
INVASION BIOLOGY

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Invasion biology is a scientific discipline that studies the human transport and introduction of species throughout the world, as well as the subsequent spread of these species and their health, economic, and environmental impacts. Although some scientists and naturalists observed and commented on the introductions of new species as long as several centuries ago, and even though Charles Elton published his famous book on invasions (*The Ecology of Invasions by Animals and Plants*) in 1958, a formally defined field of invasion biology did not emerge until the early 1980s. Since then, the field has grown enormously. While only a few dozen articles were published annually during most of the 1980s, this number exceeded 1,000 by the early years of the twenty-first century. Today, thousands of biologists around the world are studying introduced species and contributing to the field of invasion biology.

THE HISTORY OF INVASION BIOLOGY

One would imagine that as far back as several thousand years ago, careful observers would have noticed the establishment and spread of species brought into their region by travelers. The first known documented accounts of such observations appeared in Western writings in the 1700s, when European naturalists traveled to North America and described some of the European plants and insects they observed there. During the 1800s and into the twentieth century, as global travel became more common, biologists and geographers often reported on nonnative species that had become established in regions far from their native environments. However, despite the observations and accounts, and even though some of the species were causing problems in their new regions, few scientists focused on introduced species as a specific research topic during this time. Somewhat surprisingly, even in the immediate decades following the 1958 publication of Elton's famous book on animal and plant invasions,

there was little widespread interest in studying nonnative and invasive species.

By the early 1980s, concerns over the undesirable impacts of some introduced species had grown, and in 1983, the Scientific Committee on Problems of the Environment (SCOPE), an international network of scientists and scientific institutions, created a special advisory committee and charged it with encouraging and facilitating research and understanding of species introductions and their impacts, and with applying this knowledge to management of such species. During the remainder of the 1980s, a small but committed group of scientists focused their studies on invasive species. Although the number of publications during the 1980s was modest, the efforts by the founding group of scientists had attracted the attention of a large number of ecologists throughout the world. As a result, the field of invasion biology experienced exponential growth during the 1990s (Fig. 1). In the last few years of the twentieth century, the Global Invasive Species Programme (GISP), a new international collaborative effort, was initiated to minimize the spread and impacts of nonnative invasive species. At the same time, two journals with a primary focus on species introductions were founded: *Diversity and Distributions*, in 1998, and *Biological Invasions*, in 1999. The intense and widespread interest in species introductions and their effects continued throughout the first decade of the twenty-first century. During this time, invasion biologists began to work more with scientists in other disciplines, including geographers, molecular biologists, climatologists, and computer scientists, collaborations that have increased our understanding of the invasive process and heightened our ability to manage invasive species.

PRIMARY RESEARCH AREAS WITHIN THE FIELD OF INVASION BIOLOGY

Species Transport and Dispersal

Before a species can spread in a new region and cause problems, it must first be transported to the new environment. While transport does not assure establishment and spread of a species, it is a necessary first step. Some species are able to disperse very long distances by themselves (e.g., aerial-borne microbes and plant seeds), but the vast majority of species introduced into new regions of the world during the last few centuries have been transported by humans. In some cases, these species have been introduced intentionally (e.g., plants for horticulture, animals for pets, and both plants and animals for agriculture). Some of the species introduced for these purposes

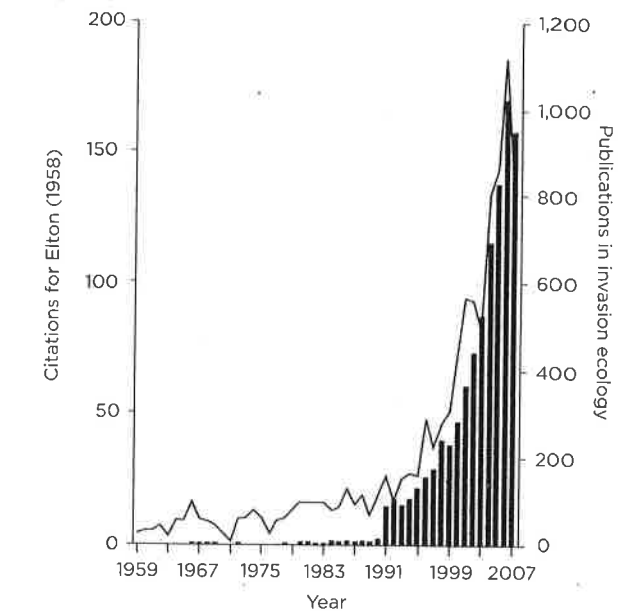


FIGURE 1 The number of biological invasion publications (columns) since Charles Elton published *The Ecology of Invasions by Animals and Plants* in 1958. Also shown are the number of publications that cited Elton's 1958 book during this time period (line). (Reprinted, with permission, from Anthony Ricciardi and Hugh MacIsaac, 2008, copyright Nature Publishing Group.)

escaped and have been able to establish and persist in surrounding environments without any further assistance from humans. Other introductions are not intentional. For example, some marine organisms attach themselves to the hulls of oceangoing ships and then become disengaged or disperse their eggs in waters distant from their native range. In other instances, plants and animals intentionally introduced often serve as hosts for parasites and pathogens, which are then transported and introduced along with their hosts. Some human diseases, once confined to particular regions of the world, are becoming more widespread as a result of the pathogens' being transported when their human hosts travel from one region of the world to another. When crop seeds are transported from one region of the world to another, seeds of other plant species are often inadvertently transported as well. When the crop seeds are planted, so are the seeds of the other species.

Many studies have shown that the likelihood that an introduced species will become established in a new region is a function of the number of propagules (e.g., seeds, eggs, larvae) in a transport or dispersal event, as well as of the number of dispersal events. The combination of these two variables, number of propagules in a dispersal event and number of dispersal events, is often referred to as *propagule pressure*. Because humans are responsible for

the long-distance transport of most species, as the number of human travelers has increased, so has propagule pressure, and hence the number of introductions. In recent decades, owing to the dramatic increase in international commerce, most regions of the world are experiencing an increase in propagule pressure for many types of organisms.

Establishment

Establishment of an individual in a new region can be defined as propagules' persisting long enough in the new region to be able to reproduce. To do this, they need to accomplish four tasks. First, they need to find an abiotic environment (e.g., temperature, salinity, moisture) they can tolerate. Second, they need to be able to access resources (e.g., water, soil nutrients, space) needed for growth, maintenance, and reproduction. Third, unless the initial propagule is a fertilized female, or capable of reproducing asexually, propagules need to find one another to mate. And, fourth, founding propagules must avoid pre-reproductive mortality—e.g., getting eaten by a predator or herbivore. The ability of the founding propagules to accomplish these tasks is influenced by their own traits as well as by the characteristics of the new environment.

The susceptibility of an environment to the colonization and establishment of a species is often referred to as its *invasibility*. Many factors can influence an environment's invasibility, including the availability of resources, abiotic factors, and the presence or absence of enemies (e.g., predators and pathogens) or mutualists, which help the new species to establish (e.g., pollinators and species that may modify the environment to the advantage of the new species) (Fig. 2). In any case, invasibility is not a static or permanent characteristic of an environment. Because invasibility is influenced by an array of biotic and abiotic

events and processes, as these change, so will the environment's invasibility. It is also important to remember that invasibility varies from species to species. The same conditions that may make an environment quite invasible to one species may make it quite resistant to another.

Charles Darwin suggested that a species should be better able to establish in a new region if it is not closely related (in an evolutionary sense) to the resident species in the new environment, his reasoning being that the new species would not experience a high level of competition from the resident species if they are not close relatives. Now referred to as Darwin's Naturalization Hypothesis, this prediction has been tested in many studies in recent years. The results have been mixed, some supporting the hypothesis and some not. It may be that Darwin's hypothesis can be supported in situations in which invasibility is primarily being determined by competition for resources or by the presence of enemies shared by the new species and its resident relatives. In cases in which invasibility is determined more by the presence of shared mutualists or by the abiotic conditions, species more closely related to resident species may actually enjoy greater establishment success.

Persistence and Spread

Ultimately, the field of invasion biology is not interested in all the species that have been transported to and become established in new regions of the world. The subject of the field is primarily the subset of these species that spread widely once established, often producing undesirable consequences (health, economic, or environmental) while doing so. Once a species has been transported to a new region, its subsequent dispersal and spread may still be primarily facilitated by humans. For example, many introduced freshwater organisms are accidentally

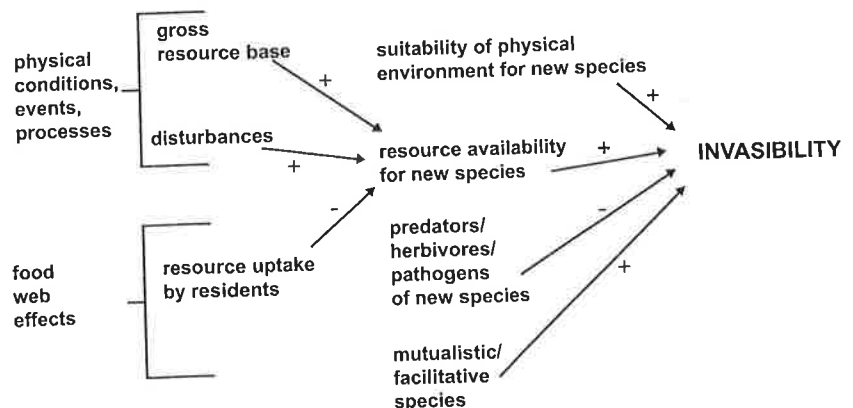


FIGURE 2 The invasibility of an environment is a composite attribute, influenced by both physical and biological conditions, events, and processes operating at the local scale. Invasibility of communities is expected to vary over time owing to changes in the local conditions, events, and processes that, together, define invasibility.

dispersed from one lake or river to another by recreational boaters. And many introduced plants are distributed into national parks accidentally by tourists when seeds of the plants are brought into the parks on the tourists' shoes and clothing. However, in many cases, after the human-mediated initial transport, secondary dispersal within the new region takes place mostly independently of direct human activity using traditional dispersal vectors of the species (e.g., wind, water, and animals).

Many studies have been conducted to try to determine whether certain species traits are associated with invasiveness (the ability to spread rapidly in the new environment). If such traits can be identified, they can be used to evaluate the invasive potential of species not yet introduced into a region, a process known as risk analysis. While some traits do seem to be associated with invasiveness in some organisms (e.g., rapid growth rate and phenotypic plasticity, or the ability of an organism to change some of its traits, such as behavior or amount of energy allocated to reproduction), the best predictor of invasiveness seems to be whether the species has been invasive elsewhere.

Evolution after Introductions

It was originally thought that founding populations would exhibit low genetic diversity, since they likely would have been established by only a few individuals, and that this low genetic diversity would impede the ability of the species to adapt to its new environment. However, a number of studies have shown that founding populations often are not lacking in genetic diversity at all. It is believed the high genetic diversity in many established populations of nonnative species is due to the fact that introduced individuals are often transported from a variety of different gene pools in their native range. This genetic diversity means that many introduced species are able to adapt to new biotic and abiotic conditions. For example, some introduced species have been found to adapt genetically to new climatic conditions. The new species can be similarly affected by resident predators and pathogens. Over time, and as a result of its adaptations with the residents, a recently arrived species may be able to evolve adaptations enabling it to persist in and exploit its new environment better. At the same time, the new species begin to affect the evolution of the residents. If the new species is a predator or pathogen, it will represent a new selection pressure that would favor better predator avoidance behavior among resident prey, and pathogen-resistant strains among resident hosts.

Although rapid spread of nonnative species has received the most attention from invasion biologists,

rapid declines of an introduced species after a period of rapid spread have commonly been documented as well. Researchers believe that this boom–bust phenomenon may be partly the result of the evolution within resident species that enable them to adapt better to the new species and to impose some regulation over its growth and spread. It is important to remember that genetic adaptation takes place only over generations. If an introduced predator is too successful, or an introduced pathogen too virulent, the resident prey and hosts may not have sufficient time to adapt before being extirpated by the new species.

One important type of evolutionary process that can occur following the introduction of a new species to a region is hybridization. In this case, the new species mates with a related resident species, or another recently introduced related species, thereby bringing together two sets of gene pools, which previously had been separate. Sometimes biologists view this blending of two gene pools as undesirable, since it can lead to a loss of species uniqueness and diversity. However, the new combination of genes resulting from hybridization also creates new genotypes and thereby new evolutionary opportunities.

Impacts of Nonnative Invasive Species

Like native species, nonnative species can affect human health, local and national economies, and ecosystems. Although most nonnative species do not have large impacts, a small proportion of introduced species are considered harmful or undesirable owing to their effects. The greatest threats involve human pathogens that are being transported throughout the world spreading disease, including avian influenza, AIDS, severe acute respiratory syndrome (SARS), West Nile encephalitis, Ebola hemorrhagic fever, dengue hemorrhagic fever, and avian influenza. Many of these and other diseases are zoonotic, which means that the pathogens can also use other animals as hosts. As a result, these diseases can be spread by the global transport of animals (e.g., for food production, and through the pet trade). Some nonnative species are causing great economic harm, costing countries billions of dollars. Examples are species that substantially reduce the productivity of crops, timber, and fisheries, contaminate or otherwise disrupt water supplies, and kill farm animals through disease.

Many invasion biologists study how introduced species affect the species and ecosystem processes in their new environment. In some instances an introduced species reduces the abundance of some of the native species (e.g., through predation, disease, or competition). Although

there are few instances of introduced species causing extinctions in marine systems or in terrestrial environments on continents, many cases are documented of introduced predators and pathogens driving native species to extinction on islands and in freshwater systems (e.g., lakes and rivers). Other introduced species have been found to alter dramatically some ecosystem processes, such as the rate at which nutrients are cycled and the availability of certain resources, such as nutrients and water. Still other introduced species are known to alter the frequency and intensity of disturbances, such as fire.

Although the undesirable impacts of introduced species are usually emphasized, it must be remembered that some new species produce desirable effects. Some species have been found to increase the diversity of native species in an environment. For example, many sessile invertebrates require a hard surface to which to attach themselves, and in some aquatic environments, hard surfaces are uncommon and ultimately limit species diversity. In some of these environments, the shells of introduced mussels have served as attachment sites for these other invertebrates, thereby increasing the number of resident native species. Some nonnative trees have been found to alter the soil conditions in previously deforested environments, thereby making it possible for native trees to reestablish on these sites. The ecological impacts of introduced species are many, and they vary from species to species and environment to environment. Invasion biologists have only begun to understand the array and extent of these effects.

Management of Nonnative Invasive Species

In addition to learning how nonnative species may impact their new environments, and sometimes cause economic harm and health threats as well, invasion biologists also try to learn how to manage these species in order to reduce their undesirable effects. One way is to reduce the likelihood that undesirable species are transported from one region of the world to another. Education, regulations and laws, the use of inspectors, and screening efforts to identify which species should be targeted during inspection procedures are all strategies currently employed to try to reduce the initial introductions. Even if introductions of undesirable species can be reduced, prevention will never be one hundred percent successful for all species. Some invasion biologists are investigating the use of early detection or early warning programs to identify the arrival of undesirable species before they have had time to spread. Experience has shown that efforts to eradicate unwanted species are very expensive and usually fail once the species has become widespread. In some cases, biological control

efforts have succeeded in dramatically reducing the abundance of undesirable nonnative species. However, because many biological control efforts involve introducing new nonnative species (e.g., parasites, pathogens, or predators of the target species), considerable testing needs to be conducted prior to the release of the control organism to make sure that it will not adversely affect other species.

A fundamental challenge of most invasive species management is that regardless of success in removing the undesirable species, management efforts may produce other undesirable consequences. Because all species in an environment exist within a web of interactions with other species and the physical environment, removing one species, particularly an abundant species, inevitably produces an array of effects, some predictable and some not. In some instances, the nonnative species may have been providing some unknown desirable effects that will be eliminated upon its removal. In many cases, a nonnative invasive species is more a symptom than the cause of a problem. For example, nonnative plant species are often believed to be the cause for the decline of native plant species, but studies have shown that in many instances, the decline of the native species is due mainly to other factors, such as changes in disturbance regimes and resource availability, which then favored the establishment of the nonnative species. In such cases, removing the nonnative species will likely not substantially benefit the native species unless the underlying causes are also addressed.

CHALLENGES FACED BY THE FIELD OF INVASION BIOLOGY

The field of invasion biology is a very young discipline. Like any growing enterprise, the field has experienced some growing pains. In recent years, scholars within and outside the field have raised questions regarding value-laden terminology that has often been used within the field of invasion biology—e.g., referring to species introductions as “invasions” and to nonnative species as “biological pollution.” Some common claims of invasion biologists have also been recently challenged—e.g., claims that nonnative species threaten native species with extinction through competition, or that introduced species cause declines in biodiversity. In fact, much evidence suggests the opposite is true. At regional and local scales (e.g., state and county scales), introductions often far exceed the number of extinctions that they cause, thereby resulting in an increase in species diversity. Some scientists have not been happy with the dichotomous nature of invasion biology, in which species are declared to be either native or nonnative, because they believe this distinction has no sound

ecological or evolutionary basis. Other invasion biologists disagree. These sorts of disagreements are common within science, particularly when a field is just developing.

The field of invasion biology also faces fundamental challenges from its very subject, species introductions. Theory has suggested, and empirical data have shown, that species introductions are usually very difficult to predict ahead of time. The reason seems to be that very small changes in environmental conditions or in the number of arriving propagules can sometimes dramatically change the likelihood of successful establishment. The apparent presence of a tipping point (a point at which small changes can produce very large consequences) in the invasion process likely explains many well-known aspects of invasion dynamics, including why invasions are often episodic, why there is often a lag phase prior to invasion spread, why some invasions experience a rapid collapse following a period of irruption, and, in general, why invasions typically have been so difficult to predict (and, unfortunately, why invasions are likely always going to be difficult to predict). This finding has important management implications. For example, managers working to prevent initial establishment of a species could be deluded into thinking that their prevention efforts were very successful since no establishment had yet occurred, when, in fact, the system they were managing was moving closer and closer to the tipping point at which successful establishment becomes very likely.

THE FUTURE OF INVASION BIOLOGY

Current developments in the field indicate that interdisciplinary research will become more common. Geographers, computer scientists, molecular biologists, and even social scientists (economists, anthropologists, sociologists) and humanists (philosophers and ethicists) have much to offer to the field. Within the field of ecology, invasion biology is reconnecting to other subdisciplines that also study species movements. For example, climate change is causing ranges of many species to shift, creating new combinations of species in much the same way that introduced species create new combinations. Whether produced by climate change or species introductions, these new communities are being referred to as "novel communities" or "novel environments" by some ecologists, who are calling for the field of ecology to focus on this general phenomenon of ecological novelty.

The field of invasion biology has exhibited remarkable growth since the creation of the SCOPE advisory committee in 1983. In recent years there has been a remarkable influx of new investigators, many bringing with them new ideas, and some challenging old ones. This

bodes very well for the field's future. Disciplines begin to stagnate in the absence of new participants and new ideas. The influx of new minds and perspectives into the field is what will ensure the field's vitality in upcoming years. The new investigators and ideas represent opportunities, perhaps not unlike the ecological and evolutionary opportunities created when new species are introduced into an environment.

SEE ALSO THE FOLLOWING ARTICLES

Elton, Charles S. / Evolution of Invasive Populations / Invasibility, of Communities and Ecosystems / Invasion Biology: Historical Precedents / Propagule Pressure / SCOPE Project

FURTHER READING

- Cadotte, M. C., S. M. McMahon, and T. Fukami, eds. 2006. *Conceptual Ecology and Invasion Biology: Reciprocal Approaches to Nature*. Dordrecht, the Netherlands: Springer.
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