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# Human Health Link to Invasive Species

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## Introduction

Invasive species are currently a far-reaching, interdisciplinary topic given their impacts on biodiversity, economics, and human health. Invasion ecology, which was proposed as a subdiscipline of ecology by Charles Elton in his book *The Ecology of Invasions by Animals and Plants* (1958), aims to understand the causes and consequences of species invasions by focusing on factors that affect the dispersal, establishment, and impact of non-indigenous species (NIS). Later authors expanded on Elton's compendium of cases of invasive species impacts and general hypotheses by linking tools and approaches from other disciplines, such as biogeography, genetics, population biology, conservation biology, and evolution. In particular, large efforts have been devoted to capture the essence of the invasion phenomenon through mathematical models. Recently, researchers have highlighted the utility of species introductions as natural experiments, which can be used to obtain a more profound understanding of general ecological theory. Current studies highlight the role of species invasions as both a consequence and cause of global change, with direct and indirect effects on biodiversity, economics, and environmental and human health.

## Phenomenon of Invasion

The term invasive species has been widely used in both scientific and nonscientific frameworks. As a consequence of this widespread use, the meaning of the term invasion often differs between authors. In general, the term invasive has been used to describe a species that presents at least one of the following characteristics:

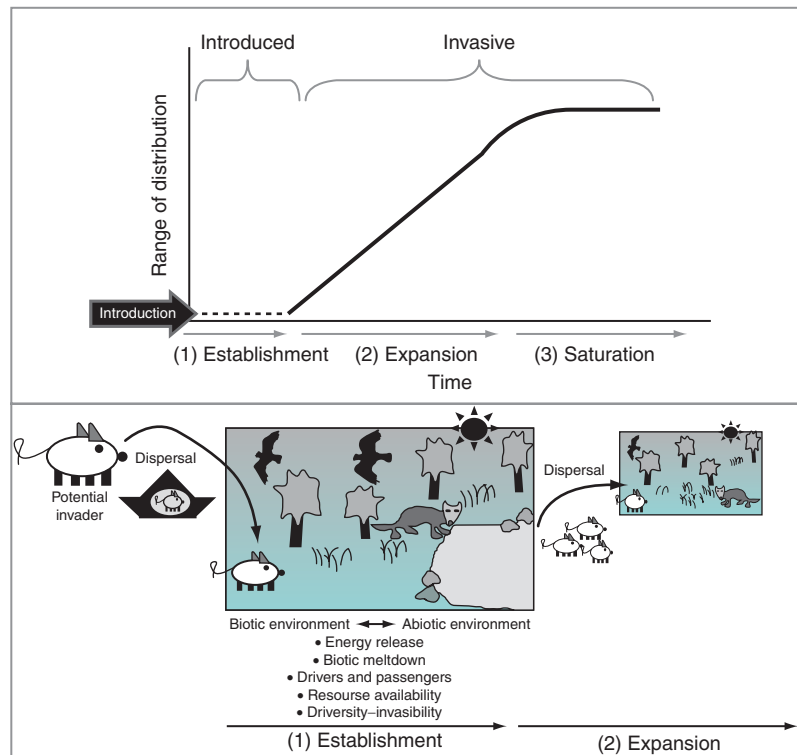
- inhabits an area outside of its current or historical range of distribution
- reaches high abundances and dominates space
- competes with native species for limiting resources
- has 'recently' or is currently increasing its range size
- causes or is likely to cause harm to human health, economics, or environments.

Biologists have suggested that to recognize patterns and make accurate predictions about invasive species, it is necessary to have a working definition that does not change according to case studies or individual

researchers. There is some controversy regarding the appropriate way to define invasive species and the invasion process. For example, a species that is nonindigenous and invasive in one area is also native in another area, or a species that is considered to be an invasive pest to one person may be considered an 'imported resource' to another.

Although scientists have not unambiguously identified taxa-independent characteristics that define all invasive species, the invasion process has been observed to progress through the same sequence of stages regardless of taxonomic identity. This involves (1) an initial establishment phase, where a species arrives to a new region, and during which little or no range expansion occurs, (2) an expansion phase, and (3) a saturation phase, where range expansion reaches a plateau (**Figure 1**). Under this framework of range expansion, stages 1–3 describe an introduced, exotic, or NIS, whereas an invasive species (i.e., a species in expansion) applies only to stages 2 and 3. Williamson's Tens Rule captures the idea that potential invaders must overcome barriers at each stage of the invasion process to successfully establish and invade new environments. This rule suggests that only a small fraction of the species in a region will arrive to a new environment, that only a small fraction of arriving species will become established in the new environment, and that only a small fraction of established species will invade new environments. The true proportions of potential invaders that succeed at each stage of the process are likely quite variable, with reports ranging from 5% to 50% in some areas. Further work to explicitly evaluate the success of invaders will provide insight into the magnitude of this problem.

The initial movement of a species to a new region may involve natural dispersal by individuals, as well as vector-related dispersal, the latter of which may greatly increase the distance that a propagule is able to disperse (e.g., to another continent). Many anthropogenic activities serve as vectors for the movement of species around the planet. Such human-aided transport of species has occurred for over 10 000 years, as humans dispersing around the world frequently bring other species with them, both deliberately (e.g., species imported for agriculture, decoration, and medicinal purposes) and fortuitously (e.g., species that are transported in the ballast water of ships, seeds, or microorganisms transported on the shoes of travelers). The current degree of global



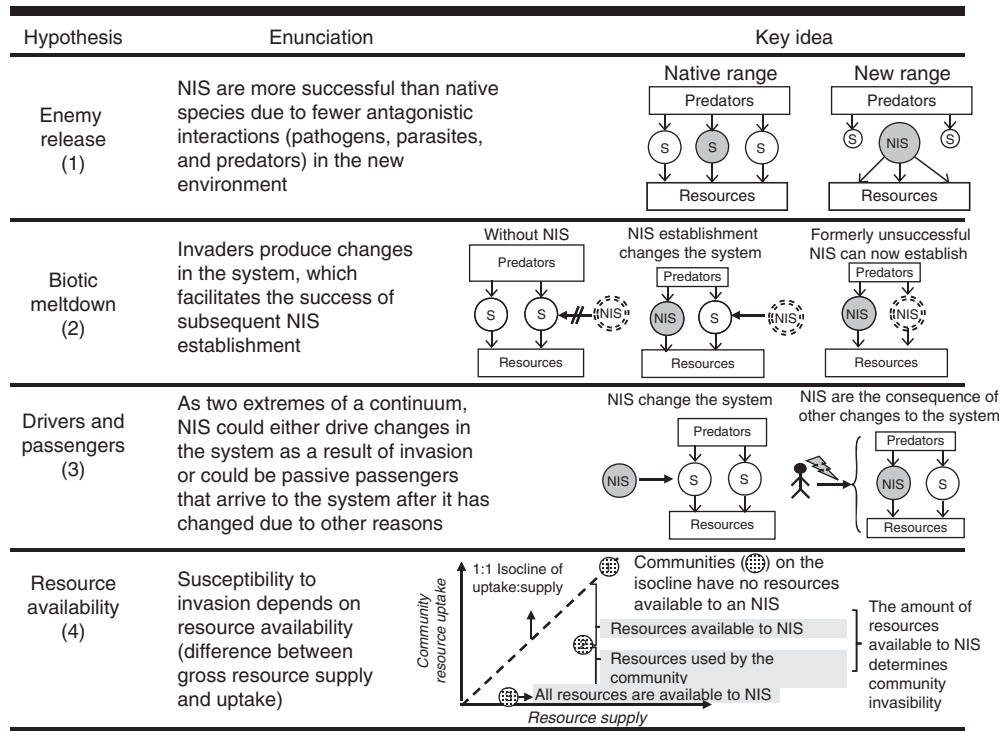
**Figure 1** Stages of the invasion phenomenon expressed as changes in spatial occupancy (upper panel) and types of ecological interactions (lower panel). A potential invader arrives to a new area through natural dispersal or vector-related transport. The current degree of global connectivity has intensified the frequency and velocity of organismal transport around the world. Human-related vectors may be deliberate or accidental. On arrival to a new region, successful establishment can only occur if a species is able to cope with the abiotic and biotic conditions of the environment, and the demographic variability due to small population size. Many potential invasions fail at this stage of the phenomenon, which also corresponds to the stage where eradication and control efforts are most successful. During the establishment stage (1) a species arrives to a new area, but little or no range expansion occurs. Several hypotheses have been proposed to explain the successful establishment of a species' population in a new environment (see details in [Figure 2](#)). Following successful establishment, individuals may disperse beyond the initial sites of introduction to colonize new areas. The subsequent movement of individuals may occur through natural dispersal or human-mediated vectors. The rate and type of range expansion may depend on life history and genetic traits that interact with environmental properties. If there is a geographical limit to available space for colonization, expansion may reach a plateau. In the latter two stages of the invasion process, efforts to eradicate or control an invader are often futile. Under this framework of range expansion, stages 1–3 describe an introduced, exotic, or nonindigenous species, whereas an invasive species (i.e., a species in expansion) applies only to stages 2 and 3. Based on Shigesada N and Kawasaki K (1997) *Biological Invasions: Theory and Practice*. Oxford: Oxford University Press.

connectivity has intensified the frequency and velocity of organismal transport around the world, which has increased the rate of successful NIS establishment.

Following arrival to a new region, to become successfully established a species must first be able to cope with and survive the abiotic and biotic conditions of the environment, and demographic variability due to small population size. Various hypotheses have been proposed to explain the successful establishment of a species' population in a new environment ([Figures 2 and 3](#)). It should be highlighted that the majority of species introductions do not move beyond the establishment phase. Furthermore, the duration of the establishment period is variable for different species and even for different populations of the same species. In this sense, a species may arrive to a new environment and be present for a long period of time without expanding its initial

distribution, and then it may suddenly increase in abundance and rapidly expand to new areas. Such latent invasions may be explained by changes in resource availability linked to disturbance, as well as to genetic adaptations. The establishment phase is a critical period for conservation biologists and managers, given that it is during this phase that measures to eradicate or control abundance and spread are most likely to be successful. In fact, for most invasions, once an organism has arrived to a new area the opportunity for successful control is limited exclusively to this phase.

After a population has become successfully established, individuals may disperse beyond the initial sites of introduction to colonize new areas. The subsequent movement of individuals from the initial points of introduction may occur through natural dispersal and human-mediated transport. The rate and type of



1: Elton 1958; 2: Simberloff and Von Holle 1999; 3: MacDougall and Turkington 2005; 4: Davis et al. 2000

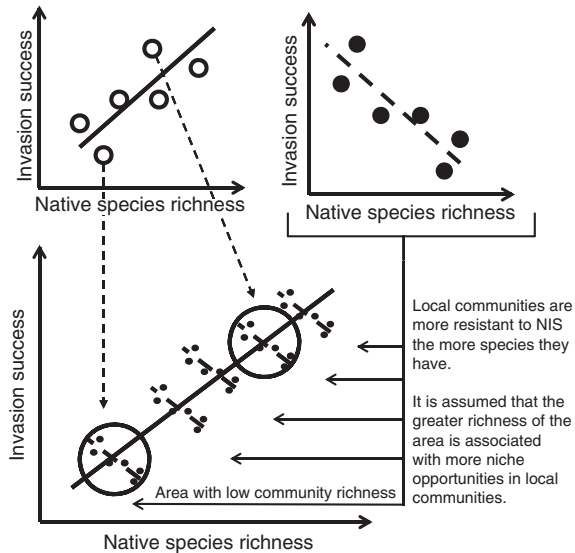
**Figure 2** Principal hypotheses that explain nonindigenous species (NIS) establishment and spread. In all panels, circles represent native (S) or non-indigenous (NIS) species. (1) The enemy release hypothesis states that an NIS experiences a new environment free of antagonistic interactions (pathogens, parasites, and predators). In this environment, the NIS reaches high abundance and could out-compete native species. (2) The biotic meltdown hypothesis states that NIS establishment implies changes in the system that facilitates the successful establishment of subsequent NIS. For example, species that fail to establish in a community because of competition with or predation by native organisms could be favored when a previous invader reduces the abundance or diversity of native organisms. In some cases, the first NIS could be a disease that reduces the abundance of native competitors, but does not have a significant impact on the NIS. (3) The drivers and passengers hypothesis develops the idea that NIS probably plays simultaneous roles as both determinants and consequences of observed changes in natural ecosystems. Given the global extent to which human activities impact natural ecosystems, it is difficult to disentangle when the arrival of an NIS represents a main determinant of system changes and when NIS are part of a general trend in large-scale system change. The left-hand figure of the third panel indicates a system where the NIS is the driver of system change, whereas the right-hand figure illustrates how NIS occurrence in the new environment is a response to changes originating from another source (e.g., anthropogenic impacts). (4) The fourth hypothesis is based on the difference between the gross resource supply in an ecosystem and the amount of this resource that is taken up by the community. If all of the resource is used, the chance of successful establishment by NIS will be minimal. However, if community uptake is only a small fraction of the supply, availability of free resources will improve NIS success. In general, it is considered that the larger the amount of unused resources (supply–uptake), the more prone a community is to invasion. This hypothesis explains the observed increase in NIS establishment when communities present variations in resource supply, or when disturbances reduce the relative uptake of resources. In both cases the relative amount of resource that the community uptakes is reduced, leading to free resources for the new NIS.

expansion may depend on life history and genetic traits that interact with environmental properties. When available space for colonization is geographically limited, the rate of expansion may slow and level off as appropriate habitat becomes scarce, and density-dependent interactions (e.g., intraspecific competition) increase. In these latter two stages of the invasion process efforts to eradicate or control an invader are often futile.

Several hypotheses have been proposed to explain the successful invasion of NIS to new areas (Figures 2 and 3). In particular, the enemy release hypothesis proposes that NIS have an advantage over native species since the new environment may be free of antagonistic interactions

(pathogens, parasites, and predators) due to a lack of evolutionary relationships with native species, which may not recognize NIS as appropriate prey or disease hosts. The biotic meltdown hypothesis states that one NIS may provoke changes in the environment that facilitate the successful establishment of subsequent NIS. The drivers and passengers hypothesis develops the idea that the establishment of introduced species in natural ecosystems may be the result of NIS-induced changes in a system, or NIS may become established as changes in the system originating from another source provide windows of opportunity for successful introduction. The resource availability hypothesis describes how NIS may take

Empirical patterns support the existence of both, positive and negative associations, between native species richness and NIS colonization success.



**Figure 3** The diversity–invasibility hypothesis proposes that species-rich communities are more resistant to invasion than species-poor communities at a local spatial scale. The principal mechanism accounting for this relationship is interspecific competition for niche opportunities, where higher numbers of native species lead to less niche opportunities for invaders. Variation in niche opportunities over broad spatial scales, and an assumed positive relationship between native species richness and availability of niche opportunities for invaders, would result in the observed positive relationship between native species richness and invasion success at broader spatial scales. Clusters of black dots represent the relationship between native species richness and invasion success within local communities; white dots represent the relationship of the same variables at a broader spatial scale.

advantage of a surplus between gross resource supply in an ecosystem and the amount of the resource utilized by the community, where communities with larger amounts of unused resources are more prone to invasion. This hypothesis provides an explanation for the observed increase in NIS establishment in communities with variable resource supply, and the positive relationship between NIS establishment and disturbances, which may reduce the relative uptake of resources by native species leading to free resources for NIS. The diversity–invasibility hypothesis, presented by the British ecologist, Charles Elton, proposes that species-rich communities are more resistant to invasion than species-poor communities, as a greater number of native species would leave fewer ‘niche opportunities’ available to NIS due to interspecific competition. Empirical evaluations of this hypothesis support the existence of both positive and negative associations between native species richness and NIS colonization success, leading researchers to propose that the

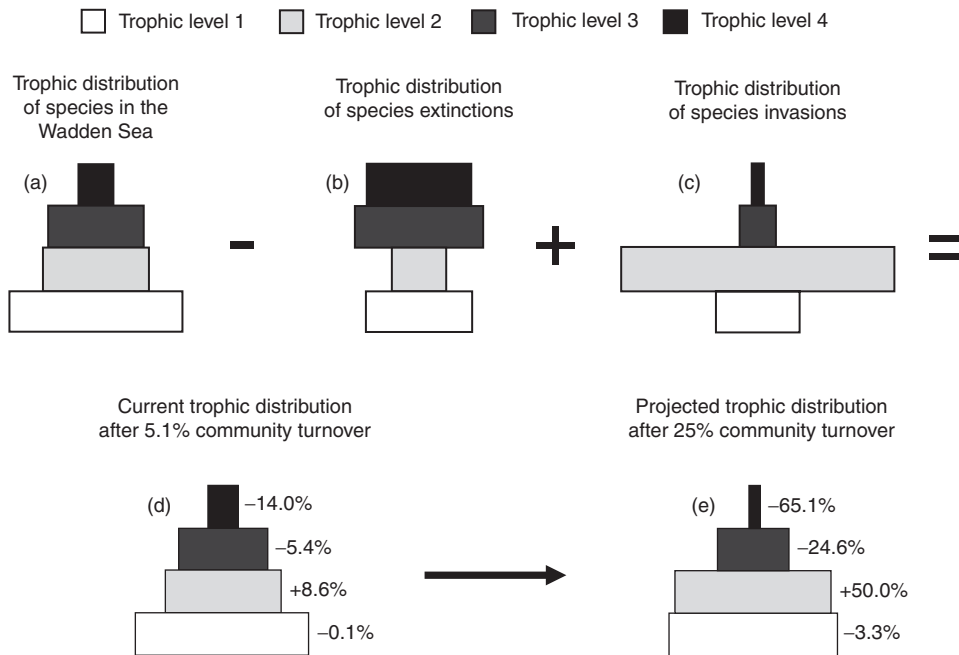
variation in niche opportunities over broad spatial scales, and an assumed positive relationship between native species richness and availability of niche opportunities for NIS would explain the positive relationship at broader spatial scales.

## Importance of NIS in Global Change

Species introductions and invasions are currently a major topic in society due to their impacts on biodiversity, economics, and human and environmental health. The introduction and spread of NIS occurs as both a consequence and a cause of global change. Changes in global climate, habitat availability, biogeochemical cycles, and biodiversity can provide niche opportunities for NIS introduction and expansion. For example, studies have found that the spread of many invasive species is related to climatic variables such as temperature, disturbed habitats are less resistant to invasion, and changes in biodiversity, such as extinctions, may provide a window of opportunity for NIS to enter a system. Similarly, species invasions are considered to be a principal component of global change due to their effects on habitat, biogeochemical cycles, biodiversity, economics, and human health. A notable example of the dual role of NIS is observed in the Wadden Sea of northwestern Europe (Figure 4). In this ecosystem, food webs have been dramatically altered due to human-caused species extinctions at high trophic levels (top predators and other carnivores), combined with species introductions occurring mainly at lower trophic levels (macroplanktivores, deposit feeders, and detritivores).

## Impacts of NIS

Although all species are capable of some degree of dispersal, anthropogenic activities have facilitated an unprecedented, massive movement of species across major biogeographic barriers that historically separated the flora and fauna of different continents. This deliberate and accidental mixing of species has resulted in global changes to the structure and function of ecosystems, where a lack of biotic controls in the invaded community can lead to unchecked population growth. Changes in ecosystems and ecosystem services have further led to repercussions on economies and human societies. Invasive species are known from all taxonomic levels (e.g., viruses, bacteria, algae, plants, invertebrates, and large mammals). Some well-known aggressive invaders include the alga *Caulerpa taxifolia*, which covers a large portion of benthic habitats in the Mediterranean Sea; the aquatic plant *Eichhornia crassipes* (water hyacinth), which grows quickly and forms thick mats that clog waterways, impedes many human activities such as fishing, and can



**Figure 4** A notable example of nonindigenous species (NIS) impacts in ecosystems as both a cause and a consequence of global change. Here the combined effects of species loss due to human-caused extinctions and species gain through introductions result in altered trophic structure of food webs in coastal marine systems of the Wadden Sea. In the trophic pyramids bar widths are scaled to the proportion of species in each trophic level and numbers indicate the percentage of species loss or gain at each trophic level. Colors indicate trophic level (white = level 1, light gray = level 2, dark gray = level 3, black = level 4). (a) Predisturbance pyramid, (b) skew of extinctions, (c) skew of invasions, (d) current distribution after invasions and extinctions resulting in 5.1% community turnover (i.e., equal numbers of extinctions and invasions), (e) projected change in the trophic distribution of species in the Wadden Sea for 25% community turnover. Since most extinctions occur at high trophic levels (top predators and other carnivores), and most invasions are from species at lower trophic levels (macroplanktivores, deposit feeders, and detritivores), the shape of the food pyramid is dramatically altered. The implications of this transformed food web on ecosystem functioning is largely unknown. From Byrnes JE, Reynolds PL, and Stachowicz JJ (2007) Invasions and extinctions reshape coastal marine food webs. *PLoS ONE* 2(3): e295. doi:10.1371/journal.pone.0000295.g004. Reproduced under an open-access license (<http://journals.plos.org/plosbiology/license.php>).

foster the breeding of disease-transmitting mosquitoes; and the rabbit, *Oryctolagus cuniculus*, which has a high population growth rate and may cause serious soil erosion by overgrazing and burrowing.

The general impacts of NIS can be grouped into three broad (nonexclusive) categories:

- Ecological impacts
- Economic and social impacts
- Human health impacts.

Researchers from different fields are working to build a framework for understanding how to best evaluate, quantify, and predict different kinds of impacts. Identifying and quantifying impacts is not always straightforward. For example, impacts may be dependent on the variable that is used (e.g., richness or diversity indices versus community composition); may depend on the system that is studied (e.g., the green alga *Codium fragile* is reported to have greatly altered community structure off the coast of Maine, but to coexist with native congeners on Irish shores); and may depend on the scale that is used

for evaluation (e.g., impacts at the population level may not be correlated with impacts on ecosystem functions).

### Ecological Impacts of NIS

In spite of the large amount of literature available on invasive species, few studies actually quantify the impacts of NIS in the field. A review by Bruno and collaborators of published papers on exotic and invasive species found that of the published scientific papers on exotic species cited between 1981 and 2003 in the ISI Science Citation Index only approximately 17% considered the occurrence of biotic interactions, and fewer than 9% of studies performed some type of controlled and replicated manipulation (Figure 5).

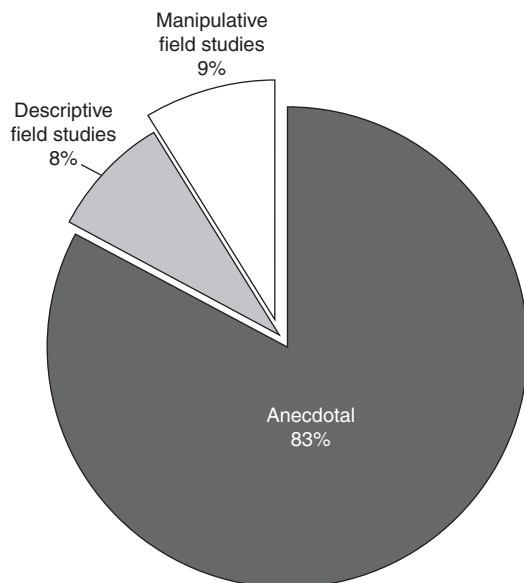
Documented ecological impacts of NIS include examples of both negative and positive changes in the richness and diversity of local communities as a result of different biotic interactions. NIS-caused decreases in richness and diversity due to competition, predation, and parasitism are evidenced by the displacement and, in some cases, the extinction of native species. However,

given the complex role of NIS as both causes and consequences of global change, in many cases it is a challenge to untangle the determinant role of NIS as a causal agent in species extinctions. In addition to negative effects on diversity, increases in local richness and diversity result from facilitation between NIS and native species. Such increases may include exotic ‘ecosystem engineers,’ which increase local species richness and abundance by providing habitat. Examples include the introduced tunicate *Pyura praeputialis* in Chile, which increased species richness at local and seascape scales, and the introduced green alga *Codium fragile*, which increased mussel recruitment and survival in the Adriatic Sea. Facilitation between exotic species (biotic meltdown) has also been observed, such as the introduction of feral pigs (*Sus scrofa*) in Hawaii, which are reported to spread exotic plants, reduce the abundance of some native plants through selective consumption, facilitate exotic invertebrates, and spread the invasive climbing vine *Parsiflora mollissima*. Moreover, the spread of these feral pigs may be facilitated by introduced earthworms, which are a readily consumed source of protein by feral pigs. NIS may also present more complex, indirect effects, where

one species modifies the impact that a second species has on a third.

The overall effects of NIS on species diversity are varied. At smaller scales, there is evidence of both local decreases and increases in species richness associated with NIS. However, at a global scale, researchers agree that species introductions and invasions are an important threat to the planet’s biodiversity. As species are moved between continents, previously dissimilar communities begin to become more alike, resulting in homogenization of the planet’s biota, and the resulting loss of diversity at larger scales.

NIS may also affect genetic diversity. Hybridization between introduced species and native species (and between individuals from different populations of the same species), and posterior introgression can lead to the loss of native local genotypes. Hybridization and introgression may result in sterile or less-fit populations, increasing the threat of extinction. Examples of genetic mixing include introductions of rainbow trout, *Oncorhynchus mykiss*, which hybridize extensively with native, threatened trout species (*O. apache* and *O. gilae*) in the southwestern United States and have greatly reduced the abundances of the native trout; reductions in the populations of rare, native ducks of New Zealand, Hawaii, and Florida due to hybridization with introduced mallard ducks, *Anas platyrhynchos*, and crop-to-wild gene flow in species such as the sugar beet, *Beta vulgaris*. Furthermore, hybridization and introgression can result in the origin of new variation and new species.



**Figure 5** Percentage of published scientific papers on invasive/exotic species cited between 1981 and 2003 in the ISI Science Citation Index reporting anecdotal occurrence of biotic interactions, evidence from descriptive field studies, and quantitative evidence from controlled and replicated manipulative studies. It is notable that in spite of the large amount of literature about invasive species, few studies actually quantify the occurrence of NIS impacts in the field. Data from Bruno JF, Fridley JD, Bomberg KD, and Bertness MD (2005) Insights into biotic interactions from studies of species invasions. In: Sax DF, Stachowicz JJ, and Gaines SD (eds.) *Species Invasions: Insights into Ecology, Evolution and Biogeography*, 1st edn., pp. 13–40. Massachusetts: Sinauer Associates, Inc. Publishers.

### Economic and Social Impacts of NIS

Although much of the concern regarding species introductions has been motivated by public perception of social and economic impacts (e.g., damage to crops and aesthetic changes to native landscapes), there is some controversy regarding the appropriate way to quantify these impacts, especially considering that the perception of impact may change over time and space. For example, in South Africa the introduced mussel, *Mytilus galloprovincialis*, which has dramatically altered intertidal systems, is not considered an important food item for subsistence by local human populations, but recently this species has been recognized as a commodity for export by other stakeholders.

Many NIS imported for agriculture and aquaculture generate economic gains through retailing of the species and their associated services. Direct economic loss caused by NIS can be divided into two categories: (1) loss of potential output, such as reduction in the survival, fitness or production of crops, domesticated animals, or fisheries and (2) direct costs incurred as efforts to assuage impacts, including control, eradication and quarantine, as well as increased spending on the application of

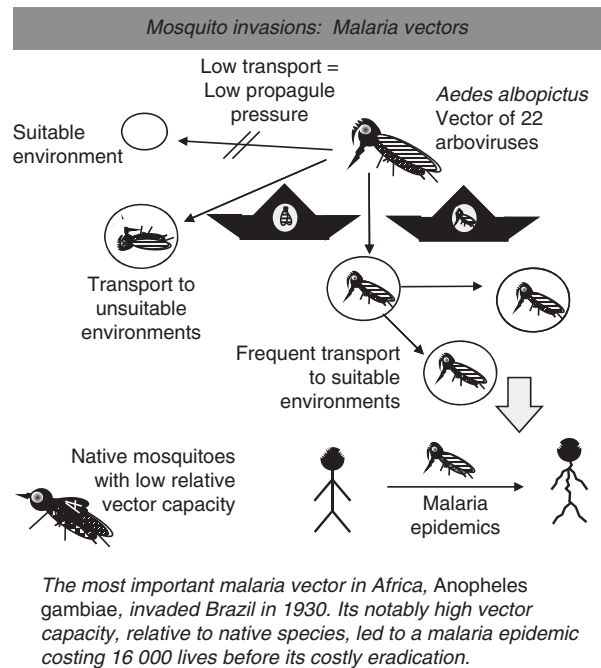
chemicals such as pesticides and herbicides to crop species, or money spent to remove or prevent the settlement of fouling organisms on shipping and aquaculture-related equipment. In the United States, the cost associated with loss or reduction in commodities due to NIS and the cost of controlling invasive species are estimated at nearly \$137 billion per year. Indirect costs generated by NIS are more difficult to quantify, such as the cost of changes in biological, physical, and chemical attributes of invaded ecosystems. For example, overgrazing by introduced ungulates results in reduced plant cover and enhanced soil erosion, and exotic fish species reduce water quality due to eutrophication.

### Human Health Impacts of NIS

One of the most direct effects of NIS on human health is the spread of pathogens. Epidemics, which have been well studied for over a century, are recognized as a particular case of biological invasions. Modeling approaches developed to study disease spread can be aptly applied to the spread of other invasive taxa. Direct effects of NIS on human health and well-being occur when an NIS

- is a pathogen
- is a vector for a native or exotic pathogen
- provokes changes in ecosystems that favor outbreak of native and exotic pathogens.

Examples of pathogenic NIS effects on human health include well-known pandemics and epidemics, such as the Spanish flu, caused by a strain of the influenza virus that resulted in the deaths of several million people all over the planet in a period of approximately 2 years; the bubonic plague, caused by the bacterium *Yersinia pestis*, which spread through Asia, Europe, and Africa using a flea vector on the invasive rat species, *Rattus rattus*, also resulting in massive mortality; and the numerous outbreaks of cholera all over the world, including an outbreak in South America during the 1990s when the cholera bacterium, *Vibrio cholerae*, was likely introduced to local ecosystems through ballast water. Current NIS affecting human health include the spread of emerging diseases such as the virus causing severe acute respiratory syndrome on many continents and the spread of introduced West Nile virus by mosquitoes in Europe and the United States. In addition, many pathogens affect human well-being through their impacts on animal and crop species, such as the introduced foot and mouth virus in ungulates of Great Britain, and introduced soybean rust in domesticated legumes of South America. NIS that act as vectors for pathogens include the introduced mosquito, *Anopheles gambiae*, which has spread endemic malaria in Brazil (Figure 6). Furthermore, NIS may provoke ecosystem changes that favor the outbreak of



The most important malaria vector in Africa, *Anopheles gambiae*, invaded Brazil in 1930. Its notably high vector capacity, relative to native species, led to a malaria epidemic costing 16 000 lives before its costly eradication.

**Figure 6** Mosquitoes are a paradigmatic example of invasions that affect human health and economy, and in which classical components of the invasion phenomenon can be observed. In this example, the distributions of two malaria vectors (i.e., the mosquitoes *Aedes albopictus* and *Anopheles gambiae*) can be well explained by climatic and traffic data. While *A. albopictus* has greatly expanded its range from Asia, likely associated with shipping routes, *A. gambiae* has rarely spread from Africa, probably due to a lower volume of shipping traffic from this continent. Information taken from Tatem AJ, Hay SI, and Rogers DJ (2006) Global traffic and disease vector dispersal. *Proceedings of the National Academy of Sciences* 103: 6242–6247.

pathogens, such as the case of selective filtration of plankton by the introduced zebra mussel, *Dreissena polymorpha*, in the Great Lakes of the United States, which promotes blooms of the native, toxic, blue-green alga, *Microcystis* sp.

Other effects on human well-being include increased exposure to hazards. Examples include elevated fire risk due to invasion by the highly flammable gorse plant, *Ulex europaeus*; weakening of a variety of wooden structures – from boats to high-rise condominiums – by the introduced termite *Coptotermes formosanus*; and increased erosion of sediment banks and increased flooding due to the burrowing activity of the introduced Chinese mitten crab, *Eriocheir sinensis*.

See also: Air Transportation and Human Health, Aquaculture Effluent: Impacts and Remedies for Protecting the Environment and Human Health, Avian Influenza Viruses: Environmental Influence, Biological



Agents and Infectious Diseases in War and Terrorism, Biological Pathways Between the Social Environment and Health, Cholera: Environmental Risk Factors, Climate Change and Health, Composite Measures of the Environmental Burden of Disease at the Global Level, Environmental and Health Costs in the European Union: Policy-Making, Global Climate Changes and International Trade and Travel: Effects on Human Health Outcomes, Global Development and Population Health, Overview of How Ecosystem Changes Can Affect Human Health, SARS, Shipping and Maritime Transport, Sustainable Management of Agricultural Systems: Physical and Biological Aspects of Soil Health, Vector Borne Disease and Climate Change, West Nile Virus, WHO-QOL Instrument and Environmental Health Assessment.

## Further Reading

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## Relevant Websites

- <http://www.issg.org>  
IUCN. Invasive Species Specialist Group.
- <http://www.gisp.org>  
IUCN. The Global Invasive Species Programme.
- <http://www.who.int>  
World Health Organization (WHO): Global Outbreak Alert & Response Network.