Invasive alien species in an era of globalization

Laura A Meyerson^{1*} and Harold A Mooney²

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 políticas. 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 dedicados 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.

Front Ecol Environ 2007; 5(4): 199-208

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 (DiCastri 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

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

Authors' contact details are on p208

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.

Invasive plants, animals, and pathogens are indelibly altering ecosystems and shaping how we live in them. Meeting the challenges associated with IAS requires the



Figure 1. Percent of non-native species as a fraction of US biota. These data report watersheds in the lower 48 US states with different percentages of established, non-native species. Data include plants, mammals, birds, fishes, amphibians, snakes, lizards, and mussels, although data on mussels was available for only a fraction of the watersheds. No pathogen data were available. Data provided by the Biota of North America Program, NatureServe, and the US Geological Survey.

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/glnpo/ baltic). This partnership is modeled on the Great Lakes

LA Meverson and HA Moonev

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/interregional 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 nonclimatic 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



Figure 2. World Mediterranean climate regions (circled). The Mediterranean basin serves as a source for many IAS introductions to both California and Chile, which in turn become sources for invasion of these species to other areas of the world (Arroyo 2006). Map produced by the University of Rhode Island Environmental Data Center. Data provided by Environmental Systems Research Institute (Redlands, CA).

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 Motzkin 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-



Figure 3. Invasion of the palm, Trachycarpus fortunei, in southern Switzerland. T fortunei was introduced to Europe in the early 19th century. By 1920, occasional occurrence of the palm was recorded in southern Switzerland, and the palm has been spreading since 1961. By 2003, dense stands were established up to 400 m above sea level and saplings were found at elevations as high as 800 m (Walther 2003; Walther et al. in press). Inset: Seedling of T fortunei establishing in oak, chestnut, and sycamore leaf litter.

tion cover (Von Holle *et al.* 2007). Any kind of soil disturbance contributed to the presence of higher proportions of non-native species, including at those sites not currently disturbed but which had "plow layers" in their soil horizons from past cultivation. Interestingly, recent work by Hierro *et al.* (2006), which compared the effects of disturbance on *Centaurea solstitialis* in its native and introduced ranges, suggests that disturbance alone does not fully explain invasion success. Instead, it appears that, for *C solstitialis*, it is the combination of disturbance and escape from soil pathogens in the native range that has encouraged invasion.

Projected increases in CO_2 are expected to stimulate the growth of many plant species, and invasive plants are expected to respond with greater growth rates than non-invasive plants (Dukes 2000; Ziska and George 2004; Mooney *et al.* 2006). For example, introduced *Phragmites australis*, invasive in North America, may have higher growth rates, greater maximal photosynthetic rates, and earlier leaf emergence than native plants (including native *Phragmites*) under elevated CO_2 (Farnsworth and Meyerson 2003). 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 a).

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 (Rodriguez 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

203

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



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).

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 nonnative 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 (Crall *et* *al.* 2006). The results of this study make it clear that pooling disparate data can be a challenge, but not an insurmountable one, as was also demonstrated by Mark Lonsdale (1999) in his global analysis of plant invasion patterns and invasibility. Consistent, compatible, and statistically sound sampling designs are needed to collect data that are comparable across a variety of species, scales, and ecosystem types. Two of the most useful, but to date least available, datasets needed are those for invasive pathogens and invasive invertebrates. Most data are siteand species-specific, and the problem lies in transitioning from local-scale case studies to syntheses and predictions at multiple spatial scales. Datasets not limited by these scaling difficulties would remove many current barriers to examining questions in invasion biology.

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. Smallerscale 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 (eg 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 prickly 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 cladodes at 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-

Network Information type Partnerships and collaborations **Global Invasive Species Information** · Catalog of 200+ invasive species • Invasive Species Specialist Group (ISSG) Network (GISIN) information systems NISbase http://www.gisinetwork.org • National Biological Information Infrastructure (NBII – USGS) • Invasive Species Profile Schema Global Biodiversity Information Facility (GBIF) IABIN Invasives Information Network (I3N) • Global Invasive Species Programme (GISP) BioNET-INTERNATIONAL • CABI **IABIN** Invasives Information Descriptions of species, habitats. InterAmerican Biodiversity Information Network (IABIN) • National Biological Information Infrastructure (NBII – USGS) Network (I3N) occurrences (or invasion events), http://www.iabinus.org/projects/ projects, experts, and references Clearing-House Mechanism (CHM; Convention • Databases are maintained in English, i3n/i3n_project.html on Biological Diversity) Spanish, and Portuguese • Global Biodiversity Information Facility (GBIF) • Ocean Biogeographic Information System (OBIS) • GISIN **Non-indigenous Species Network** Species information, including NAS Database (NISbase) taxonomy, life history, native and • NEMESIS National Exotic Marine and Estuarine Species Information System (Smithsonian Environmental Research http://www.nisbase.org introduced ranges, photos, and maps Bibliographic searches Center; http://invasions.si.edu/nemesis/) ANS Research Projects • Nonindigenous Species in the Gulf of Mexico Ecosystem (http://nis.gsmfc.org/) • NIMPIS (National introduced Marine Pest Information System www.marine.csiro.au/crimp/nimpis/) CIESM Atlas of Exotic Species in the Mediterranean Sea (www.ciesm.org) • Bishop Museum Introduced Marine Species of Hawaii Guidebook, www2.bishopmuseum.org/HBS/invertguide/index.htm) • Great Lakes-St. Lawrence Research Directory (International Joint Commission; http://ri.ijc.org/) AIRD Aquatic Invasions Research Directory (Smithsonian Environmental Research Center, http://invasions.si.edu/aird/) • Taxonomy, life history, native and Nonindigenous Aquatic Species (NAS) NISBase http://nas.er.usgs.gov/ introduced ranges photos, maps, and National Exotic Marine and Estuarine Species Information impacts of introduced aquatic species System (Smithsonian Environmental Research Center; in the US http://invasions.si.edu/nemesis/) · Spatial information on presence of Great Lakes ANS Information System (GLANSIS; introduced vertebrates, invertebrates, NOAA, Great Lakes Environmental Research Center) and plant species in the US • Alert system for new introductions · Pathways search by US state and taxonomic group Bibliographic searches National Cactus Moth Detection Volunteer network to monitor cactus USGS BRD, USDA APHIS, NBII, state agencies (states' populations and report new Network Departments of Agriculture), universities (Mississippi http://www.gri.msstate.edu/research/ observations of Cactoblastis moth State University) cmdmn/ infestations Integrated Taxonomic Information Global taxonomic information on • Smithsonian Institution System (ITIS) plants, animals, fungi, and microbes • US Geological Survey http://www.itis.usda.gov/ • NBII • Species 2000 • Global Biodiversity Information Facility (GBIF) • Global Mountain Biodiversity Assessment (GMBA, a cross-cutting Mountain Invasion Research Network • Reference databases on mountain (MIREN) network of DIVERSITAS; http://gmba.unibas.ch) invasions http://www.miren.ethz.ch/ • Mountain Research Initiative (MRI; http://mri.scnatweb.ch/)

Table 1. Examples of international and national information networks; many of these databases and networks are working together to share information and to achieve increasingly global coverage of IAS



Courtesy of P Stiling/USF

Figure 5. Cactoblastis cactorum feeding inside cladode of prickly pear cactus (Opuntia sp). There are about 63 native prickly pear species in the southern United States and Mexico; all are susceptible to predation and destruction by C cactorum (R Westbrooks pers comm).

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 these 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 invasibility.

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, landuse 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 preexisting 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.issg.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.* 2005). However, policy clearly plays an important role in information sharing, standardization of data collection, and management that facilitates multiscale analyses in both economics 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).

Acknowledgements

The authors thank the organizers of the Ecological Society of America International meeting in Merida, Mexico, particularly J Herrick, J Sarukhan, and O Sala. The authors also thank all of the presenters in the invasive species sessions for their generosity and support in this endeavor and I Carroll of The Heinz Center (currently at UC Santa Barbara), for preparation of the illustration in Figure 1. LAM received support from The H John Heinz III Center for Science, Economics and the Environment and the University Of Rhode Island College Of Life Sciences.

References

- Arroyo M. 2006. The invasion of climatically-similar Chile and California: similarities and differences/La invasion de Chile y California con climas similares: similitudes y diferencias. Ecology in an era of globalization: challenges and opportunities for environmental scientists in the Americas. Proceedings of the Ecological Society of America International Conference; 2006 Jan 8–12; Merida, Mexico. Washington, DC: ESA.
- Byers JE, Reichard S, Randall JM, *et al.* 2002. Directing research to reduce the impacts of nonindigenous species. *Conserv Biol* **16**: 630–40.
- Crall AW, Meyerson LA, Stohlgren TJ, et al. 2006. What data currently exist for non-native species? Front Ecol Environ 4: 414–18.
- Crawley MJ. 1989. Chance and timing in biological invasions. In: Drake JA, Mooney HJ, DiCastri F, *et al.* (Eds). Biological invasions: a global perspective. Chichester, UK: John Wiley.
- D'Antonio C, Levine J, and Thomsen M. 2001 Ecosystem resistance to invasion and the role of propagule supply: a California perspective. J Mediterr Ecol 2: 233–45.
- D'Antonio CM and Meyerson LA. 2002. Exotic plant species as problems and solutions in ecological restoration: a synthesis. *Restor Ecol* **10**: 703–13
- DiCastri F. 1989. History of biological invasions with special

- Drake JM and Lodge DM. 2004. Global hot spots of biological invasions: evaluating options for ballast-water management. P Roy Soc Lond B Bio 271: 575–80.
- Dudley TL, DeLoach CJ, Lovich JE, and Carruthers RI. 2000. Saltcedar invasion of western riparian areas: impacts and new prospects for control. In: McCabe RE and Loos SE (Eds). Transactions of 65th North American Wildlife and Natural Resources Conference; 2000 March 24–28; Chicago, IL. Washington, DC: Wildlife Management Institute.
- Dukes JS. 2000. Will the increasing atmospheric CO₂ concentration affect the success of invasive species? In: Mooney HA and Hobbs RJ (Eds). Invasive species in a changing world. Washington, DC: Island Press.
- Executive Order. 1999. Presidential executive order 13112 of 3 February 1999, invasive species. www.nepa.gov/nepa/regs/eos/ eo13112.html. Viewed 11 Jan 2007.
- Farnsworth EJ and Meyerson LA. 2003. Comparative ecophysiology of four wetland plant species along a continuum of invasiveness. Wetlands 23: 750–62.
- Fofonoff P, Ruiz GM, Steves B, Carlton JT. 2003. In ships or on ships? Mechanisms of transfer and invasion for nonnative species to the coasts of North America. In: Ruiz GM and Carlton JT (Eds). Invasive species: vectors and management strategies. Washington, DC: Island Press.
- Hierro JL, Villarreal D, Eren O, *et al.* 2006. Disturbance facilitates invasion: the effects are stronger abroad than at home. *Am Nat* **168**: 144–56.
- Jenkins PT. 2002. Paying for protection from invasive species. Issues Sci Technol Fall 2002: 67–72.
- Jenkins PT and Mooney HA. 2006. The United States, China, and invasive species: present status and future prospects. *Biol Invas* 8: 1589–93.
- Keller RP, Lodge DM, and Finnoff DC. 2007. Risk assessment for invasive species produces net bioeconomic benefits. P Natl Acad Sci USA 104: 203–07.
- Klotz S, Kühn I, and Durka W (Eds). 2002. BIOLFLOR Eine Datenbank zu biologisch- ökologischen Merkmalen der Gefäßpflanzen in Deutschland. Schriftenreihe für Vegetationskunde 38. Bonn, Germany: Bundesamt für Naturschutz.
- Křivánek M and Pyšek P. (2007). Forestry and horticulture as pathways of plant invasions: a database of alien woody plants in the Czech Republic. In: Tokarska B, Brock JH, Brundu G, et al. (Eds). Plant invasions: human perception, ecological impact and management. Leiden, Netherlands: Backhuys.
- Levine JM and D'Antonio CM. 2003. Forecasting biological invasions with increasing international trade. *Conserv Biol* 17: 322–26.
- Lodge D. 2006. Six degrees of separation? Trade globalization and changing linkages among freshwater ecosystems. Ecology in an era of globalization: challenges and opportunities for environmental scientists in the Americas. Proceedings of the Ecological Society of America International Conference; 2006 Jan 8–12; Merida, Mexico. Washington, DC: ESA.
- Lockwood JL, Cassey P, and Blackburn T. 2005. The role of propagule pressure in explaining species invasions. *Trends Ecol Evol* 20: 223–28.
- Lonsdale WM. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**: 1522–36.
- Madrigal EC and Saborío-R G. 2006. Análisis taxonómico de las plantas introducidas en Costa Rica. Ecology in an era of globalization: challenges and opportunities for environmental scientists in the Americas. Proceedings of the Ecological Society of America International Conference; 2006 Jan 8–12; Merida, Mexico. Washington, DC: ESA.
- Madsen JD, Ervin GN, Westbrooks R, *et al.* 2006. The national cactus moth detection network and database. Ecology in an era

of globalization: challenges and opportunities for environmental scientists in the Americas. Proceedings of the Ecological Society of America International Conference; 2006 Jan 8–12; Merida, Mexico. Washington, DC: ESA.

- McKinney ML and LaSorte FA. Invasiveness and homogenization: synergism of wide dispersal and high local abundance. *Global Ecol Biogeogr.* In press.
- MA (Millennium Ecosystem Assessment). 2003. Ecosystems and human well-being: a framework for assessment. Washington, DC: Island Press.
- Meyerson LA and Reaser JK. 2002. A unified definition of biosecurity. *Science* **295**: 44.
- Meyerson LA, Saltonstall K, and Chambers RM. a. *Phragmites australis* in eastern North America: a historical and ecological perspective. In: Silliman BR, Grosholz E, and Bertness MD (Eds). Salt marshes under global siege. Berkeley, CA: University of California Press. In press.
- Meyerson LA, Carroll I, O'Malley R, *et al.* (Eds). b. Tracking nonnative species: indicator design and data assessment for the United States. Washington, DC: The Heinz Center. In press.
- Mooney HA and Hobbs RJ. (2000). Invasive species in a changing world. Washington, DC: Island Press.
- Mooney HA, Zavaleta ES, and Hobbs RJ. 2006. Invasive alien species – are we up to the challenge? In: Preston C, Watts JH, and Crossman ND (Eds). 15th Australian Weeds Conference Papers and Proceedings: Managing Weeds in a Changing Climate; 2006 Sept 24–28; Adelaide, South Australia. Adelaide, South Australia: Weed Management Society of South Australia.
- Perrings CS, Dalmazzone S, and Williamson M. 2005. The economics of biological invasions. In: Mooney HA, Mack RM, McNeely JA, *et al.* (Eds). Invasive alien species: a new synthesis. Washington, DC: Island Press.
- Pimentel D, Zuniga R, and Morrison D. 2005. Update on the environmental and economic costs associated with alien–invasive species in the United States. *Ecol Econ* **52**: 273–88.
- Pyšek P, Sádlo J, and Mandák B. 2002. Catalogue of alien plants of the Czech Republic. *Preslia* **74**: 97–186.
- Reaser JK, Meyerson LA, and Gutierrez A. 2003. Biological invasions: does the cost outweigh the benefits? *BioScience* 53: 598–600.
- Ricciardi A. 2005. Facilitation and synergistic interactions among introduced aquatic species. In: Mooney HA, Mack RN, McNeely J, *et al.* (Eds). Invasive alien species: a new synthesis. Washington, DC: Island Press.
- Richardson DM, Rouget M, Raltson SJ, *et al.* 2005. Species richness of alien plants in South Africa: environmental correlates and the relationship with plant species richness. *EcoScience* **12**: 391–402.
- Rodriguez LF. 2006. Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. *Biol Invas* 8: 927–39.
- Rouget M and Richardson DM. 2003. Inferring process from pattern in plant invasions: a semimechanistic model incorporating propagule

pressure and environmental factors. Am Nat 162: 713-24

- Roman J and Palumbi SR. 2004. A global invader at home: population structure of the green crab, *Carcinus maenas*, in Europe. *Mol Ecol* 13: 2891–98.
- Roman J. 2006. Diluting the founder effect: cryptic invasions expand a marine invader's range. P Roy Soc Lond B Bio 273: 2453–59.
- Ruiz G, Fofonoff P, Miller W, and Hines A. 2006. Biological invasions in coastal marine ecosystems: past, present, and future. Ecology in an era of globalization: challenges and opportunities for environmental scientists in the Americas. Proceedings of the Ecological Society of America International Conference; 2006 Jan 8–12; Merida, Mexico. Washington, DC: ESA.
- Saltonstall K. 2002. Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. *P Natl Acad Sci USA* **99**: 2445–49.
- Sher AA and Hyatt LA. 1999. The disturbed resource-flux invasion matrix: a new framework for patterns of plant invasion. *Biol Invas* 1: 107–14.
- Simberloff D and Von Holle B. 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biol Invas* 1: 21–32.
- Stinson KA, Campbell SA, Powell JR, *et al.* 2006. Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. *PLOS Biol* **4**: 140.
- Stohlgren TJ, Barnett D, Flather C, *et al.* 2006. Species richness and patterns of invasion in plants, birds, and fishes in the United States. *Biol Invas* 8: 427–47.
- Tatem AJ, Hay SI, and Rogers DJ. 2006. Global traffic and disease vectors. *P Natl Acad Sci USA* **103**: 6242–47.
- US DOH (US Department of Health and Human Services). 2002. Protecting the nation's health in an era of globalization: CDC's global infectious disease strategy. www.cde.gov/globalidplan.htm. Viewed 14 Mar 2007.
- Von Holle B and Simberloff D. 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology* 86: 3212–18.
- Von Holle B and Motzkin G. 2007. Historical land use and environmental determinants of nonnative plant distribution in coastal southern New England. *Biol Conserv* 136: 33–43.
- Walther G-R. 2003. Wird die Palme in der Schweiz heimisch? Bot Helv 113: 159–80.
- Walther G-R, Gritti ES, Berger S, et al. Palms tracking climate change. Global Ecol Biogeogr. In press.
- Westbrooks R, Maden J, and Brown R. 2006. Detection and reporting of cactus moth in the United States. Fact Sheet. Starkville, MS: Mississippi State University.
- Ziska LH and George K. 2004. Rising carbon dioxide and invasive, noxious plants: potential threats and consequences. W Resour Rev 16: 427–46.

¹University of Rhode Island, Natural Resources Science, Kingston, RI 02881 *(laura_meyerson@uri.edu); ²Department of Biological Sciences, Stanford University, Stanford, CA 94305