established extensively on previously unvegetated dunes from plantings across the North American West Coast in the late nineteenth century; some biologists interpret this as a case of the beachgrass occupying a habitat that the native vegetation could not colonize. There are many potential examples of this in the literature of global plant invasions. Timberline species in New Zealand, for example, are less cold-tolerant than conifers from the northern hemisphere; when introduced, these conifer species have increased the elevation of timberline and established reproductively individuals in areas formerly uninhabited by trees.

SEE ALSO THE FOLLOWING ARTICLES
Competition, Animal / Competition, Plant / Disturbance / Elton, Charles S. / Islands / Landscape Patterns of Plant Invasions / Propagule Pressure / Succession

FURTHER READING

INVASIONAL MELTDOWN

BETSY VON HOLLE
University of Central Florida, Orlando

Invasional meltdown is the process by which two or more nonnative species facilitate each other’s establishment or exacerbate each other’s impact on native species. These interactions need not be between species with a shared evolutionary history. Interactions between two or more nonnative species have the potential to lead to synergistic impacts on the recipient ecosystem, wherein the impacts of a group of nonnative species are greater than the summed impacts of the individual species. The outcome of species introductions could result in accelerating rates of invasion, driving ecosystems to be invaded by greater numbers of species, each invasive species having the potential to facilitate further invasions or enhance impacts of other nonnative species.

BACKGROUND

In 1958, in the seminal book The Ecology of Invasions by Animals and Plants, Charles Elton popularized the notion of “biotic resistance” to invasion, whereby negative interactions such as predation, parasitism, and competition with native species act to resist the invasion of nonnative species into communities. This hypothesis was in line with the reigning paradigm at the time that negative interactions were the primary forces structuring ecological communities. Thus, the primary research focus of nonnative species impacts traditionally centered on negative interactions between nonnative invaders and native resident species. Daniel Simberloff and Betsy Von Holle introduced the term invasional meltdown in a paper published in the first issue of the journal Biological Invasions in 1999 and suggested that there are many reports of mutual facilitation between nonindigenous species in the literature. However, many of these reports of facilitation were incidental, and usually not the focus of the research. In this paper, as well as a paper published in 2000 in Biological Review by David Richardson and colleagues, it was posited that positive interactions between nonnative species had largely been ignored by the research community. Simberloff and Von Holle suggested that community-level invasional meltdown should be investigated as a potential phenomenon that could lead to an accelerating accumulation of introduced species, contrary to the deceleration of species accumulation predicted by the biotic resistance model. This term was met with great favor in the scientific community and garnered media attention as well. In 2006, six years after the original invasional meltdown paper, Daniel Simberloff reviewed invasional meltdown studies conducted thus far and found that most studies reporting invasional meltdown had demonstrated the weakest degree of facilitation (one species aiding another), and very few had clearly demonstrated population-level impacts using demographic studies. Additionally, only a handful of studies had clearly quantified a mutualism between populations of two or more species. The community-level phenomenon of invasional meltdown, whereby facilitations between nonnatives lead to increasing rates of establishment or increasing impacts, has rarely been demonstrated. Jessica Gurevitch
commented on the review paper and suggested that positive feedbacks should be the focus of future research on the topic, rather than facilitation between two species. Gurevitch (2006) distinguishes between simple facilitation, whereby one or more species has a positive effect on another, and positive feedbacks, whereby “r[unaway] positive feedbacks in a system create snowball effects in which a phenomenon builds on itself in an accelerating fashion, becoming unstoppable.” She suggested that to assess the relative magnitude and/or importance of the effect, quantitative approaches such as metaanalysis are necessary. In a rejoinder, Simberloff responded that ecology is a highly idiosyncratic science, and one best served by amassing a catalogue of case studies to understand species- and community-level interactions and impacts on specific regions and habitats. Both authors agreed that more empirical research on the positive interactions between nonnative species should be undertaken.

**EMPIRICAL EVIDENCE FOR THE HYPOTHESIS**

**Indirect Effects**

There are many examples of the weakest form of facilitation, with one species facilitating another, though indirect effects. The invasion of bullfrogs in Oregon is facilitated by the presence of a coevolved nonnative sunfish, which increases tadpole survival by reducing predatory native macroinvertebrate densities.

Pollinator visitation rates and seed output of the invasive annual species Italian thistle (*Carduus pycnocephalus*) in Argentina are increased when it grows in association with shrubs of the invasive, nitrogen-fixing yellow bush lupine (*Lupinus arboreus*), with the yellow bush lupine acting as a magnet species for the thistle. There was no difference in soil nitrogen content with and without lupine; thus, the increased seed set of the thistle is attributed to the increased pollinator visitation rate associated with lupine. The magnet effect of facilitated pollination and reproduction of *C. pycnocephalus* by *L. arboreus* could promote its naturalization in the community.

On Isla Victoria, Argentina, two nonnative species of deer, the red and fallow deer (*Cervus elaphus* and *Dama dama*, respectively) preferentially browse seedlings of the two native dominant species of tree: a conifer, *Austrocedrus chilensis*, and a broadleaf, *Nahuelagus dombeyi*. The deer avoid browsing the introduced species of conifer, the Douglas fir (*Pseudotsuga menziessii*) and the ponderosa pine (*Pinus ponderosa*), which could potentially facilitate the invasion of these nonnative pines.

In a metaanalysis of the effects of native and nonnative herbivory on more than 100 nonindigenous plant species, it was found that native herbivores suppressed nonnative plants, while nonindigenous herbivores facilitated both the abundance and species richness of nonnative plants. Furthermore, the replacement of native with nonnative herbivores eliminates the intrinsic biotic resistance of native herbivores to nonnative plant invaders, facilitating plant invasions.

**Population-Level Effects**

**AQUATIC INVASIONS** A historically benign invasive species, the gem clam (*Gemma gemma*), introduced from the east coast of the United States to the west coast, became much more abundant in Bodega Bay, California, after the introduction of the European green crab (*Carcinus maenas*) which was introduced 30 years after the introduction of the gem clam. This supports the idea that lag times of nonnative species—the length of time from introduction to spread—may be due to successive introductions of nonnative species having the potential to facilitate one another. Evidence for facilitation of the gem clam by the nonnative green crab was found, but there was no evidence of the gem clam’s facilitating the green crab. Further tests need to be conducted to understand whether the interaction between these two species is a mutualism.

A literature review of the interactions between nonnative species of the Great Lakes revealed 3 cases of mutualisms as well as 14 cases of commensalisms, more than the number of documented negative interactions between invasive species in the Great Lakes. These population-level impacts were, for the most part, not tested empirically.

**TERRESTRIAL INVASIONS** South African succulent plant species of the genus *Carpobrotus* are considered major pests across the Mediterranean. Two species of *Carpobrotus* were introduced to southeastern France in the early 1800s: *C. edulis* and *C. aff. acinaciformis*, which became naturalized on Mediterranean coastlines in the early 1900s. These species are invading the littoral ecosystems of southeastern France, and their rapid vegetation growth threatens rare plant communities. On coastal islands, *Carpobrotus edulis* and *C. aff. acinaciformis* are readily dispersed by two species of nonnative mammals: rabbits (*Oryctolagus cuniculus*) and the ship rat (*Rattus rattus*), both of which were introduced into this region prior to 1751 (with the potential for rats invading the coastal islands as early as 2400 BP). Low levels of dispersal of *Carpobrotus* occur on the mainland, and, when dispersal does occur, it is by native mammal species. Seed digestion by rats and rabbits on the islands significantly enhances the speed and seed germination of *Carpobrotus* as compared to dried fruits.
removed from the same site, with seeds from rat feces having significantly greater germination than seeds from rabbit feces, which have greater germination than dried fruits from the plants. Feral cats (Felis catus) on the islands also occasionally eat Carpobrotus seeds. The maximum seed dispersal distances for cats is far greater than that of rats and rabbits, so they serve as a potential long-distance vector of Carpobrotus. The prolific Carpobrotus fruits are twice as large as native fruits and provide nonnative island mammals a source of water and energy-rich food during the summer drought season. In this mutualism, Carpobrotus gains seed dispersers which enhance germination success, and the nonnative mammals obtain an energy and nutrient-rich food source. The continued spread of Carpobrotus threatens the natural vegetative communities of these islands, and other impacts of the nonnative mammals may not yet have been quantified. Thus, the facilitation between these species may result in synergistic impacts on the native biota of these islands.

**Community-Level Effects**

**AQUATIC INVASIONS** The introduced Asian hornsnail, Batillaria attramentaria, occurs in very high densities in the mudflat ecosystem of northern Puget Trough, in Washington state. The Asian hornsnail facilitates two other nonnative species that use the hard substrate provided by the shells of this species, with no comparable native species filling this role. The nonnative Atlantic slipper shell, Crepidula convexa, and the introduced Asian anemone, Diadumene lineata, use the hard substrate provided by the shells of B. attramentaria almost exclusively. Batillaria indirectly facilitates the nonnative eelgrass, Zostera japonica, by modifying oxygen and nutrient levels. Selective grazing by Batillaria may indirectly augment the preferred diatom resources of the nonnative mudsnail, Nassarius fraterculus, which may be the cause for the higher densities of this species associated with Batillaria. Additionally, two native hermit crabs, Pagurus hirsutiusculus and P. granosimanus, habitually use the shells of Batillaria. The invasibility of this mudflat ecosystem is enhanced by the Asian hornsnail, as this species increases the densities of four nonnative species, which may enhance their population sizes and the probability (and impacts) of persistence. However, empirical evidence of increased impacts on native fauna or positive effects on Batillaria by the four associated nonnative species has not been determined.

**TERRESTRIAL INVASIONS** The yellow crazy ant, Anoplolepis gracilipes, is one of the six most widespread and damaging invasive ant species in the world. This species invaded Christmas Island, located in the northeastern Indian Ocean, in the early twentieth century, persisting at low population densities and having negligible impacts on the native biota for the first 70 years of its invasion. Starting in 1989, supercolonies became more widespread and by 2001 had covered one-quarter of the rain forest on this island, attaining densities of up to 2,254 foraging ants per m² in invaded supercolony sites. Anoplolepis gracilipes kills the dominant native omnivore, the red land crab (Gecarcoidea natalis), by spraying formic acid over the eyes and mouthparts of the crab. The expansion of the yellow crazy ant supercolonies on the island results in the occupation of red crab burrows by the ants, which kill and consume the native crab and occupy the burrows as nest sites. Red land crab abundance is 42 times lower in ant-invaded sites. As a result of the severe reduction of the red crab, the dominant consumer of understory vegetation in this system, there is a doubling of litter cover, a thirtyfold increase in understory seedling density, and 3.9 times greater seedling species richness. Population outbreaks of two species of scale insects, the lac insect of unknown origin, Tachardina annantiaca, and the nonnative Coccus celatus are associated with sites invaded by the yellow crazy ant. The ants feed on the carbohydrate-rich honeydew of the scale insects and are assumed to defend the scales from predators and parasites. Furthermore, outbreaks of the scale insects and their associated honeydew spur the growth of a sooty mold in the canopy, causing widespread tree dieback and altering canopy and understory species composition. In areas with high densities of the yellow crazy ant the abundance of the native ground foraging emerald dove, Chalcophaps indica, has been significantly reduced. In sum, the yellow crazy ant has a direct negative effect on the red land crab, and the reduction of populations of the dominant herbivore of this system results in dramatic changes in understory community composition and litter cover. Nonnative scale insects are used by the yellow crazy ant as an energy source and spur the growth of sooty mold, resulting in widespread canopy dieback. This ant–scale insect mutualism results in an invasional meltdown whereby the impacts of the mutualism on this ecosystem are greater than the summed impacts of each individual species (Fig. 1).

Introductions of nonnative mammalian predators to islands have additive impacts on island avifauna, with the probability of bird extinction related to predator species richness as a positive logistic function. If competition occurred between island bird predators, or if there was functional redundancy of these species, the impact on native bird fauna would be expected to saturate with
from the interactions between earthworms and nitrogen-fixing plant species. Cascading community-level effects from the changes in soil biogeochemistry are prone to occur in areas with naturally low levels of soil nutrients. These impacts include increased colonization and persistence of other nonnative plants in the elevated nutrient areas, as well as the attraction of native and nonnative bird species that serve as vectors for the nonnative plants that thrive in these elevated nutrient environments. Additionally, in the highly invaded system of Hawaii, nonnative earthworms are a protein source for invasive feral pigs, which may have been a causal factor for the increased densities and expansion of feral pigs in the twentieth century. Feral pigs are estimated to disturb one-third of the diggable area of the mountain rain forest of Hawaii every year, increasing nutrient levels through fecal deposition as well as spreading propagules of nonnative plants such as the nitrogen-fixing nonnative firetree (Morella (Myrica) faya), which is associated with high levels of earthworms across this landscape. The runaway effects of changes in soil biochemical properties, as well as concomitant community-level impacts caused by the positive feedback loop between nonnative earthworms and nonindigenous nitrogen-fixing plants, is an example of invasional meltdown.

Accelerating Rates of Invasion

Observational studies of historical invasions have documented accelerating rates of invasion for a wide variety of taxa over time in the aquatic ecosystems of the Chesapeake Bay, the Great Lakes, San Francisco Bay, and the Baltic Sea; the marine systems of coastal North America, the Mediterranean Sea, and the Northeast Pacific Ocean; and terrestrial island ecosystems. Accelerating rates of invasion could be due to invasional meltdown, increased anthropogenic vectoring of species, increased detection rates, greater sampling efforts, or changes in the resistance of the recipient ecosystem to invasion. A model has been built using constant introduction rates and invader success that generated the exponential distribution of introduction times that has been observed in a variety of systems. Thus, without careful demonstration of direct and indirect interactions at the population and community levels, observational studies of systems demonstrating accelerating rates of invasion cannot be used as examples of invasional meltdown.

CONSEQUENCES OF INVASION MELTDOWN

Facilitations between a group of nonnative species can lead to greater impacts on native species than their individual impacts summed. This has been demonstrated increasing numbers of introduced predators. Empirical evidence suggests that every additional nonnative mammal predator added to islands results in an increased likelihood of island bird extinctions, suggesting that the impact of each additional predator may be facilitated by those present, rather than the impacts of predators being dampened via competition or functional redundancy.

Mutual facilitations between nonnative earthworms and nonindigenous nitrogen-fixing plant species have been found in the continental United States and Hawaii. Earthworm growth rates and carrying capacities are increased in the field through the provision of higher-quality food that nitrogen-fixing plant species provide in the form of nitrogen-rich litter. Additionally, populations of earthworms are thought to be enhanced through the modification of soil properties by nitrogen-fixers, including increased nitrogen, soil moisture, and pH. Earthworms act to increase the rate of nitrogen burial and litter breakdown with their feeding activities, rapidly increasing soil biogeochemical impacts. Thus, a mutually reinforcingpositive feedback cycle results
empirically with the devastating ant-scale mutualism on Christmas Island and the interaction between nonnative earthworms and nitrogen-fixing plant species. In order to understand the relative frequencies of facilitative versus detrimental interactions between nonnative species, there is a pressing need for additional empirical studies that quantify interactions between nonnative species. It is possible that invasional meltdown may occur infrequently, but with devastating impacts. Thus, ecosystem managers and scientists should be aware of its existence in order to record and predict the species and ecosystems most likely to experience invasional meltdown. The potential for positive interactions with invaders counters the criticism that prevention efforts are wasted if some future invasions are inevitable. It has been clearly demonstrated that there is the potential for a new species introduced into an ecosystem to have facilitative interactions with future and present nonnative resident species of that ecosystem. Thus, this warrants increased efforts and policies for preventing new invasions by dramatically reducing the frequency of new introductions to reduce the successful establishment of invaders in the future, as well as overall ecosystem susceptibility to invasion. Some of the greatest challenges of invasion biology have been the prediction of nonnative species likely to invade a given habitat, impacts of those species, as well as highly invisible habitats. Likewise, identifying high-impact species likely to form facilitations with established nonnative species, as well as the habitats and ecosystems most susceptible to invasional meltdown, may become the focus for future research on this topic.

SEE ALSO THE FOLLOWING ARTICLES
Dispersal Ability, Plant / Earthworms / Invasibility, of Communities and Ecosystems / Mutualism / Mycorrhizae / Pollination

FURTHER READING


INVASION BIOLOGY

MARK A. DAVIS
Macalester College, St. Paul, Minnesota

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,