ELSEVIER

The Science of the Total Environment 262 (2000) 253–261

the Science of the Total Environment
An International Journal for Scientific Research into the Environment and its Relationship with Man

www.elsevier.com/locate/scitotenv

Global climate change and introduced species in United States forests

Daniel Simberloff*

Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA

Received 21 November 1999; accepted 31 March 2000

Abstract

Introduced species already cause billions of dollars of damage annually in United States forests, plus massive ecological damage whose economic value has often not been estimated. The variety of impacts is staggering and includes herbivory, predation, disease, parasitism, competition, habitat destruction, hybridization, and changed disturbance regimes and nutrient cycles. How global climate change will affect these impacts has scarcely been assessed. Range changes of existing introduced species will be prominent, as many species' biogeographic ranges are set primarily by climate. Similarly, some species that might otherwise not have survived will be able to establish populations in a changed climate. It is more difficult to predict what the impacts of the introduced species will be. What is most needed are studies of the combined impacts of changing climate, CO_2, and nutrients. Certain aspects of the biology of introduced species, such as evolution and autonomous dispersal, greatly complicate the prediction of spread and impact of introduced species.

Keywords: Biogeographic range; Forest pests; Global climate change; Introduced species; Nitrates

1. Introduction

To predict how global climate change will affect the impact of introduced species on US forests, it is necessary first to understand the scope and variety of current impacts by such species, not only on forest trees but on all inhabitants of forest communities. The full panoply of such impacts would require a monograph. Estimates of the economic and ecological costs of most have not been attempted. But a quick scan suggests that such species are already an expensive scourge. Herbivory, predation, habitat destruction, competition, and disease are the most prominent effects. In addition to causing disease, a non-indigenous species can vector a disease, which can itself be either native or non-indigenous. Similarly, non-indigenous species can dis-

* Tel.: +1-423-974-0849; fax: +1-423-974-3067.
E-mail address: dsimberloff@utk.edu (D. Simberloff).

0048-9697/00/$ - see front matter
PII: S0048-9697(00)00527-1

perse weedy plants, which are most likely non-indigenous. A major sort of impact by non-indigenous species is modification of natural cycles and disturbance regimes, such as nutrient cycling and fire frequency and intensity (Mack and D'Antonio, 1998). Finally, non-indigenous species can hybridize with one another or with native species (Rhymer and Simberloff, 1996). The consequences can include genetic extinction of a native species, major genetic changes and elimination of locally adapted genotypes, and even production of an entirely new, highly invasive species.

2. Types of impacts

The following cases from US forests exemplify most but not all of the types of impacts that non-indigenous species can have (Simberloff, 1997).

2.1. Insects

Approximately 360 non-indigenous insect species are found in US forests (Liebhold et al., 1995). Pimentel et al. (2000) estimate the annual damage these cause as $2.1 billion. Gypsy moth (*Lymantria dispar*) alone infests approximately 125 million acres of US forest and defoliates up to 12 million acres annually. The USDA Forest Service spent $10.6 million in 1993 on gypsy moth suppression (Campbell and Schlarbaum, 1994). Insect invaders of our forests do more than just destroy valuable timber. For example, the balsam woolly adelgid (*Adelges piceae*) has caused extensive death of Fraser fir (*Abies fraseri*) in relict stands in the southern Appalachians, even local elimination. This damage threatens native species associated with the fir (Liebhold et al., 1995).

2.2. Snails

The Central American and Floridian carnivorous rosy wolf snail, *Euglandina rosea*, introduced to the Hawaiian islands for the biological control of the giant African snail, has instead caused the extinction of many populations of native *Achatinella* and other tree snails in the upland forests (Civeyrel and Simberloff, 1996).

2.3. Birds

Although the data exist to allow an estimate (e.g. Lever, 1987), no one has tallied the number of avian invaders of US forests. This is doubtless because, though there are a substantial number in the continental US and another suite in Hawaii, they are not as damaging economically or ecologically as insects, pathogens, and plants. Nevertheless, their impact is sometimes substantial. For example, the Asian myna (*Acridotheres tristis*) plays a major role in dispersing the plant *Lantana camara* in the Hawaiian islands, including into forest habitats where it has heavily impacted native plants (Smith, 1985). The myna and other Eurasian birds have contributed heavily to the devastation of native Hawaiian forest birds by vectoring avian pox and malaria (van Riper et al., 1986).

2.4. Reptiles

Although introduced reptiles are not prominent components of continental forests (e.g. Butterfield et al., 1997), the brown tree snake (*Boiga irregularis*) from the Admiralty Islands, introduced to Guam in approximately 1950, has completely eliminated 10 of the 12 native forest bird species and subspecies and caused the other two to become very rare (Williamson, 1996). At least seven individuals of the snake have been found at airfields on Oahu and destroyed; one turned up at Corpus Christi, TX.

2.5. Mammals

European wild boar, feral domestic hogs, and hybrids between them have wreaked havoc in both bottomland and upland forests in the continental US and Hawaii. For example, in the Great Smoky Mountains National Park, they 'root' primarily in high-elevation deciduous forests in the summer, greatly reducing understory cover and number of species. By selective feeding, they can

locally extinguish plant species with starchy bulbs, tubers, and rhizomes (Bratton, 1975). They greatly modify soil characteristics by thinning the forest litter, mixing organic and mineral layers, and accelerating mineral leaching (Singer et al., 1984). Annual expenditures for pig control in forests in the three Hawaiian national parks, aside from the costs of the damage they cause, are estimated at approximately $500 000 (Pimentel et al., 2000).

2.6. Plants

Non-indigenous plants can affect native forests in a variety of ways. Trees can outcompete natives, for example. Chinese tallow (*Sapium sebiferum*), introduced to the US Gulf coast in the early 20th century, is shade-tolerant. Its seeds are dispersed by native migratory birds, and it is invading wet forests and replacing native forest trees in Texas, Louisiana, and Florida (Bruce et al., 1997; Miller, 1997). Chinese privet (*Ligustrum sinense*) is a shade-tolerant tree or large shrub that is replacing native riparian species and preventing regeneration of bottomland hardwood-pine forests (Miller, 1997).

Several introduced tree species are particularly able to invade forests in either naturally disturbed sites or, increasingly, in the wake of anthropogenic disturbances: black locust (*Robinia pseudoacacia*) (Hunter, 1996a; Peloquin and Hiebert, 1999), Norway maple (*Acer platanoides*) (Webb, 1996), and tree-of-heaven (*Ailanthus altissima*) (Hunter, 1996b) are examples. Such species can greatly interfere with forest restoration projects. For instance, the princess tree, *Paulownia tomentosa*, outcompetes native trees in disturbed areas in eastern US forests (Williams, 1993; Langdon and Johnson, 1994; Johnson, 1996). It is replacing native pines in some areas of the Great Smoky Mountains National Park to which natural fire cycles have been returned (K. Johnson, personal communication, 2000).

Similarly, introduced ground cover plants have replaced native ground cover plants in many US forests. In the Great Smoky Mountains National Park, nepalgrass (*Microstegium vimineum*) invades even shady areas, forms dense mats, and excludes native plants from large areas (Clements, 1998). In the Midwest, European garlic mustard (*Alliaria petiolata*) invades wet to dry-mesic forests, but also oak savannas and other habitats, displacing numerous native groundcover plants (Nuzzo, 1993).

Introduced plants can also alter ecosystem processes. For instance, in a tallow-dominated forest, the leaf litter of Chinese tallow has been shown to alter rates of nutrient cycling, enhancing populations of the non-indigenous isopod *Armadillidium vulgare* while depressing populations of native invertebrates (Cameron and Spencer, 1989). Australian paperbark tree (*Melaleuca quinquenervia*) covers 200 000 ha of south Florida. By its impacts on fire frequency and hydrology, it has invaded and heavily impacted several forest types (Schmitz et al., 1997).

2.7. Pathogens

There are more than 20 introduced plant pathogens in US forests (Liebhold et al., 1995). Pimentel et al. (2000) estimate the annual cost of damage to US forests from these as $2.1 billion, equal to that of insects. However, some ecological costs of plant pathogen attack are incalculable. For example, the Asian chestnut blight fungus (*Cryphonectria parasitica*) spread in less than 50 years over 80 million ha of the eastern US, virtually eliminating the American chestnut (*Castanea dentata*), a dominant or co-dominant tree in many forests, comprising up to 25% of canopy trees (von Broembsen, 1989). Many direct and indirect impacts followed this invasion, including the extinction of several insects host-specific to chestnut (Opler, 1979), the rise of oak wilt disease (Quimby, 1982), and lower litter decomposition rates (K. Cromack, personal communication, 1987).

White pine blister rust (*Cronartium ribicola*), evolved in Asia, was widespread in Europe by mid-19th century, and was probably introduced to North America from Europe in nursery stock during 1890s (Liebhold et al., 1995). It is the most important disease of trees in the white pine group. Control programs in the US, including research, chemical treatment, and eradication of *Ribes* (the other host in its life cycle), cost hundreds of millions of dollars (Liebhold et al., 1995). Up to

95% of original stands of western white and sugar pines have been killed or damaged by white pine blister rust (Liebhold et al., 1995). The impact on forest ecosystems is profound and complex. For example, grizzly bears (*Ursos arctos horribilis*) use seeds of whitebark pine (*Pinus albicaulis*) because of their high fat content and abundance. In years of prolific seed crops, bears tend to remain and feed in high elevation areas until hibernation. When seed crops are small, as they are now because of white pine blister rust, the bears range closer to human facilities, with increased bear mortality and decreased populations (Mattson et al., 2000).

Non-indigenous pathogens need not act in isolation. For example, flowering dogwoods (*Cornus florida*) have rapidly disappeared throughout eastern forests since the late-1970s because of an introduced fungus, dogwood anthracnose (*Discula destructiva*). This fungus is particularly likely to strike trees where acid rain is prevalent, and its impact tends to be exacerbated there (Anderson et al., 1993; Britton et al., 1996).

3. Global change and non-indigenous species

Scenarios for how global climate change will affect the impact of introduced species generally, and on forests in particular, are just that — scenarios. There has been little direct experimentation on the topic, and the entire field of invasion biology has not proven very adept at forecasting the impacts of invasions. Nevertheless, some plausible hypotheses suggest that climate change will be important.

Foremost among the likely impacts of global climate change will be a simple change in the geographic ranges of many species. Although direct experimental evidence on the determinants of range limits is surprisingly scarce, the most detailed studies usually implicate climate as a major if not the chief reason why species' ranges terminate where they do (e.g. Gleason and Cronquist, 1964). For example, Neilson and Wullstein (1983) showed that Gambel's oak (*Quercus gambelii*) is not found further north than it is in the western US because of a complex interaction of several climatic factors with the physiology of the plant. This range limit is determined by seedling mortality caused by spring freezes and summer drought. The fact that Florida and Hawaii are the two states most afflicted by introduced species is very likely partly due to their mild climates (Simberloff, 1997). One can therefore easily envision that a given rise in temperature, for example, will allow a spread northward of at least some species currently restricted in their northern ranges by some function of temperature — for example, the probability of an early freeze. A prediction of the precise range change would require detailed knowledge of all the factors that combine to determine the range, as exists for Gambel's oak, but the general outlines of the change are clear. Roughly, to find a 3°C increase in temperature nowadays in the continental US, one would have to move southward 250 km (US Congress, 1993).

A scan of past rates of migration of tree species with climate change (e.g. Davis, 1981) suggests the predicted climate change is fast enough that dispersal limitation alone will prevent many species from keeping pace with their changing potential ranges as the latter expand. However, invasive non-indigenous species should in general have an advantage in this race, as many are typified by good dispersal abilities and other 'weedy' traits that are, in fact, the very features that render them invasive, such as light seeds (Rejmanek and Richardson, 1996). A number of forest pests and pathogens are predicted to spread by this means, their range boundaries shifting in concert with climate change (Peters, 1991). Some ecologists go further, and predict that, as climate changes and ranges even of native species do not shift in lock step with one another, longstanding, co-adapted communities of species will be sundered and the new communities that replace them will be inherently less stable and more invisible (Kareiva et al., 1993). This is a more speculative scenario, and there is debate about just how highly coadapted existing native communities are.

Aside from range changes, there are other ways in which increased temperature could affect invasive non-indigenous species in forests. For example, insect development is generally temperature-

dependent. Many researchers have predicted that increasing temperatures will lead to increasing winter survival and increasing numbers of generations per year, thus greatly increasing pest pressures (Mooney, 1996). For a number of forest pests, there are accurate models of environmental controls of population growth. Often these depend heavily on temperature. For instance, Williams and Liebhold (1995) predicted changing distributions and population sizes of the European gypsy moth (*Lymantria dispar*) in Pennsylvania with changing temperature and rainfall, as well as impact on forests (as measured by fraction of 2 × 2-km grid cells in the state in which at least 30% of the foliage was lost). The key point to emerge from this exercise was that a 2°C increase in temperature alone would be predicted to cause a great decrease in defoliation in Pennsylvania, while the same temperature increase combined with a 0.5-mm/day precipitation increase would be predicted to cause a major increase in defoliation. Under both the Geophysical Fluid Dynamics Laboratory general circulation model (GFDL-GCM) and the Goddard Institute for Space Studies general circulation model (GISS-GCM), defoliation would vanish within a century.

However, this exercise assumed a static resource base and did not account for changes in forest composition independently of gypsy moth impacts, only gypsy moth activity and population dynamics. This is an important consideration; for example, under both the GISS and GFDL models, two potential hosts of gypsy moth [yellow birch (*Betula alleghaniensis*) and sugar maple (*Acer saccharum*)] will ultimately shift their ranges northward almost entirely out of Pennsylvania (Davis and Zabinski, 1992). Of course, new hosts may also shift their ranges to include Pennsylvania. Further, this modeling effort, and all others of which I am aware, do not account for possible impacts of evolution. The host and/or its natural enemy could evolve different tolerances of climatic factors, or the host-natural enemy interaction itself could evolve (as, for example, when a host evolves greater resistance to a natural enemy).

Ranges and abundances of many tree species within the eastern United States have recently been predicted, based on the GFDL and GISS models (Iverson and Prasad, 1998). If the distribution, abundance, and activity of other introduced (and native) insect pests as a function of temperature and precipitation were modeled as gypsy moth was by Williams and Liebhold (1995), the combination of such modeling with that of the tree distributions and abundances could be used to forecast specific damages of particular insects on particular tree species and, perhaps, on the forest as a whole.

Increased CO_2, in addition to driving temperature change, could affect range and population sizes of forest invaders (Mooney, 1996; Dukes and Mooney, 1999). For plants, photosynthetic rates increase, and the effects differ for C_3 and C_4 plants. The C_4 plants saturate their photosynthetic capacity at relatively low concentrations. Thus, C_3 plants will gain an advantage that they currently lack. Most of the worst agricultural weeds are C_4 plants (e.g. *Echinochloa crusgalli*, *Cyperus rotundus*), but forest invaders can be C_4 also. For example, nepalgrass (*Microstegium vimineum*) as noted above invades large forest areas of the Great Smoky Mountains National Park, excluding native plants; it is a C_4 annual grass. However, the increased CO_2 is not the only change occurring. C_4 plants use water and nutrients more efficiently, and they tolerate temperature extremes better. Thus, probably all we can say at present is that certain competitive balances between native and introduced species will be changed. Increased CO_2 increases not only photosynthetic rates but also the ratio of carbon fixed to water lost. The soil water savings could potentially provide habitat for late-season annuals, a category that includes many invasive introduced pests (Mooney, 1996).

Generally, changes in CO_2, temperature, water availability, nutrient availability, and cloud cover can all affect the resistance of trees to herbivores, including introduced ones (Ayres, 1993). For example, increased CO_2 tends to reduce leaf nitrogen, and herbivores can respond with either decreased growth or increased consumption (Ayres, 1993; Watt et al., 1995). Elevated CO_2 increases leaf toughness in red oak and quaking aspen, but not sugar maple (Lindroth et al., 1993); this is potentially important to non-indigenous insects,

as degree of folivory for several phytophagous insects is known to be affected by leaf toughness. Perhaps most importantly, increased CO_2 can affect the phenology of plant development (e.g. budburst and budset) (Watt et al., 1995). It has already been shown for native grassland plants that the impact of a non-indigenous weevil is highly dependent on the precise timing of development (Louda, 1998). In Scotland, Dewar and Watt (1992) showed that a major forest pest, winter moth (*Operophtera brumata*), would become asynchronous with an introduced host, Sitka spruce (*Picea sichensis*), if there were a warming of 1–2°C. However, increased CO_2 could restore the synchrony (Watt et al., 1995).

Increased cloud cover tends to reduce plant secondary metabolism and increase susceptibility to herbivory (Ayres, 1993). Changes in temperature also can effect plant secondary chemistry and nitrogen content. It is difficult to predict the net effect of these changes plus others, and responses are likely to be non-linear, but there is every reason to think they will be substantial (Ayres and Reams, 1997).

Finally, the increasing deposition of nitrates from the atmosphere because of fossil fuel combustion has already caused large vegetational changes in forests of western Europe (Berendse et al., 1993). Increased nitrogen deposition could easily change US forest composition, including the relative abundances of introduced species (Dukes and Mooney, 1999), by altering the competitive balance between species adapted to nutrient-poor vs. nutrient-rich environments, but the nature of such changes has not been explored in detail.

4. Research needs

Although it seems safe to predict certain general impacts of global climate change (and associated changes, such as CO_2 increase and nitrate deposition) on how non-indigenous species will affect forests, it is clear from the above survey that specific predictions will require additional research. In some instances, the research is straightforward and could be completed expeditiously. This is particularly true for certain types of modeling efforts, especially the concatenation of existing models. In other cases, fundamental empirical knowledge is lacking, so that useful models cannot be parameterized or even constructed.

(1) The most urgent need is to model the combined effects of climate, CO_2, and perhaps nutrients such as nitrogen (Lawton, 1995; Watt et al., 1995). Furthermore, the models need to study jointly, on the one hand, the impacts of these factors on both tree or other native forest species themselves and, on the other, non-indigenous species that might interact with the natives. It is apparent from examples above that the joint effects of climate and other factors can be very different from those of temperature and precipitation alone.

(2) Models of impacts of climate change and other factors on forest pests (insects and pathogens) must be combined with models of range and abundance changes of hosts.

(3) As the spread of many introduced species is related to disturbances, models of the impact of climate change on disturbance regimes (fires, hurricanes, ice-storms, etc.) must be melded with models of the direct impacts of various invaders.

(4) Certain empirical gaps must be filled. For example, almost all research on the impact of both climate and CO_2 changes on herbivorous insects has been conducted on plant-chewing insects. Impacts might be very different for plant-sucking insects, leafminers, gallmakers, and borers. As some of the worst introduced forest pests are among the latter groups (e.g. the Asian longhorned beetle, *Anoplophora glabripennis*), it is important to diversify the empirical base. Also, little research has focused on the impacts of climate and CO_2 changes on insect predators and parasitoids. Obviously the trajectories of phytophagous insect populations can depend on those of their natural enemies.

(5) Even if climate were not changing, there is an urgent need for better prediction of the impacts of introduced species. The combination of non-indigenous species and a globally changing climate exacerbates that need. Current models of risk assessment for non-indigenous species (and

pathways for introduction of species, such as wooden packing material and untreated logs) rely on a model for chemical stressors that is woefully inadequate for biological stressors (Simberloff and Alexander, 1998). In particular, living organisms (including introduced species) all have two traits that are inherently at least somewhat stochastic and that complicate prediction. First, they evolve, and second, they disperse autonomously. Both of these features will come into play as climate changes. For example, range limits set by climate can be overcome, to an extent, by evolution of new tolerances. I know of no example among forest species, but the evolution of cold-tolerance by the aquarium strain of the tropical alga *Caulerpa taxifolia* has led to one of the most publicized and damaging marine invasions in the northwest Mediterranean (Meinesz, 1999). Similarly, though I know of no forest example, in agriculture, pests and natural enemies evolve different degrees of effectiveness and resistance. For instance, the ichneumonid wasp *Bathyplectes curculionis* evolved to become more adapted to a new host, the Egyptian alfalfa weevil (*Hypera brunneipennis*), while its original host in the US, the alfalfa weevil (*Hypera pastica*), evolved to become more resistant to the same wasp (Salt and van den Bosch, 1967). Autonomous dispersal also ensures that species will shift their ranges in response to climatic changes, although different species will move at different rates (e.g. Iverson and Prasad, 1998). Other aspects of the impact of non-indigenous species will be affected by these traits as well — for example, herbivorous insects evolve new host ranges. There is general agreement among invasion biologists that we are currently quite inept at predicting the impacts of introduced species (e.g. Mack et al., 2000). Without new research, this situation will only be exacerbated.

5. Conclusions

As range limits of US trees shift with changing climate, the ranges of non-indigenous species already established on them (such as herbivorous insects) will change concomitantly. Similar changes should be expected for non-indigenous plants that are forest pests. The fact that high-impact introduced species generally have 'weedy' traits suggests that dispersal limitations will not impede the movement of many established introduced pest species to keep pace with range changes of their hosts or habitats.

Additionally, some non-indigenous species that are now either precluded by climate (their propagules die or fail to reproduce) or whose ranges are restricted by climate will survive and/or spread. Invasive forest trees currently restricted to the South, like Chinese tallow, will probably spread northward.

At least some non-indigenous insect forest pests will probably have greatly increased populations because they will develop faster. Many insects currently are multivoltine in the southern part of their range and univoltine in the north.

Changes in both climate and CO_2 will lead to changing phenological relationships between introduced (and native) forest insects and their host trees; these could either exacerbate or attenuate damage caused by these pests. Similarly, climatic changes and nitrogen deposition will change plant nitrogen content, and this change in turn will affect insect feeding rate and, ultimately, population sizes. As increased CO_2 tends to reduce leaf nitrogen, and nitrogen deposition tends to increase it, there may be a tendency for these two effects to compensate for one another partially.

Past experience on the astounding variety of impacts of non-indigenous species, and the complexity of some aspects of this problem, suggest that further research will be needed to produce specific predictions.

References

Anderson RL, Berrang P, Knighten J, Lawton KA, Britton KO. Pretreating dogwood seedlings with simulated acidic precipitation increases dogwood anthracnose symptoms in greenhouse-laboratory trials. Can J For Res 1993;23:55–58.

Ayres MP. Global change, plant defense, and herbivory. In: Kareiva PM, Kingsolver JG, Huey RB, editors. Biotic interactions and global change. Sunderland, Massachusetts: Sinauer Associates, 1993:75–94.

Ayres MP, Reams GA. Global change and disturbance in southern forest ecosystems. In: Mickler RA, Fox S, editors. The productivity and sustainability of southern forest ecosystems in a changing environment. New York: Springer-Verlag, 1997:741–753.

Berendse F, Aerts R, Bobbink R. Atmospheric nitrogen deposition and its impact on terrestrial ecosystems. In: Vos CC, Opdam P, editors. Landscape ecology of a stressed environment. London: Chapman & Hall, 1993:104–121.

Bratton SP. The effect of the European wild boar, *Sus scrofa*, on grey beech forest in the Great Smoky Mountains. Ecology 1975;56:1356–1366.

Britton KO, Berrang P, Mavity E. Effects of pretreatment with simulated acid rain on the severity of dogwood anthracnose. Plant Dis 1996;80:646–649.

Bruce KA, Cameron GN, Harcombe PA, Jubinsky G. Introduction, impact on native habitats, and management of a woody invader, the Chinese tallow tree, *Sapium sebiferum* (L.) Roxb. Nat Areas J 1997;17:255–260.

Butterfield BP, Meshaka Jr. WE, Guyer G. Nonindigenous amphibians and reptiles. In: Simberloff D, Schmitz DC, Brown TC, editors. Strangers in paradise. Impact and management of nonindigenous species in Florida. Washington, DC: Island Press, 1997:123–138.

Cameron GN, Spencer SR. Rapid leaf decay and nutrient release in a Chinese tallow forest. Oecologia 1989;80: 222–228.

Campbell FT, Schlarbaum SE. Fading forests. North American trees and the threat of exotic pests. Natural Resources Defense Council, New York, 1994:47.

Civeyrel L, Simberloff D. A tale of two snails: is the cure worse than the disease? Biodiv Conserv 1996;5:1231–1252.

Clements R. Survey of exotic plants in the Great Smoky Mountains National Park. In: Fifth Annual Tennessee Exotic Pest Plant Council Symposium, Abstracts, 1998:8.

Davis MB. Quaternary history and the stability of forest communities. In: West DC, Shugart HH, Botkin DR, editors. Forest succession: concepts and applications. New York: Springer, 1981:132–153.

Davis MB, Zabinski C. Changes in geographical range resulting from greenhouse warming: effects on biodiversity in forests. In: Peters RL, Lovejoy TE, editors. Global warming and biological diversity. New Haven: Yale University Press, 1992:297–308.

Dewar RC, Watt AD. Predicted changes in the synchrony of larval emergence and budburst under climatic warming. Oecologia 1992;89:557–559.

Dukes JS, Mooney HA. Does global change increase the success of biological invaders? Trend Ecol Evol 1999;14: 135–139.

Gleason HA, Cronquist A. The natural geography of plants. New York: Columbia University Press, 1964:420.

Hunter J. Ailanthus altissima. In: Randall JM, Marinelli J, editors. Invasive plants. Weeds of the global garden. New York: Brooklyn Botanic Garden, 1996a:27.

Hunter J. Robinia pseucoacacia. In: Randall JM, Marinelli J, editors. Invasive plants. Weeds of the global garden. New York: Brooklyn Botanic Garden, 1996b:40.

Iverson LR, Prasad AM. Predicting abundance of 80 tree species following climate change in the eastern United States. Ecol Monogr 1998;68:465–485.

Johnson K. Paulownia tomentosa. In: Randall JM, Marinelli J, editors. Invasive plants. Weeds of the global garden. New York: Brooklyn Botanic Garden, 1996:38.

Kareiva PM, Kingsolver JG, Huey RB, editors. Biotic interactions and global change. Sunderland, Massachusetts: Sinauer Associates, 1993:559.

Langdon KR, Johnson KD. Additional notes on invasiveness of *Paulownia tomentosa* in natural areas. Nat Areas J 1994;14:139–140.

Lawton JH. The response of insects to environmental change. In: Harrington R, Stork NE, editors. Insects in a changing environment. London: Academic, 1995:3–26.

Lever C. Naturalized birds of the world. Harlow, UK: Longman, 1987:615.

Liebhold AM, MacDonald WL, Bergdahl D, Mastro VC. Invasion by exotic forest pests: a threat to forest ecosystems. For Sci Monogr 1995;30:49.

Lindroth RL, Kinney KK, Platz CL. Responses of deciduous trees to elevated atmospheric CO_2: productivity, phytochemistry, and insect performance. Ecology 1993;74: 763–777.

Louda SM. Population growth of *Rhinocyllus conicus* (Coleoptera: Curculionidae) on two species of native thistles in prairie. Environ Entomol 1998;27:834–841.

Mack C, D'Antonio CM. Impacts of biological invasions on disturbance regimes. Trend Ecol Evol 1998;13:195–198.

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz F. Biotic invasions: causes epidemiology, global consequences and control. Issues Ecol 2000;5:1–20.

Mattson DJ, Kendall KC, Reinhart DP. Whitebark pine, grizzly bears, and red squirrels. In: Tomback DF, editor. Whitebark pine communities: ecology and restoration. Washington, DC: Island Press, 2000:in press.

Meinesz A. Killer algae. Chicago: University of Chicago Press, 1999:360.

Miller JH. Exotic invasive plants in southeastern forests. In: Britton KO, editor. Exotic pests of eastern forests, Conference Proceedings. U.S.D.A. Forest Service and Tennessee Exotic Pest Plant Council, Nashville, 1997:97–105.

Mooney HA. Biological invasions and global change. In: Sandlund OT, Schei PJ, Viken A, editors. Proceedings of the Norway/UN Conference on Alien Species. Directorate for Nature Management and Norwegian Institute for Nature Research, Trondheim, Norway, 1996:123–126.

Neilson RP, Wullstein LH. Biogeography of two southwest American oaks in relation to atmospheric dynamics. Biogeography 1983;10:275–298.

Nuzzo V. Distribution and spread of the invasive biennial *Alliaria petiolata* (garlic mustard) in North America. In: McKnight BN, editor. Biological pollution. The control and

impact of invasive exotic species. Indianapolis: Indiana Academy of Science, 1993:137–145.

Opler PA. Insects of American chestnut: possible importance and conservation concern. In: McDonald W, editor. The American Chestnut Symposium. Morgantown, West Virginia: University of West Virginia Press, 1979:83–85.

Peloquin RL, Hiebert RD. The effects of black locust (*Robinia pseudoacacia* L.) on species diversity and composition of black oak savanna/woodland communities. Nat Areas J 1999;19:121–131.

Peters RL. Consequences of global warming for biological diversity. In: Wyman RL, editor. Global climate change and life on earth. New York: Chapman & Hall, 1991: 99–118.

Pimentel D, Lach L, Zuniga R, Morrison D. Environmental and economic costs of nonindigenous species in the United States. BioScience 2000;50:53–65.

Quimby PC. Impact of diseases on plant populations. In: Charudattan R, Walker HL, editors. Biological control of weeds with plant pathogens. New York: Wiley, 1982:47–60.

Rejmanek M, Richardson DM. What attributes make some plant species more invasive? Ecology 1996;77:1655–1661.

Rhymer JM, Simberloff D. Extinction by hybridization and introgression. Annu Rev Ecol System 1996;27:83–109.

Salt G, van den Bosch R. The defense reactions of three species of *Hypera* (Coleoptera, Curculionidae) to an ichneumon wasp. J Invertebrate Pathol 1967;9:164–177.

Schmitz DC, Simberloff D, Hofstetter RH, Haller W, Sutton D. The ecological impact of nonindigenous plants. In: Simberloff D, Schmitz DC, Brown TC, editors. Strangers in paradise. Impact and management of nonindigenous species in Florida. Washington, DC: Island Press, 1997:39–61.

Simberloff D, Alexander M. Assessing risks to ecological systems from biological introductions (excluding genetically modified organisms). In: Calow P, editor. Handbook of environmental risk assessment and management. Oxford: Blackwell, 1998:147–176.

Simberloff D. The biology of invasions. In: Simberloff D, Schmitz DC, Brown TC, editors. Strangers in paradise. Impact and management of nonindigenous species in Florida. Washington, DC: Island Press, 1997:3–17.

Singer FG, Swank WT, Clebsch EEC. Effects of wild pig rooting in a deciduous forest. J Wildl Manage 1984;48: 464–473.

Smith CW. Alien plants: impacts, research, and management needs. In: Stone CP, Scott JM, editors. Hawaii's terrestrial ecosystems: preservation and management. Honolulu: University of Hawaii Cooperative National Park Resources Studies Unit, 1985:180–250.

US Congress. Office of Technology Assessment. Harmful non-indigenous species in the United States. US Government Printing Office, Washington, DC, 1993:391.

van Riper III C, van Riper SG, Goff ML, Laird M. The epizootiology and ecological significance of malaria in Hawaiian land birds. Ecol Monogr 1986;56:327–344.

von Broembsen SL. Invasions of natural ecosystems by plant pathogens. In: Drake JA, Mooney HA, diCastri F et al., editors. Biological invasions: a global perspective. UK: Wiley, Chichester, 1989:77–83.

Watt AD, Whittaker JB, Docherty M, Brooks G, Lindsay E, Salt DT. The impacts of elevated atmospheric CO_2 on insect herbivores. In: Harrington R, Stork NE, editors. Insects in a changing environment. London: Academic Press, 1995:197–217.

Webb SL. Acer platanoides. In: Randall JM, Marinelli J, editors. Invasive plants. Weeds of the global garden. New York: Brooklyn Botanic Garden, 1996:26.

Williams DW, Liebhold AM. Potential changes in spatial distribution of outbreaks of forest defoliators under climate change. In: Harrington R, Stork NE, editors. Insects in a changing environment. London: Academic Press, 1995: 509–513.

Williams CE. The exotic empress tree, *Paulownia tomentosa*: an invasive pest of forests? Nat Areas J 1993;13:221–222.

Williamson M. Biological invasions. London: Chapman & Hall, 1996:244.