

Understanding the long-term effects of species invasions

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We describe here the ecological and evolutionary processes that modulate the effects of invasive species over time, and argue that such processes are so widespread and important that ecologists should adopt a long-term perspective on the effects of invasive species. These processes (including evolution, shifts in species composition, accumulation of materials and interactions with abiotic variables) can increase, decrease, or qualitatively change the impacts of an invader through time. However, most studies of the effects of invasive species have been brief and lack a temporal context; 40% of recent studies did not even state the amount of time that had passed since the invasion. Ecologists need theory and empirical data to enable prediction, understanding and management of the acute and chronic effects of species invasions.

Changing impacts

The red imported fire ant *Solenopsis invicta* is an invasive species in the southern USA, where it is a nuisance to humans, an agricultural pest and a threat to wildlife [1,2]. As it spreads into new areas, *S. invicta* becomes abundant and reduces the populations of other insects, particularly native ants [3]. Yet 12 years after fire ants invaded an area in Texas, local populations of native ants and other insects that had been reduced early in the invasion had increased to pre-invasion levels [4]. If ecologists had studied *S. invicta* only just after it arrived, they would have concluded that it had devastating impacts on the native insect fauna. If they had studied it 12 years later, they would have concluded that it was a benign presence in the insect community. Each of these contradictory short-term assessments is technically correct but inadequate to describe the roles of an invading species whose effects change over time.

As we show here, there are good reasons to think that the effects of many invaders change over time. In fact, it might be helpful to think of invasions as generally having an acute phase immediately after a new species arrives, followed by a chronic phase after various ecological and evolutionary processes have come into play. Yet most studies of the effects of invaders are of short duration and are conducted more or

less indiscriminately along the time course of invasions instead of being placed in an explicit temporal context (Figure 1). Such studies will not provide an adequate basis for understanding and managing the temporally variable effects of individual invaders. Furthermore, the uncritical mixing of data from different times along the course of invasions makes comparative studies of the effects of invaders imprecise and difficult.

Invasive species have large effects on native biodiversity, cause hundreds of billions of dollars in economic damages, and complicate the management of natural ecosystems around the world [5,6]. Their effects are pervasive and varied, changing variables such as the genetics and population size of individual species, diversity and structure of communities, disturbance regimes and biogeochemical cycles. Here, we focus mainly on the impacts of invaders on ecosystem-level properties such as biogeochemical cycling and hydrology, which change ‘the basic rules of existence’ [7] for all species living in the ecosystem. We use the words ‘impacts’ or ‘effects’ without suggesting a negative connotation. Invasions can either increase or decrease populations or pools of materials in an ecosystem, and can provide both benefits and costs to humans who use ecosystems.

Previous attempts to explain the ecological effects of an invader have focused on two attributes: its functional distinctiveness (i.e. how much its characteristics such as nitrogen fixation, flammability, phenology, chemical defenses and diet differ from those of species already in the community) and its abundance [7–9]. As we show here, evolutionary or ecological processes can change either of these attributes over time, thereby modulating the effects of the invader (Figure 2). Thus, a third factor (time since invasion) needs to be explicitly considered to understand adequately the effects of many invaders.

Several common ecological or evolutionary processes should modulate the effects of an invading species over time. For convenience, we divide them into four somewhat arbitrary classes: (i) changes in the species that invades; (ii) changes in the biological community that is invaded; (iii) cumulative changes in the abiotic environment that is invaded; and (iv) interactions between the invading species and other variables that control the ecosystem.

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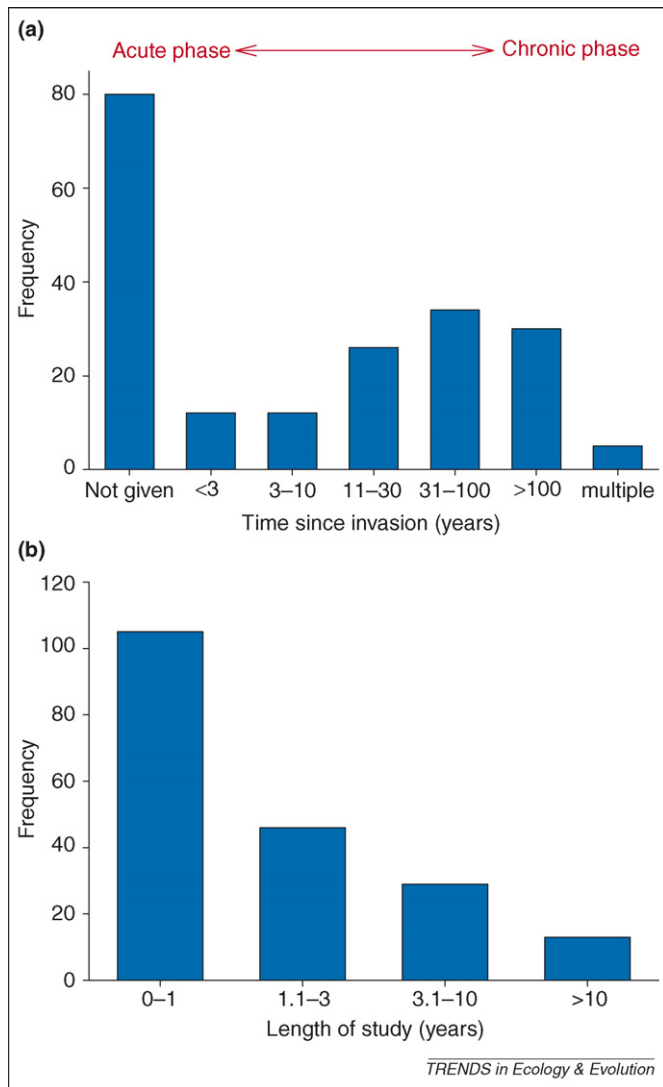


Figure 1. Characteristics of recent scientific studies on the effects of invading species. We define a study as the report of a single invading species in one ecosystem; a single paper could therefore include more than one study. We scanned all papers published in *Biological Invasions*, *Conservation Biology*, *Ecological Applications*, *Ecological Monographs*, *Ecology*, *Ecology Letters*, *Journal of Animal Ecology*, *Journal of Applied Ecology* and *Journal of Ecology* in 2001 through 2005 and found 185 papers that included 199 studies of the effects of an invading species. ‘Multiple’ means that a study included several sites that were invaded at different times. Studies were done at various times since the establishment of the invader; few studies included multiple points in time, and 40% of the studies did not record the time since invasion (a); in addition, most studies were of short duration (b). Few studies were done at multiple times since invasion or for durations long enough to reveal any temporal changes in invader effects.

Changes in the invader

Nongenetic responses

A species can change through time by acclimatization, including shifts in gene expression, resource allocation, or morphology and physiology within the lifespan of an individual. Such changes can influence many community and ecosystem processes [10], and might be especially important in invasive species, which tend to be phenotypically plastic [11]. Acclimatization can occur rapidly and, therefore, can be adequately captured by short-term studies done immediately after an invasion. However, acclimatization can also be important in responding to the biotic and abiotic changes that occur later in the invasion process.

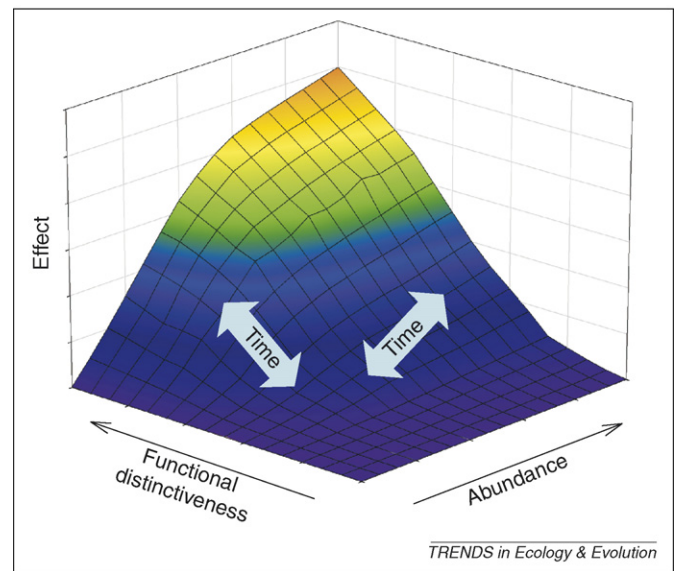


Figure 2. The effects of an invading species increase with its abundance and functional distinctiveness (i.e. how much its functional characteristics differ from those of species in the community that it is invading). Abundance and functional distinctiveness can increase or decrease through time, thereby altering the effect of the invader.

Thus, the tree *Bischofia javanica*, which invaded the Bonin Islands of Japan, is better able than native species to increase its photosynthetic rate, production of ‘sun’ leaves, and growth rate in response to sudden increases in light; it can therefore benefit from forest disturbances (e.g. typhoons) years after its initial invasion [12].

Likewise, ontogenetic changes in a long-lived invading species can cause long-term changes in its effects. For instance, the ability of a tree to form debris dams in streams, which retain organic matter, alter biogeochemical cycles and create distinctive habitats [13], is a function of the size (and hence age) of the tree, and so might not fully develop for more than a century [14]. We know of no published examples of such ontogenetic effects of invaders, but they are likely to occur and should be considered.

Genetic responses

After an invasive species arrives in a new region, evolution should tailor it to better fit the physicochemical environment and biota that it encounters, increasing its local population size and spread, and thereby its impacts. Such evolution, which can be based on existing genetic variation, hybridization or new mutations, has been discussed and studied widely [5]. For instance, because invaders often arrive in a new region without their associated specialized enemies [15,16], invading species might divert resources away from chemical defenses to growth and reproduction, resulting in highly vigorous invasive genotypes [17]. Evidence for this process (the ‘evolution of increased competitive ability’) has been mixed (e.g. [18]), but it appears to be important in some species (e.g. [19,20]). For example, specimens of the tallow tree *Sapium sebifera* from North America grow faster and produce lower concentrations of tannins than do those from their native Asia (Figure 3). Likewise, invasive species can evolve to use local species as food [21], avoid local enemies, or match their life-history traits to local environmental conditions [22,23]. Velvetleaf

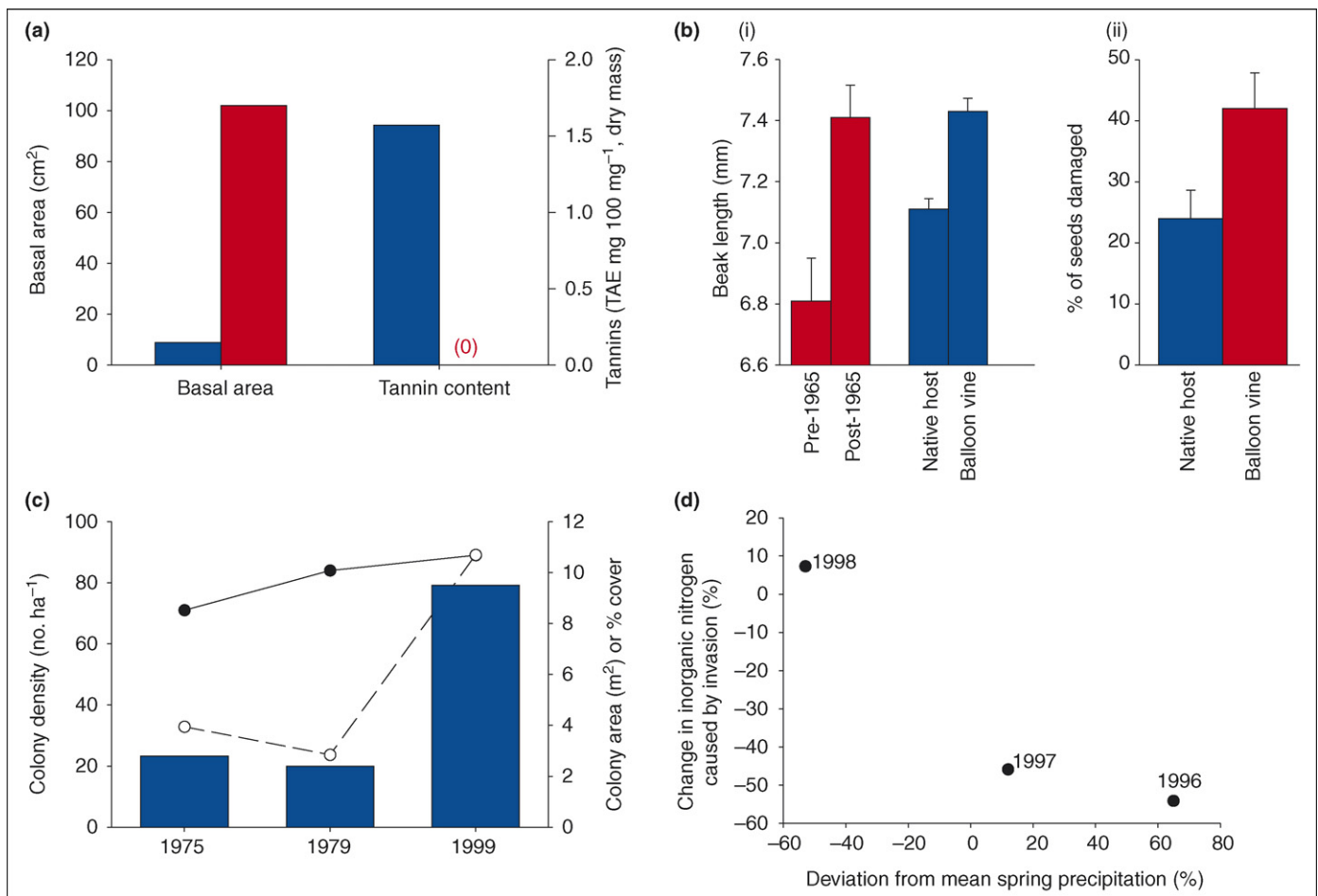


Figure 3. Examples of long-term changes in species invasions. **(a)** Probable evolutionary change in an invader. When grown together in a common garden in Texas, tallow trees *Sapium sebifera* from North American seeds (red bars) grew faster (as expressed by basal area) and had fewer chemical defenses (tannins, expressed as tannic acid equivalent = TAE) than did trees grown from seeds from their native Asia (blue bars) [19]. **(b)** Evolutionary change in a member of an invaded community. (i) The beak length ($\bar{X} \pm 1SE$) in female Australian soapberry bugs *Leptocoris tagalicus* has increased since the arrival of the invasive balloon vine *Cardiospermum grandiflorum* in ~1965 (red bars), leading to differences in beak length in bugs living on native plants and balloon vine (blue bars); (ii) long-beaked bugs collected from balloon vine (red bars) are more capable ($\bar{X} \pm 1SE$) of damaging seeds of this invasive plant than are short-beaked bugs (blue bars) collected from native plants [78]. **(c)** A cumulative change in the abiotic environment. The size (blue bars, % cover; open circles, area covered) and number (closed circles, density) of reefs of the invasive polychaete *Fycopotamus enigmaticus* in an Argentine lagoon increased substantially from 1975 to 1999. Such reefs interact with water and sediment movement and affect the composition of benthic animal communities [53,54]. **(d)** Interactions between an invasion and other controlling variables. The magnitude and even the direction of the effects of the invasive grass *Bromus tectorum* on the nitrogen status of soils depends on Spring precipitation [79].

Abutilon theophrasti, an invasive agricultural pest in North America, can rapidly adjust its life history and growth form to meet demands imposed by local competitors; these genetic changes occur within as little as 10–50 years [24]. Geographical variation in biotic or abiotic conditions in its new range can lead to genetic diversification or even speciation in the invading species [5], which could enable it to occupy an increased range of habitat types or change its functional characteristics at different sites. Invading species can hybridize with species already present at the site. This is especially common among plants, and has produced highly invasive genotypes such as common cordgrass *Spartina anglica* in Europe or hybrid cordgrass *Spartina foliosa* x *alterniflora* along the North American west coast [25,26].

Although details remain to be worked out, it appears that post-invasion evolution by invading species is common and will tend to increase their ecological effects by increasing their local population size or range. To influence ecosystem functioning, however, evolutionary changes must have substantial effects on the abundance or geographical

distribution of the invading species, its interactions with native species, or its functional traits that influence ecosystem processes. The consequences of evolutionary change for ecosystem functioning have been less studied than have the evolutionary changes themselves, but might be common and important. For instance, the new species of *Spartina* produced by hybridization can colonize formerly unvegetated mudflats [25], making them unsuitable for the sandpipers that used the mudflats; they also rapidly accumulate sediments, a process with profound biogeochemical, hydrodynamic and geomorphological implications.

The lag that is often observed between the arrival of an invader and its explosive population growth or spread might be caused by its need to adapt evolutionarily to its new environment, which should cause corresponding lags in the effects of invaders [27]. Even the initial matching of a species to its new environment can take decades to millennia, particularly if the species has a long life span. Genetic changes might occur in the invading population over the long term, so evolution can affect the impacts of a species for a long time after its arrival in a new range.

Changes in the community that has been invaded

The proliferation of an invading species can represent either an opportunity or a stress for other members of the community. Their responses to this opportunity or stress can extend over timescales from days to centuries, and involve changes in the species composition of the community and in the characteristics of the individual species. Although there are many examples of such responses, we do not yet know how often they are strong enough to moderate materially the impacts of the invasion.

Changes in community composition

Predators, parasites, and diseases of the invader, for which the invader is a valuable resource, might arrive or proliferate to take advantage of the invader, thereby reducing its population size or distribution. In Long Point Bay, Ontario, three different duck species feed heavily on invasive zebra mussels *Dreissena polymorpha* and quagga mussels *Dreissena bugensis*. The number of waterfowl-days in Long Point Bay increased from 43 200 in 1986 (before mussel invasions) to 3.6 million in 1997, reducing mussel biomass by 83% [28]. Of course, deliberate biological control is a special but widespread case of enemy proliferation.

Species composition within invaded communities can shift over the long term towards species that are resistant to the effects of the invader. In many grasslands worldwide, cespitose grasses that are vulnerable to grazing and trampling were the dominant perennials before European settlement. The introduction of domestic ungulates led to the extensive replacement of these grasses by species that are resistant to grazing and trampling [5]; for example, in Australia, overgrazing by introduced cattle *Bos taurus* led to a substantial increase in woody vegetation [29]. Similarly, the introduction of zebra mussels caused phytoplankton communities of several North American lakes to shift towards inedible Cyanobacteria (e.g. [30]). The result of these species shifts is to moderate the initially severe impact of invading herbivores on plant biomass and primary production.

Changes in the characteristics of individual species in the community

Analogous changes that moderate the impact of invaders can occur within the species of the community that is invaded, either as a result of genetic or phenotypic changes. Although research on the evolutionary aspects of species invasions has focused on the evolution of invasive genotypes of the invader (e.g. [31]) or of genotypes of consumers able to eat the invader (e.g. [32,33]), evolutionary responses could occur throughout the invaded community, especially where invaders have strong effects [34–36].

Native species can evolve to better use invaders as food or habitat. For example, the Australian soapberry bug *Leptocoris tagalicus* has evolved larger mouthparts that are better suited for attacking fruits of the invasive balloon vine *Cardiospermum grandiflorum* (Figure 3). Likewise, the Colorado potato beetle *Leptinotarsa decemlineata*, a native North American insect, evolved to feed first on the introduced potato *Solanum tuberosum* and then the introduced bittersweet *S. dulcamara* after these plants established in North America [37].

Shifts to forms resistant to the invader can occur within as well as across species through the evolution of resistant genotypes. For example, some North American perennial grasses have become more tolerant to grazing by introduced livestock (reviewed in [5]), and native North American plants appear to be evolving resistance to the root exudates of the invasive spotted knapweed *Centaurea maculosa* [38], diminishing the impact of this dominant invader. Native Australian snakes that are at risk of dying from the toxin of invasive cane toads *Bufo marinus* have evolved morphologically by decreasing their relative head size so that they cannot swallow toads that are large enough to kill them [39].

As with the invading species, physiological, behavioral, or morphological plasticity of native species can ameliorate the effects of an invader. For example, the crustacean *Sida crystallina* produces hemoglobin when exposed to the low-oxygen water beneath canopies of the invasive aquatic plant *Trapa natans* [40]. Such changes can be long term if the species is long lived.

Cumulative changes in the invaded environment

Invasive species often change the abiotic characteristics of the ecosystem through their feeding or engineering activities. A range of variables can be affected, including chemical concentrations, forms and fluxes, and the physical structure of the ecosystem. These changes can be cumulative and slow, taking many years to play out, and provide another example of how slow responses in important ecosystem components can prevent the full effects of an invader from appearing for many years [9,27].

Invasive plants often alter carbon and nitrogen cycling, water use and soil properties [41]. For example, *Myrica faya*, a nitrogen fixer, altered nitrogen cycling on Hawaiian lava flows [42], *Spartina alterniflora* converted mudflats on the west coast of the USA to marsh by trapping sediment [43] and salt cedar *Tamarix* spp. salinized soils and lowered water tables in the western USA [44]. The effects of *Tamarix* on the abiotic environment, as well as its susceptibility and rapid recovery from fire, promoted its long-term dominance to the exclusion of other riparian tree species [45,46].

These environmental effects might not be fully realized for many years, although little is known about their actual time courses. For example, it often takes decades before a shift in plant species changes soil characteristics, such as shifts from podzols to brown earth [47,48], and soil weathering [49]. Likewise, high litter inputs from melaleuca *Melaleuca quinquenervia* are gradually modifying the soil and topography of the Florida Everglades, converting wetlands to uplands (reviewed in [50]). Many invasive plants transform ecosystems by increasing sedimentation over time [51,52]. Similarly, the polychaete *Ficopotamus enigmaticus*, an invasive reef builder in the lagoons of Argentina, has significantly enhanced sedimentation, altered water flow and changed biological communities [53]. As the reefs have increased in size, number and density over decades, their effects on hydrology and sedimentation have also changed substantially [54].

Just as the cumulative effects of invasive species on the environment can take years to decades to be fully

expressed, the effects of displaced native species can take years to centuries to disappear. For example, the displacement of woody species can lead to massive erosion only decades after their removal, because woody roots persist in the soil [55,56].

Long-term effects from the accumulation of invasive species effects and the decay of native species effects are likely to be common and important in modulating the effects of species invasions. They should be most prevalent among plants and species with strong engineering effects, and will be especially important in determining the long-term impacts of the invader if they feed back either negatively or positively onto the population of the invader itself [57]. For instance, zebra mussels appear to have increased their distribution, population size and impacts on other benthic animals by converting open sandy sediments to mussel beds and shell gravels [58,59].

Interactions between the invader and other controlling variables

Invading species are not the only factor controlling the ecosystems that they invade. Factors such as disturbance, hydrology and weather (e.g. precipitation or temperature) often are important and can interact strongly with the invading species. Because the size of the invasive species population and environmental factors typically vary over time, the full effects of the invader might not be seen for a considerable time after the initial invasion.

For example, many invasive plants change the fire regime of ecosystems that they invade [60,61]. Fire initiation, spread and intensity depends on meteorological

conditions such as lightning frequency, precipitation, relative humidity and wind, as well as fuel characteristics [61]. As a result, it will be difficult to understand the effect of an invader on fire regimes until the ecosystem has experienced extreme meteorological conditions. Likewise, flood-plain morphology and function depends on the interaction between vegetation and hydrology [62], and the biomass of estuarine phytoplankton is determined jointly by grazing and hydrology [63,64]. If we are to understand how invasive riparian plants such as *Fallopia japonica* or invasive bivalves such as *Potamocorbula amurensis* affect ecosystem function, our perspective on the system must be long-term enough to include extreme hydrological events (Box 1).

Why we need to include time in our thinking about invaders

Both acute and chronic effects of invasions are important. Chronic effects represent the eventual outcomes of a species invasion and are of ecological and economic interest. However, acute effects also are important to understand, as they might last long enough to have serious ecological and economic consequences, some which might be irreversible (e.g. extirpation of native species). Also, knowing the severity and length of the acute phase will help guide efforts to provide temporary mitigation against the worst effects of the invasive species (e.g. [65]).

At present, we have neither the empirical foundation nor the theoretical frameworks needed to predict how the ecological effects of a particular invader will change over time. The current situation of accumulating knowledge from a limited number of case studies is clearly

Box 1. How to study long-term effects of species invasions

Although the ideal way to determine how the effects of a species invasion change temporally might seem to be to study a species invasion for a long time, this is a direct approach that has been used in a only few studies of species invasions (e.g. [64]), and it can be expensive, logistically difficult and slow to provide timely answers. As with other long-term phenomena, such as forest succession and soil development, species invasions can also be studied using short-term approaches [66]. For instance, retrospective studies using lake sediments, tree rings, museum specimens, human historical records and so on can be used to reconstruct past dynamics of communities and ecosystems over long periods of time [67–69]. Thus, Zangerl and Berenbaum [70] analyzed herbarium specimens to show how the chemical defenses of wild parsnip *Pastinaca sativa* declined and then increased as this invasive plant escaped from and then re-encountered its specialist herbivore, the parsnip webworm *Depressaria pastinacella*, in North America.

Chronosequences (a series of study sites that differ primarily in the time since an event occurred, such as clearcutting, deglaciation, or a species invasion) are another short-term approach to reconstructing long-term dynamics that have been used widely in studies of vegetation succession [71,72]. For example, studies of a series of *Pinus radiata* stands of different ages showed that the diversity of native and non-native plants changed through time in plantations of this non-native tree in New Zealand (Figure 1). However, because chronosequences make crucial assumptions, they should be used cautiously [71].

Instead of waiting for hundreds of years for the effects of an invasion to play out, a model system with fast dynamics (a microcosm) can be used to develop and test theories about the temporal dynamics of invasive species effects. Such systems are especially well suited to experimental studies that can be hard to

sustain over the long term in slow systems [73]. Again, crucial assumptions about scaling and container effects make it difficult to generalize the results of microcosm studies to the natural world [74–76]. Finally, mathematical models can be used to great advantage to study long-term phenomena and can be invaluable in guiding field programs. We think that progress in understanding the long-term effects of species invasions will be best achieved by using a mix of all these methods.

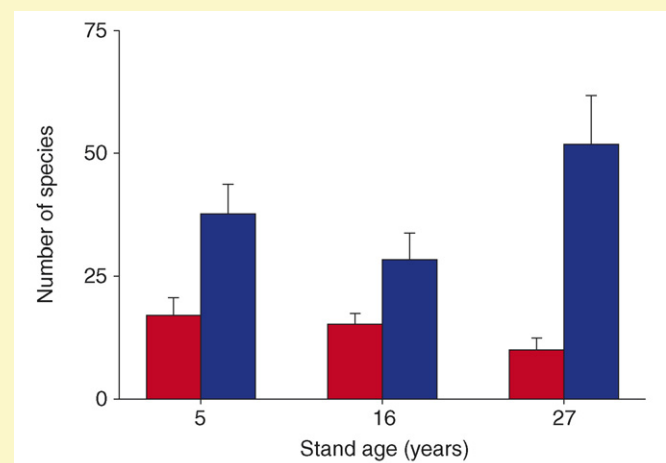


Figure 1. Number of species ($\bar{X} \pm 1SE$) of native (blue bars) and non-native (red bars) plants in plantations of the non-native tree *Pinus radiata* in New Zealand, as a function of the age of the plantation [77].

insufficient. By focusing on how ecological effects change temporally, we can improve our ability to draw generalities from available case studies and to design experiments to expose the mechanisms by which species effects change through time. This will require identifying and classifying important attributes of invaders, and understanding how the functional characteristics of invaders affect systems immediately after an invasion as well as over the longer term, when chronic effects set in. By understanding the long-term feedbacks between invasive species and their communities and ecosystems, we will be able to evaluate alternative management approaches for well established invaders, and be better able to identify which new invaders should be targeted for early eradication because of unacceptable acute or chronic impacts.

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