

The spread of invasive species and infectious disease as drivers of ecosystem change

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Invasive species, disease vectors, and pathogens affect biodiversity, ecosystem function and services, and human health. Climate change, land use, and transport vectors interact in complex ways to determine the spread of native and non-native invasive species, pathogens, and their effects on ecosystem dynamics. Early detection and in-depth understanding of invasive species and infectious diseases will require an integrated network of research platforms and information exchange to identify hotspots of invasion or disease emergence. Partnerships with state and federal agencies that monitor the spread and impacts of invasive species and pathogens will be critical in developing a national data and research network that can facilitate a full understanding of the resulting effects on ecosystems and society. Citizen science can also play a role; individuals can report new invasions, record phenological changes associated with invasions or disease outbreaks, and can participate in efforts such as the Breeding Bird Survey, which may reveal long-term biotic change following species invasions and disease spread. The ecological and societal impacts of invasive species and pathogens differ across gradients of climate and land use, and in the presence of global climate change may exacerbate both their propagation and impacts. Understanding the interactions of invasive species, disease vectors, and pathogens with other drivers of ecosystem change is critical to human health and economic well-being.

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The increased connectivity of the global human population has amplified the frequency and effect of biological invasions and disease outbreaks. New trade routes among previously disconnected countries (Aide and Grau 2004) as well as enhanced transportation technology (eg airplanes and barges) have increased both the frequency and magnitude of invasions and potentially deadly disease outbreaks worldwide. In addition, land-use and climate change interact with human transportation networks to

facilitate the spread of invasive species, vectors, and pathogens from local to continental scales (Dukes and Mooney 1999; Sakai *et al.* 2001; Benning *et al.* 2002; Patz *et al.* 2004; Smith *et al.* 2007). The introduction of non-native species and range expansions of native species with changing land use and climate may have profound consequences for the ecosystems they occupy. Invasive species drive ecological dynamics at multiple spatial scales and levels of organization, through local and regional extinctions of native species (eg chestnut blight; Mack *et al.* 2000) and entire communities, shifts in native species richness and abundance (Parker *et al.* 1999), and altered fire regimes, water quality, and biogeochemical cycles (D'Antonio and Vitousek 1992; Vitousek *et al.* 1996; Strayer *et al.* 1999; Bohlen *et al.* 2004). Invasive species are the second leading cause (after human population growth and associated activities) of species extinction and endangerment in the US (Pimentel 2002). An estimated cost of non-native species in the US alone is over \$120 billion annually (Pimentel *et al.* 2005). Because climate change and land use can exacerbate the spread and effects of invasive species across scales (Dukes and Mooney 1999; Simberloff 2000), identifying invasion and curtailing the spread of invaders is an enormous ecological and societal challenge (Lodge *et al.* 2006).

Several recent reviews of invasive species and disease focus on modeling spatial spread (Hastings *et al.* 2005), species interactions and ecosystem processes (Lovett *et al.* 2006), evolutionary change (Strayer *et al.* 2006), and policy recommendations (Lodge *et al.* 2006). The objectives of this review are (1) to frame questions and hypotheses

In a nutshell:

- Invasive species and infectious diseases are becoming more prevalent and widespread with increased connectedness and globalization
- Alien species are the second leading cause of extinction in the US and cost approximately \$120 billion annually
- Disease vectors and pathogens are spreading across continents due to human transport, land-use change, and climate change
- To adequately understand and predict the spread of invasive species and disease, we must coordinate the many existing networks at local, regional, continental, and global scales
- Both observational and experimental approaches are required to fully understand the effects and impacts of invasive species and diseases and, more importantly, to understand the biotic and abiotic factors that enhance or diminish their effects

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for linking regional and continental-scale processes that govern the spread and impact of invasive species and disease and (2) to highlight the need for a continental-scale network of sites for monitoring and predicting the spread and impact of invasive species and disease.

To adequately address the environmental and societal problems of invasive species and the spread of diseases, such as avian-dispersed H5N1 avian influenza or severe acute respiratory syndrome (SARS), we must develop a continental-scale network to: (1) monitor changes in the local and geographic distributions of invasive species and infectious disease (Peterson *et al.* 2003; Drake and Bossenbroek 2004); (2) predict the processes and environmental conditions that promote the spread of invasive species and disease vectors from individual sites to regions and the continent (Hufnagel *et al.* 2004); and (3) understand the long-term ecological and evolutionary responses to ecosystem invasion (Mooney and Cleland 2001; Strayer *et al.* 2006). A coordinated cyber-infrastructure, along with improved data portals, would enable a more effective integration of databases from state and federal partner agencies that monitor invasive species or infectious diseases (including the US Department of Agriculture, US Geological Survey, Centers for Disease Control, US Environmental Protection Agency, US Fish and Wildlife Service, National Parks Service, and US Department of the Interior). A national database on invasive species and vectors, as well as key environmental features to identify potentially suitable habitat, would help scientists to forecast the spread and effects of invasive species and of diseases (Ricciardi *et al.* 2000). A number of such networks currently exist, including the Global Invasive Species Information network, the Inter-American Biodiversity Information Network, the Non-indigenous Species Network, and the Non-indigenous Aquatic Species Network. A complete description of these networks can be found in Meyerson and Mooney (2007).

Because exotic species and disease spread encompass multiple scales of interacting biotic and environmental factors (Figure 1), it is necessary to carry out large-scale monitoring while conducting fine-scale experiments and observations. Understanding new species and pathogen introductions and subsequent invasion success requires an understanding of the transport vectors, the local environmental conditions, organismal ecology, and the population and community ecology of the organisms (Figure 1). This framework can only be successfully employed if it is designed with scale-specific hypotheses and questions.

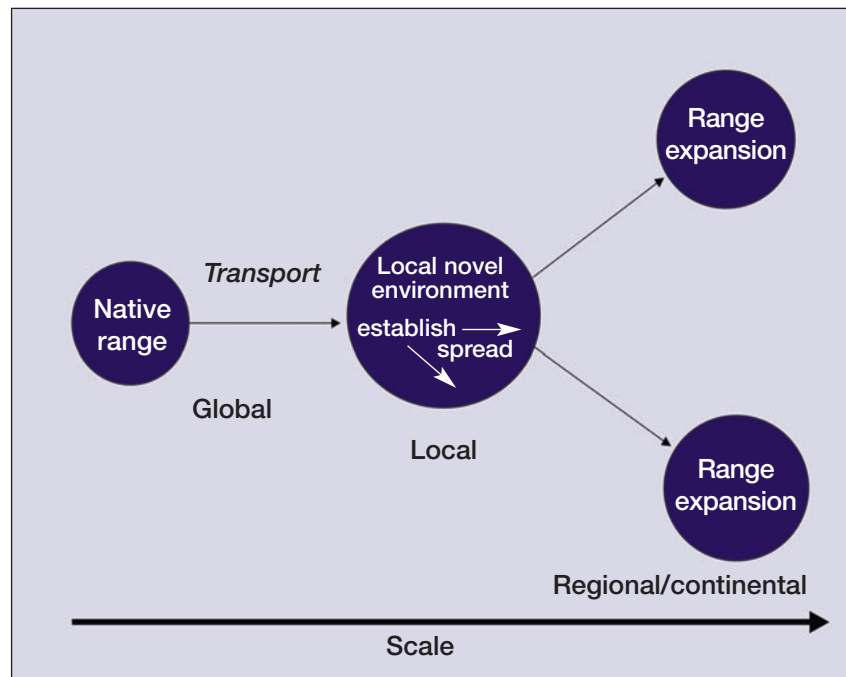


Figure 1. Invasion sequence from left to right. Species and pathogens first move via a transport mechanism from their native range to a novel habitat (global scale). Once they have arrived in a novel environment, they may (1) not survive, (2) persist but fail to spread, or (3) begin to reproduce and expand their local distribution. Finally, as the population continues to increase due to available resources, and lack of competitors, predators, or parasites, the species or pathogen may begin to expand its distribution both regionally and continentally, resulting in multiple, discrete, expanding populations.

■ Continental hypotheses and questions

The overarching questions that must be addressed include:

- (1) What societal and environmental factors can we use to accurately forecast the spread of invasive species and infectious diseases globally and at continental and local scales?
- (2) What are the population-, community-, and ecosystem-level causes and consequences of invasive species and infectious diseases, how do these vary across land-use and climatic gradients, and what suite of environmental variables predict these consequences?
- (3) How will ecosystems and their components respond to changes in natural and human-induced effects, such as climate, land use, and invasive species, across a range of spatial and temporal scales? What is the rate and pattern of the responses?

Environmental measurements for invasive species and pathogens must be coordinated with continental-scale gradient initiatives on climate change (Marshall *et al.* [2008] in this issue), coastal instability (Hopkinson *et al.* [2008] in this issue), and land use/urbanization (Grimm *et al.* [2008] in this issue). Linking aquatic habitats (lakes and rivers) to terrestrial systems is essential, because invasive species are one of the most important drivers of

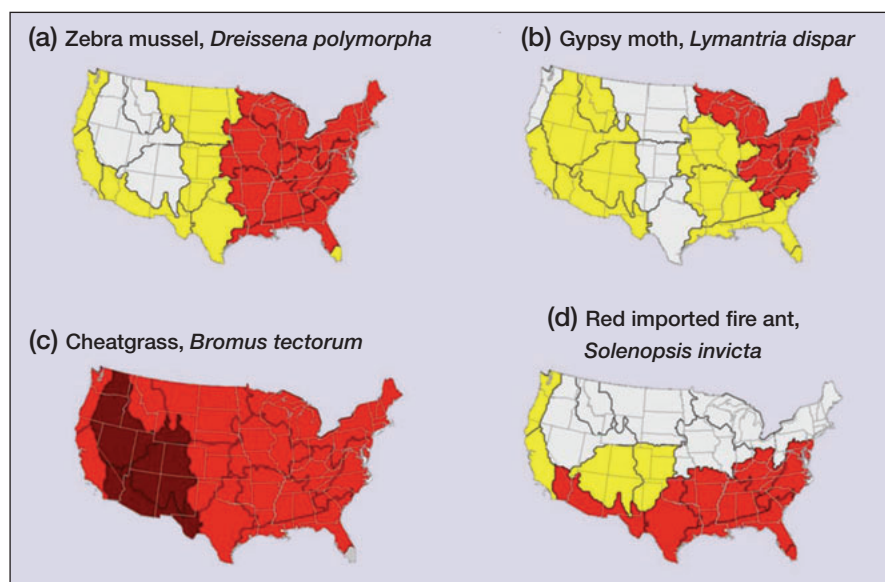


Figure 2. Present (red) and potential (yellow) geographic ranges of four invasive species among NEON climate domains. (a) The potential range of *Dreissena polymorpha* includes southeastern Alaska. (b) Gypsy moths, *Lymantria dispar*, currently show a restricted range but are predicted to spread widely. (c) *Bromus tectorum* occurs in nearly all NEON climate domains, but its impact is greatest in three climate domains (dark red). (d) The potential range of *Solenopsis invicta* includes Hawai'i.

biotic change in aquatic environments (Sala *et al.* 2000), and many terrestrial diseases and their hosts and vectors have links to aquatic systems (Williamson *et al.* [2008] in this issue). This is especially true as the connectedness among watersheds through human development increases the scale across which organisms can readily move (Peters *et al.* [2008] in this issue). Spatial coverage of monitoring will be greatly expanded through partnerships with several state and federal agencies.

New techniques for monitoring and forecasting the spread of invasions using remote sensing techniques will greatly extend the coverage of ground-based data (Asner and Vitousek 2005). Regional and continental-scale forecasting will also require data on human population densities, rates of land-use change, and the major transportation corridors connecting urban, recreational, and wildland areas. In addition, information on the pathways of species introductions and vectors of transport will be needed to prevent the introduction of non-native species and diseases (Kilpatrick *et al.* 2006). These include commerce in food and non-food plants and animals, shipping containers and ballast water, aircraft and shipping cargo areas, and intentional introductions by fish stocking, horticulture, and the pet trade (Lodge *et al.* 2006).

The general research questions listed above can be parsed into hypotheses that put infectious disease and the spread of invasive species into the context of increased connectedness, especially with respect to human development and climate change:

- (1) Connectedness of plants, animals, goods, and people predict disease and invasive species emergence.

- (2) Transportation vectors, land use, and climate interact to alter the mode, rate of spread, and effect of invasive species on natural and managed ecosystems.
- (3) Diseases affect not only human health and welfare, but also ecosystem functions.

Testing these hypotheses requires two kinds of measurements to understand and forecast the occurrence and effects of invasive species and infectious disease: (1) population, community, and ecosystem effects, and (2) rates and modes of spatial spread. Given the wide range of possible responses to species invasions, several kinds of measurements at multiple spatial scales with nearly continuous data collection are needed. The development of the National Ecological Observatory Network (NEON) should go far toward fulfilling these needs.

A few examples of invasive species with current or potential continental-scale distributions serve to illustrate how each invasive species varies among climate regions (as defined by NEON) in terms of their potential spread and in their effects on local ecosystems. The invasion of the zebra mussel (*Dreissena polymorpha*) into the Great Lakes and its subsequent spread to major river systems of the Midwest has altered abiotic factors, such as water transparency, nutrient cycling, and benthic habitat structure, as well as biotic factors, such as food-web structure, the bioaccumulation of contaminants, and the diversity of native freshwater mussels (Strayer *et al.* 1999). The presence of this invader has also led to the introduction of a roundworm parasite (*Bucephalus polymorphus*), which is responsible for dramatic impacts on cyprinid freshwater fish, the parasite's intermediate host. Models that use abiotic variables to predict the potential range of zebra mussels project further spread into river systems in virtually all of the eastern climate domains, and distinct focal points of invasion in the Pacific and southwestern US (Drake and Bossenbroek 2004; Figure 2a). Recreational boating will probably act as the transport vector, linking geographically isolated mussel populations.

Outbreaks of the gypsy moth (*Lymantria dispar*) cause regional defoliation in eastern forests, especially in stands containing oak, aspen, or birch. Short-term impacts include effects on light penetration, nitrogen (N) cycling, and primary production; the long-term effects of defoliation are unclear, but could involve interactions with other stressors such as pathogens or atmospheric N deposition (Lovett *et al.* 2006). The potential range encompasses most forested regions of the US (Figure 2b);

spatial spread is characterized by slow diffusion coupled with pulsed, long-distance establishment via anthropogenic transportation, ahead of the invasion boundary (Johnson *et al.* 2006).

Cheatgrass (*Bromus tectorum*) has established in all 50 states and is invasive in arid and semi-arid shrublands and grasslands of the Intermountain West (Figure 2c). As with other annual-grass invaders, cheatgrass promotes fire, creating a positive feedback cycle favoring further invasion, the exclusion of native plants, and loss of carbon (C) to the atmosphere (D'Antonio and Vitousek 1992; Young and Allen 1997). Cheatgrass is also of low nutritive value, and its unpredictable and ephemeral primary production threatens livestock.

The red fire ant (*Solenopsis invicta*) is increasing its range in the southern US (Figure 2d). Fire ant invasion is especially important in disturbed areas, where it causes declines in invertebrate biodiversity and nesting success of birds (Holway *et al.* 2002). Fire ants affect pollination mutualisms, kill livestock, and affect human health, and lead to pesticide use in attempts to control the ants. Invasive ants alter ecosystem processes by displacing native ant species that construct deep, long-lived nests, rich in organic matter (MacMahon *et al.* 2000). Climate change will probably extend the range of fire ants northward (Morrison *et al.* 2004).

Many other consequences to ecosystem functions and services occur with regionally important species. The following are just a few examples. Invasion of the N-fixing tree, *Myrica faya*, into nutrient-poor soils in Hawai'i affects the trajectory of plant community development and biogeochemical cycling (Vitousek *et al.* 1996). Salt cedar (*Tamarix* spp) invasions of riparian zones alter stream flow, increase evaporative water loss and soil salinity, and negatively affect native stream invertebrates and riparian plants (Morissette *et al.* 2006). Non-native earthworms (*Lumbricus* spp) in northern temperate forests have accelerated decomposition and C flux from soil, altered N and phosphorus (P) cycling, changed soil micro-organisms and invertebrates, and even facilitated the invasion of understory plants (eg garlic mustard, *Alliaria petiolata*; Bohlen *et al.* 2004). The rapid invasion of the African tulip tree (*Spathodea campanulata*) into Puerto Rico has affected nutrient cycling and decomposition processes (Crowl *et al.* 2006; Abelleira Martínez and Lugo in press) and is predicted to spread throughout moist, subtropical, and warm temperate (*sensu* Holdridge 1967) areas in the southeastern US and the Caribbean. This species restores forest conditions on abandoned lands, thus promoting the re-establishment of native tree species (Abelleira Martínez and Lugo in press), and its dominance after invasion lasts about 50 years (Lugo 2004). The regional expansions of native species as a result of climate change or land-use change can also transform ecosystems. For example, desertification of perennial grasslands by the expansion of desert shrubs, such as mesquite (*Prosopis glandulosa*) and creosotebush

(*Larrea tridentata*), alters hydrologic and biogeochemical cycling, decreases biodiversity and range productivity, and facilitates invasions by non-native plant species (Peters *et al.* 2006). In Puerto Rico, mesquite restores forest conditions in degraded dry forest lands and promotes the re-establishment of native species on these lands (S Molina Colon pers comm).

An integrated network of ecological research sites spanning the North American continent would also allow us to develop a comprehensive understanding of the ecological effects of invasive or emerging disease vectors and pathogens. While the majority of initial "detections" of new regional pathogens will undoubtedly come from public health workers and wildlife specialists, a network of established, long-term research sites would provide the resources and "continuity" to increase our understanding of the life cycles and ecology of targeted vectors and pathogens. For example, Lyme disease was first discovered in the northeastern US in 1977 (Steere *et al.* 2004), but it took nearly 25 years of ecological research to develop an understanding of the complex interactions between the bacterium, vector, and hosts in the environment (Randolph 2004; Tsao *et al.* 2004; Ostfeld *et al.* 2006). In the American Southwest, a new strain of hantavirus (*Sin Nombre* hantavirus; Nichol *et al.* 1993) emerged in 1993, and once CDC scientists had identified the deer mouse (*Peromyscus maniculatus*) as the host (Childs *et al.* 1994), ecologists in New Mexico were able to immediately apply the results of ongoing studies to explain the ecological causes of the disease outbreak (Parmenter *et al.* 1993). Subsequent long-term research at sites in Montana, Colorado, New Mexico, Utah, and Arizona (Mills *et al.* 1999) have led to a detailed understanding of the evolution and ecology of rodent-virus dynamics (Yates *et al.* 2002) and the development of remote sensing-based predictive models (Glass *et al.* 2002, 2006, 2007).

■ How can measurements be used in predictive models for forecasting?

The actual spread of invasive species has been forecast using analytical models based on diffusion, network, and gravity models that incorporate human-mediated transport (Hastings *et al.* 2005; Johnson *et al.* 2006; Bossenbroek *et al.* 2007). Another approach is to use climate-based niche models that predict the suitable habitats and potential geographic ranges of invasive species (Peterson *et al.* 2003; Drake and Boessenbroek 2004; Morissette *et al.* 2006). For many species, airborne and satellite imagery can be used to parameterize models on the spatial spread of invasive species. Remotely sensed data and embedded sensor networks can provide the detailed environmental measurements that are needed for more predictive climate- or habitat-based niche models of potential species distributions across ecosystems, regions, and geographic ranges. Ground-based measure-



Figure 3. (a) Operating out of a mobile laboratory, (b) field biologists sample blood and fleas from deer mice (*Peromyscus maniculatus*) for plague, hantavirus, and *Bartonella* in northern New Mexico.

ments are also needed to provide information on prevalent abiotic and biotic conditions, data required for predictions of ecosystem invasibility and impacts. Measurements of the spread and ecosystem effects of invasive species must be obtained across gradients of climate, land use, and human population densities. Gradient-based measurements will be critical in developing models to predict the interacting effects of invasive species, climate change, and land-use change. Benning *et al.* (2002) show how landscape models can be used to predict changes in the distribution of native birds in Hawai'i, in response to the interacting effects of climate warming, deforestation, and invasion by avian malaria.

Models that forecast disease outbreaks require data on host, vector, and pathogen populations and their environments, including spatial distribution, demography, and behaviors. Data on abiotic and biotic environmental conditions are also needed, since host or vector populations may show time lags in response to climate or food supply (Jones *et al.* 1998; Yates *et al.* 2002). New modeling approaches incorporate climatic variability (Altizer *et al.* 2006), hydrologic dynamics (Shaman *et al.* 2002), or host diversity (Keesing *et al.* 2006) as drivers of disease risk.

For this new generation of models, the goal will be to develop the predictive forecasting capability that will use past and current environmental information to assess future infection risks in plants, wildlife, and humans.

■ Multispecies approaches to monitoring invasive species and pathogens

The numbers of non-indigenous species of plants, birds, and fishes vary predictably across the US, according to native species richness and human population density (Stohlgren *et al.* 2006). Native plants and birds are characterized by high species richness in the eastern and southwestern US, with higher values in coastal and mountainous areas. Native fish species richness is highest in the large drainages of the Mississippi and Ohio River Valleys, which are also hotspots of diversity for other freshwater taxa, such as unionid clams. Areas of high native richness and high human population size and road densities are strongly associated with non-indigenous species occurrence and invasion success (Stohlgren *et al.* 2006). Broad-scale patterns lead to a continental-scale selection of sampling sites based on: (1) areas of high native and non-indigenous species richness, (2) gradients of urban to wildland areas within regions, and (3) areas with invasive species that have impacts over broad geographic ranges. The third criterion is important because the impacts of a particular invasive species or infectious disease may depend on local ecosystem characteristics and the presence of other non-indigenous species (Parker *et al.* 2005).

Collection of data on infectious diseases requires other considerations. Once an invasive or emergent disease has been identified, sampling locations should be selected within suitable habitats for hosts, vectors, and pathogens. Additional vertebrate and invertebrate species, as well as aquatic fauna and terrestrial plants, will need to be monitored at the appropriate sites to adequately quantify pathogen transmission. Sampling must include inter-site locations across continental-scale gradients of temperature, elevation, and latitude. At local sites, appropriate habitats should be sampled by rapid mobile units (Figure 3) to assess pathogens in particular vectors and reservoir host species. For example, mosquitoes will need to be sampled across North America, as their distributional ranges cover vast regions of latitude, longitude, and elevation (Figure 4); however, at the local site, mosquitoes should be sampled along river and stream corridors, ponds and lakes, and in selected wetlands, irrigated fields, and urban drainage fields at core sites and along inter-site gradients.

Migratory birds, which represent a major reservoir hosts for some human diseases, can be live-captured during both breeding seasons and migratory movements and sampled for introduced viruses such as H5N1 influenza, West Nile, or other potential invasive pathogens. Mosquito populations can be assayed for potential invasive pathogens that cause human disease, such as malaria,

Rift Valley fever, and dengue. Pathogens and hosts of aquatic fauna (eg shellfish, fish, amphibians) will also need to be sampled with both regional and continental patterns in mind. Similarly, field-sampling efforts for targeted plant diseases will necessarily be directed toward locations along gradients where host plants exist. The continental-scale approach will provide comparative data on disease dynamics among and within different ecosystems under varying environmental conditions, which will allow the further refinement of predictive models.

■ Conclusions

Invasive species and new diseases pose the same problem; each is a new species with the potential to modify the existing structure and function of ecosystems and the ecosystem services upon which people rely. Furthermore, some new pathogen species can directly impact human health. Thus, the addition of new species (invasives or diseases) to an ecosystem can affect the well-being of people, whether through economics or health. Many species already present influence human well-being positively or negatively, and we must be concerned that the introduction of new species may result in novel biotic interactions and modify existing ones in the current ecosystems (natural and managed; Figure 5).

Whether introduced species impact ecosystem services, the economy, or human health, we need to understand species interactions and the consequences to local ecosystems. Traditional epidemiology has often ignored the ecological perspective, but it largely corresponds to host–pathogen or host–vector–pathogen population ecology. Therefore, local biotic understanding is necessary to assess (and reduce) the impacts of invasive species and disease.

While new species exert their impacts at the local biotic scale, we know that, in many cases, their establishment, their effects, and the success of countermeasures can vary from one location to another. We therefore need to examine the problem at much greater geographical scales (Figure 5), using networks of study sites to address a series of questions.

First, what causes the variability between locations in the establishment of, impact of, and success of countermeasures against new species? This knowledge will improve our ability to predict which locations will be susceptible to invasion by a particular species, the potential effect on the local ecosystem and people, and what the most effective local

countermeasures will be. Detailed ecological study will be required at a variety of locations selected a priori, to address how specific species characteristics (eg growth, reproduction, survival) under different local “driver” values (eg gradients of temperature, moisture, elevation, human activities) influence biotic interactions and, thereby, human well-being. Too often in the past, answers to these questions have emerged slowly or not at all, because sampling has been implemented in limited locales, based on specific observations, and are not adequate to measure landscape-level patterns.

Second, how do new species’ propagules arrive at a location? This requires knowledge at regional and global scales, so we can assess how a particular new species becomes available for invasion, what controls invasion rates, and how preventative measures can be developed. Only at this larger scale can invasion fronts and their movements be monitored and studied (Hengeveld 1989). This requires specific biotic information such as species characteristics related to propagule numbers emerging from surrounding populations and vagility, but today this may largely be a function of external “drivers” such as markets (eg plant and animal trades) and transportation systems (eg regional connectedness and modes of transportation providing “friendly” transient environmental conditions for propagules). Compared to the previous question, above, the network of study sites addressing this question needs to contain a greater number of uniformly distributed sites, because proximity to propagule sources, rather than “driver” differences, is the key factor.

Finally, how might invasibility change in the future, and among different classes of species? Obviously, answers to

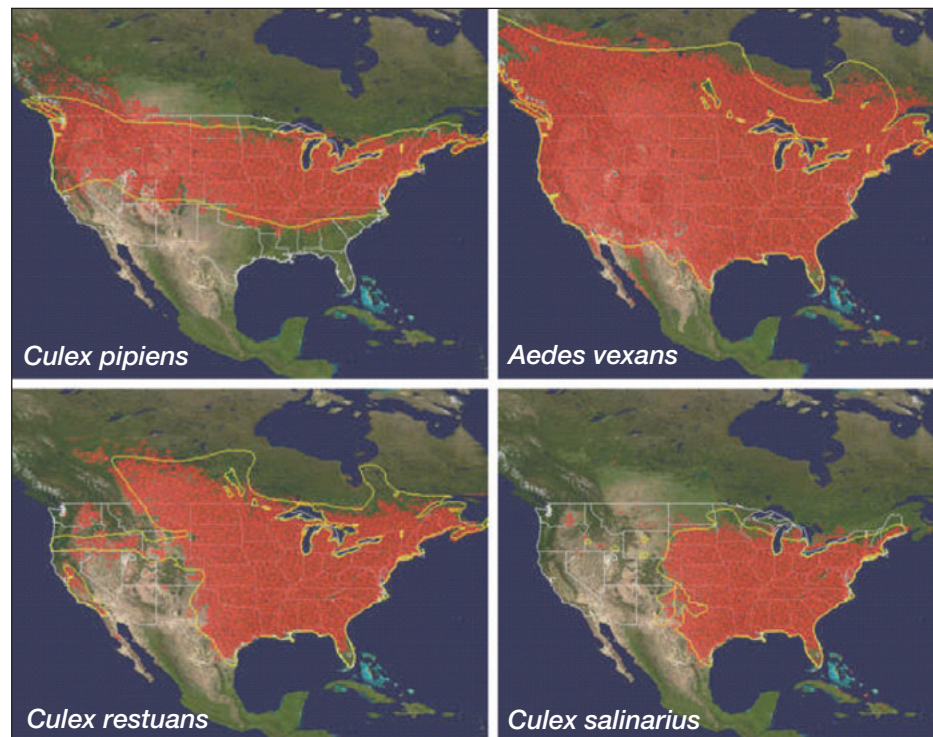


Figure 4. The geographic distribution of mosquito disease vectors, *Culex* spp and *Aedes vexans*, in North America.

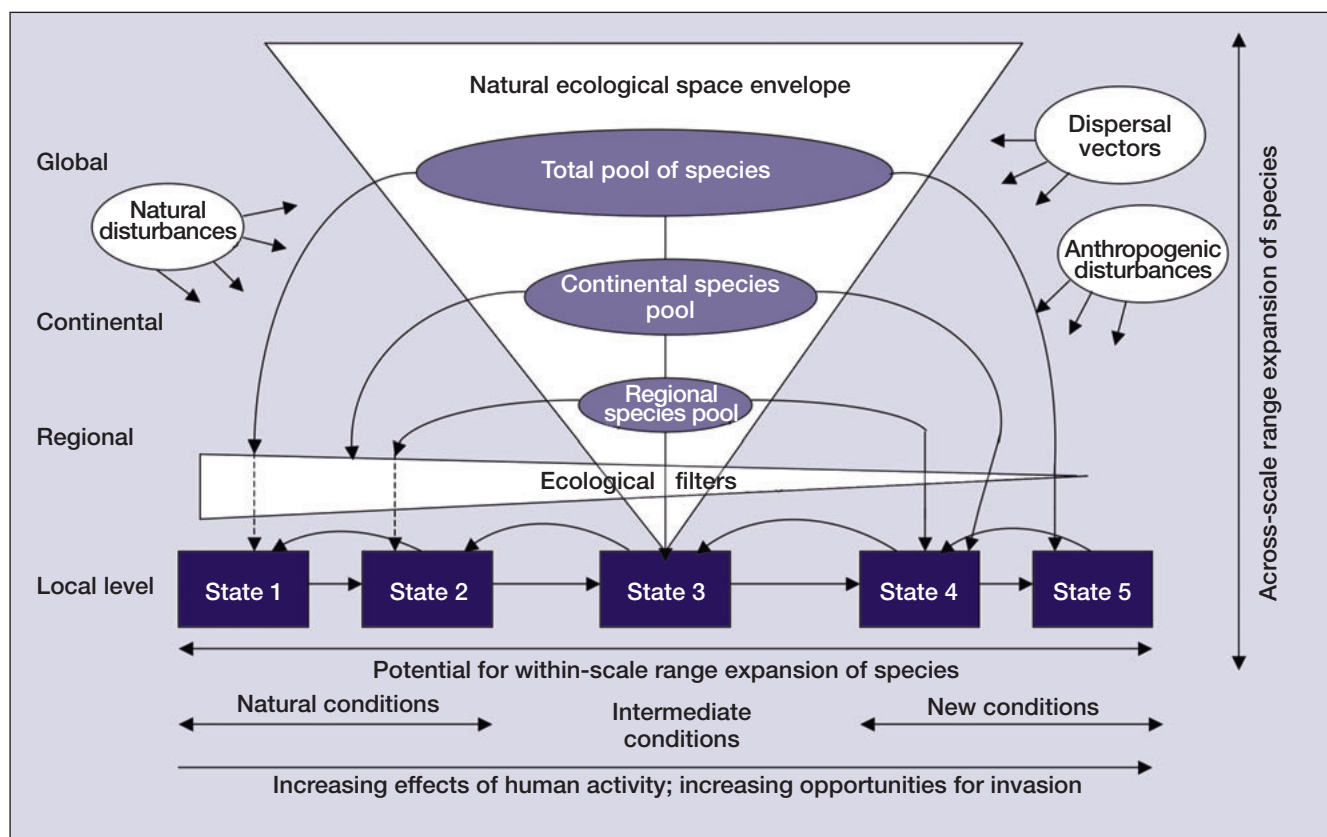


Figure 5. Summary diagram illustrating the factors that influence the spread of invasive species and diseases across geographic and ecological space and their interaction with native species in the formation of new species assemblages (novel ecosystems *sensu* Hobbs *et al.* 2006). The lines with arrows represent the movement of species and dashed lines represent negligible rates of species movement. Geographic space is represented vertically from global to local scales, while ecological space is represented by the inverted triangle. There are more species and diversity of ecological conditions at global than at local scales. However, natural and anthropogenic disturbances, as well as many other vectors, disperse species across geographical and ecological space. For a species to actually invade an ecosystem (represented at the local level by boxes, each at a different state of maturity along a gradient of human activity: states 1 and 2 without measurable human effects, states 4 and 5 exposed to heavy human activity, and state 3 an intermediate level of anthropogenic impact), it must pass through an ecological filter. We expect that the ecological filters that determine the success of an invasion are weaker to the right of the diagram and, thus, are conducive to greater invasion success in ecosystems of states 4 and 5 than in ecosystems of states 1 and 2. Under extreme anthropogenic impact, new conditions develop, which in turn select for novel ecosystems dominated by invasive species.

this question require knowledge from the previous two questions. The first question provides insight into how future conditions may influence which species are able to invade, how their presence could affect ecosystems and human well-being, and how best to develop countermeasures. The second question provides insight into where and when these invasions might take place. However, additional information is required to assess how the spatial matrix and “drivers” are changing over time in terms of, for example, climate and human activity. Therefore, a network of locations needs to be distributed across the landscape in a manner that allows us to assess not only current conditions, but how they may change in the future. It is the combination of information from the first and second question, in the spatial context of temporally changing conditions, that will provide us with the ability to forecast.

Each hierarchical level of question presented above poses different challenges to the number, spacing (local-

tion), and measurements considered in network design. Consequently, a network designed to address one hierarchical level is useful, but only slightly greater design effort may permit all hierarchical levels to be addressed and synergisms to emerge when cross-hierarchical questions are simultaneously addressed. These considerations will allow network construction to better address issues in invasion and disease ecology, and better enable networks to predict and forecast emerging threats.

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