biosecurity measures can result from independent policy actions. For example, the EU Regulation (1143/2014) on non-native species has resulted in stakeholders focusing on biosecurity programs that limit the export of live animals and plants, but it neglects new introductions. Moreover, contemporary national biosecurity programs are generally designed to protect the interests of individual countries (Black and Bartlett 2020), with relatively little consideration given to the "greater good"—i.e., protecting all nations from invasions. The mission of most national plant protection organizations, for example, includes regulating imports that pose high risks of harmful introductions, while simultaneously promoting exports from their own countries; scant attention is given to minimizing risks associated with such exports (MacLeod et al. 2010). Cooperation is urgently needed among countries to craft biosecurity programs that are more cost-effective than those where countries act largely in isolation (Latombe et al. 2017). Despite long-standing calls for a binding international convention on invasive alien species (Perrings et al. 2010; Stoett 2010), there has been no progress towards this goal in over a decade. Within individual countries, there are often political and economic obstacles to adopting truly cooperative biosecurity. Thus, rather than a top-down multilateral approach to regulation, it is likely that closer integration of national biosecurity strategies will occur through a coalition of the willing. A fine example is the

Fig. 5. The "bridgehead effect" illustrated by the global spread of the harlequin ladybird beetle *Harmonia axyridis*, based on genetic analyses by Lombaert et al. (2010). Intentional biocontrol introductions are shown in green, whereas accidental invasions are shown in red. In this example, most of the global spread of this species has originated from non-native populations established in Eastern North America, which has functioned as a bridgehead region (adapted from Lombaert et al. 2010).



Consultative Group on Biosecurity Cooperation established by Australian and New Zealand ministers in 1999 under the terms of the Australia–New Zealand Closer Economic Relations Trade Agreement. This group has led efforts to harmonize animal and plant health measures affecting trade between the two countries as well as coordinating biosecurity responses. The Plant Health Quadrilaterals is a strategic coalition composed of the national plant protection organizations of Australia, Canada, New Zealand, and the United States that enables the respective plant health and biosecurity officials to address plant health and biosecurity issues, particularly as they affect international trade of plants, plant products, and other regulated articles. In 2016, a similar quadrilateral group involving the same four nations was established to coordinate efforts to address marine biosecurity. These coalitions do not have any regulatory power, but through dialogue and cooperation they can address emerging issues in biosecurity in an open and collaborative manner. For multilateral initiatives, a useful model for research on cooperative biosecurity would be studies on cooperation between different countries to optimize harvest from shared fisheries (Bailey et al. 2010). These studies apply game theory, which could also be applied to biological invasions to explore how cooperative biosecurity might yield higher benefits to all countries by collectively reducing the flow of species globally, rather than just preventing invasions at the national level. Lampert (2020) applied a dynamic game-theoretic model to identify a Nash equilibrium corresponding to optimal contributions that various countries or other entities could adopt for managing invading species with shared adverse impacts. This approach could be expanded to explore cooperation by countries to fund various pre- and post-border biosecurity activities.

5.3. The role of the bridgehead effect in managing invasions

A key consideration driving the need for internationally cooperative biosecurity strategies is the tendency of organisms to invade new regions from locations where they have already established, a phenomenon referred to as the "bridgehead effect" (Lombaert et al. 2010; Bertelsmeier and Keller 2018) or "hub-and-spoke" invasion topology (Carlton 1996). This phenomenon has been documented in historical global patterns of invasions for several plant and animal species (e.g., Bertelsmeier et al. 2018; Correa et al. 2019; Javal et al. 2019). The term was first coined by Lombaert et al. (2010), who used molecular analyses of the global spread of the harlequin ladybird beetle *Harmonia axyridis* and found that even though the species is native to east Asia, its invasions of Europe, Africa, South America, and western North America all originated from eastern North America (Fig. 5). Evidence exists that invasions from bridgehead regions may be promoted by genetic changes, demographics, or simply by the topologies of trade networks (Bertelsmeier and Keller 2018). More work is needed on the drivers of bridgehead dynamics to determine whether management-relevant generalizations exist.

From the perspective of designing biosecurity programs, an important implication of such bridgehead dynamics is that benefits will accrue from preventing a species from establishing within a hub or bridgehead region—that is, an invaded location from which spread to other regions is more easily facilitated. Furthermore, cooperation among countries to eradicate or control species established in bridgehead regions could yield greater benefit than attempts by individual countries to exclude these species from arriving and establishing.

The current unilateral approach that dominates national biosecurity has roots in the close relationship between trade and import quarantines. Quarantine is an effective and important tool for excluding arrivals of new species, but there is a history of quarantine being abused to justify protectionist trade policies (Castonguay 2010). For example, the World Trade Organization (WTO) recognizes the International Plant Protection Convention (IPPC) as the authority for setting standards for plant quarantine, and the WTO uses its Appellate Body for settling quarantine-related trade disputes. However, while the IPPC identifies quarantine practices and harmonized standards that individual countries should follow, it generally does not implement actions to minimize the movement of species worldwide. However, the IPPC has developed a National Phytosanitary Capacity Development Strategy that facilitates investment by member countries in the development of biosecurity capacities in economically underdeveloped countries. Interdisciplinary research between invasion scientists and international trade economists is required to develop frameworks and justifications for globally collaborative biosecurity efforts (Horan and Lupi 2005). Among the topics this research could address is how countries with varying economic resources can share resources for preventing the global movement of non-native species (Early et al. 2016).

This research could also focus on developing strategies to identify bridgehead regions and initiate cooperative biosecurity negotiations with governments responsible for such regions. Border inspection data provide information on the identity of the geographical sources of species arriving at ports and are thus valuable resources for identifying bridgehead regions (Bertelsmeier et al. 2018). Biosecurity agencies often consider inspection data as confidential (because of their possible significance in trade dispute litigation). Given the potential value of such data for identifying and delimiting bridgehead regions and global invasion risk (Turner et al. 2020), a challenge for invasion science is to ensure that such data are made more widely available and in a timely way to prevent regions that have received an invasive species from serving as sources for new invasions even before the bridgehead population has been discovered. Ultimately, such data sharing could help inform biosecurity practices in individual countries, thereby reducing risks of future invasions. The world has recently witnessed an unprecedented case of international sharing of spatiotemporal spread data for SARS-CoV-2 from its earliest stages, which should serve as an example for tracking other invasive organisms (Bertelsmeier and Ollier 2020).

5.4. Managing conflicting interests in biosecurity

A related problem is that of cooperative approaches to transboundary biosecurity. The establishment of non-native populations can span regions managed for varying purposes, often with conflicting priorities (Epanchin-Niell et al. 2010). Conflicts of interest frequently bedevil attempts to manage non-native species, especially when the focal species is simultaneously perceived as both beneficial and harmful by different sectors of society or in different areas of the landscape (e.g., van Wilgen and Richardson 2014). For example, the ornamental horticulture industry benefits from importing and propagating non-native plant species while its actions conflict with other societal segments (e.g., ranchers, farmers, conservation managers) who suffer from the impacts of plant invasions (Niemiera and Von Holle 2009). Invasion scientists must collaborate with economists and other researchers to devise approaches to engender cooperation among stakeholders who are differentially impacted by the same non-native species and to explore how to optimize diverse management interests. In responding to changing perceptions of non-native species, their impacts, and their value to society, invasion science is facing challenges similar to those confronting other disciplines including the medical profession with regard to how best to communicate information about risk (Alaszewski and Horlick-Jones 2003). Social science research must also develop effective strategies or models for systematic engagement of stakeholders seeking sustainable solutions to invasions (Shackleton et al. 2019).

Conflicting interests among stakeholders that affect management of invasions sometimes manifest as “wicked problems”. These are characterized by diverse, opposing perspectives, objectives, and management goals that make them almost impossible to characterize or frame, let alone resolve, to the satisfaction of all stakeholders (Woodford et al. 2016). Woodford et al. (2016) suggest that systematic framing of “wickedness” by mediators can lead to negotiated solutions – either by reaching agreement on the dimensions and implications of unavoidable conflicts, or by circumventing the conflict by seeking alternative management perspectives. To this end, Novoa et al. (2018) developed a 12-step process designed to place stakeholders at the center of the development and implementation of decisions relating to conflicts of interest in invasive species management. Fundamental requirements for achieving such aims are (*i*) to ensure that decisions and management actions are co-designed, co-produced, and co-implemented to promote social learning and provide feedback to stakeholders, and (*ii*) to increase levels of collaboration and partnerships beyond the natural sciences and academia (Shackleton et al. 2019). Further work is clearly needed to achieve integration of broad stakeholder engagement and co-operation in invasion research and management. Opportunities abound to apply existing economic theory on governing common-pool goods (Ostrom 2010) to solve problems related to the increasingly complex conflicts between stakeholders relating to invasive non-native species.

6. Conclusions

Invasion science is an increasingly interdisciplinary field that addresses questions and hypotheses of fundamental and applied importance to ecology, conservation biology, ecosystem management and restoration, and biosecurity (Ricciardi et al. 2017; Pyšek et al. 2020). We have identified four overarching issues that are critically important for the field to further adapt to societal demands in the face of rapid global change. Reflected in these issues are burgeoning challenges posed by new sources and pathways (e.g., evolving trade routes and transportation systems) of invaders. Understanding and predicting invasions and their consequences are scientific endeavors, whereas managing them successfully largely rests with society; the former informs the latter, and both tasks are complicated by context-dependencies that are becoming increasingly significant as rapid environmental change ensues.

Solutions to these challenges require innovations in theory and methods that potentially could be found through linkages with other disciplines. For example, factors promoting the emergence and spread of novel infectious disease could be better understood and managed through collaborative research involving medical science and invasion science, to the benefit of both fields (Nuñez et al. 2020). In addition, within the broad discipline of ecology there are disparate concepts and methods that have not yet been well integrated into invasion science (e.g., species interaction networks; Hui and Richardson 2019), or that are only now becoming broadly applied (e.g., the use of functional response metrics in risk assessment; Dick et al. 2017*a*, 2017*b*; Dickey et al. 2020).

New approaches are needed to forecast candidate invaders, probable invasion success, and consequent invader impacts under future terrestrial, freshwater, and marine conditions that have little or no analogue reference point in the past. A key growth point for the field would be to develop a better understanding of temporal invasion dynamics, including invasion debt and time lags. The concept of invasion debt (Essl et al. 2011; Rouget et al. 2016), in which invasions are the end result of processes currently at play (e.g., increasing propagule transport and introduction in the face of reduced environmental resistance), is analogous to the emergence of disease symptoms following viral or bacterial exposure resulting from lapses in hygienic measures or failed social behaviors. A more predictive understanding of invader impact could be advanced, in part, through research on interacting and cumulative time lags in biodiversity and ecosystem responses to invasions (Essl et al. 2015*a*, 2015*b*).

Fundamental taxonomic skills are essential for biosecurity and a deeper understanding of biogeography and evolutionary history – the foundations of invasion science. The application of invasion science to early detection is compromised without expertise suitable to identify non-native species rapidly. Misidentifications have led and will lead to spurious conclusions in ecological studies and, ultimately, to inappropriate and ineffective management and policy. The necessary expertise could be cultivated through application and enhancement of infrastructure support (e.g., cybertools, specimen collections linked with permanent custodial care), and re-establishment of training of both classic and advanced taxonomic skills in biology programs.

Finally, invasion science must address transcultural sociopolitical challenges including how best to communicate information and uncertainty about risk, how to engage diverse stakeholders who are differentially impacted by the same non-native species, and how to inform transboundary biosecurity policies. There is still much work required to harmonize the definition and application of biosecurity policies across different multilateral organizations such as the Convention on Biological Diversity, the International Plant Protection Convention, and the World Organisation for Animal Health. Invasion science must continue to inform the rapidly evolving landscape of international biosecurity agreements designed to control pathways that create bridgehead populations, which can drive widespread invasions. International data-sharing will be needed to reduce invasion risk at regional and global scales. The remarkable example of the rapid cooperative sharing by most countries of spatiotemporal spread data for SARS-CoV-2 from its earliest stages should inspire global efforts to track other invasive organisms.

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