

## Review

## Invasion Science: A Horizon Scan of Emerging Challenges and Opportunities

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**We identified emerging scientific, technological, and sociopolitical issues likely to affect how biological invasions are studied and managed over the next two decades. Issues were ranked according to their probability of emergence, pervasiveness, potential impact, and novelty. Top-ranked issues include the application of genomic modification tools to control invasions, effects of Arctic globalization on invasion risk in the Northern Hemisphere, commercial use of microbes to facilitate crop production, the emergence of invasive microbial pathogens, and the fate of intercontinental trade agreements. These diverse issues suggest an expanding interdisciplinary role for invasion science in biosecurity and ecosystem management, burgeoning applications of biotechnology in alien species detection and control, and new frontiers in the microbial ecology of invasions.**

### Emerging Challenges and Opportunities in the Science and Management of Invasions

Invasions by alien species are a growing threat to biodiversity, ecosystem services, regional economies, and public health. Risks of invasion are shifting rapidly on a global scale owing to expanding transportation networks, technological advancements, landscape transformation, climate change, and geopolitical events [1–4]. For example, enhanced shipping promoted by the recent expansions of the Suez and Panama canals could escalate marine invasions at regional and continental scales [3,4]. The rise of internet-based commerce in living organisms (e.g., pet trade) is creating unique invasion pathways that are difficult to regulate [5]. Early warning of the risks surrounding such events is essential for preventing, controlling, and mitigating invasion threats and could reduce environmental and economic damage, just as disaster preparedness does for natural hazards [6]. However, ecologists have invested little effort in forecasting global events that could shape future invasions.

To identify future challenges and opportunities facing invasion science, an international team of ecologists (the authors) convened a horizon-scanning workshop in Cambridge, UK, in September 2016. Horizon scanning is a systematic approach for exploring emerging trends, issues, opportunities, threats, and events, which can facilitate proactive responses by

#### Trends

Expanding transportation networks, technological advances, global environmental change, and geopolitical forces are transforming risks of invasion worldwide.

Genomic modification tools offer novel risks and potential solutions to managing invasions.

Rapid warming and intensified human activities in the Arctic will alter invasion patterns and risks across the Northern Hemisphere.

Anthropogenic stressors promote rapid evolutionary shifts that cause native and alien populations to become invasive.

Microbial ecology is becoming increasingly relevant to understanding and managing invasions.

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## Box 1. Identification and Ranking of Issues

Issues were identified and evaluated using a modified iterative Delphi technique [8] and methods of expert consultation, such as voting and anonymity [9], similar to procedures used in recent horizon scans of conservation issues (e.g., [10]). Each team member submitted at least two topics, in some cases following consultation with colleagues within their organization or professional network to ensure wide coverage. In August 2016, short (200–300 word) synopses of 40 submitted topics were circulated to all members, each of whom independently ranked all 40 topics by taking into consideration the probability of emergence, pervasiveness (scope of influence), potential impact, and degree of novelty; for the latter criterion, priority was given to issues whose mechanisms, implications, or impacts are not currently widely known or well understood. The median scores of these ranks were calculated as a starting point for discussion. In September 2016, the team convened in Cambridge, UK, and discussed all topics in random order, with the constraint that the individual who proposed the topic was not among the first three people to comment on it. Team members then confidentially scored each topic on a scale from 1 (well known, or poorly known but unlikely to have substantial impacts on the study and management of invasions globally within the next two decades) to 1000 (poorly known and likely to have substantial impacts), which reduced the probability of ties. These scores were subsequently converted to ranks, and the median rank of each topic was calculated (see Table S1 and Figure S1 in the supplemental information online). Scoring summaries identified a clear inflection in rankings between the top 15 topics and the remainder, so we chose to retain this distinct subset. A dozen additional topics emerged during discussions of the initial set, and these were considered and voted upon. By such democratic decisions, the team decided that one of the new topics would replace one of the original topics, and two original topics were merged, resulting in a final set of 14 issues.

scientists, managers, and policy makers [7]. Through consensus (Box 1), we sought to identify emerging scientific, technological, and sociopolitical issues that are likely to affect how invasion processes and dynamics are studied and managed within the next 20 years. Here, we present 14 issues that are relevant to a broad range of taxa, environments, and geographical regions. Our goal in highlighting these issues is to encourage scrutiny and debate that spurs the development of new research foci and policy objectives. These issues are not presented in rank order, but are instead grouped into broad themes.

## Biotechnological Issues

### Managing Invasions through Genomic Modification: Gene Drives and Autocidal Control

Advances in molecular biology have provided potentially useful but risky options for invasive species management. The advent of gene-editing tools (e.g., CRISPR/Cas9) and synthetic gene drives enables the spread of beneficial or detrimental alterations through wild populations by biasing the inheritance of particular altered genes [11]. One potential application is to modify mosquitoes genetically so they cannot transmit diseases [12]. An example of obvious value to conservation and restoration would be the control of avian malaria introduced to Hawaii [13], where most native birds are restricted to high elevations beyond the range of alien mosquitoes carrying the parasite; the fate of these birds is precarious because their mountain refuges are threatened by climate change [14]. Advances in recombinant genetics are also providing new autocidal ('self-killing') technologies to combat invasive species by modifying their genomes such that the modification spreads through the population in a way that reduces the abundance or impact of the species. Genetic modifications can be used to create conditional lethality or sterility, or to create synthetic selfish genetic elements that drive genes into pest populations [15]. Proof of concept has largely been restricted to modeling studies or experiments on short-lived organisms [11], but important test cases include planned releases of recombinant autocidal mosquitoes (*Aedes aegypti*) in Florida and Brazil. The ease of application of these techniques will increase the scope of their utility, including, for example, in conservation [13]. However, they face uncertain public and political acceptance and might require legislative changes designed to limit the spread of recombinant species [16]. They also present environmental and biosecurity concerns, such as altered ecosystem functioning and potentially the increased invasiveness of the target species [17].

**Opportunities and Challenges of Using eDNA for Alien Species Surveillance and Monitoring**  
eDNA (genetic material gathered from bulk environmental sources [18]) provides researchers with information on species presence without the need for capture or direct observation

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(e.g., [19]). Although eDNA has already begun to be used to study invasions, we expect that rapid growth, widespread deployment, and automation of this technique over the next decade will transform the sensitivity, speed, and scale with which we detect alien species. For example, we foresee citizen scientists being recruited to collect eDNA samples, a mobilization that could enhance monitoring efforts across large geographical ranges [20]. However, while eDNA offers considerable promise for increasing the timeliness and ease of detecting alien species, it suffers from uncertainties in species identification, runs a risk of false positives, has limited capacity for estimating abundance, and could have weak statistical power, leading to overconfidence when no detections are recorded. Furthermore, it can capture signals that do not distinguish between dead and living organisms (e.g., in ship ballast water), or contamination (e.g., feces, pupal cases, or egested prey) when, in fact, the species is absent. Finally, a greater standardization of sampling and processing methods is required. Application of such techniques to support quarantine in trade or large-scale invasive species management remains in its infancy, but the power of these technologies and the risks and challenges to their adoption will become a major focus of invasion science.

#### Changing Agricultural Practices and the Emergence of New Invaders

Efforts to develop new commercially farmed species and the industrial use of mutualistic organisms to increase crop yields will promote a new suite of invasive taxa. For example, Eurasian field pennycress (*Thlaspi arvense*) is proposed for widespread commercial production in North America [21]. Introductions of such new crops will enable plant pathogens to jump from cultivated hosts to native species [22]. Two other emerging trends of food production pose novel risks. Insects as a protein source for humans offer an emerging market predicted to be worth US\$723 million by 2024 [23]. Those species selected for farming, such as crickets, mealworms, and lepidopteran larvae, grow quickly, often have a generalized diet, and thrive in high densities, properties associated with invasiveness. Commercially produced house cricket, *Acheta domesticus*, has already established in the wild outside its native range. Moreover, because commercial house cricket farms in North America and Europe have been devastated by *Acheta domesticus* densovirus, farmers have imported other crickets that are similarly easy to rear and potentially invasive [24]. Another emerging trend is investment by commercial agribusinesses in seeking and rearing soil bacterial and fungi that facilitate crop production [25,26]; such products are expected to be used on 50% of US farmland by 2025 [26]. Widespread application of these mutualists could trigger invasions by formerly non-invasive crops or co-occurring plants.

#### Ecological Issues

##### Adaptation to New Environments: Genetics versus Epigenetics

Colonizing species can respond rapidly to local environmental and biotic interactions with epigenetic changes, thereby producing heritable, adaptive, and divergent phenotypes in differing environments [27]. Epigenetic changes result in up- or downregulation (transcription) of genes responsible for phenotypes, including physiological, morphological, life-history, and behavioral traits. Recent cases demonstrating that strong epigenetic variation contributed to invasion success include both plants and animals [28,29]. Epigenetic changes provide tremendous scope for rapid adaptation [29], despite the low genetic diversity observed in some colonizing populations. The full impact of epigenetic mechanisms and the relative importance of epigenetic versus genetic processes in invasion dynamics remain poorly understood and is likely to vary by context and taxon.

##### Greater Recognition of the Impact of Soil Biota on Invasions

The soil biota (invertebrates, fungi, and bacteria) is increasingly recognized as playing a crucial role in shaping plant and animal communities via diverse pathways and mechanisms. An emerging research area examines how alien plants and animals interact with this biota and the

consequences of such interactions [30–32]. Some alien plants undergo more positive (or fewer negative) feedbacks with soil biota in their invaded than in their native ranges [31,32], and alien animals influence plant communities and soil biota as well as their interactions [33]. There is also strong context dependency in how alien species and soil biota interact [30,34], the basis of which remains poorly understood owing to two issues. First, most studies have treated soil biota as a ‘black box’ and, therefore, we know little about which organisms are involved in regulating the success and impact of alien species. Second, we have a poor understanding of the mechanistic basis by which the soil biota interacts with alien plants and animals. We expect these issues to receive significant research attention in the future, driven in part by urgencies to enhance global food production and to manage ecosystem services against growing anthropogenic stressors.

#### Global Emergence of Invasive Microbial Pathogens

Invasions by pathogenic microorganisms increasingly threaten biodiversity resources, wildlife conservation, forest sustainability, food security, fisheries, and human health [35–40]. Drivers of this phenomenon are poorly understood, but include tourism and global commerce in living plants and animals [33,35]. Accidental transport of fungi, bacteria, viruses, oomycetes, and protists in terrestrial, freshwater, and marine systems can catastrophically affect host populations of plants and animals that lack prior evolutionary contact. Frequently, pathogens have formed novel associations with insects or other organisms, with consequent elevated pathogenicity (e.g., [37]). In other cases, infections by invading pathogens have been facilitated by climate change or other shifting environmental conditions. Microbial taxa can undergo swift genetic changes, either through natural selection or via hybridization with other species or strains, and such changes can result in elevated virulence, the ability to infect new hosts, or the emergence of entirely new invasive pathogens [39]. A key problem in managing pathogen invasions is our currently limited ability to detect or identify emerging pathogens, owing to the lack of comprehensive global databases, existence of nonsymptomatic reservoir hosts and cryptic pathogen spillovers, and the potentially enormous number of undescribed taxa (which can remain obscure until a host die-off; e.g., [37]). New molecular methods will increasingly reveal impacts of invading microbial pathogens, especially where host die-offs were previously thought to result from abiotic causes.

#### Rapid Evolution of Invasiveness

An existing but restricted alien population can undergo rapid evolution that promotes a greatly expanded invasion. Such a shift is believed to have affected a newly introduced US population of the Asian harlequin ladybird (*Harmonia axyridis*), by the purging of deleterious alleles through a genetic bottleneck effect. This invasive ‘bridgehead’ population of a previously non-invasive species facilitated subsequent invasions of North America, South Africa, South America, and Europe [41,42]. Prolonged lag times preceding the sudden expansion of an alien population could be attributed to rapid evolution, although each case needs intensive research on this possibility. Similarly, a human disturbance triggering an evolutionary change can cause a formerly innocuous native or alien population to become highly invasive [43]. Invasions by the little fire ant (*Wasmannia auropunctata*) in many areas all appear to originate from a clonal genotype that occurs only in human-disturbed habitats within the native range of Brazil [44]. The sudden spread in North America and beyond of the Colorado potato beetle (*Leptinotarsa decemlineata*, native to South America) originated not from native populations but from an introduced population in North America that switched from burweed (*Solanum rostratum*) to potato as its preferred host plant [43]. Genetic mechanisms underlying these cases differ and require intensive study to decipher, but research on rapid change in contemporary time is at the forefront of modern evolution [45]. We predict that ongoing massive changes to natural ecosystems driven by land conversion, rapid climate change, and invasions will increase the opportunity for the rapid evolution of increased invasiveness in particular local populations.

## Sociopolitical Issues

### Creation and Destruction of Intercontinental Trade Agreements alter Long-Distance Dispersal Opportunities

International trade agreements will increase the volume and distance traveled of merchandise and thus magnify the translocation of associated species as commodities, stowaways, and contaminants (e.g., pathogens, parasites, commensals, and symbionts) [46,47], and have a vastly greater spatial coverage than intracontinental agreements: the Trans-Atlantic Trade and Investment Partnership, and the Comprehensive Economic and Trade Agreement link the European Union with the USA and Canada, respectively. The fate of these agreements can change with shifting political landscapes; protectionism by some countries in the future will shift the balance of trade in new directions with consequences for existing agreements (e.g., the Trans-Pacific Partnership). Intensified translocations across distant regions are associated with significantly higher invasion risks than intracontinental translocations, because a higher proportion of incoming organisms will be novel alien species, and species in recipient regions are less likely to have evolved traits to cope with the invader [47,48]. By contrast, an opportunity exists for developing more effective cooperative frameworks for plant and animal quarantine measures that would reduce invasion risk. While the International Plant Protection Convention is designated by the World Trade Organization as the standard-setting agency for plant protection activities, individual nations could implement these standards differently depending upon desired risk levels. A consequence of these heterogeneous standards is the establishment of new alien species populations that pose a risk even to nations with strong quarantine programs, owing to the connectedness of international transportation networks.

### Globalization of the Arctic

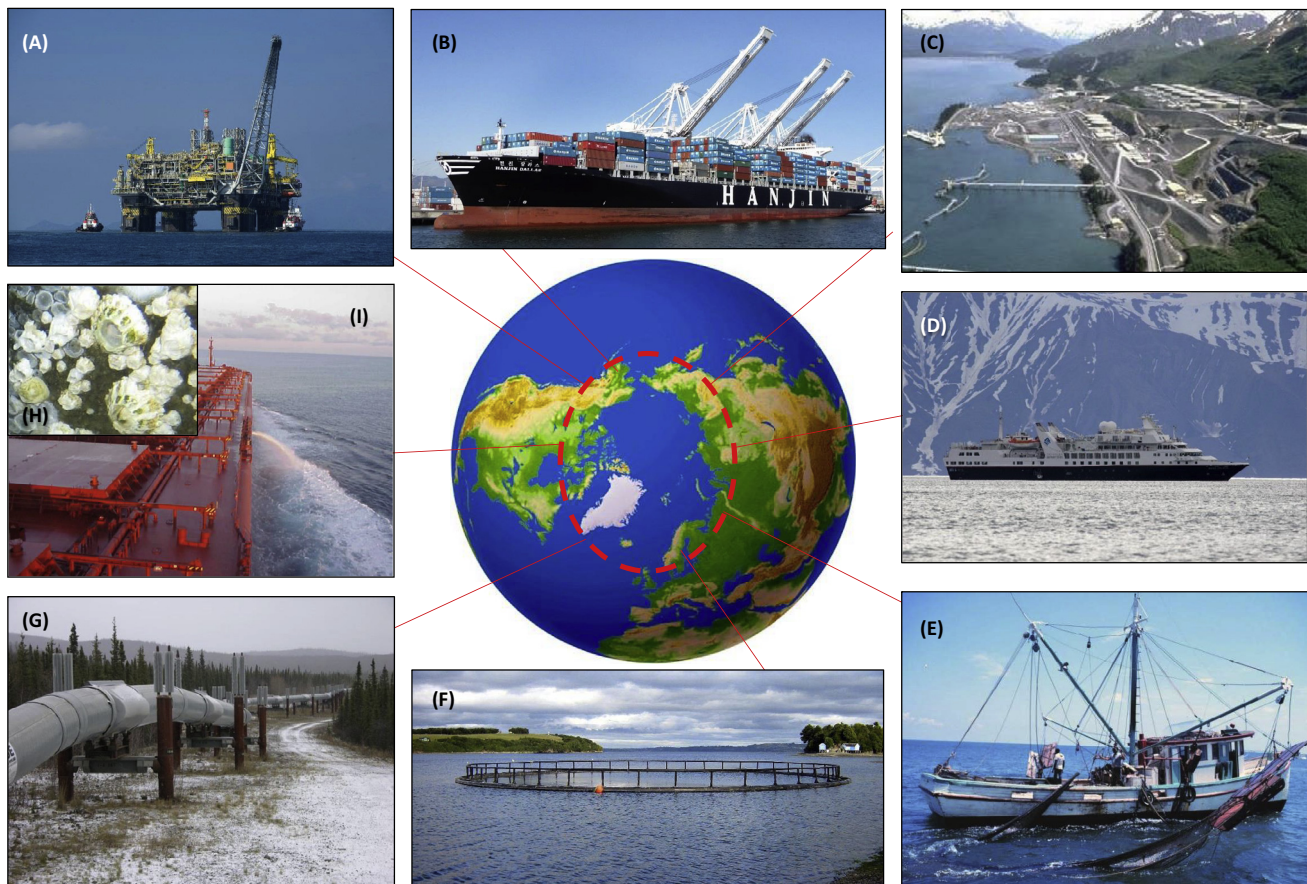
Although few established populations of alien species are documented in coastal marine or terrestrial habitats above 66°N (e.g., [49]), the Arctic is poised to emerge as a global hub of biological interchange. Loss of Arctic sea ice is occurring more rapidly than predicted and is facilitating a cascade of human activities, including shipping, mineral and energy exploration, shoreline and offshore development, fishery exploitation, and tourism, which will all generate opportunities for invasion, locally and in distant regions (Figure 1). Prospective access to new energy resources, raw materials, and a major shipping route has attracted keen interest from many nations, including China, India, and South Korea. Propagule supply to Arctic habitats will increase dramatically [50,51], challenging efforts to protect northern fisheries and endemic biodiversity under increasing disturbance from alien species. Transport on the hulls of ships of fouling organisms could ultimately pose a greater threat than ballast water discharge, if the latter vector abates in importance owing to recent ratification of a global convention requiring the treatment of ballast water.

Climate warming will not only render the region more vulnerable to new invasions [52], but also make it a conduit for them [53]. Indeed, some species have already begun traversing this region [54]. Overland supply chains and a major new transoceanic trade route are emerging. Ship transits have grown exponentially along the northern coast of Russia in recent years [55], and the first large luxury cruise ship traversed the Northwest Passage in 2016. The new sea routes and infrastructure will create stronger linkages with existing global transportation networks, while shortening voyages and likely reducing metabolic stress for organisms moved between distant temperate regions (in contrast to the temperature stress of moving through tropical systems). These changes will affect invasion risk in terrestrial, freshwater, and marine habitats worldwide.

### Increased Invasion Risk Driven by Geopolitical Conflict

The next few decades could see substantial increases in global conflicts and large-scale refugee movements provoked, in part, by climate change [56]. Geopolitical conflict directly leads to the erosion of infrastructure needed for conservation and biosecurity, redistribution of





Trends in Ecology &amp; Evolution

**Figure 1. Activities Expected to Drive Increased Invasions to and through the Arctic.** Loss of Arctic sea ice will intensify oil and mineral extraction (A), movement of commodities, including live organisms (B), port development (C), tourism and cruise ships (D), commercial fishing (E), aquaculture (F), and construction of overland pipelines (G). Shipping through the region will facilitate species dispersal via hull fouling [see (H), barnacles on the hull of a vessel docked at Iqaluit, Canada)] and ballast water discharge (I). See the supplemental information online for image attributions.

resources, border policy changes, reconfigured transportation networks, greatly altered land-use patterns, and large-scale refugee movements [57]. Collectively, these changes have major consequences for the ingress, spread, and impact of alien biota through a variety of mechanisms, such as international military shipments. Indeed, the post-World War II relocation of military equipment allowed the brown tree snake (*Boiga irregularis*) to be introduced to Guam [58]. Similarly, military transport is assumed responsible for the establishment of 10 species of insects in Japan [59]. Military activity has also been linked to the movement of alien plants since the 19th century, amounting to the translocation of almost-entire weed floras, a phenomenon so universal that such plants are known as ‘polemochores’ [60]. Moreover, human colonization and immigration history, including the displacement of people following geopolitical conflicts, have profoundly influenced the composition of alien species found in any given region [61]. Thus, impending geopolitical conflicts fueled by climate change are likely to produce new waves of biological invasions.

#### Capitalizing on Citizen Participation for the Early Detection, Surveillance, and Management of Invading Populations

Government agencies face constraints on resources available for conducting surveys and surveillance of alien species, limiting the ability of traditional programs to detect and respond

quickly to invading populations when eradication and control are most feasible. The opportunity exists to harness and mobilize extensive citizen observations for surveillance [62]. Increasingly available tools and technology can support robust, efficient, and rapid data acquisition and reporting. National programs for citizen science surveillance of invasions are lacking in most countries. Organized frameworks and infrastructure are required, including systems for citizen reporting, outreach campaigns (effective information and education delivery), quality control, and data management. Additional opportunities exist for citizen effort in management and eradication programs as well as in broadening public awareness of biological invasions [63]. To realize this potential fully, social science research is needed to determine how best to engage the public in alien species recording [64], as is technical work on how to integrate citizen information into data systems.

#### Sociocultural Resistance to Management Tools: An Empty War Chest?

Five global trends will challenge our capacity to manage established alien species populations. First, pest management often requires the use of traps, pesticides, and repellents, among other methods. Increasingly, the humaneness of control techniques is given at least as much consideration as their effectiveness, resulting in more humane but less effective tools being available for pest control [65]. Second, the public increasingly opposes using pesticides, forcing managers to reduce application rates or to apply alternatives perceived to be more environmentally friendly [66]. Third, many species are evolving resistance to commonly used chemical controls [67,68]. Research is needed to find alternative chemicals and nonchemical approaches. However, and fourth, the rate at which new pesticides are being registered is slower than that at which active ingredients are being removed from the market. A fifth emerging trend is public distrust of gene drives and similar genetic interventions. These trends suggest that alien species management will become increasingly difficult, thereby challenging science to develop new tools to replace unacceptable current approaches.

#### Invasive Species Denialism

Coverage of alien species and their threats is increasingly mainstream. Previously, such coverage reflected the scientific consensus that invasions often have negative biodiversity and socioeconomic impacts. More recently, however, a surge of articles in the popular press has attempted to reframe, downplay, or deny the role of invasions in global change (e.g., [69–72]). We distinguish between scientific skepticism (i.e., calling into question the assumptions or quality of data supporting conclusions regarding impacts of invasions; e.g., [73]) and denialism (in which assertions are repeated in the face of substantial scientific evidence to the contrary [74]), similar to post-truth political discourse. Science denialism attempts to manufacture uncertainty in the expert consensus on an otherwise undisputed topic, exploiting the fact that all scientific knowledge contains an element of uncertainty, and policymakers have invoked a perceived lack of expert consensus to prevent action on environmental problems [75]. As has been the case with its impact on mobilizing widespread societal response to climate change, denialism in the context of invasions could significantly hamper efforts to mitigate or control deleterious effects of alien species [76]. Therefore, invasion scientists will need to find more effective ways to communicate facts to the public, media, policymakers, and other researchers [77].

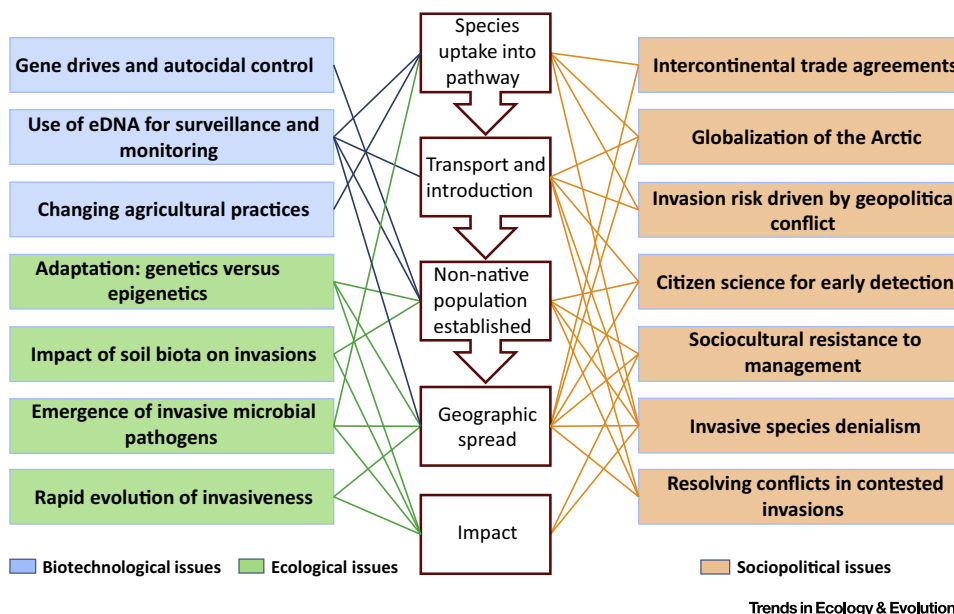
#### New Frameworks for Resolving Conflicts of Interest in Contested Invasions

Many species that provide commercial benefits for aquaculture, horticulture, or forestry are invasive. Consequently, the management of alien species is increasingly contested in social arenas where such species are valued differently by stakeholders [78]. For example, although invasion researchers and conservationists perceive the spread of trout as a serious ecological problem, some sport fishermen see attempts to manage and legislate against such invasions as infringements of their rights. Such conflicts between stakeholders harm efforts directed at

building long-term conservation programs. A new approach to this problem lies in developing a framework that more clearly presents issues pertaining to biological invasions and reflects contemporary invasion science, which seeks to evaluate impacts using objective protocols that incorporate ecological, economic, and human-value assessments. Woodford *et al.* [79] propose applying concepts underpinning the notion of ‘wicked problems’ to achieve clearer, more transparent framing and communication of these complex problems. Such a framework would need to show that effective management of invasions requires either recognizing unavoidable complexity or circumventing it by seeking alternative management perspectives [77,80,81].

### Concluding Remarks

Current issues of well-recognized importance concerning alien species have attracted much research attention (e.g., effects of climate change on the spread of biota; alien plants as biofuel crops; international trade in live species). However, additional consideration should be given to issues whose full significance is, at present, somewhat speculative or not yet fully elaborated but that exhibit indications of their importance increasing in the future. Our horizon scan identified 14 such issues, relevant to a broad range of taxa and environments (terrestrial, freshwater, and marine), that could cumulatively shape invasion science (Figure 2). We foresee a rapid shift in the significance of these issues in coming decades. Advances in genetic modification techniques, for example, will provide both challenges and solutions to invasive species management. We considered biotechnologies that are in early stages of development and likely to involve releasing novel biological entities (e.g., synthetic cells or products of de-extinction), but these were not prioritized in our rankings because their importance was predicted to be realized only in the more distant future. However, the release of genetically modified organisms, already underway but recognized for decades as an issue for invasion science, is likely to become increasingly significant to the field over time.



**Figure 2. Horizon Scanning Topics and their Relevance to the Invasion Process and Impact.** Each of the biotechnological, ecological, and sociopolitical issues identified here has a direct influence on multiple stages of the invasion process: uptake of the species into a vector-pathway system, survival during transport, introduction to a new region, establishment of a reproducing population, and subsequent spread within the region. Several issues also directly challenge our understanding of, and capacity to manage, the ecological impacts of invasions. These links are not meant to be comprehensive, but rather to illustrate the breadth of relevance of these issues.



We identified the globalization of the Arctic region as a highly influential phenomenon affecting future invasions (Figure 1). Although it is well known that diminishing Arctic sea ice is facilitating greater ship traffic, less attention has been given to the role of a warming Arctic in generating new opportunities for invasion through diversified and intensified human activities. It is not widely appreciated that the region will become a major trade corridor between the Atlantic and Pacific oceans, thereby forming a new hub within existing global transportation networks [55]. While altering regional and global invasion dynamics, the magnitude of these effects will depend on how effectively management and policy responses reduce transfers of associated species. The Arctic Council, which seeks to address diverse environmental issues in the Arctic by coordinating legal instruments (agreements and regulations), infrastructure, and communication among countries [82], is exploring strategies to limit invasions [83].

Our horizon scan also recognizes emerging trends involving potential sociopolitical conflicts that could render invasions ‘wicked problems’ for management [79]. These include conflicts among stakeholders, public resistance to management tools (e.g., driven by perceived risks of pesticides), and the rise of invasive species denialism in opinion articles and the popular media. By contrast, we anticipate that citizen science (i.e., public participation in the initial detection, surveillance, recording, and eradication of alien species) will have a prominent role in management at local-to-regional scales and also lead to a greater public awareness that could significantly impact policy. Sociopolitical issues in general are expected to have a significant influence on all stages of the invasion process and on the impacts of alien species (Figure 2).

The composition of our team (with its biases in gender, race, and geographical representation) likely influenced the selection and ranking of the issues presented here. In particular, participants from developing countries might have proposed alternative issues (e.g., effects of conversion of agricultural land for urban development) that have added significance, given that most developing countries have limited capacity to respond to invasions [2] and can act as hubs to spread species into developed regions. Nevertheless, the diverse issues identified here signal: (i) an expanding interdisciplinary role for invasion science in biosecurity and ecosystem management; (ii) burgeoning applications of biotechnology in invasive species detection and control; and (iii) greater recognition of the microbial ecology of invasions. They also foretell a rapidly growing demand for more effective methods of assessing and predicting ecosystem-level impacts of invasion, especially for microbial and ‘belowground’ biota. Evolving management and policy frameworks will affect the full impact of the issues presented here; however, advanced warning of global shifts in invasion risks and opportunities is essential for developing strategies that can more effectively mitigate invasion threats.

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### Supplemental Information

Supplemental Information associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.tree.2017.03.007>.

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