with the basal body are needed for membrane anchoring and for cytoskeletal organization.

***Where do basal bodies come from?*** The basal body is considered to be a self-replicating organelle. In a process that is not yet completely understood, the daughter basal body is assembled adjacent and orthogonal to the mother organelle. Although this was long speculated to be a templated assembly process, it is likely that the mother basal body acts as the site where components required for assembly of a new organelle are gathered. In addition, two other variations of basal-body biogenesis have been observed. First, basal bodies can be assembled using a *de novo* pathway that does not require a mother organelle. Second, centrioles can migrate from the nucleus to the plasma membrane and assemble a cilium, thereby becoming a basal body.

***Are basal bodies evolutionarily conserved?*** The basal body is an evolutionarily conserved organelle thought to have originated from ancient protists. Not only has the structure and function of the basal body been conserved through time and across species, the protein components within the organelle have been evolutionarily conserved as well.

***Are any human diseases caused by basal body defects?*** Cells lacking functional basal bodies are often able to survive, albeit in a diseased state. Many human diseases can be attributed to defects in the basal body and associated cilium, including polycystic kidney disease, retinal degeneration, Bardet–Biedel syndrome and oral–facial–digital syndrome.

***Where can I find out more?***

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Molecular, Cellular and Developmental Biology (MCDB), 347 UCB, University of Colorado at Boulder, Boulder, Colorado 80309, USA.
E-mail: mark.winey@colorado.edu

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**Primer**

# Biological invasions

**Jonathan M. Levine**

Biological invasions pose a leading threat to biodiversity world-wide. Through competition, predation, and habitat alteration, invaders can radically change both the species composition and functioning of native ecosystems. Biological invasions also impact world economies, with economic costs estimated at over 100 billion US dollars per year in the United States alone.

Invasions occur when species are intentionally or accidentally introduced outside of their native or historic range, and successfully spread in their new environment. The term 'exotic species' is used for a broader group that includes any species not native to a region, including livestock, crops and garden plants. Only those exotic species that spread outside the human-dominated environment are considered biological invaders. Two spectacular examples illustrate the defining features of invasions (Figure 1).

Shortly after World War II, the brown tree snake was introduced to the island of Guam, probably as accidental cargo from its native range in the South Pacific. Guam, like many remote islands, lacked snakes or similar top predators, rendering the native vertebrates particularly vulnerable to snake invasion. The brown tree snake grew to tremendous densities on Guam, causing most forest-dwelling bird species to go extinct on the island, and decimating lizard and mammal fauna. In addition, its habit of climbing power poles has caused thousands of power outages on the island, contributing to millions of dollars of economic losses.

Another highly successful biological invasion involved the balsam woolly adelgid. This plant-sucking insect was introduced to the United States on nursery stock from Europe in the early part of the twentieth century. Its salivary secretions are toxic to the certain trees, and in the southern Appalachians, it has decimated entire stands of mature Fraser firs. Although younger trees persist, the adelgid has fundamentally altered the structure of the forest ecosystem it has invaded.

Although the current rate of species introductions is unprecedented, the process itself is not a recent phenomenon. Rare, long-distance colonization events, often-times facilitated by tectonic movement, have been an ever-present feature of the earth's biogeographic history. But the current rate at which species move across biogeographic barriers is several orders of magnitude greater than in the fossil record. This by-product of human activities can be regarded as a form of biological pollution, analogous to elevated concentrations of a chemical pollutant otherwise present in trace amounts.

The recent surge of interest in biological invasions is partly rooted in concerns over invader impacts. But this interest also results from the fact that invasions present outstanding

Figure 1. The Brown tree snake and damage from the balsam woolly adelgid.

The Brown tree snake (*Boiga irregularis*) has devastated populations of forest-dwelling vertebrates on the island of Guam, while the balsam woolly adelgid (*Adelges piceae*) has killed large stands of adult Fraser Fir trees in the Appalachian mountains of the United States. Credit to John Fowler and Todd Long for the left and right images, respectively.

natural experiments for understanding the structure and function of ecological communities. Examining how ecosystems respond to the addition of new species provides unparalleled insights into how these systems are organized.

Ecologists study biological invasions by examining the controls over the different stages of the invasion process: Introduction, Establishment, Spread and Impact (Figure 2). Importantly, only a small fraction of introduced species successfully establish; moreover, only a small fraction of these successfully spread and impact native communities. The factors that constrain success at each of these stages are the focus of this article.

## Introduction

Introduction describes the transport of invaders from their native to exotic range, as well as transport within the exotic range. Of all stages in the invasion process, it is the best understood. Nearly all biological invasions begin as accidental introductions with trade and travel, or as intentional introductions that spread outside their intended use.

The fraction of invaders that were intentionally versus accidentally released varies greatly by taxonomic group. With the exception of biological control agents, insect pests and forest pathogens tend to be accidental introductions, often with the importation of nursery stock and other natural products. Aquatic invertebrates also tend to be accidental introductions, with many species having arrived in ship ballast water. By contrast, invasive vertebrates were often intentionally introduced for hunting, livestock, or as pets. Invasive plants include large numbers of both intentional and accidental introductions.

For those groups accidentally introduced with trade activity, there is growing interest in using economic forecasts to project future introduction rates. One general result to emerge from these studies is that even though trade is projected to increase rapidly over the next several decades, the number of biological invasions should increase much more slowly. This is because each unit of trade transports some species that were already introduced in previous trade activity. And the more trade increases with any biogeographic region, the fewer *new* species available for transport.

## Establishment

Establishment describes the process by which the populations of introduced species increase from rarity. This feat is accomplished by only a small fraction of introduced species. Moreover, their ability to establish varies greatly among communities. These observations have made establishment the most studied stage of the invasion process. Ecologists focus on two main questions: What species traits distinguish successful from unsuccessful invaders? And what types of ecological communities are most resistant to invasions? One challenge in studying these problems is that the failed invasions are often unknown.

Any successfully establishing invader must possess traits necessary for tolerating the climate conditions in the exotic range. For example, many plant invaders found in Mediterranean-climate regions — cool wet winters and warm dry summers — originated in other Mediterranean-climate regions of the world. Ecologists have developed a range of statistical modeling techniques that input the climatic conditions of the invader's native range and use this information to project its distribution in the exotic range. Such approaches tend to be broadly predictive of non-native distributions, but in some cases, the empirically observed exotic range encompasses a broader or more narrow range of climatic conditions than projected from the native range. These observations challenge ecologists' understanding of the controls over biogeographic distributions.

Ecologists have also attempted to predict the life history traits required by successful invaders. Very often, these traits correspond to those of rapidly growing, generalist species. For example, multivariate statistical approaches have been used to compare the traits of pines that successfully spread outside of cultivation to those that do not. Just three key reproduction-related traits, all of which correspond to the degree of weediness, discriminate the successful from unsuccessful pine invaders. Still, not all invaders are at the weedy end of the life history spectrum; the traits underlying invasion success vary with the resident community.

In addition to questioning the traits of successful invaders, ecologists also examine the traits of communities that allow them to resist invasions. Resistance arises from two sources. Abiotic resistance is the reduction in invasion success due to stresses imposed by the physical environment, such as temperature, moisture, or salinity. Biotic resistance is the reduction in invasion success due to interactions with the resident species, including competitors, predators, or disease.

Abiotic resistance is likely the major factor acting to repel invaders from specific ecosystems. Its role in regulating invasion success is most often appreciated at large biogeographic scales, as typified by work on the climate requirements of invaders. The role that abiotic factors play in regulating invasion success at the local scale of individual communities has been less studied. But where abiotic resistance has been examined, it often overwhelms biotic resistance. For example, the distribution of Argentine ants within various communities in southern California is largely constrained by moisture availability; competition from the native harvester ants is of little importance. In other systems, abiotic and biotic resistance interact to regulate invasion success.

Biotic resistance may be the single most studied process in the ecology of biological invasions. Numerous experimental and observational studies have asked how resident competitors, predators or disease influence the success of biological invasions. Recent meta-analyses of the plant invasions literature indicate that across studies, removing resident competitors or herbivores increases invader establishment and performance. Nonetheless, biotic resistance rarely repels invaders outright. Rather, interactions with resident species tend to reduce the population growth and spread of invaders that have successfully established.

Ecologists have not only asked how resident competitors influence invasion success, but more subtly, whether a high *diversity* of competitors enhances community resistance to invasion. Ecological theory has suggested that more diverse communities more fully use their resource base than species poor communities, and should therefore better resist invasions. Indeed, experimental manipulations of resident species diversity almost always support this expectation. By contrast, observational studies of natural gradients in species diversity tend to find the opposite result — more diverse areas are more invaded than their species poor counterparts. Although useful for predicting invasion across the landscape, this latter result is a spurious correlation. Extrinsic factors such as environmental heterogeneity that support a high richness of native species also facilitate invasion, clouding the causal but much weaker effects of diversity.

A final factor known to influence the establishment success of invaders is simply the number of propagules introduced. Evidence for the importance of propagule supply emerges from various efforts to intentionally introduce species. For example, 'naturalization societies' once purposely introduced birds to different biogeographic regions around the world, and kept excellent records of their efforts. For birds introduced to New Zealand, the most important determinants of invasion success were simply the number of birds released and the number of release attempts. Similar results have been found for insects released for biological control, another group of well recorded intentional introductions.

## Spread

Spread describes the process by which biological invasions move across the landscape. Classic studies use direct observations and/or spatially referenced museum records to reconstruct the movement of invaders across broad spatial scales. Not only can these results be used to project future expansion, but they often show surprisingly fast spread rates. European starlings spread across North America in less than a century.

Spread is a fascinating process because it integrates the factors controlling establishment with the dispersal of propagules across the landscape. Because this integration can be complicated, much of our understanding of the spread process comes from mathematical models.

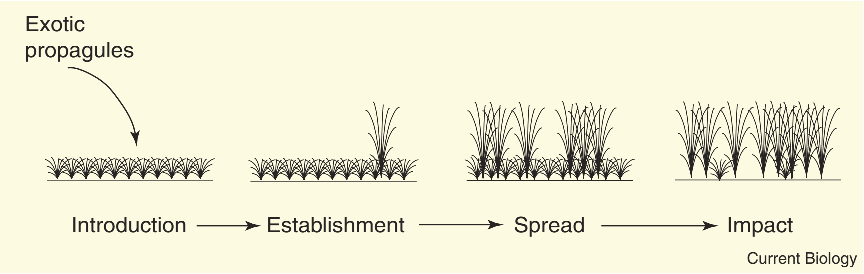

Figure 2. Different stages of the invasion process, with the tall form representing the invader.

A large body of theory suggests that spread though spatially homogeneous landscapes is regulated by the low density population growth rate of the invader interacting with dispersal. Counter-intuitively, invader population growth at higher densities is unimportant for spread. This result changes, however, if individuals produce more offspring or suffer lower mortality when population size grows. Such 'Allee effects' emerge when a critical number of individuals is required to ameliorate harsh physical conditions or attract pollinators or other mutualists. For invader populations experiencing Allee effects, the performance of the population at higher densities can strongly influence the speed of advance.

In most theoretical studies, invaders spread through spatially homogeneous landscapes. Yet real invasions move through heterogeneous regions of suitable and unsuitable habitat. How landscape structure, fragmentation, and corridors influence the speed of advance and the demographic traits controlling this advance are of growing interest to ecologists. A concerning possibility is that habitat corridors established to facilitate the persistence of native species might also facilitate the spread of exotic invaders.

## Impact

Most invaders, even those that successfully spread, exert little impact. Yet the minority that do can have devastating effects. The factors distinguishing invaders with large versus small impacts are thus of considerable interest. One emerging generalization is that high impact invaders possess traits differing significantly from those of the resident species. Indeed, the massive impacts of the brown tree snake on Guam relate to the absence of similar top predators in the native fauna.

The most commonly envisioned impacts of invaders arise through competition, predation, and disease. Argentine ants, for example, are far more aggressive competitors than the native ant fauna they often replace. Exotic zebra mussels in North American aquatic systems overgrow native bivalve competitors, and so effectively filter feed that they cause massive plankton declines. Less obvious are exotic pathogens, but their damage can be devastating. Chestnut blight, a fungal pathogen accidentally introduced from China is responsible for the near elimination of the American Chestnut tree.

Some of the most dramatic impacts of invaders are exerted through changes in ecosystem processes such as nutrient cycling, hydrology, and fire regimes. Exotic grass invasion of arid and semiarid shrublands and woodlands can dramatically increase fire frequency by changing fuel loads. Fires are disproportionately damaging to the woody taxa, feeding back to favor grass invasion. Invasive coqui frogs in Puerto Rico, which reach among the highest recorded densities for terrestrial amphibians, eat massive quantities of insects. Not only does this consumption reduce arthropod numbers, frogs convert resources bound up in insect biomass into plant-available compounds in their excretion. This alters forest nutrient cycling and increases plant growth.

One of the most obvious, yet challenging questions in the study of biological invasions is whether invasions cause native species to go extinct. Despite the fact that invaders are regarded as one of the leading threats to native species diversity, and the fact that invaders reduce population size, surprisingly few species have gone extinct due to invasions. Refuges from the invader often remain at some place in a native species' range. Whether native species can stably persist within these refuges is an open question. But in the short term, the number of invasions has far exceeded the number of resulting extinctions. This result has emphasized that most ecological systems are not 'saturated' with species.

### Two puzzles

Nearly all problematic invasive species experience rapid population growth at some point in the invasion process. However, many of these invaders were seemingly present in the exotic range for a considerable period of time prior to exploding in numbers. A number of hypotheses have been proposed for this 'invasion lag', but the true explanation can be hard to pin down and likely varies by system. It may be that the invaders remain sparse until the climatic conditions appropriate for rapid expansion happen to occur. Alternatively, initially small invader populations may require time or multiple introductions to overcome 'Allee effects' or build-up the genetic diversity necessary for population expansion. Lastly, the lag may simply reflect that fact that exponential growth only becomes obvious once populations get relatively large.

A second invasions puzzle is why species that are apparently benign in their native range become so dominant in their exotic range. Classic thinking holds that in the introduced range, the invader escapes the specialist predators or pathogens that control its populations in its native range. Indeed, many exotic plants and animals have fewer specialist predators and pathogens in their exotic versus native range. However, the enemies release hypothesis also requires that consumers actually control the exotic species in its native range, and further, that generalist enemies in the exotic range do not compensate for the loss of specialist predators and pathogens. There is much weaker evidence for these more subtle, but equally important requirements of the hypothesis. Moreover, recent work suggests that generalist enemies often prefer exotic over native plants, counteracting benefits of specialist enemy release. In sum, the long-held hypothesis that enemy release is responsible for the run-away success of exotic species is not nearly as well-supported as commonly believed. Developing alternative hypotheses to explain invader dominance in the exotic range may become a key priority.

### Generality

The explosion of research into biological invasions over the last several decades has generated considerable understanding of the patterns and dynamics of individual invasions. The challenge, however, comes when moving from individual case studies to the development of general principles that apply across a broad range of invasions. Meta-analytical approaches over the last five years or so have yielded some of the most general conclusions in this research area, many of which form the basis of the principles outlined in this article.

Future insights on biological invasions will likely emerge from the current focus of the ecological community on the impacts of climate change. Worldwide, numerous studies are manipulating environmental factors such as temperature and precipitation to better understand how ecosystems will respond to forecasted changes in these variables. Many of these projects include exotic species and therefore present excellent opportunities to evaluate the role that climate plays in regulating invader establishment and impact. Through studies such as these, ecologists can begin to predict how biological invasions will alter the way ecological communities respond to a changing climate.

### Further reading

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Department of Ecology, Evolution, and
Marine Biology, University of California,
Santa Barbara, California 93106, USA.
E-mail: levine@lifesci.ucsb.edu

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**Correspondences**

# Head turns bias the brain's internal random generator

**Tobias Loetscher, Urs Schwarz, Michele Schubiger and Peter Brugger**

Numerical and spatial cognition rely on common functional circuits in the parietal lobes of the brain [1]. While previous work has established that the mere perception of numbers can bias a subject's attention in space [2], the method of random digit generation has only recently been introduced to a rapidly growing literature exploring asymmetries in number space [3]. Here we show that human subjects' attempts to generate numbers 'at random' are systematically influenced by lateral head turns, which are known to reallocate spatial attention in the outside world. Specifically, while facing left, subjects produced relatively small numbers, whereas while facing right they tended to produce larger numbers. These results support current concepts of parietal cortex as mediating the interplay between spatial attention and abstract thought [4].

Numerical magnitudes supposedly are represented on a 'number line' that extends from left (small numbers) to right in mental space. Several lines of evidence suggest that this analogue, oriented representation of numbers is mediated by those parietal lobe regions of the brain that also process left and right in outside space. First, patients who have suffered damage to the right parietal lobe, and who consequently fail to attend to the left side of space ('hemispatial neglect'), also exhibit neglect in number space. For instance, when they are asked to indicate the median number of orally presented number pairs — "which number is halfway between 9 and 17?" — they deviate towards too large, 'right-sided' numbers [5]. Second, work with healthy subjects showed that the universal left-sided attention bias in spatial exploration ('pseudoneglect' [6,7]) is also found