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Invasive alien species in an era of globalization

Laura A Meyerson* and Harold A Mooney**

Globalization facilitates the spread of invasive alien species (IAS) as international commerce develops new trade routes, markets, and products. New technologies increase the pace at which humans and commodities can move around the world. Recent research on IAS at the global scale has examined commerce and travel in order to inform predictions, risk analyses, and policy. Due to limited data, regional-scale studies have primarily focused on invasion patterns rather than impacts. Local-scale experimental research can identify mechanisms and impacts of biological invasions, but the results may not be applicable at larger spatial scales. However, the number of information networks devoted to IAS is increasing globally and may help integrate IAS research at all scales, particularly if data sharing and compatibility can be improved. Integrating ecological and economic factors with trade analysis to explore the effectiveness of different approaches for preventing invasions is a promising approach at the global scale.

La globalización facilita la extensión de especies invasoras no-nativas (EIN) por medio del aumento del comercio internacional en nuevas rutas, mercados y productos. Nuevas tecnologías incrementan la tasa de movimiento de seres humanos y sus comodidades alrededor del mundo. Investigaciones recientes sobre las EIN a la escala mundial han examinado el comercio y la transportación para poder informar predicciones, riesgos ecológicos y políticos. Debido a los datos limitados, los estudios a la escala regional se han concentrado en los patrones de invasión de las EIN en lugar de sus impactos. Los estudios experimentales a la escala local pueden identificar mecanismos e impactos de estas invasiones biológicas, pero los resultados no pueden ser aplicados a grandes escalas. Sin embargo, el número de redes de información dedicadas a las EIN esta incrementando a nivel mundial y podrán ayudar integrar este tema de investigación a todas las escalas, particularmente si se mejora la accesibilidad y la compatibilidad de los datos. La integración de factores ecológicos y económicos con el análisis de patrones de comercio es un método prometedor para explorar la eficacia de diferentes estrategias diseñadas para prevenir invasiones a la escala global.


For hundreds of years, humans have been introducing plants, animals, and other organisms around the world, in a relatively slow process of globalizing the Earth's biota (DiCastris 1989). More recently, the pace of this process has increased with modern trade, travel, and technology, so that biological invasions have become a consequence of globalization. Globalization facilitates and intensifies the spread of invasive alien species (IAS) – defined here as “alien species whose introduction does, or is likely to, cause economic or environmental harm or harm to human health” (Executive Order 1999) – through intentional or accidental introductions. Researchers can approach critical questions surrounding IAS by focusing on global-scale phenomena such as international trade and regional scale patterns (Figure 1), or by focusing more specifically on particular species or an ecosystem that has been colonized by IAS. For example, global research may examine commerce and travel trends over time to inform predictions, risk analyses, and policy. Regional-scale analyses often focus on patterns of invasion such as rates of introduction or the presence of invaders because data on IAS impacts are rarely collected at large spatial scales. Local-scale experimental research frequently uses observation and manipulation to tease apart the complex ecological relationships that promote invasions and may seek to specify IAS impacts. However, research is rarely conducted at these three scales simultaneously.

In a nutshell:

- Invasions are driven by interacting factors across global, regional, and local scales
- Information networks can assist with data integration across spatial scales and with managing invasions on the ground
- Innovative applications of economic analyses are needed to assist in the prevention of IAS introductions and the management of existing infestations

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application of new science, the integration of other disciplines into this scientific research, and the engagement of policy makers and the public. Where possible, the multiple scales of invasion research should be integrated to advance the science of invasion biology and to increase our ability to control invasion rates and manage the effects of undesirable species introductions that do occur. Working across multiple disciplines, across spatial scales, and within the policy arena will enhance the success of such efforts. This paper discusses the interaction between IAS and globalization at multiple spatial scales and explores opportunities to work across scales and disciplines.

Factors that drive biological invasions

Trade

At the global scale, commercial trade propels rising annual and cumulative rates of invasion due to the development of new source and recipient regions, trade routes, and markets, as well as new products, larger and faster ships, and increased air transport (Lodge 2006; Ruiz et al. 2006). These rates of invasion are expected to increase, as are the associated environmental and social costs (Levine and D’Antonio 2003). Although many vectors are responsible for species introductions, the rising volume of air and ship transport has been identified as the primary driver of marine invasions (Lodge 2006) and the spread of insect disease vectors (Tatem et al. 2006). A major opportunity to intervene and better manage species introductions exists, but, in practice, using trade and vector information to reduce invasions is difficult. It requires cooperation across multiple sectors, including international trade organizations, national and local regulators, suppliers, distributors, and buyers. Cooperation at the global scale to reduce invasions requires changes in business practices by all parties and trade-offs, but may ultimately produce benefits that outweigh the costs.

For example, as major forces in the world economy, China and the US both import and export substantial quantities of goods, which makes these two nations leading sources and recipients of IAS (Jenkins and Mooney 2006). Both countries have diverse flora and fauna and both have increasing reservoirs of established and incipient IAS from around the globe, poised for secondary introductions elsewhere (Lodge 2006). The US and China also share similar ecogeographic regions, so both countries are primed for enhanced biotic interchange. Furthermore, neither nation has a consistent, proactive regulatory framework applied across all sectors to prevent the introduction and spread of IAS (Jenkins and Mooney 2006). There are, therefore, a number of reasons for the US and China to work together to decrease invasion vectors and to strengthen regulatory frameworks and cooperative agreements. While environmental concerns alone are not likely to spur this kind of cooperation, Chinese and American economists and others could conduct cost–benefit analyses for reducing species introductions, which may produce a more compelling argument.

Another example involves the Great Lakes region, which is considered to be an “invasion beachhead” for the rest of North America, because so many aquatic invasive species have been introduced there from the Baltic region and have subsequently spread to other North American waters (Lodge 2006). These multistage invasions include vectors such as transcontinental commercial trade and inter-lake recreational boating and fishing. Effectively addressing such complex invasion webs requires internationally coordinated policy and monitoring efforts, commercial, economic, and ecological assessments at all scales, and an informed and invested public sector in all affected countries.

The Great Lakes/Baltic Sea Partnership developed by the US Environmental Protection Agency seeks to achieve some of these goals by fostering the sharing of information, data, and technology and by encouraging collaborative research between these two regions (www.epa.gov/glmpo/baltic). This partnership is modeled on the Great Lakes Partnership.
binational initiatives of the US and Canada, such as the US–Great Lakes Fisheries Commission (www.glfc.org) and the US–Canada International Joint Commission (www.ijc.org). Another continental example is the North American Plant Protection Organization, which “coordinates the efforts among Canada, the United States and Mexico to protect their plant resources from the entry, establishment, and spread of regulated plant pests, while facilitating intra/inter-regional trade” (NAPPO; www.nappo.org). These are large and multifaceted agendas, but such coordinated initiatives in other regions could bring similar important benefits.

At regional and local scales, comparisons of climatically similar sites can reveal non-climatic factors that facilitate species invasions. For example, comparisons of invasion rates over time in the Mediterranean climates of California and Chile clearly show that, while climatic and temporal factors are roughly equivalent, rates of invasion are not (Arroyo 2006). California has substantially more invasions than Chile, perhaps because Chile has lower propagule pressure, greater biotic resistance, less disturbance, and fewer transport corridors (eg lower road density), or because it has fewer available niches for introduced species to exploit than California (Arroyo 2006). Like the US–China example given above, California and Chile have become sources for secondary invasions elsewhere in the world (Figure 2). A more global analysis that included exogenous factors such as trade balances and IAS propagule pressure might lead to the discovery of additional causes that have contributed to high invasion rates in California.

Propagule pressure

Propagule pressure has been implicated in successful species invasions (D’Antonio et al. 2001; Rouget and Richardson 2003). It includes both the absolute number of individuals introduced to a new system and the number of introduction events that occur (Lockwood et al. 2005). Propagule pressure occurs at regional and local scales, but often results directly from international trade and globalization. Understanding the role of propagule pressure in invasion success requires examination at both the species and population levels. Distinct populations reflect particular trade patterns and transport vectors, which supplement existing introduced populations in terms of absolute numbers and genetic variation (Lockwood et al. 2005; Roman 2006).

Positive interactions occur between propagule pressure and disturbance (ie the more disturbed an area, the easier it is to invade when a window of opportunity opens; Crawley 1989; D’Antonio et al. 2001). However, recent experimental work in a floodplain forest in southwestern Virginia manipulated species diversity, abiotic conditions, and propagule pressure and found evidence that the overwhelming factor in invasibility was propagule pressure rather than disturbance (Von Holle and Simberloff 2005). Nonetheless, it is reasonable to conclude that these effects are additive rather than distinct.

Ships now often introduce species that are already present in recipient ports, so that, even as commercial trade volumes increase, the number of introductions of new species may eventually saturate (Levine and D’Antonio 2003). However, repeated introductions of the same species increase propagule pressure (including the genetic diversity of introduced populations), so that there is an increased probability that a species or genotype will become invasive in the recipient port or in a tertiary site (Lockwood et al. 2005). While the genetic distinctions among populations of the same species with potentially differing ecological impacts may seem subtle or irrelevant to those unfamiliar with biological invasions, the potential consequences are not. Therefore, instigating actual policy and behavioral change requires not only good data, but also compelling examples and effective communication.

Disturbance

Disturbance at both global (eg climate change; Figure 3) and local (eg roads) scales is clearly an important factor in facilitating species invasions (eg Sher and Hyatt 1999; Mooney and Hobbs 2000; D’Antonio and Meyerson 2002). Even disturbances occurring more than 100 years ago may influence current invasions (Von Holle and Motzkun 2007). Research on Cape Cod, MA, tested multiple factors that could account for non-native species invasion: anthropogenic disturbance, natural disturbance, soil, environmental conditions, or current vegeta-
When Mooney and Meyerson work negatively, invasion occurs and currently is expected to spread. Phragmites australis, a species introduced to North America, may have higher growth rates, greater maximal photosynthetic rates, and earlier leaf emergence than native plants, including native Phragmites. Invasive species like introduced Phragmites (Figure 4) can also exhibit plastic responses to changing environmental conditions, which may translate into a relatively greater ability to respond to other facets of global change, including increasing temperatures and sea level rise (Farnsworth and Meyerson 2003; Meyerson et al. in press).

**Negative and positive interactions**

When a negative interaction among species favors invasives over natives, the invasive species can benefit greatly, particularly when the interaction involves a novel mechanism. For example, garlic mustard (Alliaria petiolata) virtually eliminates arbuscular mycorrhizal fungi (AMF) colonization, which dramatically impairs the regeneration of some native canopy species (Stinson et al. 2006). Garlic mustard’s antifungal effects reduce seedling growth of highly AMF-dependent plants. These effects persist for at least 2 years following garlic mustard removal, so that disrupted mutualisms may facilitate invasions through both direct and indirect means and can complicate attempts at ecological restoration (Stinson et al. 2006).

Recent work on the role of positive interactions in species invasions has demonstrated how facilitation among IAS can hinder our ability to predict invasion impacts and magnify the impacts of a single introduction (Simberloff and Von Holle 1999; Ricciardi 2005). To date, there has been little research on facilitation of native species by invasives. However, a review of literature from 1993 to 2004 found that facilitation of natives by invasives affects multiple habitat types, communities, and trophic levels, and plays a role in evolutionary changes through habitat modification, trophic subsidies, pollination, and competitive and predatory release (Rodríguez 2006). The implications for ecological restoration and conservation are substantial, particularly when the invader provides habitat for an endangered species (eg Tamarix and the willow flycatcher; Dudley et al. 2000) or in highly degraded sites, where restoration would be facilitated by the introduction of an invasive that ameliorates harsh site conditions (eg D’Antonio and Meyerson 2002).

**Approaches needing greater attention**

**Integrating economic analysis and policy**

Economic analysis of the trade-offs associated with IAS management gives policy makers the rationale for creating IAS policy and allocating funds to prevention and control programs. Furthermore, economic analyses can engage the public in ways that information on biological impacts may not, because the financial costs are something that most people understand. Unfortunately, there have been few large-scale, comprehensive economic studies on invasive species impacts. The economic figure quoted most often, $100+ billion annually for IAS management in the US (Pimentel et al. 2005), has been praised as comprehensive.
and compelling, but criticized for being too broad-brush to be of real use (Reaser et al. 2003; Perrings et al. 2005).

Most economic analyses focus on the effects of IAS on a particular natural resource, such as timber, aquaculture, or grazing lands (Perrings et al. 2005). However, a recent study focused on the consequences of the coqui frog (Eleutherodactylus coqui) on Hawaiian real estate values. Accidentally introduced to Hawaii from Puerto Rico in 1988, the coqui poses substantial risks to Hawaiian native biota, but it is its "piercing call"—reaching 70–100 decibels at a distance of a half meter and loud enough to induce hearing loss with sustained exposure—that has received the most attention (www.hear.org). Preliminary research shows that the presence of coqui frogs in Hawaii has major economic consequences, including average decreases of 64% in the property value of homes located near infestations (K Burnett pers comm.). Assessments such as this one tend to initiate rapid responses from policy makers, because of the relevance of real estate values to human economic well-being.

Environmental assurance bonds follow the principles of the "polluter pays" strategy used in oil spill clean ups and recently proposed for IAS (Jenkins 2002; Perrings et al. 2005). These bonds could create market incentives to identify future costs or effects of species introductions and would work by requiring those who import new species or engage in activities that may lead to invasions to post a bond to cover projected damage if an introduction becomes invasive. The bond is re-evaluated if the risks change, the funds are used to mitigate control costs if negative effects are documented, and the bond is refunded if no impact occurs. Benefits of this approach include "shifting the burden of proof" of no harm to those responsible for the introduction and providing an economic incentive for research on the impacts of species introductions (Perrings et al. 2005). For example, environmental assurance bonds could be implemented among trading partners such as the US, China, and others, as an incentive to take precautions against unintentional inclusion of organisms in packing materials, substrates, ballast water, and so on.

Filling information gaps

Recent work has synthesized large, non-native species datasets to report globally (eg Global Compendium of Weeds; www.hear.org/gcw) and nationally (eg Czech Republic: Pyšek et al. 2002; Křivánek and Pyšek in press; Germany: Klotz et al. 2002; South Africa: Richardson et al. 2005; Ireland: www.biochange.ie/alienplants; Australia: www.weeds.crc.org; Pacific Islands: www.hear.org). Some have identified taxonomic and ecosystem data gaps (eg Figure 1; Meyerson et al. in press b), and others have been used to make predictions about the relationships between non-native and native species richness and human facilitation of invasives (Stohlgren et al. 2006). One challenge for those undertaking this work is to credibly integrate data collected at different scales. More challenging, and sometimes impossible, is pooling data collected using different sampling protocols. For example, data collection methods within US federal agencies can vary by region, so that data may not be directly comparable. This is also the case at the state level; US states may each be collecting data on water quality using different methods and parameters. However, recent work by McKinney and La Sorte (in press) analyzed four large datasets available on the internet and found evidence that IAS have a more homogenizing impact on biota than those species that are simply non-native. Although these results seem self-evident, this had not been previously quantified.

Researchers may also collect data on IAS using methods appropriate to particular questions rather than standardized methods. For example, a nationwide survey of non-native species databases was undertaken to determine the relative instances of data collection at different scales and the types of data (eg pattern or impact) collected (Cral et

Figure 4. Phragmites australis is a highly successful plant invader of coastal marsh systems of North America. An aggressive Phragmites lineage was likely introduced to the northeastern US in the 19th century and is presently spreading through coastal wetlands along the Atlantic coast, parts of the Gulf and Pacific coasts, and in inland marsh systems. While native Phragmites was previously found in many of these North American habitats, observation and experimental research have made it clear that the spread of introduced Phragmites is closely coupled with human disturbance of the physical and chemical environment (Saltonstall 2002; Meyerson et al. in press).
Facilitating the globalization of information

At a global scale, integrating site-specific ecological factors with trade analyses may be a useful approach for preventing invasions. Drake and Lodge (2004) concluded that reducing the average probability of individual ships introducing species is a more effective method for reducing rates of invasion than managing sources of invaders from “hot spots”. Ballast water exchange technologies are promising in terms of decreasing the numbers of organisms transported from port to port (primary and secondary introductions), but other aspects of shipping (hull fouling, containerization) remain problematic (Fofonoff et al. 2003).

A global perspective on IAS provides at least a coarse ability to forecast risk by identifying changing vectors and routes and new donor and recipient regions, and therefore presents a better chance of managing IAS. However, global analyses are single pieces of a complicated puzzle and must be considered in multiple contexts. Smaller-scale experimental research and synthetic data analysis have disentangled many complex interactions. Coupling this work with broader-scale research may sharpen risk assessments and lead to the discovery of heretofore unrecognized patterns and relationships.

For example, the recent northern expansion of the invasive European green crab (Carcinus maenas) from the Gulf of Maine to Cape Breton, Nova Scotia, was thought to have occurred because of warming sea temperatures and/or adaptations of established southerly populations to colder northern waters (Roman 2006 and references therein). However, building on an earlier study of the population structure of C maenas in its native European range (Roman and Palumbi 2004), Roman (2006) applied molecular techniques to demonstrate that the introduction of new lineages of C maenas to Nova Scotia from the northern end of its native range in Europe was more likely. These European populations may have been better adapted to the cold temperatures of northern Nova Scotia than populations of the Gulf of Maine (Roman 2006). Furthermore, the author noted that the new “super port” in the Strait of Canso, Nova Scotia, appears to be at the epicenter of C maenas haplotype diversity (Roman 2006).

Making such explicit links can be difficult, but could be more easily achieved by integrating information networks and current and historical databases into research and management. It is very encouraging that the number of national- and regional-scale information networks is rising and that they are increasingly connected to one another (Table 1). Many networks synthesize information on IAS taxonomy, distribution, ecology, impacts, control, and management, but they are relatively new and have therefore not yet fulfilled their potential. Below, we present several examples of successful networks that are helping to prevent and manage invasions.

In North America, the US Geological Survey, Mississippi State University, and the federal land management agencies (e.g. National Park Service, US Fish and Wildlife Service) are cooperating with APHIS (Animal and Plant Health Inspection Service) to develop a National Cactus Moth Detection and Reporting Network (Madsen et al. 2006). The potential range for the invasive moth Cactoblastis cactorum reaches from North Carolina west to California and south to Mexico. The main goal of the network is to establish pricky pear cactus (Opuntia spp) sentinel sites on public and private lands to help monitor the spread of the moth from the Carolinas and Alabama (Westbrooks et al. 2006). The success of this community-based approach in early detection and rapid response efforts became evident when a sentinel site, established on the Isle of Palms, near Charleston, South Carolina, in April 2005, was confirmed in July 2005 to have cactus moths (Figure 5). The quick response to this outbreak by federal officials and local volunteers resulted in the destruction of infected cactus clades on the site. A supply of cactus moth larvae were collected and preserved for use as specimens in the national detection effort (R Westbrooks pers comm).

The Nonindigenous Aquatic Species (NAS) information resource of the US Geological Survey was established as a central repository for spatially referenced biogeographic accounts of nonindigenous aquatic species. NAS works closely with other information networks, including seven international participants (Table 1). Information collected through this network has been used to follow up on reports of new occurrences of IAS and to eradicate others. For example, before Hurricane Katrina, giant salvinia (Salvinia molesta) was so widely distributed in the lower Pascagoula River (MS) that eradication and even control was not considered worthwhile. However, post-Katrina, most of the giant salvinia was either deposited on land or killed by salt water intrusion. The small remaining patches were then sprayed by the state and effectively controlled (P Fuller pers comm). Surveys for Nile tilapia (Oreochromis niloticus hybrid) in coastal Mississippi were also undertaken after Hurricane Katrina. One population was located at an aquaculture facility destroyed by the hurricane. Tilapia remaining at the facility were located in small farm ponds that were treated with rotenone (in con-
junction with MS state officials). More than 10,000 fish were collected in the control effort (many of these have been archived at the Mississippi Museum of Natural Science) and only three tilapia have been captured in the area since this effort (P Schofield pers comm).

A final example demonstrates the potential influence of large databases on policy. The Taxonomic Analysis of Introduced Plants in Costa Rica is developing a national database of the origins, growth, habitat use, and population distribution of introduced plant species (Madrigal and Saborio 2006). Currently, the database consists of over 2000 plants from over 600 genera and 140 families. Analyses of this data have identified the horticultural industry as the primary source of introduced plants from tropical Asia, South America, Africa, and Europe. This has led to calls for increased regulation in Costa Rica to prevent further introductions (Madrigal and Saborio 2006).

Conclusions

Ecologists are attracted to the study of species introductions because they provide opportunities for addressing research questions that run the gamut from evolution to historical patterns of natural species spread to applied questions in control and restoration. The connections among the numerous drivers of these relationships are coming to light and although all of the pieces may not yet easily fit, patterns in the puzzle are beginning to emerge. Better integration of research findings with policy and management is needed and, in fact, is expected by those who fund this important research.

Global analyses have revealed large-scale patterns of IAS related to commercial trade and shipping, while smaller-scale mechanistic experiments have illuminated many complex facets of invasions. More research is urgently needed to determine the global propagule pools for IAS, how those pools are changing over time, and how they vary by taxa and region (Ruiz et al. 2006). This could potentially be accomplished by linking data on IAS propagule pressure with habitat and climate matching in major shipping ports to assist with better predictions of secondary and tertiary invasions (Byers et al. 2002; Lodge 2006; Tatem et al. 2006). Furthermore, IAS should be investigated in both their native and introduced ranges to better disentangle the species traits and other factors that contribute to invasion and invariability.

At the local scale, more experimental field studies are needed to quantify the role of propagule pressure in invasion success relative to other factors, such as ecosystem type, land-use history, and disturbance. As different species are introduced, understanding both the positive and negative economic and ecological aspects of species introductions (eg facilitation and interference) will become increasingly critical. Questions about the comparative strengths of predation, competition, and facilitation, the density dependence of positive interactions, and their interactions with pre-existing anthropogenic stressors must be addressed.

Information networks can serve an invaluable function as clearinghouses for data on IAS around the globe, particularly where the facilitation of data sharing and integration is fostered. National- and regional-level monitoring will assist with populating these accessible databases and, ultimately, identification, mapping, and modeling of IAS distributions, abundance, and impacts at local, national, and global scales. Furthermore, these efforts provide finer resolution and links to international IAS databases such as the Global Invasive Species Database (www.isgg.org/database/welcome/).

Identifying effective economic strategies for IAS at national and international levels is also critical, particularly over biologically (as opposed to politically) relevant time scales (Keller et al. 2007). This should include economic and risk assessment of the impacts of IAS on ecosystem goods and services (including degradation of natural systems) and should quantify the non-economic impacts of IAS, such as the loss of cultural services, as defined by the Millennium Ecosystem Assessment (MA 2003). In addition, national- and international-level strategies should bridge multiple temporal and spatial scales, since many invasions occur and have impacts on local and regional scales, and because the risks of some invasions may only become apparent in the medium- to long-term (Keller et al. 2006). Tools to bridge the information gaps between economic analyses and ecosystem impacts may differ, as economic issues respond to policies that permit and restrict
activities and alter behavior, while gaps in scale approaches to IAS are likely to be addressed through technology (Perrings et al. 2003). However, policy clearly plays an important role in information sharing, standardization of data collection, and management that facilitates multiscalar analyses in both economies and ecology.

The global-to-local connection for IAS has been addressed in an innovative way by a national organization, the US Centers for Disease Control and Prevention (CDC). They have adopted a global infectious disease strategy to support the concept that “it is far more effective to help other countries control or prevent dangerous diseases at their source than to try to prevent their importation” (www.cdc.gov/globalidplan). Working with other national agencies, international groups such as the World Health Organization (WHO), and with nations suffering from disease outbreaks, the CDC strives to stem outbreaks wherever they may occur (US DOH 2002). A strategy to address IAS like the one employed by the CDC would minimize the risk of unwanted introductions and strengthen biosecurity overall (Meyerson and Reaser 2002).

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