

Invasive Plants, Insects, and Diseases in the Forests of the Anthropocene

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***Abstract:** Invasive species, non-native plants, insects, and diseases can devastate forests. They outcompete native species, replace them in the ecosystem, and even drive keystone forest species to functional extinction. Invasives have negative effects on forest hydrology, carbon storage, and nutrient cycling. The damage caused by invasive species exacerbates the other forest stresses of the Anthropocene: increased human intrusion throughout natural landscapes, the fragmentation of forests, and a changing climate. Warming will open new areas for ecological invasion while the rising concentration of CO₂ (carbon dioxide) in the atmosphere gives many invasives an edge over native species. Storms and extreme climatic events are likely to become more frequent, and these events will facilitate the introduction and spread of invasive species. The cumulative effect of these stressors is impaired ecosystems that can no longer provide all the services on which humans rely. Because these changes are not possible without humans to facilitate the introduction and spread of new species, the impact of invasives is a defining element of the Anthropocene.*

INTRODUCTION

The unprecedented mixing of species from across continents and ecosystems is one of the profound changes of the Anthropocene. Species introduced into completely different ecosystems are freed from the constraints that limited their growth and expansion in their home systems (Phillips and others. 2010). For example, plants can escape the herbivores adapted to feed on them, insects can escape the pathogens that limited their population growth, and newly introduced species can find new opportunities such as hosts with little resistance to their attack (Liebhold and others. 1995). The combination of fewer constraints and new opportunities allow some introduced species to flourish in their new environments to the detriment of native species; in short, to become invasive species (Torchin and others. 2003). Executive Order 13112 (1999) defines invasive species as alien species whose introduction causes economic or environmental harm or harm to human health. In many cases, the introduction of species into new ecosystems is an unintended consequence of human movement and trade



(Bradley and others. 2011). Some invasives were introduced intentionally to bring useful plants and animals to new places for the benefit of humans (Reichard and White 2001). However, once introduced into a new ecosystem, invasive species are able expand in that ecosystem without human assistance (e.g., Gibbs and Wainhouse 1986). As invasive species expand their range, they can create novel ecosystem interactions and unforeseen outcomes (Hobbs and others. 2006; Mascaro and others. 2011).

In addition to their ecological costs, exotic forest invaders have a large economic impact on both forest products and ecosystems services (Pimentel and others. 2005; Holmes and others. 2009). For instance, a mere three invasive insects cause approximately \$1.7 billion dollars in damages in the United States annually (Aukema and others. 2011). By one estimate, the United States spends about \$1.3 million dollars a year on surveillance to keep just one pest, the Asian gypsy moth (*Lymantria dispar*), from invading (Work and others. 2005).

The negative impact of invasive species is likely to expand during the Anthropocene. Their effect is exacerbated by the warming climate (Bradley and others. 2010), more frequent extreme climatic events (Diez and others. 2012), large and severe fires (Ziska and others. 2005), and forest fragmentation (Dewhurst and Lutscher 2009). Moreover, it is not just the invasive species already in our forests that will thrive as the climate changes as the introduction of new species is almost inevitable. As global trade continues to move vast cargos across the world, the chance of new introductions is high. Work and colleagues (2005) estimate that about seven species are introduced to the United States each year via refrigerated maritime cargo alone. Even native insects, plants, and diseases may act more like invasive species in the Anthropocene under new climate conditions (Weed and others. 2013).

Invasive species will help define the forests of the Anthropocene, hence it is vital to understand the types of invaders we face, their impacts, and how they interact in natural ecosystems. While all ecosystems have been altered by invasive species, this discussion is limited to plants, insects, and diseases affecting forested ecosystems. Though animals such as the brown tree snake (*Boiga irregularis*) or feral pigs (*Sus scrofa*) have detrimental impacts on forested ecosystems, they are excluded from this paper in an effort to limit an already expansive topic. For the same reason, this paper also excludes invasion of wetland and coastal communities. While all the examples and most of the research cited is drawn from the United States, the issue of invasives in the Anthropocene is, of course, international (e.g., Yan and others. 2001).

OVERVIEW

Plants

Humans are enthusiastic about importing new species of plants for economic benefit or aesthetic appeal, but these introductions frequently go wrong and result in exotic plants invading native forests (e.g., Forseth and Innis 2004). By one estimate, the horticultural trade is responsible for over 80 percent of invasive plants in the United States (Reichard and Hamilton 1997). Other common pathways include accidental introduction with crop seeds and purposeful introductions for soil erosion control (Reichard and White 2001). Many of the invasive plants in the United States are agricultural weeds; in other words, plants that interfere with crop production or grazing, but these are generally outside of the scope of this paper. Though the focus of this paper is

on forests, the list of invasive plants is still long. In the northern forests of the United States, the major invasive plants of concern include the following species among many others (Shifley and others. 2012):

- spotted knapweed (*Centaurea biebersteinii*),
- tree-of-heaven (*Ailanthus altissima*),
- Russian olive (*Elaeagnus angustifolia*),
- multiflora rose (*Rosa multiflora*),
- garlic mustard (*Alliaria petiolata*),
- Japanese knotweed (*Fallopia japonica*), and
- bush honeysuckle (*Lonicera* spp.).

In the forest of the Southeast, the list includes (Hanson and others 2010):

- mimosa trees (*Albizia julibrissin*),
- kudzu (*Pueraria lobata*),
- Asian bittersweet (*Celastrus orbiculatus*),
- cogon grass (*Imperata cylindrica*), and
- Japanese stiltgrass (*Microstegium vimineum*).

In western forests, invasive species of concern would include (Cal-IPC 2006; Gray and others 2011):

- cheat grass (*Bromus tectorum*),
- salt cedar (*Tamarix* spp.),
- toadflax (*Linaria* spp.),
- spotted knapweed (*Centaurea maculosa*),
- Scotch broom (*Cytisus scoparius*),
- leafy spurge (*Euphorbia esula*), and
- knapweeds (*Centaurea* spp.).

Unfortunately, these 19 species are just a small sample of all the invasive species in the United States Forests and readers are encouraged to refer to publications specific to each region or state to identify invasive plants (e.g., Olson and Cholewa 2009; Miller and others. 2010; Gray and others. 2011). Mapping from programs such as the Early Detection and Distribution Mapping System (www.eddmaps.org/distribution/) shows that invasive plants cover the entire United States. Though not every forested acre has been invaded by non-native plants, at the county scale, invasive plants are ubiquitous in the coterminous United States. For example, a study of 24 northeastern and mid-western states found 66 percent of all plots had at least one invasive plant (Schulz and Gray 2013). Disturbed areas, particularly roadsides, accumulate invasive plants because many invasives are adept at colonizing open growing space (Aikio and others. 2012).

Invasive plants disturb ecosystems in a number of ways. Out of the 1,055 threatened plant species in the United States, about 57 percent are affected by invasive plants (though often in combination with other stressors) (Gurevitch and Padilla 2004). Invasive species outcompete and overwhelm native plant species. For example, kudzu covers some 7.4 million acres in the United States, where it shades out and crushes other plants (Forseth and Innis 2004). Similarly, stiltgrass outcompetes native plants, reduces herbaceous diversity, impedes native woody species regeneration, and creates extensive stiltgrass monocultures (Oswalt and others 2007; Adams and Engelhardt 2009). Invasive plants can disrupt plant reproductive mutualism such as pollination or seed dispersal, causing population reductions (Traveset and Richardson 2006). An example of a less visible influence of the presence of invasive plants is the allelopathic effect of tree-of-heaven, which has a detrimental impact on red oak regeneration (*Quercus rubra*), an important tree both economically and ecologically in the eastern United States (Gómez-Aparicio and Canham 2008). Another example is melaleuca (*Melaleuca quinquenervia*) which has converted wetlands to uplands through increased litter inputs over many years (Strayer and others 2006).

Invasive plants often negatively impact water quantity because they tend to grow fast and use more water than native species (Brauman and others 2007). Invasive plants alter, usually negatively, habitat for wildlife. Some reduction in habitat quality is to be expected where animals have adapted to a plant community that is subsequently disrupted by invasives. For example, birds that nest in honeysuckle and buckthorn (*Rhamnus cathartica*) experience higher predation rates than those that nest in native plants (Schmidt and Whelan 1999). Even when invasive species like buckthorn provide fruits for animals (birds in this case), these fruits are often less nutritious than those provided by the native species displaced by the invaders (Smith and others 2013). About 28 percent of birds listed as threatened are negatively affected by invasive plants (Gurevitch and Padilla 2004).

Insects

There are some 455 invasive insects in U.S. forests, though only about 62 cause significant ecosystem damage (Aukema and others 2011). Of those insects that have a significant impact on forested ecosystems and feed on trees, about a third feed on sap, a quarter are wood borers, and the remainder feed on foliage (Aukema and others 2010). Over the last century, an average of about 2.5 non-native insects were detected in the United States per year (Aukema and others 2010) and Koch and colleagues (2011) predict new alien forest insect species establishments every 5–15 years in select urban areas. Not every foreign insect that establishes in the United States becomes a destructive invasive, but many have. Some of these insects, such as the gypsy moth, have been in this country for over a century, and many have spread through the entire range of their new hosts. Mapping tools such as the Alien Forest Pest Explorer (www.nrs.fs.fed.us/tools/afpe/) illustrate that at least one, but often many, invasive forest insects infest every forested region in the United States.

Many invasive insects are specialists that feed on, or live in, one particular tree or shrub species or genus. For instance, hemlock woolly adelgid (*Adelges tsugae*) feeds only on species of hemlock. Others, such as the gypsy moth, attack a broad range of tree species. The Northeast and Appalachian forests have a particularly high number of destructive insects, in part because of their proximity to busy eastern ports and in part because of the large number of tree species that

can support a large number of species-specific invaders (Liebhold and others 2013). In contrast, western interior forests have fewer different species of invasive insects (Liebhold and others 2013), perhaps because of their distance from ports of entry and because they have fewer species of trees and shrubs.

Insect populations often expand and collapse in response to environmental conditions. For native insects, populations can be very low and individuals difficult to find until conditions are right for an outbreak. The population then crashes due to declines in the host, lack of available food, climate shifts, predator response, or pathogens that spread easily at high population densities. Invasive species can build large, outbreak-type populations as they invade new areas because of the lack of constraints in the new environment. Because these are novel outbreaks, native trees are ill equipped to resist or recover from them. For example, populations of hemlock woolly adelgid can be very high once they have established in a new area, but even though adelgid populations decline as the health of hemlock trees decline, the outbreaks result in significant hemlock mortality (McClure 1991).

Polyphagous insects can cause a reduction in tree growth through massive defoliation, but species- or genus-specific invaders can also have disastrous impacts on forested ecosystems. By 2006, some 15 million ash trees had been killed by the Emerald ash borer (*Agrilus planipennis*) (Poland and McCullough 2006). This widespread mortality has cascading effects through the ecosystems with ash trees, including the loss of native insects (Gandhi and Herms 2010b). The death of hemlocks from hemlock woolly adelgid affects herbaceous plants (Eschtruth and others 2006), nutrient cycling (Cobb and others 2006), stream temperatures, fish communities (Ross and others 2003), bird diversity (Tingley and others 2002), and habitat for deer and other mammals (DeGraaf and others 1992). More generally, by removing important trees from U.S. forests, invasive insects have the potential to affect fundamental forest composition, structure, and function (Ellison and others 2005; Gandhi and Herms 2010a). The complexity of interdependencies within ecosystems makes it difficult to trace the full impact of invasive forest insects (Kenis and others 2009).

Diseases

There are likely many more non-native disease-causing organisms in the United States than have been identified because they are often difficult to detect. As with non-native insects, those we are most aware of are those that cause serious damage. For example, an early introduction, chestnut blight (*Cryphonectria parasitica*), functionally removed American chestnut (*Castanea dentata*) from its ecological role as a dominant tree in eastern forests by the 1950s (Tindall and others 2004). Though the list of significant invasive forest diseases is shorter than that of insects, diseases cover most forested regions of the United States (Aukema and others 2010). Chestnut blight, Dutch elm disease (*Ophiostoma* spp.), and butternut canker (*Sirococcus clavignenti-juglandacearum*) cover the entire range of their host trees (Evans and Finkral 2010). Beech bark disease (*Ophiostoma* spp.) has spread through forests where beech trees (*Fagus americana*) are most dense (Morin and others 2007). Based on past spread rates, it is likely that other significant diseases including sudden oak death (*Phytophthora ramorum*), dogwood anthracnose (*Discula destructiva*), laurel wilt (*Raffaelea lauricola*), and phytophthora root rot (*Phytophthora cinnamomi*) will likewise expand to fill their ecological niche in the United States (Evans and Finkral 2010).

A lack of coevolution between host and pathogen can result in limited resistance in the host tree and excessive aggressiveness (i.e., greater host mortality) in the pathogen, which in turn causes disease outbreaks (Brasier 2001). For example, there is very limited genetic resistance of tanoaks (*Notholithocarpus densiflorus*) to sudden oak death (Hayden and others 2011). Because genetic resistance to invasive diseases may vary in a native tree population, identifying and protecting potential resistant individuals is an important management response (Schwandt and others 2010). Selection and breeding presents a possible route to increasing resistance to beech bark disease in American beech populations (Koch and others 2010). Diseases introduced to forests have removed dominant tree species, reduced diversity, altered disturbance regimes, and affected ecosystem function (Liebhold and others 1995, Mack and others 2000). The cascading effects of the removal of important trees species are similar to the effects of invasive insects and influence forest structure as well as the animals and plants connected to the diseased trees.

Synergies

The previous sections discussed invasive plants, insects, and diseases separately, but of course they interact with each other and with other forest stressors. An invasion by one species can facilitate other invaders (Green and others 2011). For example, the tree-of-heaven's allelopathy facilitates the secondary invasion of another invasive plant, Fuller's teasel (*Dipsacus fullonum*), by suppressing native competitors (Small and others 2010). There are numerous examples of insect invaders facilitating invasion by plants. The emerald ash borer helps buckthorn and honeysuckle invade forests by opening the canopy (Hausman and others 2010). Japanese barberry (*Berberis thunbergii*), Asian bitter-sweet, and honeysuckle often invade forests after hemlock woolly adelgid has caused canopy mortality (Small and others 2005). Defoliation by gypsy moth helped tree-of-heaven spread through the forests of Pennsylvania (Kasson and others 2013). Though less well-documented, it is likely that invasive forest diseases have also facilitated the invasion of plants by creating canopy openings. Diseases also help insects by sapping tree defenses (e.g., Parker and others 2006). The synergy between invasives that aggravate the impact on native ecosystems has been labeled "invasional meltdown" (Simberloff and Von Holle 1999). Unfortunately, evidence is beginning to accumulate that this invasional meltdown is already occurring in some ecosystems (Simberloff 2006).

INVASIVES IN THE ANTHROPOCENE

Humans are tightly linked with invasive species. They are a key factor in the introduction of invasive species as discussed above, but they are also a key factor in their spread. For example, the transportation of firewood has been identified as an important vector for invasive insects, particularly long-distance dispersal (Bigsby and others 2011; Koch and others 2012). Human development and infrastructure also help invasive species flourish. Many invasive plants such as Asian bitter-sweet and multiflora rose (*Rosa multiflora*) thrive in disturbed areas and the open edge habitat created by human development (Yates and others 2004; Kelly and others 2010). The trees of these disturbed, edge habitats may also be more stressed, and hence more susceptible to insects and diseases. For example, in one Ohio study, 84 percent of new emerald ash borer infestations were within 0.6 miles (1 km) of major highways (Prasad and others 2010). Even low-density residential areas are associated with a greater density of invasive plants (Gavier-Pizarro and others 2010). The effect of human land use on invasives lasts a long time, as demonstrated

by a study that links invasive plants in North Carolina with historic land use and reforestation (Kuhman and others 2010).

Human Development

Human development is expanding in the Anthropocene and with it the opportunity for invasives expands as well. About one third of the coterminous United States was human-dominated in 2001, and an additional 35,600 square miles (92,200 km², or roughly the size of Indiana) are likely to be converted from natural cover to development by 2030 (Theobald 2010). About 15 percent of the current acreage of southern forests could be converted to housing and other uses by 2040 (Hanson and others 2010). Although the long-term trend in the Northeast during the 20th century was one of increasing forest cover, this trend has recently reversed, and the total number of forested acres has started to decline again (Drummond and Loveland 2010). As much as 909,000 acres (368,000 hectares), or about two percent of forest land, could convert from forest to other land uses in Maine, New Hampshire, Vermont, and New York by 2050 (Sendak and others 2003). This growing human presence and increased fragmentation is a significant driver in the spread and domination of invasive species in U.S. forests (Lundgren and others 2004; Gavier-Pizarro and others 2010; Schulz and Gray 2013). An indirect effect of fragmentation and suburbanization is the population growth of animals that thrive in human environments. For instance, deer (*Odocoileus virginianus*) populations have grown significantly in many suburban/forest interface zones. The high deer populations help spread invasives and, at the same time, hamper the regeneration of native species (Evans 2008; Williams and others 2008).

Climate Change

Not only is human development making the landscape more available to invasives, but in addition, human-driven changes to the climate benefit invasives. A warming climate opens new ecosystems to invaders previously limited by cold. Warming will facilitate the spread of invasive plants such as kudzu and privet (*Ligustrum sinense*) as far north as New England by 2100 (Jarnevich and Stohlgren 2009; Bradley and others 2010). In general, invasive plants have been far better able to respond to recent climate change in New England than native species (Willis and others 2010). Warming will also facilitate the spread of invasive insects such as hemlock woolly adelgid (Evans and Gregoire 2007). Two or three times more forest in Canada will be at risk from gypsy moth by 2060 because of a changing climate (Régnière and others 2009). Similarly, climate changes will modify forest pathogen dynamics and may exacerbate some disease problems (Sturrock and others 2011). For instance, sudden oak death has potential to expand its range under a warming climate (Venette and Cohen 2006). Increasing summer temperatures appear to exacerbate outbreaks of cytospora canker (*Valsa melanodiscus*) and mortality of alders (*Alnus incana*) in the Southern Rocky Mountains (Worrall and others 2010).

A changing climate means more than just warming temperatures. Other climate changes such as increased CO₂ (carbon dioxide) concentrations and more frequent and more powerful storms will benefit invasives. Rising CO₂ concentrations commonly give invaders an extra edge in competition with native species (Manea and Leishman 2011). For example, cheatgrass is able to take advantage of increased CO₂ concentrations by increasing productivity (Smith and others 2000). Higher CO₂ levels help kudzu and honeysuckle tolerate cold temperatures and hence expand these species' capacity for invading new forests (Sasek and Strain 1990). Extreme climatic

events are likely to increase as the climate changes, and these events will facilitate the introduction and spread of invasive species (Diez and others 2012). Hurricanes, ice storms, wind storms, droughts, and fire can all create forest disturbances that invasive species can capitalize on. Many invasive species grow rapidly and can take advantage of the increased sunlight in forest gaps faster than can native species. A study in Florida found that nearly 30 percent of the species regenerating after Hurricane Andrew were invasive and that invasive vines negatively affect the regeneration of native plants (Horvitz and others 1998). Similarly, tufted knotweed (*Polygonum caespitosum*) and mile-a-minute weed (*Persicaria perfoliata*) were able to expand after Hurricane Isabel hit Maryland (though garlic mustard decreased because of the increased light) (Snitzer and others 2005).

The warming and, in many regions, drying predicted for the United States will increase the area burned in the United States over the next century (Moritz and others 2012). These predictions match the trend from the last few decades of increased fire activity in the United States (Westerling and others 2006). Some invasive species contribute to the increase in fire activity. Cheatgrass provides surface fuel that spreads fire more frequently than before its invasion (Ziska and others 2005). Sudden oak death also encourages fire by killing trees and creating more heavy fuel (Valachovic and others 2011). This synergy between sudden oak death and fire has caused a fourfold increase in the mortality risk for redwood trees (*Sequoia sempervirens*) (Metz and others 2013). While many native species are adapted to fire, altered fire regimes (more frequent or more severe fires) can benefit invasives. Uncharacteristically severe fire kills dominant vegetation that would have survived more natural fire and can create growing space for invasives.

Native species under new conditions

In addition to the effects on invasives, climate change affects native species in unforeseen ways. With a changed climate, native species may be able to expand their range to new areas and may act like invaders in these new regions. Climate change has the potential to disrupt predator-prey relationships and permit outbreak conditions (Logan and others 2003). Temperature increases will shift native species ranges northward so new areas are affected, but at the same time, some previously affected areas may no longer be suitable for certain species (Ayres and Lombardero 2000). Warmer, drier conditions have helped drive insect outbreaks in the Southwest and Alaska (Logan and others 2003). Spruce budworm outbreaks in eastern Canada are predicted to be longer and more severe because of the changing climate (Gray 2008). Not only will mountain pine beetle be able to expand its range into much of the boreal forest, but it may be able to expand eastward by infesting jack pine (*Pinus banksiana*), a new host (Carroll and others 2006). Other previously obscure native insects such as the red oak borer (*Enaphalodes rufulus*) may become serious pests under new conditions (Riggins and Londo 2009).

HOPE FOR FORESTS IN THE ANTHROPOCENE

Is there any hope for native forest ecosystems in the Anthropocene? For conservationists, ecologists, foresters, wildlife biologists, and all those who work in the woods, the answer must be yes. The first key element in any response to invasive species should be concerted effort to limit new introductions (Hayes and Ragenovich 2001; Lodge and others 2006). Increased surveillance at ports and other introduction pathways can limit the growth of the invasive problem. Improved early detection strategies directed at a quarter of U.S. agricultural and forest land would likely

be able to detect 70% of invaded counties (Colunga-Garcia and others 2010). If an invasive species avoid detection, a rapid response can help limit establishment (Anderson 2005). Similarly, policy or management actions that limit fragmentation and carbon emissions will reign in the negative interactions between invasives and these other forest stressors. There are steps that forest land owners and managers can take to increase ecosystem resistance to the effects of climate change and resilience to negative impacts of invasive pests and plants (Waring and O'Hara 2005). Eradication is impossible for many invasives and management should focus on those invasives that cause the most damage or those that can be effectively removed (Ellum 2009). A cornerstone of forest management in the face of the uncertainties of the Anthropocene is maintaining species diversity (Linder 2000). Maintaining or restoring species diversity on a site can increase the likelihood that some native species will flourish in this new epoch. Intact, diverse forest ecosystems may be more resistant to invasion (Jactel and others 2005; Huebner and Tobin 2006; Mandryk and Wein 2006). For example, the impact of sirenid wood wasp has been less dramatic in the diverse forests of the United States than in the single species plantations in the southern hemisphere (Dodds and others 2010).

Even in the Anthropocene invasives are not invincible. Much of their competitive advantage comes from escaping the predators, pests, and pathogens of their region of origin. When those predators, pests, and pathogens catch up with an invader in a new region, the invader is less able to cause unusual damage or disrupt ecosystems. For example, *Entomophaga maimaiga*, a fungus that attacks gypsy moth, appears to have begun to limit the extent and impact of outbreaks in the areas longest infested by gypsy moth (Andreadis and Weseloh 1990). Similarly, a leaf blight has been discovered on stiltgrass that can cause reduced seed production, wilting, and, in some cases, death of stiltgrass plants (Kleczewski and Flory 2010). In a third example, an insect pest that can significantly retard the growth of kudzu has recently been found in Georgia (Zhang and others 2012). Once predators, pests, and pathogens have caught up with a non-native species in its new region, the label 'invasive' may no longer be appropriate. As with biological control of invasive plants and insects, human intervention may be able to change the dynamics of some invasive pathogens. New transgenic techniques hold promise for engineering resistance into tree such as elm and chestnut to battle exotic diseases (Merkle and others 2007).

As climate change alters ecosystems, there is the possibility that new restoration opportunities may emerge. For example, canopy openings created by hurricanes and other storm events could provide ideal planting sites for the restoration of American chestnut (Rhoades and others 2009). In addition, climate change may render some areas unfavorable to invasives that previously seemed entrenched. Models suggest that cheatgrass will no longer be viable in some areas of the western United States as the climate warms (Bradley and Wilcove 2009). In these locations, cheatgrass could be replaced with native species. Managers should be ready to seize these novel restoration opportunities if and when they emerge during the Anthropocene.

Though it can be considered heresy, invasive species may not be all bad. Some can provide ecosystem services, while others might fill novel ecological niches created by climate change and inaccessible to native species. For example, invasive tamarisk provides habitat for the endangered willow fly catcher (*Empidonax traillii*) (Shafroth and others 2005). With the recent introduction of the tamarisk leaf beetle (*Diorhabda carinulata*), which reduces tamarisks competitive advantage (Pattison and others 2011), it is worth reconsidering tamarisk's potential positive role in riparian ecosystems. A study in Hawaii demonstrates that though invasives caused the decline of

native tree species, the new species were able to maintain some ecosystem functions (Mascaro and others 2011). While protecting against new invasives and fighting the spread of existing invasives are both important, it may be time to accept some non-native species.

Protecting refugia, such as parks and preserves, where threatened native species face fewer stressors may help those native species survive through the Anthropocene. Outside of parks and preserves, management that fosters diversity at both the stand and landscape scales can help minimize the threat of invasives. Managers must be ready to embrace any opportunities for proactive restoration that may emerge because of a warming climate, species shifts, or disturbances. For entrenched invasives, conservationists may have to move from denial to acceptance and adapt forest management to a new mix of species. Though invasives are a significant threat to forests in the Anthropocene, all is not lost.

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