



Management of Landscapes for Established Invasive Species

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7.1 Introduction

Long-term management strategies are invoked once an invasive species has become established and spread beyond feasible limits for eradication or containment. Although an invasive species may be well-established in small to large geographical areas, prevention of its spread to non-affected areas (e.g., sites, regions, and cross-continent) through early detection and monitoring is an important management activity. The level for management of established invasive species in the United States has increasingly shifted to larger geographical scales in the past several decades. Management of an invasive fish may occur at the watershed level in the western States, with watershed levels defined by their hydrologic unit codes (HUC) ranging from 2 digits at the coarsest level to 8 digits at the finest level (USGS 2018). Invasive plant management within national forests, grasslands, and rangelands can be implemented at the landscape level (e.g., Chambers et al. 2014), although management

can still occur at the stand or base level. Landscapes in this chapter refer to areas of land bounded by large-scale physiographic features integrated with natural or man-made features that govern weather and disturbance patterns and limit frequencies of species movement (Urban et al. 1987). These are often at a large physical scale, such as the Great Basin.

This chapter considers the continuum from application of broad-scale invasive species management to implementation of specific local tactics (Fig. 7.1). Several foundational principles are discussed in Sect. 7.2. Considerations for natural resource managers faced with invasive species issues within the context of an ecosystem (Pickett and Candenasso 2002) or ecological community of variable size, landscape, or watershed management are then presented in Sect. 7.3. In Sect. 7.4, we address strategies, approaches, and tactics but in the context of recent advances made in (1) the sciences (e.g., biology, ecology, and epidemiology) involved and (2) strategies, approaches, and tools for invasive species man-

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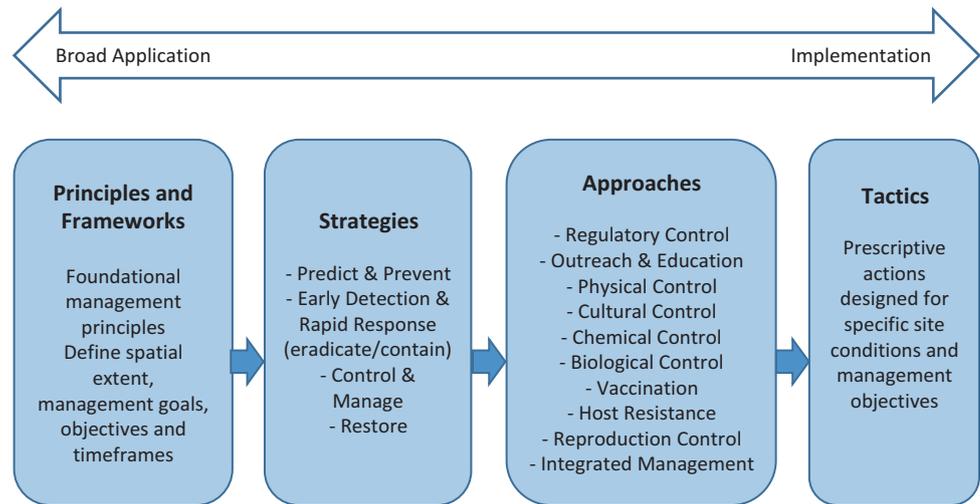
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Fig. 7.1 A continuum of management responses to address management objectives at appropriate scales. (Adapted from Fig. 4.2 in Millar et al. 2012)



agement; key findings, knowledge gaps, and needs are included. This chapter considers invasive species that affect features in landscapes containing the Nation's forests, grasslands, and rangelands. Types of invaders included in this synthesis include insect pests of trees and disease vectors, pathogens of trees and wildlife, terrestrial and aquatic plants, and terrestrial and aquatic wildlife or other animals.

7.2 Invasive Species Management Principles

Organizations and agencies have utilized various concepts or principles in written invasive species management plans such as the training module on managing invasive plants by the US Fish and Wildlife Service (US FWS 2017a). The USDA Forest Service uses the Forest Service National Strategic Framework for Invasive Species Management to prioritize and guide management of all invasive species using the Invasive Species Systems Approach (ISSA). For the purposes of this chapter, four general principles are considered relevant to natural resource managers and land managers faced with the invasive species issues in the context of this volume. The following principles apply broadly to decision-making and implementation of management strategies, approaches, and tactics (Fig. 7.1).

7.2.1 Understanding Impacts of Invasive Species Is Essential for Effective Management

Impacts of invasive species can be highly complex deriving from a variety of direct and indirect interaction pathways (see Chap. 3). Mitigating impacts of invasive species and restoring affected systems therefore require an understanding of impacts and ecological pathways leading to those impacts at all levels in the affected community (see example, Box 7.1). Invasive species management in natu-

Box 7.1 Understanding Impacts of Invasive Species for Effective Management: Example, Spotted Knapweed (*Centaurea stoebe*)

Spotted knapweed infestations impact the food chain in pine savannas in western Montana and can delay reproduction of chipping sparrows (*Spizella passerina*), increase their dispersal, and reduce return rates of resident birds to breeding sites (Ortega et al. 2006). Spotted knapweed can outcompete native plants (Maron and Marler 2008) and consequently reduce populations of native insects that serve as important food sources required by chipping sparrows while nesting and rearing their young. Hence, suppressing spotted knapweed populations and restoring some native plant species but failing to restore those plant species that support these insect foods might mitigate some but not all of the impacts caused by spotted knapweed in this system. For example, the use of broadleaf herbicides can favor native grasses over native forbs (Ortega and Pearson 2010). Whether restoring the system to native grasses at the expense of native forbs would be considered successful would depend on management objectives. If the primary objective was to restore the displaced knapweed with native grasses that are needed to increase winter forage for elk (*Cervus elaphus*), this outcome could be deemed successful (e.g., Thompson 1996). However, further restoration efforts might be required to restore these sites for chipping sparrow breeding areas. This example illustrates both the importance of understanding ecological pathways leading to impacts at all levels and the value of designing management strategies essential to address specific objectives.

ral areas can be far more complex than in managed agricultural systems, and many factors can impede management objectives (see Pearson et al. 2016a). In extreme cases, mitigation may fail even if invasive species populations have been locally extirpated. For example, invasive plants may alter soil properties in ways that persist after the invasive species is eliminated (Magnoli et al. 2013), chemical control measures may suppress nontarget natives (Ortega and Pearson 2010), and secondary invasion may result in replacement of the target invasive species with another pest (Pearson et al. 2016b). Hence, it is necessary to anticipate and understand the full range of impacts, any side effects of management actions, and complicating factors, prior to applying adaptive management to meet management objectives.

7.2.2 Effective Management Is Specific to Ecosystem, Landscape, and Forest Management Objectives

Invasive species management is an important component of a comprehensive management plan for any ecosystem, landscape, or forest. With increasing global trade (among other factors), it is likely that the number of potential invasions will continue to increase (Chornesky et al. 2005). Furthermore, the full effect of already established invasive species on US forests has not been realized. Thus, management success as defined by management objectives must include specific desired outcomes related to existing or likely invasive species. However, management objectives must be formulated in accordance with the governing processes established (land management planning process for Federal lands or other appropriate planning and decision-making process for other ownerships) for the affected system or land area and the ecological processes extant. A partial list of important factors to consider might include system resilience, or the capacity of an ecosystem to respond to a disturbance by recovering quickly (Beisner et al. 2003), susceptibility to invasion, and directional changes in abiotic conditions, e.g., anthropogenic eutrophication, climate change, and shifts in disturbance regimes (see Chaps. 4 and 5).

Much of our knowledge about resilience theory and thresholds as they relate to plant invasions has been gained through research conducted in the Great Basin (e.g., Chambers et al. 2014). For example, studies in the Great Basin that consider system resilience in relation to disturbance, susceptibility to invasion, climate change, and shifts in disturbance regimes illustrate how focusing invasive species management on sites exhibiting higher resilience to disturbance and greater resistance to invasion by cheatgrass (*Bromus tectorum*) can favor success (Chambers et al. 2014). On the other hand, in systems where humans have altered disturbance regimes to the point that they are pushed beyond

historic equilibrium states, non-natives may be better adapted than native species to thrive under the new ecosystem conditions (e.g., MacDougall and Turkington 2005), thus creating a situation where management efforts are likely to fail unless the disturbance regime itself is restored. It is important to recognize that systems are changing over global scales in ways that may favor non-native invasive species over native species that are no longer able to adapt to changing local conditions. In some cases, systems have already transitioned into novel ecosystems, with biotic, abiotic, and social components that have been altered by human influence and comprise a combination of introduced species which either have attained or are well on their way toward becoming new stable equilibrium states (Hobbs et al. 2006). In such cases, restoration to the original state is likely infeasible, and the best approach may be managing for form and function that best serve to generate the ecosystem services we desire (Hobbs 2007). Hence, management objectives must account for system processes to be successful, and management and restoration goals will tend to range along the full gradient from restoration to pre-invasion conditions to management of novel ecosystems.

7.2.3 Threshold Concept Aids Decision-Making for Invasive Species Management

In general terms, threshold is considered a defined level (e.g., magnitude or intensity) that, if exceeded, will lead to a change in condition or result in an action. Three types of thresholds (ecological, utility, and decision) are relevant to decision-making in natural resource management (Nichols et al. 2014) and, by extension, invasive species management within forest and rangelands. Ecological thresholds have been defined in various ways. Common terms to those definitions include “a point or zone at which there is a sudden change in the condition or dynamics of a biological system” (Nichols et al. 2014; see p. 10). Utility thresholds are “values of state or performance variables at which small changes yield substantial changes in the value of management outcomes” (Nichols et al. 2014; see p. 12). Human values are the “drivers” of utility thresholds, although there may be an ecological basis as well. Decision thresholds are “values of system state variables that should prompt specific management activities” (Nichols et al. 2014; see p. 13). Generally speaking, management objectives, available control actions, and predictive models of an invasive species population or other measures in system dynamics are the basis of decision thresholds. Examples include action thresholds for management of invasive plants (US FWS 2017a) and thresholds of the delimiting and priority indices within the gypsy moth (*Lymantria dispar*) Slow the Spread program which results in a recommended course of action (Tobin and Blackburn 2007).

7.2.4 Prioritization of Limited Resources for Effective Management

Invasions of non-native pests cost the US economy an estimated \$120 billion US annually (Pimentel et al. 2005). Current and future mitigations may require difficult tradeoffs about which species in which locations to address and how to allocate resources between detection, treatment, and monitoring. As a result, effective management depends on careful prioritization to ensure that the limited resources are implemented for maximal benefit. Approaches for natural resource managers to prioritize invasive species management issues for purposes of effort or resource allocation are discussed in the following section.

7.3 Framework for Management and the Prioritization or Allocation of Limited Resources

In a general sense, management is the act or skill of controlling and making decisions about a business or enterprise. The heart of decision-making comes down to the allocation of limited resources necessary to stabilize, expand, or ensure the longevity of some specific part of a, or an entire, business. The business or enterprise in this effort is the management of natural resources for beneficial use, ecosystem services, intrinsic societal value, observation, and preservation for scientific study. Invasive species are clearly capable of negatively impacting natural resources (Chap. 2) and preventing us from reaching one or more of our goals in achieving natural resource management.

For the purposes of this chapter, management of invasive species refers to any activity that is used to minimize the spread and address adverse effects of an invader. Activities used to accomplish these goals include (1) preventing, surveying, detecting, identifying, monitoring, inventorying, eradicating, containing, and controlling invasive species; (2) rehabilitating and restoring affected lands (see Chap. 8); and (3) providing technical outreach and educational activities to various audiences in support of these activities as a means to achieve the specified goals.

For the forest, grassland, or rangeland manager, prioritization of invasive species and the ecosystems they threaten is needed for wise use of resources available for their management. Multifaceted inputs are required for this prioritization exercise (Box 7.2).

At the simplest level, the outcome of this process is to allocate resources to the highest priority work. Numerous decision-support tools are available to help identify the highest priority work, such as linear optimization programs and cost-benefit analysis programs available from business. We often lack complete information about the new invaders or their impacts needed to support implementing these kinds of

Box 7.2 Inputs Required for Prioritization of Invasive Species Management

1. Level of threat or potential impact from the invading species
2. The ecological, economic, and/or societal value of the recipient ecosystem or community, its susceptibility to invasion, and capacity for restoration
3. Spatial extent and temporal stage of the invasion within the ecosystem under consideration
4. Goals and objectives of potential invasive species management effort(s)
5. Available tools and their relative effectiveness in managing invasive species under the conditions existing in the threatened or already affected ecosystem (see Sect. 7.4)

models. In this situation, other methods can be implemented for identifying relative priorities for invasive species management. These are discussed in the following section.

7.3.1 The Threat or Impact from Invading Species

Species with the greatest negative impact, such as wildfire threat, rate of spread, or ecosystem impact, would be given the highest priority if only one factor is considered. For example, an aggressive tree-killing insect or pathogen that has the potential to threaten the survival of a single genus of trees, such as emerald ash borer (*Agilus planipennis*) or Dutch elm disease (*Ophiostoma novo-ulmi*), would have a high priority. Similarly, annual invasive grasses increase wildfire threat and degrade habitat quality of greater sagegrouse (*Centrocercus urophasianus*) in the bird's western (Washington, Oregon, Idaho) and southwestern ranges (California, Nevada, Arizona, New Mexico), thus posing a significant threat to the ecosystem. With new invasive species, for which we may not have a significant level of knowledge, the threat can be estimated by examining historical data on past impacts of the species elsewhere. For example, we know the potential impacts of buffelgrass (*Pennisetum ciliare*) because Forest Service noxious weed managers have observed its expansion in the Sonoran Desert, and thus we assume that it will behave in a similar manner in other desert ecosystems. Or, in contrast, there may be a species that has displayed a very narrow habitat preference which may be listed as a lower priority because of its more limited threat of spread. Plant invader impacts can now be estimated and ranked from empirical surveys that provide managers with critical information for prioritizing invaders for management action according to their relative impacts on the system (Pearson et al. 2016b). Federal noxious weed lists and State

lists can be used to assess priority (USDA NRCS 2016a). In all cases, impacts can and should be measured or considered at multiple levels, with ecosystem transformation being listed as the most severe (see Chap. 2; Barney et al. 2013; Ricciardi et al. 2013).

7.3.2 Prioritizing Communities or Ecosystems for Invasive Species Management Based on Their Value

Unique, highly specialized ecosystems, communities, or even specific sites that provide ecological goods and services used by people or rare wildlife species may rank “high” in a single-factor priority system. For example, the North American Committee on Cooperation for Wilderness and Protected Area Conservation (NAWPA) determined that only 2% of our native grassland ecosystems remain in North America (Davidson 2009). Thus, a high priority may be assigned for invasive species management action in a native grassland ecosystem due to its rarity. Other examples of ecosystems with high ecological or societal value include the Florida Everglades, forests that produce highly valued fungi like morels (*Morchella esculenta*) and white truffles (*Tuber magnatum*) or vegetation such as western huckleberry (*Vaccinium membranaceum*) on the West Coast, or forests that produce ginseng (*Panax quinquefolius*) in the East. An ecosystem may also be prioritized based on its known susceptibility to negative impacts from invaders. A floristically simple ecosystem may be prioritized if the invader is projected to have negative impacts on key species. In the case of some high-elevation subalpine western forests that contain only two or three tree species, the negative effect of invasive species can be magnified. For example, whitebark pine (*Pinus albicaulis*), which is the only five-needle pine in some subalpine forest communities, is a significant mast-producing tree for wildlife forage. However, whitebark pine is susceptible to the invasive white pine blister rust (*Cronartium ribicola*), and thus its negative effect on whitebark pine in this system is significant because no other tree species can compensate for the amount of lost forage for wildlife, including the threatened mainland grizzly or brown bear (*Ursus arctos horribilis*). Therefore, the management of invasive species that threaten whitebark pine may be a high management priority.

7.3.3 Spatial Extent and Temporal Stage of the Invasion Within the Ecosystem Under Consideration

The spatial scale and stage of infestation can affect the outcome of mitigation efforts. Early detection and monitoring have been highlighted as key activities to discover non-native species at the initial stage of invasion, providing an opportu-

nity for rapidly initiating eradication measures and implementing responses to prevent spread and permanent establishment, reducing costs and damage. Based on a review of 53 invasive plant eradication projects in California, Rejmanek and Pitcairn (2002) found that attempts to eradicate invasive weed infestations smaller than 2.5 acres (1 ha) were generally successful, while infestations over 2500 acres had almost no chance of success. For other invader types that are inherently more mobile than plants (e.g., insects, aquatic organisms), the size of the infested area above which eradication may not be possible is likely considerably smaller. Tobin et al. (2013) published a review of over 600 different arthropod eradication programs encompassing 130 species in 91 countries to examine the effect of different factors on success or failure on eradication. They concluded that factors that most strongly influenced success included the size of the infested area, relative detectability of the target species, method of detection, and the primary feeding guild of the target species. The probability of success may be even lower for taxa that are also difficult to detect. Wood-boring beetles, for example, are notoriously difficult to detect since they spend the majority of their life cycle inside their tree host. Typically, these species are not identified until negative impacts on the landscape become widespread and are apparent. In some cases, this awareness can be years following their initial introduction and establishment, thus making eradication attempts challenging. Emerald ash borer was established in southeast Michigan in the early 1990s but was not detected and identified as the cause of extensive ash (*Fraxinus* spp.) mortality until 2002. By 2003, eradication efforts were initiated, but this management strategy was eventually terminated due to the amplified magnitude of the infestation and economic and technological constraints (Herms and McCullough 2014). However, eradication of Asian longhorned beetle (*Anoplophora glabripennis*) was successful from sites in Islip, Manhattan, and Staten Island, NY; Carteret and Jersey City, NJ; Chicago, IL; and Boston, MA, even though establishment of this woodborer likely occurred several years prior to its first US detection in 1996 (Meng et al. 2015). The rapid and coordinated detection and removal of infested trees and effective community outreach and engagement likely influenced the successful eradication of Asian longhorned beetle from these urban areas. However, the more recently detected infestations in Worcester, MA, in 2008, and Bethel, OH, in 2011 may present additional challenges to current eradication efforts since these infestations were likely established for a longer period of time prior to their initial detection. In addition, these infestations are also located within heavily wooded suburban/rural landscapes that are connected to contiguous tracts of eastern deciduous hardwood forests, thereby providing Asian longhorned beetle populations with an abundance of preferred hosts and enhancing the potential for spread (Lopez et al. 2017; Trotter and Hull-Sanders 2015). Spotted lanternfly (*Lycorma deli-*

catula), an exotic species native to Asia, was found infesting tree of heaven (*Ailanthus altissima*) on three residential properties and one commercial property within a 2-mile radius in Boyertown, Berks County, PA, in September 2014 (Parra et al. 2017). The likelihood of eradication is considered to be low pending availability of improved detection methods and availability of new control methods that do not rely as heavily on the use of trap trees and host removal (Parra et al. 2017). Aquatic species that are small in size at some point in their life cycle and may occur anywhere in an aquatic system are also particularly difficult to detect at low population levels. If the establishment of an aquatic invasive species is not detected and acted upon almost immediately, eradication is extremely unlikely (Simberloff 2003). For example, the non-native marine alga *Caulerpa taxifolia* was left untreated when first detected in the Mediterranean Sea near the coast of Monaco. It subsequently spread and now blankets thousands of hectares of coastal substrate in the region, rendering futile any hope of eradication (Meinesz et al. 2001). In contrast, *C. taxifolia* was effectively eradicated in California due to timely identification and rapid implementation of containment and treatment (Anderson 2005). Even when natural resource managers detected populations of aquatic invasive species at low population levels and acted decisively, eradication was successful in relatively few cases and usually at great expense. For instance, the polychaete *Terebrasabella heterouncinata*, a parasite of South African abalones, was detected in California and successfully eradicated by removing 1.6 million of its most preferred and susceptible hosts in the intertidal area (Culver and Kuris 2000). Although zebra mussels (*Dreissena polymorpha*) have been present in the United States for more than 30 years and have continued to spread to new waterways during that time, the only sites from which they have been eradicated are a handful of isolated, abandoned quarries, and only after heavy applications of molluscicide (Strayer 2009). In general, the smaller the infestation and the earlier the stage of invasion, the more likely eradication and mitigation efforts will have a successful outcome.

7.3.4 Goals and Objectives of Potential Invasive Species Management Efforts

It is important to clearly state and establish appropriate goals and objectives for management actions against the invasive species under consideration. For example, eradication of a species or the restoration of the ecosystem or community to both its pre-invasion species composition and functional state may not be possible. If so, decision-making and priority setting would need to incorporate integration of the negative impacts of the invasive species, importance of the invaded community, efficacy of any proposed actions, the actions

chosen, and the desired goal or “end state.” The goal may then be to build/manage/repair the affected area to a functional resilient state. For example, cheatgrass may always be present in a plant community at some reduced level, such as 10% cover. However, presence of desirable native bunch grasses such as bluebunch wheatgrass (*Pseudoroegneria spicata*) in such a community provides good wildlife habitat, domestic livestock forage, and long-term soil protection. The occurrence of these native grasses with a mix of native forbs and shrubs that existed prior to cheatgrass invasion will yield a resilient landscape that provides multiple benefits in spite of the low-level occurrence of cheatgrass. Management plans aimed at building landscape resilience, decreasing negative impacts, and preventing or slowing establishment into uninfested areas can also be adaptable, especially when developed for well-established species known to have periodically fluctuating population densities. For example, depending on current biotic (e.g., population levels and stand densities) and abiotic (e.g., climate) conditions, management of gypsy moth populations can vary yearly to encompass a variety of techniques including stand thinning, mass trapping, microbial or chemical controls, and detection and monitoring surveys (Schweitzer et al. 2014; Sharov et al. 2002).

7.3.5 Effectiveness of Available Tools or Their Potential for Success

Experiential knowledge, published reports on the effectiveness of available tools or tactics, and online maps are also useful in setting priorities. For example, the USDA Natural Resources Conservation Service has published an interactive map of ecosystem resilience and resistance for the Great Basin ecoregion (Chambers et al. 2014). The map provides an index of relative ecosystem resilience to disturbance and resistance to cheatgrass invasion based on underlying soil, temperature, and moisture regimes. Thus, the most resilient and resistant areas would have the highest potential for successful management and would receive the highest priority in a single-factor system. An overview of categories of tactics or tools and synthesis of recently developed tools are provided in the next section of this chapter.

7.3.6 Integration of Input

In reality, resource managers will seldom be operating in a single-factor priority system. Instead, they will need to integrate all five of the prioritized factors discussed above, with emphasis on (1) the potential tools or techniques that may be used and (2) the ultimate management goal. Potential tools or techniques might be implemented singly or in combinations. Integrated pest management is a site-specific, multi-

tactic, decision-making process that optimizes pest control in an economically and ecologically sound manner. Approaches such as regulatory control; education and outreach; physical, cultural, chemical, and biological control; vaccination; host resistance; and control of reproduction may be integrated and consolidated into a unified program. A discussion of these approaches is found in the next section.

7.3.7 Key Findings

- Prioritization of invasive species and the ecosystems at risk is needed in order to allocate limited resources available for their management.
- Input from many factors including the degree of threat of the invasive species, the value of the ecosystem, the spatial extent of the invasion, management goals, and available management tools must be integrated to set priorities and make management decisions.
- Early detection, inventory, and monitoring effectiveness provide the base data needed to analyze threats and define treatments.

7.3.8 Key Information Needs

- Models for analyzing risk and uncertainty to better prioritize management decision-making
- Mechanisms for feedback on the efficacy of management actions for evaluating management decisions and incorporating new information into future actions
- Large-scale predictive models on the impact of invasive species on ecosystem changes to estimate if the new invader will dominate the invaded ecosystem, be restricted to microsites, or persist at a lower population level and thereby allow the components of the pre-invasion community to also persist
- Priority-setting models that integrate inputs including ecosystem uniqueness and value, potential invader impacts, management goals, available tools, and probability of success
- Improved tools for early detection and rapid response and guidelines for optimal implementation in time and space to enhance their efficacy

7.4 Recent Advances in Understanding the Biology and Ecology of Invasive Species

More than 450 non-native forest insects (some of which are invasive) (Aukema et al. 2011), at least 197 invasive pathogens of plants and animals (CISEH 2016), over 1600 inva-

sive plants (CISEH 2016), at least 261 species of non-native terrestrial vertebrates (some of which are invasive) (Witmer et al. 2007), and more than 186 species of invasive aquatic organisms (CISEH 2016) are established in the United States. Several invasive species have caused impacts severe enough to inflict heavy damage both economically and ecologically and thus warrant management attention.

Many established non-native species are not economic pests in their native range where they coevolved with natural enemies and, along with host resistance, they typically coexist in equilibrium with native populations. When an invasive species is detected in the United States, little is generally known about its biology in its native range, and even less is known about its ecology, dispersal, and interactions with hosts and the environment, knowledge which is critical to guide management in the introduced range. Fortunately, significant advances have been achieved in understanding the biology and ecology of some of our most damaging invasive insects, pathogens, plants, vertebrates, and aquatic organisms. Additional information about the biology and impacts of damaging invasive species is given in Chap. 2.

7.4.1 Invasive Insects

Some examples of the most threatening invasive forest insects that have become established in North America and either impact trees directly or vector tree diseases are listed in Table 7.1 along with management approaches that will be discussed in Sect. 7.4.2. Native insects such as mosquitoes (Diptera: Culicidae) may also vector invasive pathogens including West Nile virus and Zika virus that impact animals and humans (Fauci and Morens 2016; Reisen 2013).

Understanding the life history of invasive insects is critical for predicting and modeling population growth and spread, timing the application of control tactics to target vulnerable life stages, and directing the location and implementation of survey and management strategies. Basic biology and life cycles have been studied for many invasive insects: environmental factors that influence 1-year or 2-year development and thus affect population growth and spread rates of emerald ash borer (Tluczek et al. 2011); factors that influence development, longevity, and fecundity of Asian longhorned beetle (Keena 2002) and goldspotted oak borer (*Agrilus auroguttatus*) (Lopez and Hoddle 2014); phenology and seasonal flight of redbay ambrosia beetle (*Xyleborus glabratus*) (Hanula et al. 2008); and the complex life cycle of siren woodwasp (*Sirex noctilio*) and its relationships with and horizontal transmission of different species of mutualistic fungi (Morris and Hajek 2014). Information on the biology, economic impacts (from damage and control), and pest management of spotted lanternfly is currently incomplete for fully informing the feasibility of eradication.

Table 7.1 Examples of significant invasive insects of forest trees and management approaches under development or in operational use^a

Insect	Scientific name	Major forest hosts	Year of introduction or detection	Management approaches ^b
Emerald ash borer	<i>Agrilus planipennis</i> Fairmaire (Coleoptera: Buprestidae)	<i>Fraxinus</i> spp.	2002	RC, PC, CuC, CC, BC, HR, IPM
Gypsy moth	<i>Lymantria dispar</i> L. (Lepidoptera: Lymantriidae)	Wide host range; preferred genera include <i>Alnus</i> , <i>Fagus</i> , <i>Betula</i> , <i>Quercus</i> , <i>Populus</i> , and <i>Salix</i>	1869	RC, PC, CuC, CC, BC, HR, R, IPM
Hemlock woolly adelgid	<i>Adelges tsugae</i> Annand (Hemiptera: Adelgidae)	<i>Tsuga</i> spp. (eastern and Carolina hemlocks are more susceptible than western and Asian species)	1951	RC, PC, CuC, CC, BC, HR, IPM
Asian longhorned beetle	<i>Anoplophora glabripennis</i> Motschulsky (Coleoptera: Cerambycidae)	Wide host range; preferred genera include <i>Acer</i> , <i>Populus</i> , <i>Salix</i> , and <i>Ulmus</i>	1996	RC, PC, CC
Sirex woodwasp	<i>Sirex noctilio</i> F. (Hymenoptera: Siricidae)	<i>Pinus</i> spp.	2004	RC, PC, CuC, CC, BC
Winter moth	<i>Operophtera brumata</i> L. (Lepidoptera: Geometridae)	Wide host range; preferred genera include <i>Quercus</i> , <i>Acer</i> , <i>Prunus</i> , <i>Tilia</i> , <i>Fraxinus</i> , and <i>Ulmus</i>	1930s	RC, PC, CuC, CC, BC
Goldspotted oak borer	<i>Agrilus auroguttatus</i> Schaeffer (Coleoptera: Buprestidae)	<i>Quercus</i> spp.	1990s	PC, CuC, CC
Balsam woolly adelgid	<i>Adelges piceae</i> Ratz. (Hemiptera: Adelgidae)	<i>Abies</i> spp.	Around 1900	RC, PC, CuC, CC
Polyphagous shot hole borer	<i>Euwallacea</i> spp. (Coleoptera: Curculionidae: Scolytinae)	Wide host range including <i>Quercus</i> spp., <i>Salix</i> spp., <i>Platanus</i> spp., and <i>Populus</i> spp.	2003	RC, PC, CuC
Spotted lanternfly	<i>Lycorma delicatula</i> (Hemiptera: Fulgoridae)	<i>Ailanthus altissima</i> is preferred but feeds on hosts from 20 plant families	2014	RC, PC, CC, IPM

^aManagement approaches listed are not “recommended”; rather, they are a summary of approaches that have been studied and may also be used in some operational invasive species management programs

^bRC regulatory control, PC physical control, CuC cultural control, CC chemical control, BC biological control, HR host resistance, R reproductive, IPM integrated pest management

Recent advances in molecular techniques and DNA analysis have been used to identify populations and country of origin for several species, including hemlock woolly adelgid (*Adelges tsugae*) (Havill et al. 2006), emerald ash borer (Bray et al. 2011), gypsy moth (Keena et al. 2008), Asian longhorned beetle (Carter et al. 2010), and sirex woodwasp (Boissin et al. 2012). Identification of the country of origin facilitates exploration for natural enemies, location of genetic material for developing host resistance, and evaluation of control strategies in the native range with well-established populations.

Sophisticated techniques have been developed and used to measure insect flight capacity and spread: harmonic radar for Asian longhorned beetle (Williams et al. 2004); computer-monitored flight mills for sirex woodwasp (Bruzzone et al. 2009), emerald ash borer (Taylor et al. 2010), and Asian longhorned beetle (Lopez et al. 2017); dendrochronology-based models for emerald ash borer (Siegert et al. 2014); geographic-, host-, and environment-based models for spread of hemlock woolly adelgid (Morin et al. 2009) and emerald ash borer (Prasad et al. 2010); and trap-based monitoring for the spread of gypsy moth (Sharov et al. 2002). Understanding dispersal by investigating a species' behavior

and physiological limits is critical for establishing quarantine boundaries and determining zones for implementation of control measures. This information is also useful for predicting the spread and subsequent distribution of new populations, thereby improving rapid detection and eradication efforts.

Determining the range of host species and host interactions of invasive insects in the introduced ecosystem is essential for effective management. Invasive insects that reach high densities, which then encounter different tree species within their host genera as well as other genera in their new environment, may respond by colonizing a range of new hosts that are not infested when densities are lower. The emerald ash borer has recently been found to infest a novel host, the native white fringetree (*Chionanthus virginicus*) in North America (Cipollini 2015). The Asian longhorned beetle attacks >100 species of trees but prefers maples (*Acer* spp.), poplars (*Populus* spp.), willows (*Salix* spp.), and elms (*Ulmus* spp.) (Meng et al. 2015); however, susceptibility among poplar species and hybrids varies considerably (Hu et al. 2009). Although all North American species of ash encountered by emerald ash borer to date are susceptible, preferences differ among species and are related to differ-

ences in host volatiles, nutrition, and defense compounds (Chen and Poland 2010; Chen et al. 2011). Sirex woodwasp infests a wide range of pine (*Pinus*) species across its global distribution; however, preferences among species are poorly understood because attacked trees are often growing in monocultures (Slippers et al. 2015). Goldspotted oak borer colonizes several species of oaks in California, including coast live oak (*Quercus agrifolia*), California black oak (*Q. kelloggii*), and canyon live oak (*Q. chrysolepis*), as well as other red oak species, but rarely infests white oaks (Coleman and Seybold 2011). Redbay ambrosia beetle attacks redbay (*Persea borbonia*) and several other tree species in the family Lauraceae, including sassafras (*Sassafras albidum*) and avocado (*Persea americana*) (Mayfield et al. 2013). The polyphagous shot hole borer (*Euwallacea* spp.) attacks over 200 species of trees in California including oaks, sycamore (*Platanus occidentalis*), cottonwood (*Populus* spp.), willow, and avocados (Eskalen et al. 2013). The spotted lanternfly is known to feed on plants in more than 20 families; however, the relationship between it and tree of heaven provides an opportunity to reduce tree of heaven populations using a combination of pest population reduction and host removal (e.g., using systemic insecticide treatments and removal or herbicide treatment of some tree of heaven, when appropriate) (Parra et al. 2017).

Significant advances have been made in analytical chemistry techniques for identifying semiochemical attractants including insect-produced pheromones and host kairomones. Semiochemical attractants are used for detecting and monitoring many species of insects which rely heavily on olfactory cues for mate and host selection. For example, the semiochemical lure quercivorol was recently found to be highly attractive to polyphagous shot hole borer and Kuroshio shot hole borer (*Euwallacea* spp.) and is being used to monitor shot hole borer invasions and dispersal (Dodge et al. 2017). Coupled gas-chromatographic-electroantennographic detection has been used to identify male-produced aggregation pheromones that attract both sexes of sirex woodwasp (Cooperband et al. 2012). Identification of insect-produced pheromones has been more challenging for Asian longhorned beetle and emerald ash borer. In these species, host volatiles are considered to be more effective for long-distance attraction and for synergizing attraction to close range or contact pheromones (Crook and Mastro 2010; Nehme et al. 2010, 2014; Ryall et al. 2012). Volatiles from the symbiotic laurel wilt fungus (*Raffaelea lauricola*) synergize host volatiles present in manuka (*Leptospermum scoparium*) oil in facilitating attraction of redbay ambrosia beetle (Kuhns et al. 2014).

7.4.2 Invasive Pathogens of Trees

There have been recent advances in knowledge and understanding of the basic biology, ecology, dispersal, and host interactions of invasive tree pathogens. Examples of some of the most significant diseases caused by invasive pathogens infecting trees and wildlife in North America are summarized in Table 7.2.

Understanding genetics of invasive pathogens aids in accurate identification of causal agents of disease. Multi-locus microsatellite genotyping of *Phytophthora ramorum*, the causative agent of sudden oak death (Garnica et al. 2006; Ivors et al. 2006; Prospero et al. 2007), has led to characterization of clonal lineages and their distributions (COMTF 2016). Results are organized in a searchable database that is categorized by three lineages (PRMGP 2016). A previously undescribed and presumably non-native pathogen, *R. lauricola*, the causative agent of laurel wilt that is also a fungal symbiont of the invasive redbay ambrosia beetle, was recently discovered (Fraedrich et al. 2008; Harrington et al. 2008). In addition, other related fungal symbionts of the same insect have been identified and described (Harrington et al. 2010).

Confidence in detection methods used to assess expanding disease distributions and an understanding of dominant modes of pathogen spread also are important in the management of invasive tree pathogens. For example, study of *P. ramorum*-caused disease of tanoaks (*Notholithocarpus densiflorus*) and documentation of disease patterns in the forest landscapes of Oregon led to understanding the correlation between aerial dispersal of inoculum and disease pattern and the lack of correlation with dispersal of inoculum in streams and soil (Hansen et al. 2014). These findings support the continued use of aerial surveys for *P. ramorum* in Oregon's forested landscapes. Investigation of the relative importance of multiple putative insect vectors of *Ceratocystis fagacearum* (the oak wilt fungus), a long-established pathogen, led to the conclusion that a nitidulid beetle is the principle vector species of oak wilt (Ambourn et al. 2005; Juzwik et al. 2004), whereas the smaller oak bark beetle (*Pseudopityophthorus minutissimus*) is minimally important in pathogen transmission in Minnesota (Ambourn et al. 2006). Frequencies of pathogen-contaminated nitidulid beetles (*Colopterus truncatus* and *Carpophilus sayi*) present in freshly made wounds, and the nearly immediate arrival of *C. truncatus* to such wounds, have fostered greater adherence for following guidelines for removing recently wilted red oaks (sanitation), disposing of diseased material, and developing harvesting guidelines to reduce the potential for new infections via insect transmission.

Better understanding of spatial patterns of trees that survive disease may indicate environmental differences that affect the pathogen. For example, a recent analysis of surviv-

Table 7.2 Examples of some of the most significant invasive pathogens and associated diseases of trees and wildlife of forests, grasslands, and rangelands and management approaches^a

Disease	Pathogen/parasite and key insect associates	Major forest/grassland/rangeland hosts	Year of introduction or detection	Management approaches ^b
<i>Tree diseases</i>				
Rapid `ōhi`a death	<i>Ceratocystis</i> A and <i>Ceratocystis</i> B	<i>Metrosideros polymorpha</i>	2014	RC
Laurel wilt disease	<i>Raffaelea lauricola</i> (pathogen); <i>Xyleborus glabratus</i> (insect vector)	Lauraceae, e.g., <i>Persea borbonia</i> , <i>Sassafras albidum</i> , <i>Litsea aestivalis</i> , <i>Lindera melissaefolia</i>	2003	PC, CuC, HR
Sudden oak death	<i>Phytophthora ramorum</i>	<i>Quercus</i> spp., <i>Lithocarpus</i> spp.	2002	RC, PC, CuC, CC, IPM
Butternut canker	<i>Ophiognomonia clavignenti-juglandacearum</i>	<i>Juglans cinerea</i>	1967	PC, CuC, HR
Oak wilt	<i>Ceratocystis fagacearum</i> (pathogen); sap beetle vectors (<i>Colopterus</i> spp.; <i>Carpophilus sayi</i>) and bark beetle vectors (<i>Pseudopityophthorus</i> spp.)	<i>Quercus</i> spp.	1942	RC, PC, CuC, CC, IPM
Beech bark disease	<i>Neonectria</i> spp. (pathogen); <i>Cryptococcus fagisuga</i> , <i>Xylococcus betulae</i> (scale insects provide entry wound)	<i>Fagus grandifolia</i>	~1890	PC, CuC, HR
Dutch elm disease	<i>Ophiostoma novo-ulmi</i> , <i>O. ulmi</i> (pathogen); <i>Scolytus multistriatus</i> , <i>S. schevyrewi</i> , <i>Hylurgopinus rufipes</i> (insect vectors)	<i>Ulmus</i> spp.	~1928 (<i>O. ulmi</i>); ~1940 (<i>O. novo-ulmi</i>)	PC, CuC, CC, HR
Chestnut blight	<i>Cryphonectria parasitica</i>	<i>Castanea dentata</i>	1905	PC, HR
White pine blister rust	<i>Cronartium ribicola</i>	Five-needle pines, e.g., <i>Pinus strobus</i> , <i>P. albicaulis</i> , <i>P. lambertiana</i> , <i>P. monticola</i>	~1900	RC, PC, CuC, HR
<i>Wildlife diseases</i>				
Sylvatic plague	Gram-negative bacterium <i>Yersinia pestis</i> (pathogen); fleas on rodents (vectors)	Prairie dogs (<i>Cynomys</i> spp.); black-footed ferret (<i>Mustela nigripes</i>)	1900	PC, CuC, V
West Nile virus	Arbovirus (<i>Flavivirus</i> spp.) (<i>Flaviviridae</i>) (pathogen); mosquitos (<i>Culex</i> spp.) (vectors)	Wide range of bird species, e.g., bald eagle (<i>Haliaeetus leucocephalus</i>), greater sage-grouse (<i>Centrocercus urophasianus</i>), western scrub-jay (<i>Aphelocoma californica</i>), red-tailed hawk (<i>Buteo jamaicensis</i>), great horned owl (<i>Bubo virginianus</i>)	1999	PC, CuC, V
White nose syndrome	<i>Pseudogymnoascus destructans</i>	Many species of bats, e.g., little brown bat (<i>Myotis lucifugus</i>), northern long-eared bat (<i>M. septentrionalis</i>)	2006	RC, CuC, PC

^aManagement approaches listed are not “recommended”; rather, they are a summary of approaches that have been studied and may also be used in some operational invasive species management programs

^bRC regulatory control, PC physical control, CuC cultural control, CC chemical control, BC biological control, HR host resistance, V vaccination, IPM integrated pest management

ing butternut (*Juglans cinerea*) trees indicated that drier, upland sites were correlated with increased likelihood of butternut survival (LaBonte et al. 2015). These findings suggest the need for further disease assessment of butternut plantings on open, well-drained sites.

7.4.3 Invasive Pathogens of Animals

Research on the biology of invasive pathogens of animals increases our understanding of how they are vectored and might be managed through preventing transmission. West

Nile virus is an arbovirus typically vectored by non-native mosquitos (*Culex* spp.). Successful transmission of the virus to uninfected birds depends on the engorged female mosquitos living long enough for virus in the blood to replicate to transmissible levels in their salivary glands. West Nile virus may persist in mosquito hosts through facultative diapause or localized adaptation to overwintering of infected mosquito adults, or through vertical transmission of the virus to F1 progeny (Reisen 2013). Overwintering persistence of West Nile virus in vertebrate hosts has not been confirmed; however, recent research suggests that the house finch (*Carpodacus mexicanus*), house sparrow (*Passer domesti-*

cus), and western scrub-jay (*Aphelocoma californica*) could serve as overwintering reservoirs (VanDalen et al. 2013; Wheeler et al. 2012). The source of initial viral infection in uninfected mosquitos in spring has not been conclusively attributed to relapse and recurrence of viral activity and symptoms in persistently infected birds; however, viral transmission to avian predators feeding on West Nile virus-infected live or dead avian prey is possible (Nemeth et al. 2009; Pérez-Ramírez et al. 2014; Reisen 2013).

White nose syndrome is a cutaneous infection of bats caused by the invasive (Leopardi et al. 2015) psychrophilic fungus *Pseudogymnoascus* (formerly *Geomyces*) *destructans* (Gargas et al. 2009; Lorch et al. 2011) (Table 7.2). The disease is named for the white fungus that grows on the muzzles, ears, and wing membranes of infected bats (Blehert et al. 2009). White nose syndrome has led to the local extirpation of bat populations and may eventually cause the extinction of the endangered little brown bat (*Myotis lucifugus*). The six native bat species currently known to be susceptible to infection by *P. destructans* are insectivorous and hibernate under thermally stable, cool, and moist conditions in caves and mines where they congregate to overwinter and effectively reduce their metabolic function during the seasonal absence of food (Blehert and Meteyer 2011). These behavioral and physiological adaptations for overwintering survival, coupled with geographic features and environmental factors (Maher et al. 2012), may explain why white nose syndrome has spread so rapidly. Deleterious physiological (Cryan et al. 2010; Verant et al. 2014; Warnecke et al. 2013; Willis and Wilcox 2014) and behavioral (Brownlee-Bouboulis and Reeder 2013; Wilcox et al. 2014) changes during hibernation have been linked to *P. destructans* colonization of bat dermis and epidermis.

Amphibian chytridiomycosis likely originated from regions of Asia, Africa, and/or Brazil and is caused by the amphibian generalist fungal pathogen *Batrachochytrium dendrobatidis* (*Bd*), which releases aquatic flagellated zoospores (Berger et al. 1998). Infection by *Bd* disrupts cutaneous osmoregulatory function among phylogenetically distant amphibian taxa (Voyles et al. 2009) by inhibiting electrolyte transport across the epidermis, thus causing significant reductions in plasma sodium and potassium concentrations, leading to asystolic cardiac arrest.

A morphologically, genetically, and functionally distinct congeneric species, *B. salamandrivorans* (*Bsal*), likely originating from Asia and first detected in the Netherlands (Martel et al. 2013), has not yet been confirmed as present in the United States (Grant et al. 2016). Since the Eastern United States has the highest diversity of salamanders (Salamandridae) in the world, high-risk areas have been identified (Richgels et al. 2016) and a national response strategy has been developed (Grant et al. 2016).

A greater understanding of the distribution of *Bd* and areas with amphibians at risk of infection with chytridiomycosis is required to effectively manage this disease. Recent analyses of database information accessed from the Global *Bd* Mapping Project indicate that *Bd* was prevalent in many countries, amphibian families, and species and that sites in the montane grasslands and shrublands biome had the highest probability of *Bd* occurrence (Olson et al. 2013). A comprehensive species distribution model for *Bd* in the Americas based on habitat parameters projected higher suitability of *Bd* infection in Western North America (James et al. 2015) than earlier models (Liu et al. 2013; Rödder et al. 2009). The optimal (17–25 °C) and physiological (4–28 °C) temperature ranges for growth of *Bd* ultimately constrain its distribution (Piotrowski et al. 2004), and the probability of *Bd* infection was found to shift between seasons along a latitudinal/precipitation gradient. Prevalence of early-season infections was associated with higher latitudes receiving decreased (recent) precipitation, while late-season prevalence was higher at low elevations receiving increased (recent) precipitation (Petersen et al. 2016).

Recent research has provided insights into mechanisms of amphibian resistance to *Bd* infection. MCH (major histocompatibility complex) alleles encode receptors at the cell surface that are responsible for induction and regulation of acquired immune responses to pathogens. *Bd*-resistant amphibians across four continents share common amino acids in three peptide binding pockets of the MCH class II antigen binding groove (Bataille et al. 2015). Characterizing MCH class II-based resistance in the North American native lowland leopard frog (*Lithobates yavapaiensis*) serves as an important initial step in developing genetically informed breeding programs for amphibian species recovery (Savage and Zamudio 2011).

7.4.4 Invasive Plants

A summary of the most common invasive plants is presented in Table 7.3.

The successful invasion and persistent establishment of non-native plants can frequently be attributed to their mating system (Pannell 2015). Further, mating system plasticity, as exemplified by purple viper's bugloss (*Echium plantagineum*) and yellow star-thistle (*Centaurea solstitialis*), has allowed for some obligate native-range outcrossers to be self-compatible in the invaded range (Petanidou et al. 2012). Mixed-mating systems also exist in invasive plants such as Japanese stiltgrass (*Microstegium vimineum*), with both cleistogamous (obligate selfing) and chasmogamous flowers (may outcross) (Cheplick 2005). It may be possible to manipulate rates of inbreeding depression to reduce the invasion potential of selfing species. Indeed, Japanese stiltgrass

Table 7.3 The most common significant invasive plants in forests and management approaches^a

Plant	Common name	State and/or Federal regulation (if any)	States in which found	Approx. year of introduction or detection	Management approaches ^b
<i>Acer platanoides</i>	Norway maple	CT; MA	MT; ID; WA; OR; MN; WI; MI; IL; IN; OH; KY; TN; WV; VA; NC; VA; MD; PA; NY; NJ; CT; MA; RI; VT; NH; ME	1756	PC, CC, IPM
<i>Ailanthus altissima</i>	Tree of heaven	CT; MA; VT; NH	All but AK; MT; WY; ND; SD; MN; VT; NH	1784	PC, CC, IPM
<i>Akebia quinata</i>	Chocolate vine	None	LA; MO; IL; MI; IN; OH; KY; WV; PA; GA; SC; NC; VA; MD; DE; NJ; NY; MA; CT; RI	1845	PC, CC
<i>Albizia julibrissin</i>	Mimosa	None	CA; AZ; UT; TX; NM; OK; LA; AR; MO; IL; IN; OH; KY; TN; NC; SC; GA; MS; FL; WV; VA; MD; DE; NY; PA; RI; MA; CT; AL; NJ	1745	PC, CC
<i>Alliaria petiolata</i>	Garlic mustard	AL; CT; MA; MN; VT; NH; OR; WA	WA; OR; ID; UT; CO; KA; NE; OK; AR; MO; IA; MN; WI; IL; IN; KY; TN; OH; MI; WV; PA; GA; SC; NC; VA; MD; DE; NJ; NY; CT; MA RI; NH; VT; ME; AK	1868	PC, CuC, CC
<i>Berberis thunbergii</i>	Japanese barberry	CT; MA; MI	WA; WY; ND; SD; NE; KA; MO; IA; MN; WI; IL; MI; IN; KY; TN; OH; WV; PA; VA; NC; SC; GA; MD; DE; NJ; NY; CT; MA; RI; VT; NH; ME	1875	PC, CuC, CC, IPM
<i>Bromus tectorum</i>	Cheatgrass	CO; CT	All 50 States; not PR or VI	1890s	PC, CC
<i>Celastrus orbiculatus</i>	Oriental bittersweet	CT; MA; VT; NH; NC	AR; GA; SC; NC; TN; VA; WV; KY; IL; IN; OH; WV; MD; DE; PA; NJ; NY; VT; NH; MA; CT; RI; ME	1736	PC, CC
<i>Centaurea diffusa</i>	Diffuse knapweed	AZ; CA; CO; ID; MT; NE; NV; NM; ND; SD; UT; WA; WY; OR	WA; OR; CA; NV; AZ; NM; UT; CO; WY; MT; ID; NE; IA; MO; MI; IL; IN; KY; TN; OH; NY; MA; CT; NJ	1907	PC, CC, BC
<i>Centaurea solstitialis</i>	Yellow star-thistle	AZ; CA; CO; ID; MT; NV; NM; ND; OR; SD; UT; WA	All but AR; LA; MI; AL; GA; HI; AK; PR; VI	1852	BC, PC, CC
<i>Elaeagnus umbellata</i>	Autumn olive	CT; MA; NH; WV	WA; OR; MT; NE; KS; IA; MO; AR; LA; MI; WI; IL; IN; OH; KY; TN; AL; MS; GA; FL; SC; NC; WV; VA; MD; DE; NJ; NY; PA; CT; MA; RI; VT; NH; ME; HI	1830	PC, CuC, CC
<i>Euonymus alatus</i>	Winged burning bush	CT; MA	MT; IA; MO; IL; WI; MI; IN; OH; KY; WV; PA; VA; NC; SC; GA; NY; NJ; DE; MD; VT; NH; MA; CT; RI	1860	PC, CC
<i>Euonymus fortunei</i>	Wintercreeper euonymus	None	TX; KS; MO; WI; IL; IN; MI; OH; KY; TN; MI; AL; GA; SC; NC; VA; MD; PA; NJ; DE; RI; NY; CT; MA; RI	1907	PC, CC
<i>Euphorbia esula</i>	Leafy spurge	AK; AZ; CA; CO; CT; HI; ID; IA; KS; MA; MN; MT; NE; NM; ND; SD; UT; WA; WI; WY	All but TX; OK; AR; LA; MI; AL; KY; TN; NC; SC; GA; FL; HI; PR; VI	1827	PC, CC, BC
<i>Falcataria moluccana</i>	<i>Albizia</i> ; peacocks plume	None	HI	1917	PC, CuC, CC, IPM

(continued)

Table 7.3 (continued)

Plant	Common name	State and/or Federal regulation (if any)	States in which found	Approx. year of introduction or detection	Management approaches ^b
<i>Fallopia japonica</i>	Japanese knotweed	AL; CA; OR; WA; CT; MA; VT; NH	All but ND; WY; NV; AZ; NM; TX; AL; FL; HI; PR; VI	Late 1800s	PC, CC, IPM
<i>Fallopia sachalinense</i>	Giant knotweed	CA; OR; WA; CT	AK; WA; OR; CA; MT; ID; MN; WI; IL; MI; KY; TN; LA; OH; WV; VA; NC; PA; MD; DE; NJ; NY; CT; VT; MA; RI; ME	Late 1800s	PC, CC, IPM
<i>Ficaria verna</i>	Lesser celandine	CT; MA	WA; OR; TX; MO; WI; IL; IN; MI; OH; KY; TN; WV; PA; VA; MD; DE; NY; NJ; CT; MA; RI; NH	1867	PC, CC
<i>Frangula alnus</i>	European buckthorn	MN; CT; MA; VT; NH	ID; WY; CO; NE; IA; MN; IL; IN; MI; KY; TN; OH; NC; WV; PA; MD; NJ; NY; CT; RI; MA; VT; NH; ME	1864	PC, CC, IPM
<i>Hedera helix</i>	English ivy	OR; WA	HI; WA; OR; CA; ID; UT; AZ; TX; LA; AR; MO; IL; IN; MI; AL; GA; FL; OH; KY; VA; WV; NC; SC; MD; DE; PA; NJ; NY; CT; MA	1800	PC, CC
<i>Hedychium gardnerianum</i>	Himalayan ginger	None	HI	Mid-1900s	PC, CC
<i>Heracleum mantegazzianum</i>	Giant hogweed	Federal noxious weed; AL; CA; FL; MN; NC; OR; SC; WA; CT; MA; VT; NH; PA	WA; OR; IL; WI; NC; PA; NY; CT; MA; ME; MI	1917	PC, CC
<i>Hydrilla verticillata</i>	Hydrilla	Federal noxious weed; AL; AZ; CA; CO; FL; ME; MS; NV; NM; NC; OR; SC; TX; WA; CT; MA; VT	WA; CA; AZ; TX; LA; AR; IA; MS; AL; FL; GA; SC; NC; TN; KY; IN; VA; MD; PA; DE; NJ; NY; CT; MA; ME	1960	PC, CC
<i>Imperata cylindrica</i>	Cogongrass	Federal noxious weed; AL; CA; FL; HI; MN; MS; NC; OR; SC; VT	OR; TX; LA; MS; AL; GA; FL; SC; VA	1912	PC, CC, IPM
<i>Lespedeza bicolor</i>	Shrubby lespedeza	None	TX; KS; IA; MO; AR; LA; IL; IN; KY; TN; MS; AL; GA; FL; SC; NC; VA; WV; OH; PA; MD; DE; NJ; NY; CT; MA; MI	1856	PC, CC
<i>Lespedeza cuneata</i>	Sericea lespedeza	CO; KS	HI; NE; KS; OK; TX; LA; AR; MO; IA; WI; IL; IN; MI; IN; KY; TN; MS; AL; FL; GA; SC; NC; VA; WV; OH; PA; MD; DE; NJ; NY; CT; MA	1896	PC, CuC, CC
<i>Ligustrum obtusifolium</i>	Privet	CT; MA; NH	WA; IA; MO; IL; IN; MI; OH; KY; TN; NC; VA; MD; PA; NJ; NY; CT; MA; RI; NH; VT	1860	PC, CC
<i>Ligustrum sinense</i>	Chinese privet	None	TX; OK; MO; AR; LA; MS; AL; FL; GA; TN; KY; VA; NC; SC; MD; NJ; CT; MA; RI; HI	1852	PC, CC
<i>Linaria dalmatica</i>	Dalmatian toadflax	CO; ID; MT; NV; OR; SD; WY	All but TX; MO; AR; LA; MS; AL; TN; KY; WV; GA; FL; VA; MD; DE; HI; PR; VI	Late 1800s	PC, CC, BC, IPM
<i>Linaria vulgaris</i>	Yellow toadflax	ID; MT; NV; OR; SD; WA; WY; NM	All but HI; PR; VI	Late 1600s	PC, CC, BC, IPM

(continued)

Table 7.3 (continued)

Plant	Common name	State and/or Federal regulation (if any)	States in which found	Approx. year of introduction or detection	Management approaches ^b
<i>Lonicera × bella</i>	Bell's honeysuckle	CT; MA; VT; NH	WA; WY; NM; MN; IA; IL; IN; MI; KY; OH; PA; VA; NC; SC; NJ; MD; NY; CT; RI; MA; NH; VT; ME	Hybrid of <i>L. tatarica</i> and <i>L. morrowii</i>	PC, CC
<i>Lonicera japonica</i>	Japanese honeysuckle	CT; MA; VT; NH	All but OR; ID; MT; WY; CO; ND; SD; MN; IA; VT; VI	1806	PC, CuC, CC, IPM
<i>Lonicera maackii</i>	Amur honeysuckle	CT; MA; VT; NH	OR; ND; NE; KS; TX; IA; MO; AR; WI; IL; IN; MI; KY; TN; OH; WV; VA; NC; SC; GA; MS; PA; NY; MD; NJ; DE; CT; MA	1855–1860	PC, CC
<i>Lonicera morrowii</i>	Morrow honeysuckle	CT; MA; VT; NH	WY; CO; NM; MN; IA; MO; AR; WI; IL; MI; OH; KY; TN; WV; PA; NY; VA; NC; SC; NJ; MD; DE; CT; RI; VT; NH; MA; ME	1975	PC, CC
<i>Lonicera tatarica</i>	Tatarian honeysuckle	CT; MA; NH; VT	All but NV; AZ; OK; MO; AR; LA; AL; MS; TN; GA; FL; SC; NC; HI; VI	1752	PC, CC
<i>Lygodium japonicum</i>	Japanese walking fern	AL; FL	TX; AR; LA; MS; AL; GA; FL; SC; NC; PA; HI; PR	1930s	CC
<i>Lythrum salicaria</i>	Purple loosestrife	AL; AZ; AR; CA; CO; FL; ID; IN; IA; MI; MN; MO; NV; NM; NC; ND; OH; OR; PA; SC; SD; TN; TX; UT; VA; WA; WI; WY; CT; MA; VT; NH	All but AZ; LA; GA; FL; SC; HI; AK; PR; VI	1800	PC, CC, BC, IPM
<i>Melaleuca quinquenervia</i>	Cayeput; melaleuca	Federal noxious weed; AL; CA; FL; MA; NC; OR; SC; TX; VT	LA; FL; HI; PR	Early 1900s	PC, CC, BC, IPM
<i>Mesembryanthemum crystallinum</i>	Iceplant	None	CA; AZ; PA	Early 1800s	CC
<i>Miconia calvescens</i>	Miconia	HI	HI	1960s	PC, CC, BC, IPM
<i>Microstegium vimineum</i>	Japanese stiltgrass	AL; CT; MA	TX; LA; AR; MO; IL; MS; AL; IN; KY; TN; GA; FL; OH; WV; VA; NC; SC; MD; DE; PA; NJ; NY; CT; MA; PR	1919	PC, CC
<i>Miscanthus sinensis</i>	Chinese silvergrass	CT	CA; CO; LA; MO; IL; KY; MI; MS; AL; GA; FL; SC; NC; TN; WV; OH; PA; MD; DE; NJ; NY; CT; RI; MA	Early 1940s	PC, CuC, CC
<i>Morella faya</i>	Fire tree	HI	HI	1800s	PC, CC, BC
<i>Oeceoclades maculata</i>	Monk orchid	None	FL; PR; VI	1960s	PC
<i>Paulownia tomentosa</i>	Princess tree	CT	WA; TX; OK; LA; MO; AR; IL; IN; KY; TN; MS; AL; GA; FL; WV; VA; NC; SC; PA; MD; MD; DE; NJ; PA; NY; CT; RI; MA	1834	PC, CC
<i>Pennisetum setaceum</i>	Fountain grass	HI	OR; CA; AZ; NM; CO; LA; KY; TN; FL; HI	Early 1900s	PC, CC
<i>Persicaria perfoliata</i>	Mile-a-minute weed	AL; CT; MA; OH; NC; SC	OR; OH; KY; WV; VA; NC; PA; MD; DE; NJ; NY; CT; MA	1930s	PC, CC, BC, IPM

(continued)

Table 7.3 (continued)

Plant	Common name	State and/or Federal regulation (if any)	States in which found	Approx. year of introduction or detection	Management approaches ^b
<i>Phragmites australis</i> ssp. <i>australis</i>	Common reed	AL; SC; WA; CT; MA; VT	WA; OR; CA; NV; UT; ID; WY; NE; TX; LA; MN; IA; WI; IL; IN; OH; PA; VA; NC; SC; MD; DE; NY; NJ; CT; VT; NH; MA; RI; ME	1800s	PC, CC
<i>Psidium cattleianum</i>	Strawberry guava	None	FL; HI; PR	1800s	PC, CC, BC
<i>Pueraria montana</i> var. <i>lobata</i>	Kudzu vine	FL; KS; KY; MS; OR; WA; MO; TX; CT; MA; IL; PA; WV	WA; OR; NE; KS; OK; TX; MO; AR; LA; IL; IN; KY; TN; MS; AL; GA; FL; WV; OH; VA; NC; SC; MD; DE; PA; NJ; NY; CT; MA	Late 1800s	PC, CuC, CC, IPM
<i>Pyrus calleryana</i>	Callery pear	None	TX; OK; AR; LA; MS; IL; IN; OH; KY; TN; AL; GA; FL; SC; NC; VA; WV; PA; MD; DE; NJ; NY; CT; MA	1908	PC, CC
<i>Rhamnus cathartica</i>	Common buckthorn	IA; MN; MA; VT; NH	CA; ID; UT; MT; WY; CO; ND; SD; NE; KS; MN; IA; MO; WI; IL; IN; MI; KY; TN; OH; WV; VA; NC; MD; PA; DE; NY; CT; RI; VT; NH; MA	Early 1800s	PC, CC, IPM
<i>Rhodotypos scandens</i>	Black jetbead	None	WI; MO; IL; IN; OH; KY; WV; VA; PA; NJ; DE; NY; CT; VT; NH; MA; SC; AL	1866	PC, CC
<i>Rosa multiflora</i>	Multiflora rose	AL; KY; MO; SD; CT; MA; IA; IN; NH; PA; WI; WV	WA; OR; CA; NM; TX; NE; KS; OK; MN; IA; MO; AR; LA; WI; IL; IN; MI; KY; TN; MS; AL; GA; FL; SC; NC; VA; WV; OH; PA; MD; DE; NJ; NY; CT; RI; VT; NH; MA; ME	1868	PC, CuC, CC, IPM
<i>Rubus armeniacus</i>	Himalayan blackberry	OR	WA; OR; CA; NV; AZ; UT; ID; MT; CO; NM; MO; AR; IL; KY; TN; AL; OH; VA; PA; DE; NJ; MA; HI	1885	PC, CuC, CC
<i>Rubus ellipticus</i>	Himalayan raspberry	None	HI	Mid-1900s	PC, CC
<i>Rubus phoenicolasius</i>	Wineberry	CT; MA	MI; IL; IN; AR; OH; KY; TN; GA; SC; NC; VA; MD; WV; DE; NJ; PA; NY; CT; RI; VT	1890	PC, CuC, CC, IPM
<i>Rumex acetosella</i>	Sheep sorrel	AR; CT; IA	All 50 States	1700s or earlier	PC, CC
<i>Schinus terebinthifolius</i>	Christmas berry, Brazilian peppertree	FL; TX	CA; TX; AL; FL; HI; PR; VI	1891	PC, CC, BC, IPM
<i>Senecio jacobaea</i>	Tansy ragwort	AZ; CA; CO; CT; ID; MT; OR; WA	WA; OR; CA; ID; MT; WY; IL; IN; MI; PA NY; NJ; MA; ME	1922	CC, BC, IPM
<i>Senecio madagascariensis</i>	Fireweed	HI	HI	Early 1980s	PC, CC, BC
<i>Syzygium jambos</i>	Rose apple	None	FL; PR; VI	1800s	PC, CC
<i>Taeniatherum caput-medusae</i>	Medusahead	CA; CO; NV; OR; UT	WA; OR; CA; NV; ID; UT; MT; PA; NY; CT	1887	CC
<i>Tamarix</i> ssp. (<i>T. ramosissima</i> is one of most common)	Saltcedar, tamarisk	CO; MT; NE; NM; ND; OR; SD; TX; WA; WY	CA; NV; UT; AZ; CO; NM; TX; ND; SD; NE; KS; OK; AR; LA; MS; GA; SC; NC; VA	Early 1800s	PC, CC, BC, IPM

(continued)

Table 7.3 (continued)

Plant	Common name	State and/or Federal regulation (if any)	States in which found	Approx. year of introduction or detection	Management approaches ^b
<i>Triadica sebifera</i>	Chinese tallow tree	FL; LA; MS; TX	CA; TX; AR; LA; MS; AL; GA; FL; SC; NC	Late 1700s	PC, CuC, CC
<i>Triphasia trifolia</i>	Sweet lime	None	TX; FL; PR; VI	Possibly 1950s	CC
<i>Ulex europaeus</i>	Gorse	CA; HI; OR; WA	WA; OR; CA; NY; PA; WV; VA; MA; HI	Late 1800s	PC, CuC, CC, IPM
<i>Vinca minor</i>	Common periwinkle	WI	WA; OR; MT; UT; AZ; NE; KS; TX; MT; IA; MO; AR; LA; WI; IL; IN; MI; KY; TN; MS; AL; GA; FL; SC; NC; WV; VA; MD; OH; PA; DE; NJ; NY; CT; RI; VT; NH; MA; ME	1700s	PC, CC
<i>Wisteria sinensis</i>	Wisteria	None	TX; MO; AR; LA; IL; KY; MI; TN; MS; AL; GA; FL; SC; NC; WV; MD; DE; PA; NJ; NY; CT; MA; VT; HI	1816	PC, CC

^aManagement approaches listed are not “recommended”; rather, they are a summary of approaches that have been studied and may also be used in some operational invasive species management programs

^bPC physical control, CuC cultural control, CC chemical control, BC biological control, IPM integrated pest management

does vary its chasmogamous and cleistogamous flower ratios in response to the environment (Cheplick 2005).

Outcrossing breeding systems, including dioecy, may facilitate high genetic variation in invasive plant populations, which in turn increases the likelihood of their successful adaptation to the wide range of novel environmental conditions that may be encountered in the invaded range (Guggisberg et al. 2012). Though only ~7% of all flowering plants are dioecious (obligate outcrossing between individuals that are separate sexes) (Renner 2014), a disproportionate percentage of common US woody invaders are dioecious or partially dioecious, including tree of heaven, common buckthorn (*Rhamnus cathartica*), and Oriental bittersweet (*Celastrus orbiculatus*). The native broadleaf dioecious *Amaranthus* species Palmer amaranth (*A. palmeri*) and common waterhemp (*A. rudis*) have produced herbicide-resistant biotypes (Steckel 2007). Hydrilla (*Hydrilla verticillata*), an invasive non-native aquatic which has both monoecious and dioecious biotypes, has developed herbicide (fluridone) resistance in three of its dioecious phenotypes, all associated with mutations of the *pds* gene (Arias et al. 2005), which indicates a potential capacity for genetic adaptation as well as relationship between dioecy and the propensity for development of herbicide resistance. Dioecy in plants is positively associated with polyploidy, but it remains unclear if polyploidy is the evolutionary cause or consequence (or more likely both) of dioecy (Ashman et al. 2013). Hybridization also leads to production of polyploids (Soltis and Soltis 2009).

It has been hypothesized that hybridization improves invasion success through the generation of novel phenotypes

or increased genetic variation (Ellstrand and Schierenbeck 2000; Parepa et al. 2014; Schierenbeck and Ellstrand 2009). Hybridization may occur between two invasive species, sometimes resulting in a hybrid with superior characteristics compared to the parents, or it may occur with a closely related native species, resulting in the loss of native species alleles. Morrow honeysuckle (*Lonicera morrowii*) and Tatarian honeysuckle (*L. tatarica*) as well as Japanese knotweed (*Fallopia japonica*) (typically male-sterile in its invasive range) (Tiébré et al. 2007) and giant knotweed (*F. sachalinense*) are examples of non-native species within the same genus that hybridize. The hybrid for the *Lonicera* species is *L. × bella* which does not show any known advantage over the parent species, while the hybrid for the *Fallopia* species, *F. × bohémica*, can backcross with its parents and exhibits higher vegetative regeneration than its parents (Bimova et al. 2003) as well as novel secondary metabolites (Piola et al. 2013). Hybridization between several species within the *Spartina* genus has resulted in allopolyploid (having two or more complete sets of chromosomes derived from different species) genomes or hybrid swarms thought to contribute to the success of several invasive *Spartina* species (Ayres et al. 2004). Smooth cordgrass (*Spartina alterniflora*), which is native to the US East Coast but non-native on the West Coast, has hybridized with the native western species California cordgrass (*S. foliosa*), producing hybrids with superior fitness that have spread rapidly through California marshes (Ainouche et al. 2009; Ayres et al. 2008). In contrast, hybridization between Oriental bittersweet and the native American bittersweet (*C. scandens*) has led to significant declines of American bittersweet due to unidirectional

pollen flow from the non-native plant and poor seed set of the hybrid, essentially wasting female reproductive effort and eventually alleles of the native (Zaya et al. 2015). Invasive hybrids can invade from their native range, as exemplified by diffuse knapweed \times spotted knapweed (*Centaurea diffusa* \times *C. stoebe*) (Blair and Hufbauer 2010). Hybrids can also result when species introduced separately from allopatric or only minimally overlapping native ranges hybridize unaided once in close proximity in the invaded range, as is the case for hybrid toadflax (yellow or common toadflax \times Dalmatian toadflax) (*Linaria vulgaris* \times *L. dalmatica*) (Ward et al. 2009), Bohemian knotweed (*Fallopia japonica* \times *F. sachalinense*, also known as *F. bohemica*) (Walls 2010), and saltcedar or tamarisk (*Tamarix chinensis* \times *T. ramosissima*) (Gaskin and Schaal 2002).

Potential hybridization between non-native and native species that are similar in appearance, such as Oriental bittersweet and American bittersweet and Japanese angelica (*Aralia elata*) and devil's walking stick (*A. spinosa*), can be easy to overlook (Sarver et al. 2008). An expansion of what was thought to be the native devil's walking stick north of its traditional range has instead been confirmed as the non-native Japanese angelica, which can only reliably be distinguished from devil's walking stick by its inflorescence (Moore et al. 2009). This is another example where an invasive species may be outcompeting other native vegetation. Not only could the formation of new hybrids go undetected, managers could inadvertently remove native species or not treat invasive species because of misidentifications (Verloove 2010). The development of genetic barcodes, possibly involving the ITS2 region for morphologically similar species, may facilitate more reliable identifications in the future (Hollingsworth et al. 2011; Yao et al. 2010).

Though information on seed banks and germination requirements is lacking on many common invasive plants and native plants used for restoration of invaded sites, seed banks of various invasive plants have been estimated to range from none to a year (e.g., tree of heaven (Kostel-Hughes and Young 1998) and Amur honeysuckle (*Lonicera maackii*) (Luken and Goessling 1995)), between 3 and 7 years (e.g., Japanese stiltgrass (Barden 1987) and mile-a-minute weed (*Persicaria perfoliata*) (Hough-Goldstein et al. 2015)), to as long as 20 or more years (e.g., multiflora rose (*Rosa multiflora*) (Kay et al. 1995; Luginbuhl et al. 1999)). The cost implications in restoration involving invasive plants with long-lived (anything more than a year) seed banks are obvious. Plants possessing long-lived seed banks are often associated with more specific germination requirements; therefore, seed bank longevity of most invasive plants is likely to vary with site conditions (Huebner 2011; Kostel-Hughes and Young 1998). Likewise, successful restoration of a site requires knowledge of the site and any existing native seed banks as well as the ability to predict germination

rates and future regeneration of the native species that are being reintroduced. Unfortunately, an unintended outcome associated with using commercially produced native seed mixes for restoration purposes has been the inadvertent selection for particular genotypes which can negatively impact the genetic integrity of those species targeted for restoration (Dyer et al. 2016).

Not all discrete populations of a given invasive plant spread at equal rates, and understanding these differences will lead to more strategic management. For example, 33% of garlic mustard (*Alliaria petiolata*) populations have growth rates <1 (Evans et al. 2012). Given the relatively high variation in population growth rates, each invasive plant species and attendant strategy for control need to be considered separately. Ongoing and future detailed population studies of invasive plants that evaluate growth rates under varying biotic and abiotic conditions (topography, climate, soils, other species present) may show that some invasive plants die out on their own under certain conditions. For instance, older populations of Japanese stiltgrass show a decline in survival perhaps due to changes in the root fungal community (Cunard and Lankau 2017). In such cases, it might be more cost-effective to allow declining populations of these plants to go unmanaged, except for monitoring, so that active management efforts can be directed at populations that are expanding or spreading.

Over time, garlic mustard populations were found to select for conspecifics that released lower levels of allelopathic compounds (Lankau et al. 2009). Allelopathic suppression can be amplified in the invaded range, thus affecting overall plant community diversity (Ledger et al. 2015). Though field effects of noted allelopathic invasive plants (including tree of heaven, multiflora rose, Oriental bittersweet, and Japanese stiltgrass) on native species have not been documented (Pisula and Meiners 2010), allelopathic suppression of native species by Bohemian knotweed (the hybrid of Japanese and giant knotweed) was confirmed in field-based assessments in Europe (Murrell et al. 2011). Field-based allelopathic suppression by *Fallopia* spp. was determined to be only a contributing factor in the overall impact of *Fallopia* spp. on other plants in the United States (Siemens and Blossey 2007). The time since invasive plant introduction influences release rates, activity, and persistence of allelopathic compounds in the soil and also determines how frequently this novel weapon becomes consistently repressed among naturalized invasive plant populations of touch-me-not (*Impatiens glandulifera*) (Gruntman et al. 2016).

Evidence for the development of coevolutionary tolerance to allelopathic compounds produced by invasive plants in native plants and soil microbes has been reported for garlic mustard (Lankau 2010, 2012) and tree of heaven (Lawrence et al. 1991). Increasing tolerances may be the result of ame-

liorating effects of resident soil microbial communities; conversely, native species dependent on soil microbes can suffer negative indirect impacts when these microbes are affected by allelopathy (Cipollini et al. 2012). Evaluating evolving tolerances to allelochemicals under different site conditions might identify those soil microbial communities that are more likely to be protective against allelochemicals versus microbial communities that are more likely to be harmed by allelopathic compounds. Such responses are also likely to vary with the environment (soil type, topography, and climate) and thus be unpredictable and hard to incorporate into management plans.

Changes in soil chemistry can reflect the decomposition of invasive plant leaf litter containing highly concentrated nutrients. For example, tree of heaven is associated with high species richness beneath its canopy (Masaka et al. 2013), and this can be attributed to a facilitative effect of its high-nutrient, rapidly decomposing litter (Gomez-Aparicio and Canham 2008). Nitrogen-fixing species such as Russian and autumn olive (*Elaeagnus angustifolia* and *E. umbellata*) alter soil properties on marginal sites through the action of symbiotic actinorhizal associations that increase soil nutrients (DeCant 2008; Funk et al. 1979). One invasive species, Japanese stiltgrass, may indirectly facilitate the success of another invasive species, garlic mustard, by suppressing other plant species and thus increasing light availability (Flory and Bauer 2014). Increases in soil nutrients from invasive plants might facilitate their regeneration as well as native species leading to co-existence and changes in overall species composition in the community, instead of competitive exclusion of one or more native species.

Plant invasions alter species-area relationships such that larger invaded areas tend to have higher richness values than occur in uninvaded sites of similar size (Powell et al. 2013). This is due to a disproportionately greater impact of invasive plants on the abundance of common rather than rare native species. This finding supports the need to better understand how invasive plant species change plant community composition, rather than focusing on the extinction of native plants attributable to invasive plants (Gurevitch and Padilla 2004). The impacts of changing plant community compositions due to invasive plants are also evident at other trophic levels. For example, the abundance of native insectivorous and nectarivorous bird species decreased where the urban streetscape is dominated by non-native plants (White et al. 2005). Also, native insects have been shown to be in lower abundance on non-native plants than native plants (Zuefle et al. 2008).

Several invasive plants are known to have pathogens that impact their fitness. These include *Verticillium nonalfalfae* on tree of heaven and *Bipolaris* spp. on Japanese stiltgrass. Other pathogens do not appear to result in high mortality but help control the host plant species; these include powdery mildew (*Erysiphe cruciferarum*) on garlic mustard, rose

rosette disease on multiflora rose, and soybean rust (*Phakopsora pachyrhizi*) on kudzu (*Pueraria lobata*) (Flory and Clay 2013). In addition, many invasive plants show signs of herbivory caused by several species of insects or other invertebrates. For example, the *Ailanthus* webworm can cause extensive defoliation of the invasive tree of heaven. However, many invasive plants demonstrate greater tolerance toward generalist herbivores than associated native plant species (Jogesh et al. 2008). A better understanding of the collective role of pathogen and predator species accumulation on invasive plants may assist managers in predicting if and when certain invasive plants could become less of a threat. It has been suggested that many of these “volunteer” pathogens might be suitable for use as biocontrol agents. However, the potential impact of these organisms on native species needs to be determined before they can be considered for release.

The claim that invasive plants are successful invaders because they are more plastic may only be true in the initial stages of an invasion after which selection for optimal phenotypes is likely (Palacio-López and Gianoli 2011). Thus, attempting to define general traits that determine invasiveness is not likely to be productive, because such traits will vary with the environment and the stage of invasion. Competing and/or facilitative co-occurring plants, herbivores, pathogens, and symbionts may or may not co-migrate in response to a changing environment (Van der Putten et al. 2010). Models that incorporate these interactions will better predict future invasive plant distributions in response to global change. For example, tree of heaven has shown signs of evolving since its invasion, evidenced by the fact that its current range has expanded beyond the climatic range predicted from its native distribution (Albright et al. 2010). Range expansion is likely to be common among invasive plant species. Understanding the length of time required for range expansion to develop, what species interactions may be linked to this expansion, and the ability of an invasive plant to evolve into a new range in response to a changing climate will improve our success in managing current and future plant invasions.

Some invasive plants facilitate the presence of other invasive plants. The term “invasional meltdown” has been used to describe sites that are composed of invasive species that facilitate each other’s sustained presence at an increasing rate of establishment (Green et al. 2011; Rodriguez-Echeverria 2010; Simberloff 2006). Such complex interactions across the same and different trophic levels may make it exceptionally difficult to restore plant communities that are predominantly composed of invasive species. There may be cases where manipulation of one invasive species, which serves as an analogous “keystone” species, may improve the likelihood of restoring native species because removal of the former may have a domino effect on other invasive plants.

Outcomes of these varied considerations are additional inputs required for establishing priorities in invasive species management (Box 7.2).

7.4.5 Invasive Terrestrial Vertebrates

While a system-wide approach is often most desirable for managing invasive species (Mack et al. 2000), the most impactful invasive vertebrates represent diverse taxa that each require specific approaches, thus making it difficult to render generalizations about their management and control. Strategies often must be tailored to specific attributes of species' natural history or behavior. Some of the most threatening invasive terrestrial vertebrates are presented in Table 7.4.

The natural history of most vertebrate species has been well-understood for many years. Some invasive vertebrate groups were intentionally introduced and have been well-established for many years (e.g., horses (*Equus caballus*), cats (*Felis catus*), and swine (*Sus scrofa*)); however, feral populations cause substantial economic and ecological damage. Most recent work has been directed at either understanding impacts or testing control technologies such as evaluating various chemical or fertility control drugs. Recent advances in understanding the ecology of certain species and in improving the technological capacity of traps have enhanced the efficacy of trapping as a control tool. For example, Sparklin et al. (2007) reported evidence that matriarchal social groups of feral swine ("sounders") are territorial (i.e., they defend a home range against other sounders). This means that more effective control may be achieved on large tracts by trapping whole sounders while systematically moving across the area (Sparklin et al. 2007). The mechanics of

whole-sounder trapping have recently been facilitated by technological advances in trap designs. Historically, feral swine were captured in small corral traps with a gate that closed when a pig feeding on bait in the trap hit a tripwire or similar trigger mechanism. Any pigs not yet inside the enclosure when the gate closed were not only not captured, they also became educated as to the danger of the trap and were much more difficult to capture in future encounters. Traps now available from several manufacturers employ motion-sensing cameras and cellular technology to either send photographs (via text message) or livestream video of pig activity in the trap. Trappers then can activate the trap with a wireless command whenever they choose to do so. Thus, the trapper controls activation of the trap, not the pigs. Additional research is needed to confirm both the degree of territoriality in feral swine under variable resource conditions and the effectiveness of whole-sounder trapping.

7.4.6 Invasive Aquatic Animals

Invasive species scenarios can unfold rapidly in aquatic systems through a variety of transmission pathways and can result in ecosystem-altering effects (Penaluna et al. 2017). Aquatic invasive species are in a very high rate of flux, with many taxa in apparent early stages of invasion, many being highly managed to prevent their attaining a foothold in regional waters, and others having been more established and expanding their distribution. Some of the most damaging invasive aquatic organisms are listed in Table 7.5.

Research is progressing to understand ecosystem responses to aquatic invasive species, including food web alterations, and the ecological potential and ramifications for biotic homogenization. Warmwater aquatic invaders appear to have become more established in many ecosystems (Sanderson et al. 2009); therefore with projections of climate change, the distributions of many warmwater species are expected to increase in certain regions (e.g., with latitude and elevation) (Perry et al. 2005). Current modeling efforts are directed at identifying cool-water refuges for native aquatic species that are unlikely to be subject to such invasions (USDA Forest Service 2017) and examining climate niches of aquatic invasive species known to have adverse effects on native systems. These activities should aid managers in establishing monitoring priorities (e.g., Olson et al. 2013).

7.4.7 Key Findings

- Many non-native species established in the United States are not economic pests in their native range, and, initially, little is known about their biology, ecology, host interac-

Table 7.4 Significant invasive vertebrates and management approaches^a in the United States

Common name	Scientific name	Management approaches ^b
Rats	<i>Rattus</i> spp.	PC, TS, CC
House mouse	<i>Mus musculus</i>	PC, TS, CC
Nutria	<i>Myocastor coypus</i>	TS, CC
Feral cat	<i>Felis catus</i>	PC, TS, R
Feral horse	<i>Equus caballus</i>	PC, TS, R
Feral swine	<i>Sus scrofa</i>	PC, TS, R
Rock pigeon	<i>Columba livia</i>	PC, TS, R
European starling	<i>Sturnus vulgaris</i>	PC, TS, R
House sparrow	<i>Passer domesticus</i>	PC, TS
Nile monitor	<i>Varanus niloticus</i>	TS
Burmese python	<i>Python molurus</i>	TS
Brown treesnake	<i>Boiga irregularis</i>	TS, CC

^aManagement approaches listed are not "recommended"; rather, they are a summary of approaches that have been studied and may also be used in some operational invasive species management programs

^bPC physical control, TS trap/shoot, CC chemical control, R reproduction control

Table 7.5 Significant invasive aquatic organisms and management approaches^a in the United States

Common name	Scientific name	Management approaches ^b
Asian carp	<i>Hypophthalmichthys nobilis</i> (bighead carp); <i>Mylopharyngodon piceus</i> (black carp); <i>Ctenopharyngodon idella</i> (grass carp); <i>Hypophthalmichthys molitrix</i> (silver carp)	RC, PC
Spiny waterflea	<i>Bythotrephes longimanus</i>	RC
Sea lamprey	<i>Petromyzon marinus</i>	RC, CC
Zebra mussel	<i>Dreissena polymorpha</i>	RC, CuC
Chinese mitten crab	<i>Eriocheir sinensis</i>	RC, PC
New Zealand mud snail	<i>Potamopyrgus antipodarum</i>	RC, PC, CuC, CC, BC

^aManagement approaches listed are not “recommended”; rather, they are a summary of approaches that have been studied and may also be used in some operational invasive species management programs

^bRC regulatory control, PC physical control, CuC cultural control, CC chemical control, BC biological control

tions, and ecological and economic impacts nor management.

- There has been considerable progress in understanding the life cycle, genetics, host range, dispersal, semiochemical communication, and host interactions of many significant invasive insects, diseases, plants, vertebrates, and aquatic organisms.
- There have been recent advances in developing molecular techniques that are needed to identify new invasive species, characterize their lineages and distributions, and determine their country of origin.
- Significant advances have been made in analytical chemistry for identifying semiochemical attractants for insects that can be used for detection and monitoring.
- Sophisticated methods have been developed and used for determining rates of spread of invasive pests including the use of insect flight mills, aerial survey for inoculum and disease spread, and dispersal models for invasive pests.
- Progress has been made in understanding environmental and spatial factors that influence the risk of invasion.
- Significant advances have been made in understanding mechanisms of plant and animal resistance to diseases.
- Progress has been made in understanding plant mating and breeding systems, including how dioecy and hybridization influence genetic variation and resistance.
- Knowledge has been gained on the impact of allelopathic compounds produced by invasive plants and how they influence native plants and soils.

7.4.8 Key Information Needs

- Understanding interactions between native and invasive species, elucidating impacts of invasives on the abundance of native species and the ecosystem affected, and ascertaining if coexistence can be facilitated and is an evolutionary stable strategy
- Additional information on the accumulation and impacts of native and introduced natural enemies on invasive insects and plants
- Greater understanding of the etiology and epidemiology of emerging disease complexes
- Information on polyploidy, dioecy, and mating systems of plants necessary to manipulate reproduction, inbreeding, timing of control, and herbicide resistance
- Greater understanding of how environmental factors and soil microbial communities influence allelopathic compounds released from invasive plants and how these compounds impact native plants
- Greater understanding of how characteristics of population ecology and behavior of vertebrate invasive species can be utilized to improve their control

7.5 Approaches to Management of Invasive Species

Approaches to manage invasive species and specific control tactics used (Fig. 7.1) may vary by the general type of invading organism, whether in terrestrial or aquatic ecosystems (see Table 7.6). Some management approaches are effective for several taxa in different ecosystems, while others are practical only for certain kinds of invasive species. For instance, outreach and education are critical components of management programs for all invasive species taxa. Similarly, the application of pesticides is used across all invasive species taxa. Regulatory control is used for invasive insects, pathogens, terrestrial wildlife, and aquatic organisms, but is not as effective for control of invasive terrestrial or aquatic plants. Biological control using natural enemies is used operationally primarily for both invasive insects and plants. Vaccination control is only practical for protecting wildlife from invasive pathogens and is not used operationally for management of other invasive taxa. Similarly, reproduction control is used primarily for invasive insects or wildlife and has limited practicality for managing invasive pathogens or plants. Developing hosts resistant to invasive pests is a management approach used against invasive insects and pathogens, but is not practical for managing plants or wildlife that invade ecosystems rather than specific host trees. Table 7.6 provides a general overview of management approaches that are operationally used for each invasive taxonomic group. A more detailed discussion of management approaches and

Table 7.6 Operationally used invasive species management approaches by invader type^a

Invader type	Regulatory	Outreach and education	Physical	Cultural	Chemical or pesticidal	Biological	Vaccination	Host resistance	Reproduction	IPM ^b
Insects	X	X	X	X	X	X		X	X	X
Pathogens of trees	X	X	X	X	X			X		X
Pathogens of wildlife	X	X	X	X	X		X			
Terrestrial plants		X	X	X	X	X				X
Aquatic plants		X			X					X
Terrestrial wildlife	X	X	X		X		X		X	
Aquatic organisms	X	X	X	X	X		X		X	

^aManagement approaches listed are not “recommended”; rather, the table presents a summary of management approaches that are currently used

^bIPM = integrated pest management

examples of how they are used for specific invasive species or taxonomic groups is provided in subsequent sections.

Selection of the optimal combination of management approaches and tactics depends on the management goals and objectives, economic and ecological priorities, the invading species and its impacts, available tools, and ecosystem interactions.

7.5.1 Regulatory Control

Regulatory control is a society-based strategy designed to exclude or monitor pathways that are available for introducing an invasive species into a suitable habitat or ecosystem. State and Federal seed certification programs provide verification that seeds are free of pests such as insects, plant pathogens, and even unwanted plant seed (AOSCA 2016). Plant quarantines established by the Federal Government, States, or other countries restrict the movement of items that may result in movement of unwanted invasive species within or among states, or into the United States (see Chap. 6). Best management practices (see Sect. 7.5.4 below) developed by users or commodity groups often become regulatory controls (USDA NAL 2016).

Implementing regulations is one of the first and most effective measures available to reduce further spread and impacts of established populations of invasive pests (Liebhold et al. 1992; Vander Zanden and Olden 2008). Several significant invasive insects are regulated by Federal or State quarantines that restrict movement of the insects and any potentially infested host material including firewood, nursery stock, logs, chips, and cuttings. Other examples of regulatory control measures include inspection and removal of gypsy moth egg masses from outdoor household articles transported out of regulated areas (USDA APHIS 2010) and removal and destruction by chipping, grinding, or burning of

trees infested by emerald ash borer (Poland and McCullough 2006), hemlock woolly adelgid (NHDFL 2015), and Asian longhorned beetle (Meng et al. 2015). Research is being conducted on new regulatory treatments for infested wood, including vacuum or microwave treatment (see Chap. 6). Adaptations of regulatory policies to cover soil potentially infested with fire ants, root-knot nematode, and other pests such as invasive earthworms have been researched and are being proposed to prevent their introduction (Callahan, Jr. et al. 2006). The Pennsylvania Department of Agriculture established an internal quarantine restricting the movement of many commodities to evaluate options for managing spotted lanternfly following discovery of the insect.

Regulatory approaches are perhaps more commonly used for most recent introductions of invasive species (e.g., sudden oak death, rapid `ōhi`a death (*Ceratocystis A*, *Ceratocystis B*), and spotted lanternfly) rather than for long-established species (e.g., Dutch elm disease, white pine blister rust) that are widely distributed.

Many invasive plants are so widespread that regulatory control is impractical. Consequently, only 4 of the 79 common invasive plants in the United States listed in Table 7.3 are also listed as Federal noxious weeds (USDA NRCS 2016a). According to the Federal Noxious Weed Act, if species included on the Federal Noxious Weeds List are discovered, active management and adequately funded management programs must be implemented against them (FNWA 1974). Individual States vary greatly in how they categorize invasive plants and how they define those categories. Many States prohibit planting or selling the species, but do not require their active management. They may refer to these species as invasive rather than noxious. However, some States also use the term “noxious,” but use of the term only prohibits seed of these species from contaminating other seed supplies and does not require their removal or management. California, Massachusetts, Oregon, and Washington have more compre-

hensive lists of noxious weeds than those occurring in most of the other States (USDA NRCS 2016b), but this does not correlate with the occurrence of more invasive plant problems in other States. Indeed, Maryland has one of the shortest lists of noxious weeds (USDA NRCS 2016b), yet has a very active invasive species council that provides a much longer list of invasive species of concern (with no regulations associated with them); a similar situation exists in several other States. Consistency among the States on how they define and code regulations would assist scientists in evaluating the effectiveness of such regulations.

Range expansion of feral swine has occurred because swine are transported illegally and intentionally released in new areas in order to establish populations suitable for hunting (Mayer and Brisbin 1991). In response, several States have established or are considering tighter regulations for controlling the transport of swine as well as educating hog hunters.

Pet trade and quarantine regulations may aid in preventive management of animal diseases such as amphibian chytridiomycosis, a disease caused by a fungal pathogen (Liu et al. 2013; Stokstad 2014). The US Fish and Wildlife Service published an interim rule declaring 201 non-native salamander species as injurious wildlife under the US Lacey Act (Federal Register Docket No. FWS-HQ-FAC-2015-000; GPO 2017; USFWS 2016). A petition to include all live amphibians in trade as injurious unless certified as free of the causative fungal pathogen is also under review.

Some aquatic invasive species have status listings as nuisance or injurious species because they pose adverse effects on native ecosystems or local economies; some of these species are being targeted for significant regulatory control efforts (see Penaluna et al. 2017). The USDA highlights some aquatic nuisance species (USDA NAL 2017), and the US Fish and Wildlife Service identifies several aquatic species as injurious and covered under the Lacey Act (GPO 2017; USFWS 2017b). Aquatic invasive species trigger cross-jurisdiction considerations due to the occurrence of common waterways. Significant resources are expended to control some aquatic invasive species. For example, in the Pacific Northwest, invasive species councils are well-established in British Columbia, Canada, and the US States of Alaska, Oregon, and Washington, and each council addresses both pathways of spread and control of infestations. In Washington State, the 2015 Report to the Legislature (WDFW 2015) reported results from 2011 to 2013, which included (1) >27,000 boat inspections, with decontamination of 83 boats that contained aquatic invasive species, of which 19 boats had zebra or quagga mussels (*Dreissena bugensis*),

and (2) 6 new infestations of New Zealand mud snails (*Potamopyrgus antipodarum*). Despite region-wide efforts, some species are recognized as requiring continuous management, whereas for others, effectiveness of control methods is poor. As a result, some invasive species seem to be fully established.

Purposeful introductions of non-native aquatic species has been a norm throughout the world, because these actions have served to promote ecosystem services of local societies, such as food provisioning, recreation, pest control, and general well-being. For example, the introductions of the European brown trout (*Salmo trutta*) into South America (Soto et al. 2006) and New Zealand (Townsend 1996) and the eastern mosquitofish (*Gambusia holbrooki*) into Australia (Hamer et al. 2002) were intentional. However, we now know that these introductions have subsequently caused major reductions in native fauna, including fish, amphibians, and invertebrates (Townsend 1996; Wissinger et al. 2006). Similar adverse effects on native amphibians and other ecosystem components have been exacerbated by fish-stocking practices common throughout the United States (see reviews by Dunham et al. 2004; Kats and Ferrer 2003). Throughout the Western United States, forested lakes at higher elevations that were devoid of fish have been intentionally stocked with game fishes such as the brook trout (*Salvelinus fontinalis*), which is native to Eastern North America (Macneale et al. 2010).

In the United States, States have key jurisdiction over fish-stocking practices, and their practices have come under increasing scrutiny because State stocking of fish occurs in wildlands and affects native species including some that are threatened or endangered (T&E). For example, in California, a court-ordered moratorium was placed on non-native fish stocking of numerous water bodies due to risks to native species including those listed T&E species (CDFW 2010). Additionally, recovery efforts for the California golden trout (*Oncorhynchus mykiss aguabonita*) in the Kern Plateau of the Sierra Nevada range have included not only a moratorium on non-native fish stocking but also additional efforts to remove non-native trout (which hybridize with or prey on golden trout) by using chemical treatments and installing barriers to prevent upstream migration into golden trout habitats (Pister 2008). Stocking practices continue in other areas, however, due to the strong desire to provide positive fishing experiences. Additionally, modifying fish harvest regulations designed to increase predation pressure on invasive aquatic species such as the Asian carp species (Cyprinidae) (Hein et al. 2006; Tsehaye et al. 2013) has been effective at reducing the abundance of some invasive aquatics.

7.5.2 Outreach and Education

Besides legal or regulatory approaches, human behavior can also be influenced to manage invasive species through efforts involving outreach and education. These efforts are conducted to increase awareness of quarantines and regulations, reduce introduction and spread of invasive species, aid in identifying and reporting new detections, facilitate rapid response, and enhance support and successful implementation of control tactics. Education and outreach are components of management responses at all stages of the continuum from strategies to approaches and to tactics (Fig. 7.1). This extension of information contributes to the success of programs for prediction and prevention of invasive species, early detection, rapid response, management, and restoration. Informing and engaging the public on invasive species issues is one of the first opportunities to disrupt the progression of invasions by preventing the introduction and spread of non-native species (see Chap. 6). In managing established populations of invasive species, education and outreach tools are used across all taxonomic groups. Outreach and education can be accomplished in a myriad of ways using various media outlets to increase understanding of controversial issues that may surround approaches to manage invasive species and to increase public support for management programs and enhance their success. These engagement and communication efforts are critical to the success of cooperative management programs. While the overall management approach and optimal combination of tactics are specific to particular invasive species and ecosystems, public outreach and education are important components of management across all categories of invasive species.

Invasive species management programs can be controversial and in some cases have been delayed or halted because of opposition from organized groups (Warner and Kinslow 2013). For example, criticism and petitions from community members over aerial applications of pheromones for the eradication of light brown apple moth (*Epiphyas postvittana*) in California led to the eventual suspension of the aerial spray program and an overall change in management tactics (Ben-Haim et al. 2013). Public support can be critical to the success of management projects, and understanding the underlying attitudes of the public can help in development of outreach education activities. The level of support for control and eradication programs was generally higher among people who had prior knowledge of control and eradication projects and members of conservation organizations, indicating the important role of awareness and education in increasing public support for invasive species management projects (Bremner and Park 2007). The Pennsylvania Department of Agriculture implemented an extensive and

effective outreach program to inform affected citizens and businesses on available detection, identification, and control methods of spotted lanternfly. This program engages property owners in egg scraping, tree banding, trap tree establishment, host removal to kill all life stages, and reporting any findings (PDA 2019).

Public outreach in practice contributes to the success of regulatory control programs by enhancing awareness of quarantines and compliance with regulations (Peterson and Diss-Torrance 2012; Warner and Kinslow 2013). For example, major campaigns have been implemented that included radio and television advertisements, billboards, bumper stickers, and social media to stop the movement of firewood that may harbor invasive insects and pathogens (Poland and McCullough 2010). Pest alerts, brochures, identification cards, “wanted” posters, doorknockers, fliers, and identification kits containing pest and damage specimens have been distributed with the intent to educate the public to be on the lookout for and to report major insect pests such as the Asian longhorned beetle and emerald ash borer (Haack et al. 2002).

Cooperative Weed Management Areas (CWMA), Partnerships for Regional Invasive Species Management (PRISM), and Invasive Plant Partnerships (IPP), all hereafter referred to as CWMAs, have become common in many States, with some States, like New York, dividing the entire State area into CWMAs. Some CWMAs are actually CWPMA (Cooperative Weed and Pest Management Areas) and incorporate all invasive pests and not just plants as a focus. All of these CWMAs are partnerships of Federal, State, and local government agencies, tribes, individuals, and interested groups who manage invasive species in a defined area (MIPN 2016). The goal within these management areas is to engage all private and public landowners across a common landscape or watershed to enhance cooperation and communication and facilitate more effective management of invasive species (CISM 2016). Outreach and education are essential activities that can promote effective cooperation and communication of science-based approaches that are included in CWMA management plans.

Invasive vertebrates are perhaps unique in that they include species which, though highly impactful ecologically, enjoy considerable support among the public (Witmer et al. 2007) which often objects to their lethal control, no matter how humane the euthanasia may be or how destructive the damage is (Simberloff 2014). For example, feral horses and feral cats can be removed relatively easily as compared to many other species, but objections based on ethical, emotional, cultural, and historical grounds require that alternative approaches are used such as fertility control (Kirkpatrick et al. 1982). Unfortunately, while fertility control may limit population growth, it often permits existing problems to per-

sist. Control of vertebrate invasives is further complicated by the fact that the public generally does not distinguish between native and non-native animals, particularly if they fail to experience immediate or direct impact from damage (Witmer et al. 2007). Since most introductions of non-native vertebrates are a result of anthropogenic activity, educational and regulatory approaches to prevent such introductions are critical. For example, many reptiles and amphibians are now established in Florida as a result of accidental or intentional releases of pets (Reed 2005). While increased regulation of the pet trade may help in preventing future releases, education of the public is also important. The Florida Fish and Wildlife Conservation Commission conducts an annual Python Challenge (FFWCC 2016), a competition in which members of the public compete to capture (and remove) the most and largest Burmese pythons (*Python molurus bivittatus*). However, the objective of the challenge is not focused on population control but rather to direct attention to the issue of invasive pythons and consequently enhance public awareness and participation (Dorcas et al. 2017).

Public outreach and education are also important in the management of invasive aquatic animals. This may include posting signs at vulnerable areas, providing brochures that explain the issues, initiating programs in schools to educate youth, launching workshops at environmental centers to inform the public, and encouraging professional aquatic biologists to spread the word through face-to-face encounters with the public. For example, the “Don’t Turn it Loose” brochure, produced by Partners in Amphibian and Reptile Conservation, is available online and has been distributed nationwide (PARC 2016). These efforts are linked to cultural changes involving past practices that previously were not known to cause damage to native ecosystems. In addition, continuing education programs and online training courses are available to assist professionals in learning about newly developed approaches (USDA NRCS 2016c). Online outreach tools are continually being developed and incorporate rapid response plans, which are critical in preventing non-native aquatic species introductions.

Humans are responsible for much of the overland movement of aquatic animals among waterways (Buchan and Padilla 1999). Consequently, management activities intended to stop the movement of invasive aquatic animals must incorporate efforts to influence and manage human behavior. Research in the field of social science is investigating the influence that outreach, education, and law have on risky behaviors associated with the spread of invasive aquatic animals. High-risk behaviors include releasing unwanted pet fish or unused live bait fish into the wild (Drake and Mandrak 2014) or failure to decontaminate boats and gear when moving from one body of water to another (Puth and Post 2005; Rothlisberger et al. 2010). Multiple studies indicate that, to

date, efforts have been insufficient to reduce high-risk behaviors to acceptable levels (Drake et al. 2015; Kilian et al. 2012; Nathan et al. 2014; Prinbeck et al. 2011).

Live bait used for fishing has been linked to introductions of both non-native species and diseases (e.g., Ranavirus on salamanders in the bait trade; Picco and Collins 2008). Similarly, with the increase in residential water gardens and non-native pets, a variety of aquatic invasive species can be spread inadvertently (Keller and Lodge 2007). The pet trade along with schools (biological laboratory classes) have also been sources for introduction of non-native aquatic species (Larson and Olden 2008). Possibly a combination of such practices has led to the introduction of nine non-native freshwater turtles to Hawaii, where effects on native biota are increasing as aquatic communities are changing. In conclusion, there has been increased awareness of the adverse effects associated with releases of non-native species. Hopefully, education and outreach campaigns will be effective in forestalling these practices in the future.

7.5.3 Physical Control

Physical control is defined in this chapter as either mechanical methods of physically removing invasive species (e.g., hand-pulling small invasive plant infestations before flowering, mowing plants, trapping and removing or shooting terrestrial invasive animals) or physically precluding them from areas. Erecting barriers to prevent invasive species access to a protected stand, ecosystem, or water course is another example of controlling spread.

Controlling insects by physically removing them or using barriers to prevent their movement is difficult and often impractical due to the small size and cryptic nature of many species, large population numbers, and the ability to disperse rapidly over great distances by flight. At the individual tree or local level, burlap bands, sticky bands, glues, oils, or grease applied to the stems of trees may be used as physical barriers to prevent movement of caterpillars such as gypsy moth (Thorpe and Ridgway 1994) that crawl up from the ground to infest the tree canopy. Invasive insects such as Asian longhorned beetle may also be controlled by physically removing and chipping or burning infested trees (Meng et al. 2015). Physical control is the primary method employed to control spotted lanternfly. The trap tree/host removal method shows that populations are significantly reduced in the areas where tree removal and trap tree treatments have been conducted (Parra et al. 2017).

Several invasive plants are controlled by combining a physical control (fire, cutting, girdling, or mowing) with a chemical application. In many cases, cutting or top-“killing”

(e.g., after a burn) the plant often leads to prolific sprouting or root suckering. However, a few invasive plants can be controlled on a local level by physical control alone. Examples include garlic mustard (a biennial herb) via hand-pulling before seed production (Chapman et al. 2012) and Japanese stiltgrass (a shade-tolerant annual grass; Shelton 2012) and tall oatgrass (*Arrhenatherum elatius*, a perennial grass) (Wilson and Clark 2001) via intensive (very close to the ground) mowing prior to seed production. Conversely, whereas mowing has little effect on yellow bluestem (*Bothriochloa ischaemum*, a perennial grass of Texas prairies), a growing-season fire significantly reduces its abundance (Simmons et al. 2007).

Exclusion of invasive animals, particularly ungulates including swine and horses, via fencing has been used to mitigate damage and protect sensitive resources. Likewise, rodent damage can be minimized by using a combination of exclusion, sanitation, and habitat manipulation (Witmer et al. 2007). The use of sound devices to frighten wildlife tends to be effective only for limited periods because animals habituate to the stimulus (Bomford and O'Brien 1990). However Mahjoub et al. (2015) reported that a nonlinear ultrasonic parametric array effectively created a sonic net that repelled European starlings (*Sturnus vulgaris*). Repellents such as taste-aversive agents have been explored with varied success, mainly for use against ungulates including feral swine and horses. However, the benefits of such physical approaches are localized spatially and temporally and may serve to defer or shift the damage.

Lethal control, exemplified by trapping or shooting, is the most frequent approach used to manage many vertebrate and aquatic invertebrate invasive species. Use of baited wire-muskrat traps was more effective at reducing the most reproductive crayfish than use of predatory fish (Hein et al. 2006). Even among species such as rodents on which chemical control is used, trapping can be an important supplemental tool; however, in most cases, it has only achieved short-term population control because surviving animals become trap shy.

Shooting, either aerially from a helicopter or from the ground over baited traps, is an approach frequently used for feral swine, while shooting over bait is an effective method used to control nutria (*Myocastor coypus*) (LeBlanc 1994). Newer technologies such as night-vision and thermal optics have enhanced the efficiency of such operations (McCann and Garcelon 2008).

Some species have been controlled successfully using the Judas animal approach (McIlroy and Gifford 1997), wherein a radio-marked individual of the target species is released into a control area and subsequently tracked, directing managers to other individuals which may then be euthanized. Campbell et al. (2005) described an improved sterilization procedure for both male and female Judas goats (*Capra hircus*) that allowed for preservation of normal sex-

ual behavior (but not function) and hence drive to locate conspecifics. Similarly, preliminary evidence suggests that Judas pythons may enhance direct capture and control of Burmese pythons in Florida (Dorcas and Willson 2011; Dorcas et al. 2017).

Physical control measures have been implemented for control of aquatic invasive fauna and flora, and in some situations, citizen involvement can increase the scope of efforts. Common methods used for manual removal of fish include angling and netting. For bullfrogs (*Lithobates catesbeianus*), shooting, spears/gigs, bow and arrow, clubs, traps, and hand capture have been used, and removal of egg clutches can be effective in depleting populations over time. For aquatic plant control, manual removal can be effective; however, it can be costly in terms of time and effort involved. Furthermore, the resultant fragmentation of plants may also increase their spread.

7.5.4 Cultural Control

Cultural control refers to activities conducted by humans during the culture or management of the resource of concern with the intent to minimize the likelihood of establishment, spread, or build-up of invasive species. As used in this chapter, cultural control may include steps taken to avoid an invasive species (e.g., not planting susceptible trees on a site known to have a particular invasive insect or plant pathogen of concern) or manipulations of growth designed to maintain overall health and vigor of the resource being protected, e.g., forest trees, grassland, rangeland, wildlife, wetlands, and bodies of water.

Silvicultural thinning, increasing stand diversity, improving tree vigor, and urban tree care have been shown to reduce tree vulnerability to gypsy moth (Gottschalk 1993). Hemlock woolly adelgid density was found to be highest on seedlings grown in dense shade and decreased with increasing light; therefore, silvicultural treatments that increase light exposure might reduce hemlock woolly adelgid abundance (Brantley et al. 2017). Thinning mixed hemlock-hardwood stands may also improve tree vigor and growth of hemlock (*Tsuga* spp.) trees, thereby altering their foliar chemistry to make them less vulnerable to infestations by hemlock woolly adelgid (Fajvan 2008; Piatek et al. 2016). Sirex woodwasp infests only stressed or weakened pines, so removal of stressed trees, pre-commercial thinnings, and other silvicultural treatments that improve tree vigor can reduce the incidence of damage (Dodds et al. 2007). Healthy hemlock trees are able to withstand higher infestations of hemlock woolly adelgid than trees with low vigor (McClure 1995); therefore, mulching and irrigation can be used to help improve tree health (Ward et al. 2004). Submerging emerald ash borer-infested black ash (*Fraxinus nigra*) logs in running water for

at least 3 months kills the larvae inside, preserves the wood for use in Native American basket-making, and may help prevent spread of the beetle when logs are transported to tribal lands for basket-making ceremonies (Poland et al. 2015).

Cultural approaches are critical to management of disease epidemics (e.g., Dutch elm disease, white pine blister rust, oak wilt) and are also important in management of new invasive diseases (e.g., sudden oak death). For example, effectiveness of using a vibratory plow to sever connected roots and thus prevent belowground spread of the oak wilt fungus was evaluated over a period of 6 years in 25 mixed hardwood infection centers. Results indicate that spread was stopped in 84% of the treated centers for 4–6 years (Juzwik et al. 2010). Two sanitation options were also evaluated to reduce the potential for aboveground transmission of the pathogen by insects. Annual removal of wilted red oaks (*Quercus* spp.) within the outermost root-cutting line during the same year of plowing would have resulted in 64% fewer removals than a strategy that required felling of all red oaks (healthy or diseased) inside the outermost line (Juzwik et al. 2010).

Recent advances have been made in understanding and implementing habitat modification to control mosquito populations that vector West Nile virus. Cultural controls include sanitation involving removal of tires or other sources of standing water that serve as breeding sites for larvae and the use of pumps, culverts, and networks of shallow ditches for seasonal water flow management in marshes and wetlands that allow ecosystem function but reduce mosquito reproductive habitat (Floore 2006). Removing invasive trees and shrubs mitigates degradation of habitat and reduces breeding habitat for mosquitoes and is also a component of a program to conserve the greater sage-grouse in Montana and Wyoming (Walker et al. 2007). In comparing effects of native versus non-native shrubs on the ecology of a common vector of West Nile virus, *Culex pipiens*, leaf detritus of the invasive shrubs Amur honeysuckle and autumn olive were linked to higher adult mosquito emergence rates, while leaf litter from native blackberry (*Rubus allegheniensis*) functioned as an ecological trap because it was found to be correlated with high rate of oviposition but low adult emergence rates (Gardner et al. 2015). Trapping protocols were evaluated to determine if presence and abundance of West Nile virus-vectoring mosquitoes could explain the 2003 die-off of American white pelican chicks (*Pelecanus erythrorhynchos*) at Medicine Lake National Wildlife Refuge in northern Montana. Results indicate that significantly more West Nile virus-infected mosquitoes were associated with shelterbelts comprised of mixed dense stands of invasive Russian olive and caragana (*Caragana arborescens*) than in marshy or grassland habitats (Friesen and Johnson 2013).

Cultural control of white nose syndrome of bats includes modifying bat hibernacula environments to eliminate the dis-

ease pathogen and increase bat survival (modifying temperature and humidity, providing alternate sources of food and water, and treating hibernacula with chemical or biological control agents), conserving genetic diversity of bats to increase development of immunity and resistance, and reducing human-assisted dispersal of the disease-causing fungus by decontaminating clothing and equipment for anyone planning to enter areas where bats hibernate (e.g., US Fish and Wildlife Service National White-Nose Syndrome Decontamination Protocol – Version 04.12.2016; WNS DT 2016). Culling heavily diseased individual bats or populations was also proposed, but disease models suggest this approach may not be effective (Hallam and McCracken 2010).

Management of amphibian chytridiomycosis may involve several activities which include environmental manipulation, controlling amphibian introductions, and deploying ex situ conservation efforts to reduce the disease-causing bacteria in the environment and on hosts or to increase population buffering capacity (Scheele et al. 2014). Temperature control has also been tested to control the fungus causing amphibian chytridiomycosis. Four of five studies found that increasing water temperature eliminated infection from amphibians (Sutherland et al. 2015).

Regeneration of many native plant species in several US forest types, including most eastern forests, is accomplished by increasing the quantity of light reaching the forest understory and reducing competition from other species and often occurs following a harvest, fire, or both. Such disturbances, depending on their severity or frequency, increase the likelihood of invasion by non-native plants (Haeussler et al. 2002; Nelson et al. 2008). However, a disturbance can be so severe in some community types that the affected site is resource-limited and is more likely to be colonized by native species than by non-native plants (Hebel et al. 2009). Defining light and competition levels (and corresponding harvesting and burn frequencies) that will promote regeneration of native species but deter invasion of non-native species is needed for all forest types.

Invasion by non-native plants may occur primarily from unsustainable land management practices that have resulted in a seed bank depleted of native seed and the loss of native plant species because they are the most merchantable or most preferred by herbivores such as deer (Cervidae) or cattle (*Bos taurus*) (Beauchamp et al. 2013; DiTommaso et al. 2014). Several studies have demonstrated that most non-native plant species are not preferred forage. Though this may change with time (e.g., Japanese honeysuckle is now a preferred deer food), controlling deer alone (e.g., via fencing) may reduce current and future invasions by non-native plants. It may require decades to realize an effect, but evidence shows that non-native species decline in abundance (DiTommaso et al. 2014; Kalisz et al. 2014) and depleted

native species may recover (Tanentzap et al. 2009). Likewise, overgrazing by cattle and sheep (*Ovis aries*) may be prevented by rotating sites used for pasture and by fencing these pastures. Abandoned grazing areas that were overgrazed often become an epicenter for new plant invasions. Depending on the condition of the site and the type of grazer, simply removing the animals may not prevent invasions. For example, adding goats has proven to be effective at controlling several invasive plants, and removing goats has been detrimental to some systems (Zavaleta et al. 2001). Conversely, removal of feral sheep and cattle from Santa Cruz Island (beginning in 1981, with full eradication thought to have been achieved by 1997) initially resulted in increases in exotic fennel (*Foeniculum vulgare*) and yellow star-thistle and only a slight increase in one of the native species (Klinger et al. 1994, 2002). However, passive recovery 28 years after the removal of the feral sheep from Santa Cruz Island shows a transition from non-native plants to native woody vegetation (Beltran et al. 2014).

Changes in logging severity, fire intensity or frequency, or grazing pressure should incorporate best management practices aimed at preventing the introduction of invasive plant propagules. Plant propagules may be reintroduced via contaminated equipment used in a previous harvest or burn (Bryson and Carter 2004; Westbrooks 1998), transport of seed in animal dung via animal rotations from contaminated pastures (Bartuszevige and Endress 2008), and use of contaminated hay as forage (Bryson and Carter 2004; Westbrooks 1998) or gravel for road cover (Christen and Matlack 2009; Mortensen et al. 2009; Westbrooks 1998). Adoption of best management practices (that are not regulations) by private landowners may be enhanced by providing economic incentives. Matta et al. (2009), using a multinomial logit model, conducted a landowner survey which estimated that most private forest landowners would require an incentive of \$95.54 per ha per year to voluntarily participate in a program using best management practices that were not required at that time (2009).

For invasive aquatic plants, divers can remove some early infestations of submerged plants by hand or with hand tools. Smothering or shading with mats or bottom barrier materials can be used to control smaller patches of invasive aquatic plants such as yellow floating heart (*Nymphoides peltata*) (DiTomaso et al. 2013). Mechanical removal of aquatic invasive plants (see Haller 2014) can be achieved by deploying boats with skimmers to remove surface-growing plants such as hyacinth (*Hyacinthus* spp.) and salvinia (*Salvinia molesta*), boats with lawnmower-like blades to mow or harvest plants, and/or rotovators (large aquatic rototiller) and dredges. In a comprehensive review by Sutherland and others (2015) as part of the Conservation Evidence project that summarizes information from 156 conservation journals, removal of two invasive aquatic plants (swamp stonecrop (*Crassula helmsii*)

and reed canary grass (*Phalaris arundinacea*)) was found to increase abundance of native amphibians.

Habitat manipulation is a frequently used approach to forestall the adverse effects of aquatic invasive species on native species. Draining wetlands or reducing water levels is one approach used for both plants and animals (Hine et al. 2017; Hussner et al. 2017). Reducing wetland levels before summer or prior to extreme winter conditions can expose unwanted plants (e.g., Eurasian watermilfoil (*Myriophyllum spicatum*), Brazilian elodea (*Egeria densa*)) to freezing or drying conditions that can kill them (Haller 2014).

7.5.5 Chemical or Pesticidal Control

Chemical or pesticidal control of invasive species involves the use of natural or synthetic chemicals or microbial agents to prevent infestation, eliminate populations, reduce damage and impacts, or slow the spread by significantly reducing the population.

The use of insecticides is a very effective means of controlling many invasive insects if the insect can be effectively brought into contact with the applied material. Research is conducted to evaluate pesticide efficacy, delivery method(s), translocation within hosts, fate in the environment, and impacts on other species. Systemic insecticides applied by trunk or soil injection or basal bark sprays can provide control of emerald ash borer (McCullough et al. 2011) and hemlock woolly adelgid (Cowles and Cheah 2002; Whitmore 2014) in urban or high-value landscape trees but are not practical for large-scale management of forest stands. Similarly, horticultural oil or insecticidal soap sprays have been found to be effective in reducing hemlock woolly adelgid populations on accessible trees but are not practical at the forest landscape level (Cowles and Cheah 2002; McClure 1995). Systemic insecticides are generally ineffective in controlling ambrosia beetles such as shot hole borer and redbay ambrosia beetle; however, prophylactic spraying of bark may help prevent attacks on individual trees (Peña et al. 2011). Contact insecticides applied as a bark drench have been evaluated for controlling the crawler stage of balsam woolly adelgid (*Adelges piceae*) but must thoroughly drench the insect which is fairly well hidden on the tree, so it is not feasible for aerial spray or broad forest application (Ragenovich and Mitchell 2006). Rapid testing of insecticides to control spotted lanternfly resulted in the registration of several products for spotted lanternfly control in Pennsylvania (PSE 2019).

The microbial insecticide *Bacillus thuringiensis* var. *kurstaki* (*Btk*) and the gypsy moth nucleopolyhedrosis virus product Gypchek are used to manage gypsy moth populations (Elkinton and Liebhold 1990; USDA 2012). Aerial sprays of *Bt_k* are used to eradicate isolated populations and

control gypsy moth over large suburban or rural areas. Gypchek is highly specific to gypsy moth but can only be produced by infecting larvae; therefore, it is not mass produced commercially and is only available through the Forest Service for limited applications (Podgwaite 1999). Both chemical and microbial insecticides are also used to control mosquitos that vector West Nile virus or Zika virus.

Use of pesticides against invasive pathogens of trees and other plants is not common in forests and wildlands. Rather, they are used on a small spatial scale within higher-value landscapes where economics or other values justify its use (e.g., Dutch elm disease, oak wilt, sudden oak death). For example, the systemic fungicide potassium phosphite has been widely used in California on high-value landscape trees as a bark spray (with or without a bark penetrant) applied to lower trunks of *Quercus* species to suppress sudden oak death development in trees newly infected with *P. ramorum* or to prevent infection of “at-risk,” healthy trees (UCB FPM Lab 2017). In a current long-term study, potassium phosphite is being evaluated for its potential to protect tanoaks from *P. ramorum* in forest settings (Phytosphere Research 2013). This treatment has also demonstrated efficacy in protecting avocado, pineapple (*Ananas comosus*), and cocoa (*Theobroma cacao* L.) crops as well as jarrah (*Eucalyptus marginata*) (Pegg et al. 1990).

Chemical control is commonly used for management of invasive plants infesting small areas of refuges or other protected areas. Conducting research to identify the safest and most effective herbicides to control existing and new invasive plants is an ongoing need as are standardized protocols for systematically surveying and testing for herbicide resistance. Yellow star-thistle has developed resistance to four auxin inhibitors, including triclopyr (Miller et al. 2001), and hydrilla has developed resistance to fluridone, which inhibits carotenoid biosynthesis (Michel et al. 2004). Invasive plants that produce numerous seeds or spores and have long-distance dispersal are most likely to develop herbicide resistance after repeated applications. Most invasive plants have these characteristics. Likewise, the acetolactate synthase (ALS) inhibitor herbicides, which are commonly used in invasive plant management in natural areas and include imazapyr, imazapic, and metsulfuron-methyl, are the most likely to develop resistance in natural areas because they have shown the highest resistance development in agricultural settings (Hutchinson et al. 2007). With increasing use of herbicides in natural areas to combat invasive plants and the repeated use of the same herbicides, many of which are ALS inhibitors, the development of resistance is likely but could be prevented with the use of proper protocols. Such protocols may include developing multiple herbicides in different herbicide families that can be used in rotation to prevent herbicide resistance (Hutchinson et al. 2007). However, the rotational use of

multiple herbicides on public lands requires approval under National Environmental Policy Act (NEPA) guidelines. Control of invasive plants may require applications in consecutive years. However, the impacts of herbicide on nontarget species may also increase with the frequency of herbicide application, especially if they are applied at intervals of less than 4–5 years (Crone et al. 2009; Huebner et al. 2010). The acceptable number of herbicide applications requires a delicate balance between reducing the abundance of the non-native species and ensuring that treatments do not eliminate native species. Ideally, applied research should be combined with basic ecological assessments such as competition and demographic studies to define optimal application rates and timing of treatments.

Rodenticides have been used extensively to control invasive rats (*Rattus* spp.) and mice (*Mus musculus*), particularly on islands where extirpation is achievable. Anticoagulants such as brodifacoum are the most widely used option for treatment. Howald et al. (2007) reviewed the literature on attempts to eradicate invasive rodents on islands worldwide and reported that 332 of 387 attempts were successful. Acetaminophen baits have been shown to be effective for controlling brown treesnakes (*Boiga irregularis*; Savarie et al. 2001), although methods for optimal delivery continue to be investigated (Lardner et al. 2013).

Although no registered toxicants are currently available for use against feral swine in the United States, development is ongoing, and US Environmental Protection Agency (EPA) registration is being sought (Snow et al. 2016). Sodium nitrite, developed and licensed for use in Australia and New Zealand, works through binding hemoglobin and causing death from methemoglobinemia, which causes rapid depletion of oxygen to the brain and vital organs. Nitrite toxicosis is considered to be humane (Cowled et al. 2008; IMVS 2010; Shapiro et al. 2015), and the risk of secondary toxicosis to nontarget species is slight (Lapidge et al. 2012). Sodium nitrite baits are delivered using specialized feeding stations that are designed to minimize or prevent access by nontarget species (Campbell et al. 2013; Lapidge et al. 2012). However, additional research is needed to further evaluate and minimize nontarget effects.

Sylvatic plague is a rodent-associated, flea-borne disease of animals caused by the gram-negative bacterium *Yersinia pestis* that can be transmitted to humans. The disease affects nonurban wildlife including the endangered black-footed ferret (*Mustela nigripes*), an obligate predator of highly plague-susceptible prairie dogs (*Cynomys* spp.) (Jachowski et al. 2011). Management of plague-vectoring fleas has emerged as a significant factor in the conservation of endangered species. Reintroduction efforts for black-footed ferret are dependent on developing tools to control plague vectors that affect prairie dogs. Initial treatments focused on applications of insecticidal deltamethrin dust (DeltaDust® – Bayer

Environmental Science, Montvale, NJ) and targeted fleas in prairie dog burrows (Biggins et al. 2010; Bodenchuk et al. 2013; Dinsmore 2013). Insecticidal treatment of prairie dog burrows affected the food supply of a ground-nesting insectivorous bird, the mountain plover (*Charadrius montanus*), which preferentially nests on prairie dog colonies. Treatments effectively lowered nest survival because adults spent more time away from nests searching for prey or were forced to switch to lower-quality insect prey. Jones et al. (2012) determined that dusting not only allowed black-tailed prairie dogs (*Cynomys ludovicianus*) to persist in plague-affected areas during epizootics but also generated refugia of genetic diversity in treated colonies. Furthermore, the increased survival of resident and immigrant individuals created a more robust base population for reestablishing old colonies or starting new colonies.

Although numerous control techniques are available for use in aquatic ecosystems, once an invasive animal is established, eradication is rarely attained and meaningful control is often achieved only at great expense (Johnson et al. 2009a, b). For example, control of the sea lamprey (*Petromyzon marinus*) in the Laurentian Great Lakes using the lampricide TFM (3-trifluoromethyl-4-nitrophenol) costs more than \$20 million each year and is an ongoing annual expense that is required to keep sea lamprey populations at levels sufficient to minimize their predation on valuable sportfish (Hansen and Jones 2008). Research is progressing to develop innovative control techniques for controlling multiple high-impact aquatic invasive animals, including zebra and quagga mussels (Meehan et al. 2014) and Asian carp species (Zielinski and Sorensen 2016); methods include the application of pesticides such as rotenone and antimycin to kill invasive fish (Sato et al. 2010).

Numerous pesticides are registered for use against unwanted aquatic species. A total of 45 chemicals were identified as piscicides and are listed in a US Geological Survey report (USGS 2017). The most effective pesticides available for removing invasive fish include antimycin and rotenone, though these products may not fully remove adequate numbers of unwanted individuals. For example, rotenone was used at Diamond Lake in Oregon in 2006 to remove the invasive tui chub (*Gila bicolor*) which had been adversely altering the lake ecosystem (Finlayson et al. 2014).

Applications of herbicides and algicides are well-established treatments used to control aquatic invasive plants. Fourteen herbicides are registered for use in US aquatic systems (Netherland 2014). Foliar spray treatments are useful for free-floating plants such as water lettuce (*Pistia stratiotes*) or salvinia; however, systemic herbicides can be more selectively administered and can be more effective. In Washington, invasive Japanese knotweed has been controlled along watercourses using herbicidal mixtures, and application methods include stem injections or foliar spray incorporating glypho-

sate, imazapyr, and vegetable oil (Claeson and Bisson 2013). Altering salinity has been used in some circumstances. Reducing available nutrients is an approach available in the broader portfolio of methods used to control algae (Lembi 2014).

There is concern about the potential for the inadvertent spread of aquatic invasive species and diseases when water is drawn for wildfire management or other uses (Olson et al. 2013), transferred from fish hatcheries for stocking of non-native fishes, or used for transportation of people and supplies. Treatment of water with ammonia compounds or bleach has been instituted in some regions to forestall such disease transmission (Olson et al. 2013; USDA FS 2016).

7.5.6 Biological Control

Biological control, or biocontrol, is essentially using living organisms to reduce the numbers of pest organisms, the goal being to achieve sustainable and targeted management of the pest or invasive species. Biological control agents frequently involve insects (e.g., predators or parasitoids), but selected microorganisms such as fungi, bacteria, and viruses may also be utilized. Biological control is one of the more successful methods available for achieving long-lasting, widespread, and environmentally safe management of invasive species. Biological control is sustainable, selective, and cost-effective, and its use may successfully avoid the ecological and economic collateral damage often associated with pesticides (Rinella et al. 2009; Suckling and Sforza 2014; Van Driesche and Hoddle 2016). Developing biological control programs requires a significant investment in basic and applied research which includes exploring for natural enemies, developing rearing and release methods for selected biological control agents, evaluating impacts on nontarget species, monitoring the establishment of the released agent, and assessing control of the pest and the level of protection provided to host plants (Van Driesche et al. 2008).

Biological control has been used for many invasive forest insects (Van Driesche and Reardon 2013). For example, foreign exploration, collection, mass rearing, and release of insect and microbial biological control agents to manage the gypsy moth and brown-tail moth (*Euproctis chrysorrhoea*) began in the early 1900s and continued into the 1970s. More recently, three species of wasps were discovered parasitizing emerald ash borer in its native range in China, and following extensive host-specificity testing, these species were approved in 2007 for release in the United States. They are currently being mass reared, released, and evaluated in long-term studies to determine their impact on emerald ash borer populations and ash tree health (Bauer et al. 2015). A fourth parasitic wasp from Russia was also approved for release

beginning in 2015 (USDA APHIS 2015) and is currently being reared and released.

Biological control agents have also been evaluated for their efficacy against the Asian longhorned beetle; however, host-specificity screening indicates that several of these species that were recovered from the pest's native range have a broad host range and may have an impact on nontarget species in North America (Meng et al. 2015). Beetle predators of the hemlock woolly adelgid have been released widely to achieve biological control, and their establishment and efficacy are currently being evaluated (Havill et al. 2014). Similarly, beetle predators from Europe have been introduced for biological control of balsam woolly adelgid (MacQuarrie et al. 2016). Augmentative biological control of siren woodwasp using a nematode, *Deladenus siricidicola*, has been very successful in confining siren woodwasp infestations to small localized areas in Australia (Carnegie et al. 2005); however, in North America, differences in species and strains of nematodes and their associated fungal symbionts have been shown to affect their virulence and efficacy as biological control agents. Considerable research is currently underway to better understand these complex interactions (Morris et al. 2012). Entomopathogens, including nuclear polyhedrosis virus (NPV) and the fungus *Entomophaga maimaiga*, can cause significant mortality in gypsy moth populations. Climatic factors that favor the development of fungal epizootics, and methods to release infected gypsy moth larval cadavers, have been investigated (Siegert et al. 2012; Smitley et al. 1995) with intent to optimize the use of this pathogen for biological control of gypsy moth populations. *Ooencyrtus kuvanae* (Howard) (Hymenoptera: Encyrtidae), an egg parasite of spotted lanternfly, was discovered in Pennsylvania in 2016 (Liu and Mottern 2017). The parasite was introduced in 1908 for gypsy moth control and is known to attack multiple host species. An unidentified species of native Dryinidae (solitary wasp) parasitized spotted lanternfly nymphs in Pennsylvania, and an unidentified fungus that was found infecting nymphs is being identified (Parra et al. 2017).

Major success stories in biological control point to the great potential this tool holds for controlling invasive plants at a landscape scale (Seastedt 2015; Van Driesche et al. 2002). The use of biological control agents against invasive plants includes some fungi such as rusts (Hasan and Ayres 1990) and herbivorous insects (McFadyen 1998). However, biological control agents sometimes fail to impact weed populations even where they become established. The worldwide success rate of projects using biological control attempts against invasive plants is estimated at 20–30% (Crawley 1989; Raghu et al. 2006; Van Driesche et al. 2010; Van Klinken and Edwards 2002), as compared to 62% of projects that achieved complete control of target invasive

arthropods (Van Driesche et al. 2010). More recently, Cock et al. (2016) found the overall success rate for complete biological control of invasive insects was 10% and has been declining since the 1970s, while the number of introductions of classical biological control agents has decreased. Ineffective biological control agents, even if host-specific, can persist and may cause unwanted ecological effects (Pearson and Callaway 2003, 2005, 2006, 2008; Pearson and Fletcher 2008; Ortega et al. 2004; but see Van Driesche and Hoddle 2016). The practical application of biological control is universally challenged by difficulties in understanding (e.g., quantifying and/or verifying) single and interacting factors that influence its success or failure and predicting the efficacy of individual agents (Carson et al. 2008).

Host specificity of potential biological control agents may influence the success of biological control and potential for adverse impacts on nontarget organisms. The ability to test for and predict host specificity of herbivores has improved greatly in recent decades (Sheppard et al. 2005). However, our ability to predict efficacy of agents has not followed suit, and consequently it's currently not possible to predict with confidence if a biocontrol agent will reduce populations of the target pest once released. Several avenues of research can advance the science of biocontrol and improve its efficacy. These include (1) choosing an appropriate target plant, (2) selecting the best biocontrol agent using genetics and chemical ecology, and (3) understanding and exploiting climate change effects.

Selecting an appropriate target plant is important because recent work suggests that some plant species are more amenable to biocontrol than others. The enemy release hypothesis (Elton 1958) underlies the theory of biocontrol and proposes that non-native species transplanted outside of their native range thrive because they leave most or all of their natural enemies behind (Keane and Crawley 2002; Müller-Schärer and Schaffner 2008). Thus, biological control is most appropriate for use against plants that are "released" from their natural enemies in the invaded range, though these conditions are not usually fully demonstrated because of limited studies in the native range (Hierro et al. 2005). Other recent work indicates that plant traits could be used to predict plant species most amenable to biological control. For example, "easy targets" for biocontrol are those species that are not known to become overly abundant or negatively impactful in their native range, i.e., asexual species and/or species that occur in aquatic or wetland habitats (Paynter et al. 2012). Naturally, some invasive plants are more likely to be successfully controlled using biological control, but uncertainty exists in identifying susceptible (and unsusceptible) target plants.

Identifying, prior to release, which agents are most likely to be successful in reducing the abundance of invasives is

critical for successful biological control (McFadyen 1998). Recent advances in genetics and chemical ecology have shown promise in improving agent selection. Molecular approaches have significantly contributed to the resolution of taxonomic issues associated with both target plants and candidate biological control agents (Gaskin et al. 2011; Goolsby et al. 2006). Genetic diagnostics have also allowed us to pinpoint the geographic origin of invasive plants (Gammon and Kesseli 2010; Gaskin et al. 2013a, 2013b; Tarin et al. 2013; Williams et al. 2005) and to reconstruct routes of invasion (Buckley and Catford 2016; Estoup and Guillemaud 2010; Le Roux and Wieczorek 2009). This knowledge is essential to properly test the enemy release hypothesis and can guide the search for effective biocontrol agents. This can be especially critical when local adaptation results in herbivores and especially pathogens that have become highly host-specific to certain populations or genotypes. Examples of these include Brazilian peppertree (*Schinus terebinthifolius*) (Cuda et al. 2012; Diaz et al. 2015; Manrique et al. 2014), rush skeletonweed (*Chondrilla juncea*) (Campanella et al. 2009), and invasive knotweeds (Grevstad et al. 2013).

Plant-insect chemical ecology has only recently been applied to weed biological control (aside from host-specificity testing, which is based largely on plant chemistry). Chemistry plays a central role in determining ecological outcomes between plants and insects and should provide information that can be used to better predict those candidate agents that are most likely to be effective (Wheeler and Schaffner 2013). For example, hybridization may function as an extreme example of hypothesized evolution of increased competitive ability, whereby plants introduced into new areas in the absence of natural enemies evolve reduced allocation to costly chemical defenses, which then allows them to increase allocation to growth and/or reproduction (Blossey and Nötzold 1995). In hybrid plants, heterosis (hybrid vigor) resulting in increased allocation to growth and reproduction can be associated with novel phytochemistry, which produces confusing signals for biocontrol agents coevolved with either of the hybrids' parental species (Hubbard 2016).

Evidence suggests that some types of herbivores will be positively affected by climate change, whereas others will be negatively affected (Robinson et al. 2012; Runyon et al. 2012). Similarly, climate change will likely affect biological control responses due to phenological differences in responses of hosts and biological control agents to changes in temperature (Reeves et al. 2015). These changes could potentially be exploited in biocontrol, for example, by focusing on agents that respond most positively to climate change (see Chap. 4).

Research is underway to investigate the use of biological control against invasive diseases of terrestrial vertebrates. Cornelison et al. (2014) found that the ubiquitous soil-associated gram-positive bacterium *Rhodococcus rhodo-*

chrous strain DAP 96253 demonstrated potential for biological control of the white nose syndrome in bats by inhibiting conidial growth of the fungus in infected tissues.

Although highly desirable, biological control has not been widely used in managing invasive diseases of trees. The mycoparasitic species complexes of *Clonostachys* and *Trichoderma* have been shown to be effective against *Crinipellis royeri*, a fungal disease of cocoa in Ecuador (Evans et al. 2003). Infecting the chestnut blight fungus (*Cryphonectria parasitica*) with hypoviruses (namely, *Cryphonectria hypovirus* 1 (CHV-1), CHV-2, CHV-3, and CHV-4) has proven effective against chestnut blight in some locations in Europe and in Michigan (MacDonald and Fulbright 1991), but has failed almost completely in the Eastern United States possibly due to vegetative incompatibility among host individuals that prevents the virus from spreading (Milgroom and Cortesi 2004). Biological control of *Heterobasidion* root disease (*Heterobasidion annosum*) has been achieved by exclusion of sugar resources on freshly cut stumps by a native decay fungus, *Phlebiopsis gigantea* (BioForest Technologies 2016).

Biological control agents being considered for various invasive aquatic plants include mollusks, fungi, carp, and invertebrates such as moths, thrips, mites, and chironomid midges (Van Driesche and Bellows 1996). Beetles are the dominant insects being used for biological control of aquatic plants (Cuda 2014; Cuda et al. 2014). Aquatic predators have been considered as biological control agents, but their lack of prey specificity may restrict their utility. In 2016, the predaceous sterile hybrid tiger trout (female brown trout \times male brook trout (*Salmo trutta* \times *Salvelinus fontinalis*)) was evaluated as a control measure for reinvasion by tui chub and golden shiner (*Notemigonus crysoleucas*) at Diamond Lake, OR (Carroll and Miller 2016).

7.5.7 Vaccination

Vaccines involve the treatment (e.g., via oral or direct injection) of host organisms with killed microorganisms or attenuated strains of the invasive disease organism (e.g., bacterium, virus) to render the potential host immune or only mildly susceptible to infection and development of disease.

Recent efforts to conserve black-footed ferret populations have focused on developing a sylvatic plague vaccine and delivery system for prairie dogs (Abbott et al. 2012; Rocke et al. 2010). A vaccine, which is in the final phases of field testing for animal safety and efficacy, uses recombinant raccoon poxvirus (RCN) to vector proteins of *Y. pestis*, F1 and V, already approved for use in a human-injectable plague vaccine (Rocke et al. 2014). The vaccine is delivered in a palatable (peanut butter-flavored) bait matrix incorporating

rhodamine B, a biomarker used to track uptake (Fernandez and Rocke 2011; Tripp et al. 2014).

Vaccines and immunomodulators are also being used to increase resistance of bat populations to white nose syndrome (Lilley et al. 2017) and to treat island scrub-jays (*Aphelocoma insularis*) that occur only on Santa Cruz Island and are susceptible to infection by the mosquito-vectored West Nile virus (Boyce et al. 2011).

Vaccination and application of antifungal or probiotic agents were categorized as having low or moderate effectiveness against amphibian chytridiomycosis (Grant et al. 2016). Booroolong frogs (*Litoria booroolongensis*) infected with an isolate of the disease-causing fungus, treated with itraconazole, a triazole fungicide, to clear infection, and then re-exposed to the fungus did not acquire immunity from the initial exposure, suggesting that a vaccine is unlikely to be effective (Cashins et al. 2013).

Aquatic invasive species that are emerging infectious diseases are candidates for control using vaccination. To date, most attempts to use vaccination for control have been directed against farmed fish and widespread diseases (Gudding et al. 1999) that are not considered aquatic invasive species. Research is continuing in this area.

7.5.8 Host Resistance

Resistance is a result of genetic traits of the potential host species (e.g., tree, terrestrial animal) that render it mostly “immune” to the invasive species, results in tolerance of attack or infection by the invasive species, or is manifested as a morphological barrier to infestation by invasive species infestation (Fritz and Simms 1992).

Host resistance, if it exists, can be propagated in populations across the landscape, can be an effective long-term defense against invasive pests, and can serve as a tool for restoring impacted landscapes (see Chap. 8 for more details). Although all North American ash species encountered by emerald ash borer to date may be infested, relative preferences and susceptibility vary among species and appear to be related to differences in volatiles, nutrition, and defense compounds (Chen and Poland 2010; Chen et al. 2011; Cipollini et al. 2011; Pureswaran and Poland 2009; Whitehill et al. 2012). Within an ash species, some individual “lingering” ash trees persist in stands where all of the surrounding ash trees have succumbed to emerald ash borer within 5–6 years. Asian ash species typically have higher levels of resistance than North American species, and this trait may have a role in developing a resistance breeding program for our native ash species. Traditional and hybrid breeding programs have been utilized to select, screen, and develop

ash cultivars that exhibit increased resistance to emerald ash borer (Koch et al. 2012) (see Chap. 8). Foliar chemistry has been linked to hemlock infestation and susceptibility to hemlock woolly adelgid (Pontius et al. 2006), and the relative resistance of North American hemlock species as compared to Chinese hybrids has been evaluated (Montgomery et al. 2009).

Identification of resistance and selection or breeding for resistant species, phenotypes, or genotypes generally is a most common strategy for use against widespread, long-established invasive pathogens whose resultant diseases have broad geographic distributions. Within genetically diverse populations of trees, there can be a small number of individuals that exhibit some level of resistance to invasive diseases (see Chap. 8 for more details). Silvicultural strategies aimed at decreasing the proportion of susceptible individuals in a stand, and, therefore, increasing the proportion of resistant individuals, can, in some cases, be an effective tool for use in disease management. Single tree selection and removal of American beech (*Fagus grandifolia*) trees actively infected with beech bark disease resulted in an 11.5% increase in disease-free (apparently resistant) basal area 50 years after treatment (Leak 2006). The basal area of trees with *Neonectria* infection decreased from 67% in the untreated stands to 27% in the treated stands, indicating that removing susceptible trees may have also decreased the level of fungal inoculum (Leak 2006). Beech bark disease is caused by an introduced scale insect (*Cryptococcus fagisuga*) that provides a pathway for entry for the bark canker pathogens (*Neonectria ditissima* and *N. faginata*). Proteomic investigation of scale-resistant and scale-susceptible trees in eight geographically isolated stands led to the discovery that different protein profiles occurred in diseased and healthy trees (Mason et al. 2013). Further study of these proteins is underway with the goal of developing biomarkers that will aid managers in identifying and retaining resistant trees and removing susceptible trees as a preemptive measure to minimize the impacts of beech bark disease.

Increasing resistance of native species to infection by an emerging invasive infectious disease is a relevant topic for continuing research. For example, it was discovered that a complex microbiota appears to be interacting on amphibian skin and that some species have a controlling effect on these disease microbiota. Amphibian skin harbors symbiotic resident bacteria that possess antifungal properties that are being examined for their potential to combat the amphibian chytridiomycosis fungus. The probiotic bacteria *Janthinobacterium lividum* is thought to provide some resistance to the chytridiomycosis fungus and is being tested for that purpose in susceptible frogs (Bletz et al. 2013).

7.5.9 Reproduction Control

Reproduction control involves using a natural or synthesized chemical or genetic manipulation to impede or prevent mating or development of offspring in the invasive species population. Reproduction control includes tactics such as mating disruption of invasive insect species using pheromones or controlling fertility in terrestrial invasive vertebrates.

Mating disruption is used to eradicate or slow the spread of sparse gypsy moth and control brown apple moth populations by applying female mating pheromone to saturate the environment and thus interfere with male location of females (Leonardt et al. 1996; Soopaya et al. 2015; USDA 2012). Sterile insect release of irradiated males has been attempted for control of gypsy moth (USDA 2012) and light brown apple moth (Stringer et al. 2013), but is challenging due to reduced reproductive fitness of irradiated insects and is not practical for most invasive forest insects which are difficult to mass rear. Recent novel approaches for control of invasive fish involve the intentional release of genetically modified fish that are designed to disrupt reproduction of target invasive fish species (Kapuscinski and Sharpe 2014). This involves manipulating the chromosomes to skew sex ratios, or using recombinant DNA techniques to insert damaging genes into the genome of target invasive fish to disrupt the reproductive cycle, or a combination of both (Thresher et al. 2014).

Immunocontraceptives have been evaluated for population control in several species of invasive vertebrate pests (Fagerstone et al. 2010). OvoControl® P is an oral contraceptive approved by the EPA for use on rock pigeons (*Columba livia*). Vaccines such as gonadotropin-releasing hormone (GnRH) and porcine zona pellucida (PZP) are used in mammals such as feral horses and feral swine. A single dose of GnRH vaccine can render an animal infertile for 1–5 years (Killian et al. 2008; Massei et al. 2008). However, while such approaches enjoy greater public support than using toxicants and other lethal methods, their use has been limited due to the high costs associated with delivery as compared to other methods and the relatively low effectiveness and length of time required to achieve population reduction (Massei et al. 2011). This technology might be most appropriate on islands or other areas where immigration and emigration are limited.

7.5.10 Integrated Pest Management Programs

Integrated pest management (IPM) is the optimization of several pest control methods in an economically and ecologically sound manner. In natural ecosystems, it is an environ-

mentally based strategy that focuses on attaining long-term efficacy by deploying a combination of tactics in a compatible manner to maintain pest damage below an economic threshold, while protecting against hazards to humans, animals, plants, and the environment. IPM may involve use of several techniques such as biological control, habitat manipulation, cultural practices, pesticides, and resistant varieties incorporated into a unified program. IPM requires clear articulation of management goals, knowledge of the pest and its impacts on the ecosystem, technology to monitor the presence and abundance of the pest, guidance on when management is worthwhile, a suite of complementary tools and strategies to affect the abundance and/or reduce impact of the pest, and the methodology to evaluate the success of interventions.

IPM programs have been developed for several invasive forest species and many agricultural pests. The gypsy moth Slow the Spread program is currently the largest and most successful IPM program in the United States for managing the spread of an invasive forest pest (Sharov et al. 2002) and is recognized as a model approach for managing invasive species. A grid of pheromone-baited traps is deployed to detect the presence of adult male gypsy moths just ahead of the advancing front of the generally infested area. Analysis of the pattern of moth captures is then used to identify areas that require treatment. The network of traps identifies new infestations of gypsy moth that are well below population densities that cause defoliation; therefore management has the option to apply specific treatments aimed to eliminate or reduce sparse populations, such as trapping, mating disruption, and application of microbial pesticides such as *Btk* and gypsy moth nucleopolyhedrosis virus. The overall success of the program can be attributed to the integrated and coordinated involvement by the Forest Service, USDA Animal and Plant Health Inspection Service (APHIS), State plant pest regulatory officials, and State foresters. The project is managed at the landscape level and focuses use of standardized protocols for data collection and analysis, decision-making, and allocation of funds across all States and agencies that participate in the project (Sharov et al. 2002).

The Hemlock Woolly Adelgid Initiative also utilizes an integrated and coordinated approach to manage this invasive pest, which is currently established in 19 eastern States (Ferguson et al. 2013). Research identified the geographic region or country of origin of eastern US hemlock woolly adelgid populations, and then foreign explorations were conducted to locate candidate natural enemies that could be considered for release to control local hemlock woolly adelgid populations. The program utilizes insecticides to protect hemlocks while biological control agents become established and is investigating levels of pest resistance among hemlock species in the infested area (Onken and Keena

2008). SLOW Ash Mortality (SLAM) is an integrated program for managing the emerald ash borer (Mercader et al. 2015; Poland and McCullough 2010). This program uses a combination of detection and monitoring traps, tree removal, systemic insecticides, biological control, and behavioral modifications with clusters of girdled trap trees to achieve a greater level of control. In a large-scale multiagency pilot study of the program in an area over 350 km², both girdled trees and insecticide treatments reduced emerald ash borer densities and protected ash trees in areas surrounding the treatments. Model results indicated that emerald ash borer spread rates were reduced from areas with girdled trees. Trees treated with the systemic insecticide also reduced larval abundance in subsequent years (Mercader et al. 2015, 2016). The Pennsylvania Department of Agriculture has developed and implemented a pest management strategy to suppress the spotted lanternfly population focusing on the core of the infested area and working outward using the trap tree/host removal method as well as pesticide applications. This approach has not been fully validated, but preliminary results show that lanternfly populations are significantly reduced in the areas where trap tree/tree removal treatments have been completed (PDA 2019). Success of large-scale IPM programs requires support from residents and landowners in the affected area and can be attained by fully informing the public about the program goals, methods used, and anticipated results. Success also requires a commitment to a sustained level of resources over time. Research is also needed to evaluate and model the success of these programs.

Successful management of individual species of invasive plants requires that knowledge exists about which treatments are effective against particular species; however, many sites are invaded by multiple species of invasive plants or are surrounded by adjacent populations of non-native plants in the landscape. Success in controlling one invasive species often facilitates invasion by another invasive plant. Consequently, it's necessary to be able to predict how multiple species are likely to respond to the removal of one or more invasive plant species (Kuebbing et al. 2013).

It may not be economically feasible to restore some plant communities that incur invasional meltdowns (as discussed in Sect. 7.4.1), and even removal of some invasive plants could cause more damage than good. For example, the removal of the non-native saltcedar (*Tamarix* spp.) may initially impact the federally endangered southwestern willow flycatcher (*Empidonax traillii*), because in degraded and invaded habitats, saltcedar can serve as important habitat for the flycatcher, though some *Tamarix* stands are unsuitable (Schlaepfer et al. 2011; Sogge et al. 2008; York et al. 2011; USFWS 1997). Other examples of non-native species with potential new conservation value are non-native plant species used to reclaim coal mine grasslands which serve as habitat for Henslow's sparrow (*Ammodramus henslowii*) in

Indiana (Bajema et al. 2009), melaleuca (*Melaleuca quinquenervia*) which provides habitat for snail kite (*Rostrhamus sociabilis*) in the Everglades (Chen 2001), and European legume gorse (*Ulex europaeus*) which protects the endangered New Zealand weta (very large stenopelmatid orthopterans) from predators (Gibbs 1998) and serves as a nurse plant for native forest regeneration if grazing is stopped (Sullivan et al. 2007). These examples do not negate the well-documented harm these non-native invasive plants can do in other settings. Indeed, they may both provide a service and cost. For instance, melaleuca also decreases the primary food source for the kite (Chen 2001), and regeneration with European legume gorse as a nurse plant results in a successional trajectory toward lower species richness (Sullivan et al. 2007). Some plant communities that experience meltdown, especially those occurring in urban areas, are often labeled as novel communities. These communities are so different from the original after invasion that recovery is deemed unlikely. More importantly, the communities now appear to serve an ecosystem service (benefits provided by ecosystems including food and water, regulating climate and disease, providing nutrient cycling, crop pollination, or recreational values), because few if any other species could grow in some of these sites. In some situations, removal of non-native species could harm native species that are now dependent on services or resources provided by the non-native species (e.g., native birds using non-native shrubs as nest sites, native pollinators using non-native plants to forage for pollen or nectar) (Schlaepfer et al. 2011). The willingness to allow the existence of some non-native communities, and accept coexistence between non-native and native species, is termed "conciliation biology" (Carroll 2011). Ecological and economic costs associated with conciliation biology can be estimated, and these data would provide additional input for prioritizing invasive species management efforts (Box 7.2).

Ecosystems and invasive plants may be best managed as part of a landscape mosaic composed of dynamic land uses (Chabrierie et al. 2007; Vila and Ibanez 2011). These uses may help move invasive plants (corridors and disturbed patches), while others may serve as barriers (actively cultivated agricultural land and large uninvaded forest patches). It is also a social landscape in which some landowners who choose not to control or prevent the occurrence of an invasive species may serve as the source of invasion for other landowners. In order to successfully manage invasive plants, knowledge of the landscape spatial composition, landscape ecology, management and design, and coordinated control and prevention efforts must be shared among the various affected landowners (Epanchin-Niell et al. 2010). This is a goal of most CWMA's, but it is not clear how successful such organizations have been. Without documentation of success, it is not possible to evaluate the value of applying economic

incentives to further successful management (Hershendorfer et al. 2007).

A combination of harvesting, fire, herbicide application, strategic grazing, deer control, and/or biocontrol may be the key to ensure that sustainable forests, grasslands, rangelands, and wetlands avoid large damaging invasions by non-native plants. It may be possible to reduce the negative impacts on nontarget species attributed to repeat applications of herbicides, or prescribed burning, by rotating their application. Biocontrol treatments, when available, may be the best initial step to decrease plant population abundance where large non-native plant populations occur. In situations where invasive plants are less abundant or not widely distributed, repeat applications of herbicide may not be needed. More detailed information on the efficacy of each biocontrol agent (percent reduction in population size and spatial patterns of establishment) in different environments will help to define management objectives. For instance, garlic mustard populations are most impacted (63% reduction in population size) by a root-mining weevil (*Ceutorhynchus scrobicollis*) because it attacks both the rosette and flowering stages; adding a stem-attacking weevil (*C. alliariae*) reduced the overall population by 88% (Evans et al. 2012). Likewise, the strategy for releasing a biocontrol agent may be dependent on the distance between patches or populations of the invasive plant, as well as the micro-physiography of each patch (Pratt et al. 2003). The application of multiple biocontrol agents may be needed in sites that contain several abundant invasive plants (invasion meltdown sites). It's important to understand how biocontrol agents may interact with each other, as well as with any existing native insects and/or pathogens (some of which may also impact the non-native species with time) within the target site.

Land managers may choose a proactive approach if economic assessments demonstrate that employing sustainable forestry to promote native species recovery and deter invasions is more economically viable than treating invasions after the disturbance occurs. Such assessments should incorporate the true cost of invasion, including opportunity costs associated with the impact of invasions on future loss of forest regeneration (Holmes et al. 2009). Likewise, there needs to be an assessment of the measures used to prevent invasives associated with best management practices (BMPs) and the cost of using them, as compared to the cost of invasion when they are not utilized. Such economic assessments will provide landowners with more tangible evidence to support why investing in BMPs and lower-impact harvesting regimes is cost-effective.

IPM has been implemented for some tree diseases (e.g., sudden oak death, white pine blister rust, oak wilt). For example, an IPM program for management of white pine blister rust has been developed (Schoettle and Sniezko 2007) that consists of manipulating the forest composition, improv-

ing host vigor, using rust-resistant planting stock, reducing pest populations, and diversifying age structure. For oak wilt disease, the greatest success in management has occurred when early diagnosis is followed by creative and integrative use of control tools tailored for local sites (Juzwik et al. 2011). Similarly, appropriate site-specific strategies are the basis for management of sudden oak death in California (Swiecki and Bernhardt 2011). Many aquatic invasive species have established populations in situations that require sustained management. IPM programs may be implemented using a variety of approaches over time to control the non-native species. To manage fish populations, such programs may include barriers, manipulating water levels, targeted overharvest, stocking of predators, sterilants, toxic baits, selective piscicides, attractants and repellants, immunocontraceptive agents, viruses, chromosomal manipulations, gynogenesis, and transgenics (Faush et al. 2009; USGS 2017).

7.5.11 Key Findings

- Considerable research has been conducted to develop and evaluate management of invasive species under each of the major management approaches including regulatory control, education and outreach, physical control, cultural control, chemical control, vaccination, biological control, reproduction control, host resistance, and IPM programs.
- Federal and State quarantines regulate movement of many significant invasive pests. Recent research addresses efficacy of current regulations and has led to new regulations for treating solid wood packing material.
- Public outreach and education promote awareness and support of regulations and control actions for invasive vertebrates and aquatic animals, including trapping and shooting. Research evaluates the efficacy of various outreach activities on influencing human behavior and compliance with regulations.
- Efficacy of physical control is being evaluated for use against invasive vertebrates including fencing, sound devices to frighten animals, lethal control in the form of trapping and shooting, angling, netting, water skimmers, and hand removal of egg clutches for invasive aquatic organisms.
- Cultural control practices including mulching, irrigation, mechanical root cutting, sanitation, harvesting, prescribed fire, and silvicultural manipulations have been developed and implemented for management of invasive species.
- Research on pesticides includes evaluation of efficacy of insecticides, identification of the safest and most effective herbicides, use of rodenticides, and efficacy of toxicants for feral swine and rotenone for invasive fish.

- Biological control research has led to the identification of natural enemies of hemlock woolly adelgid, gypsy moth, and emerald ash borer in their native ranges; development and evaluation of rearing, release, and recovery methods; biological control of invasive weeds with insects; use of soil bacteria for biological control of white nose syndrome of bats; and evaluation of predators for control of invasive aquatic organisms.
- Vaccination and immunomodulation are being evaluated to control vertebrate diseases including sylvatic plague, white nose syndrome, and amphibian chytridiomycosis.
- Considerable research has been conducted on development of host resistance for many tree diseases including chestnut blight, Dutch elm disease, and beech bark disease as well as development of resistant ash against emerald ash borer, possible host resistance in hemlock against hemlock woolly adelgid, and frogs that are resistant to amphibian chytridiomycosis.
- Research on reproduction control has led to mating disruption for management of gypsy moth and immunocontraceptives for feral horses and swine.
- IPM programs incorporate multiple techniques such as biological control, habitat manipulation, modification of cultural practices, use of pesticides, and use of resistant varieties that are consolidated into a unified program. Integrated ecosystem- or landscape-level programs are being developed and evaluated for hemlock woolly adelgid, emerald ash borer, gypsy moth, invasive plants, and aquatic organisms.
- Knowledge of how climate change will affect different biological control applications, chemical pesticide efficacy, and cultural control treatments
- Better integration of methods for combining toxicant and reproductive controls for invasive vertebrates that are more society-friendly
- Better species-specific methods for assessing invasive species density/abundance in order to more effectively evaluate the relative success of control programs
- Improved decision-support tools that take into account ecological and economic factors to assist managers in prescribing management approaches, designing integrated pest management strategies, and determining conciliatory strategies when an invasive species cannot be stopped
- Development of standardized protocols for systematically surveying and testing for pesticide resistance
- Development of improved rearing, release, and recovery methods for introduced natural enemies and evaluation of their interactions with each other and native species for biological control of major invasive insects and plants
- Better assessment of efficacy of integrated pest management programs and adaptation of implementation guidelines

7.5.12 Key Information Needs

Additional research is needed on a number of issues, including the following:

- Assessment of the effectiveness of legislative control and different outreach methods related to managing human behavior and for informing the development of practical and effective strategies for employing outreach, education, laws, and other social incentives and deterrents to slow substantially the human-mediated spread of invasive species
- Posttreatment monitoring and evaluation of invasive species management responses and efficacy
- Development of improved pesticide and toxicant application delivery methods, rates, and frequencies to effectively control invasive species but minimally affect nontarget native species and the ecosystem
- Better understanding of plant-plant interactions, system-specific plant-insect chemical ecology, and cross-trophic level interactions

7.6 Recent Advances in Development of Tools for Invasive Species Management

Significant advances have been made in the past decade in developing tools for managing invasive species. One of the first steps in containing and managing an invasive species is to accurately identify the damaging agent and determine its distribution. The longer that species introductions go undetected or unidentified, the more difficult it becomes to control the introduced population (Simberloff 2003). Development of new and improved monitoring and detection technologies including traps, lures, and molecular tools has enhanced both early detection and our ability to monitor and manage invasive species. New tools are also being developed for suppressing and managing established populations of invasive species, while existing technologies must be evaluated and modified for use against new invasive species. New management tools may include discovery of new biological control agents or host resistance traits that are specific to the particular invasive species. Considerable progress has been made in developing new data management and decision systems for use in pest management.

7.6.1 Advances in Surveys and Traps for Monitoring and Early Detection of Invasive Species

Semiochemical attractants have been identified, and traps and lures have been developed for early detection of many insect species, including gypsy moth (Sharov et al. 2002), polyphagous and Kuroshio shot hole borers (*Euwallacea* spp.) (Dodge et al. 2017), and sirex woodwasp (Cooperband et al. 2012), and are being improved for other species such as emerald ash borer (Crook and Mastro 2010; Ryall et al. 2012), Asian longhorned beetle (Nehme et al. 2010, 2014), and redbay ambrosia beetle (Kuhns et al. 2014). Other technologies being evaluated include using acoustic detection for Asian longhorned beetle (Mankin et al. 2008), biosurveillance of emerald ash borer utilizing solitary ground nesting predaceous wasps (Careless et al. 2014), and using sniffer dogs to locate and identify Asian longhorned beetle (Errico 2013). The reliance on simple visual surveys to detect spotted lanternfly hinders suppression efforts. Research is needed to determine pheromone behavioral cues and trapping methods for nymphs and adults.

Intensive sampling methods that were used primarily for detection of rare plant species have been used to detect invasive plant species in early stages of invasion (Huebner 2007; Moore et al. 2011). Aerial photography combined with multispectral imagery (includes visible and near-infrared frequencies), hyperspectral sensors, or satellite imagery (e.g., LiDAR, Landsat) has been used successfully to detect invasive plant populations (Huang and Asner 2009) with distinct physical structures (Asner et al. 2008; Gavier-Pizarro et al. 2012), fruit characteristics (Rebbeck et al. 2015), or leaf phenology (many invasive species leaf out earlier in the spring and remain in leaf longer in the fall; Resasco et al. 2007). Despite the usefulness of the data obtained using aerial and remote-sensing technologies, they are limited by labor and equipment costs, safety issues, and a combination of these factors. Furthermore, this technology has no utility for detecting plants that don't possess unique characteristics.

Selection of the best tools for detecting invasive animals is also limited by cost and labor. Jarrad et al. (2011) suggest combining detection of mammals, amphibians, and reptiles for inclusion in a comprehensive surveillance program for invasive terrestrial vertebrates. This approach begins with risk analyses to identify preferred habitats of high-risk invaders, choosing survey areas that match and would therefore have a higher probability of hosting the invader. At those sites, a combination of species-appropriate traps and direct biological surveys for the target invasive species could be carried out (Jarrad et al. 2011).

7.6.2 Advances in Molecular Tools for Detection

Recent advances in molecular diagnostic tools are improving detection and identification of invasive insects, plant pathogens, plants, animal diseases, and aquatic organisms. DNA barcodes are being developed to aid in rapid identification of new invasive species (Ball and Armstrong 2006; Hollingsworth et al. 2011). A major advantage of DNA-based identification is that it provides the ability to identify morphologically indistinct immature stages of insects such as eggs and larvae, as well as damaged specimens, which would have been difficult to identify using conventional methods. Molecular methods are also useful in distinguishing between morphologically similar species that occur in a cryptic species complex (Cooperband et al. 2016; Lopez et al. 2014). Detection technology for plant pathogens has evolved rapidly over the past decade, progressing from molecular-based polymerase chain reaction methods that require 1–2 days to complete to newer techniques that are more rapid. The newer methodology does not require DNA extraction or extensive training to complete, uses portable equipment that can be utilized in the field, and is more specific than immunologically based methods. A recent example of this evolution is the development of diagnostics for *P. ramorum*-infected tissues. Application of sorption real-time assay and/or loop-mediated isothermal amplification (LAMP) assay provides sensitive and specific detection of this pathogen in 30 and 45 min, respectively (Tomlinson et al. 2007). An on-site device has been developed that can identify pathogens within 1 h and does not require specialized equipment (Tomlinson et al. 2010). Additionally, a species-specific assay for *P. ramorum* that uses recombinase polymerase amplification was developed that produces rapid results (as little as 15 min), uses portable equipment, and does not require DNA extraction or extensive training (Miles et al. 2015). Most recently, surface-enhanced Raman scattering (SERS) has been used for label-free and species-specific detection of *P. ramorum* in infected rhododendron (*Rhododendron* spp.) leaves (Yuksel et al. 2015). Accurate detection of the laurel wilt pathogen (*R. lauricola*) has been difficult, due in part to the occurrence of related fungi in the same affected plant. Because *R. lauricola* samples contain relatively low concentrations of diseased tissue, currently available diagnostic methods don't possess the sensitivity to reliably detect the fungus in woody tissue. However, using primers to amplify two taxon-specific simple-sequence repeat (SSR) loci with 0.1 ng detection limit for *R. lauricola* has improved the sensitivity of these tests. This method is now routinely used in diagnostic clinics and by researchers at the University of Florida to identify isolates obtained from suspect host tissues (Dreaden et al. 2014).

During the past decade, there has been a dramatic increase in the technical ability to conduct surveillance for invasive

aquatic animals, producing new technology that is rapid, inexpensive, and highly sensitive (Trebitz et al. 2017). Much of this progress can be attributed to the development of environmental DNA (eDNA) methods that allow researchers to screen for the presence of very rare aquatic species, using technologies which can detect just a few cells in a water sample (Jerde et al. 2011; Wilcox et al. 2013) (see Chap. 9).

Recently developed innovations in molecular diagnostics have produced accurate and conclusive confirmation that *P. destructans* is the causative agent of white nose syndrome of bats (Shuey et al. 2014). Long-wave ultraviolet (UV) light, which produces a distinctive orange-yellow fluorescence in response to microscopic skin lesions present on the wings of infected bats, is a reliable nondestructive diagnostic method that can be used to detect white nose syndrome without disturbing hibernating bats (USGS 2014). More details on eDNA tools are covered in Chap. 10.

7.6.3 Tools for Suppression of Invasive Species

Tools have also been developed to suppress established invasive pest populations. Some examples include (1) improved delivery techniques and new pesticide chemistries for chemical control of several invasive species; (2) development of rearing, release, and recovery methods for natural enemies used for biological control; and (3) traditional and transgenic breeding tools for developing resistant hosts. An improved formulation of the insecticide emamectin benzoate, TREE-äge®, was developed and tested (Herms and McCullough 2014; McCullough et al. 2011) along with new injection tools to improve its delivery into trees for protection against emerald ash borer (Doccola et al. 2015). Rearing and release methods have been developed for parasitoids of emerald ash borer (Duan et al. 2012, 2013; Gould et al. 2011) and predators of hemlock woolly adelgid (Havill et al. 2011), and trapping methods are being tested to recover released natural enemies (Abell et al. 2015). Transgenically developed resistant elm and American chestnuts have been developed and are currently being evaluated for their resistance to disease (Newhouse et al. 2007, 2014).

Recent advances in three-dimensional printing technology and computer applications have facilitated the development of highly technical tools for use in management of invasive pests. New material processes for bioreplication have furthered the development of nanoreplication of beetles that possess an accurate nanostructure of the exoskeleton and physical properties that include iridescent color reflection (Domingue et al. 2014a). Nano-fabricated and three-dimensional printed emerald ash borer decoy females, electrically charged with high DC voltage, have been developed to attract and electrocute males (Domingue et al. 2014b). A

recent application that tracks and monitors releases of parasitoids for biological control of emerald ash borer is now available for use on smart phone devices (Mapbiocontrol 2016).

7.6.4 Current Research that May Lead to the Development of New Management Tools

Development of a standardized DNA barcoding system for plants has been more challenging than those developed for animals, fungi, and insects, which use a portion of the cytochrome oxidase 1 (CO1) mitochondrial gene. Unfortunately, the low rate of nucleotide substitution in plant mitochondrial genomes precludes use of CO1 as a universal plant barcode. Most researchers now concur that multiple markers will be required to adequately discriminate among plant species. Currently, most plant DNA barcodes can only identify to species group and not species (Hollingsworth et al. 2011).

A new plant mating-disruption tool may include use of cytoplasmic male sterility (CMS). CMS has been observed in over 150 plant species and is a maternally inherited condition in which a plant is unable to produce functional pollen. It is associated with chimeric mitochondria and may be induced by interspecific crosses (Schnable and Wise 1998). It's been theorized that the use of CMS to control invasive plants is potentially effective against non-selfing species (dioecious and self-incompatible species) and should be further evaluated. CMS could spread in some populations despite causing severe reduction in the invasive species' fitness, resulting in rapid population extinction (Hodgins et al. 2009).

It has been suggested for several years that unmanned aerial vehicles (drones) could be deployed to locate invasive plants in remote areas (Jay et al. 2009; Pajares 2015a, b); deposit biocontrol agents, herbicides, or ignition sources; and monitor the efficacy of control measures; however, current regulations and safety guidelines have limited their use.

The opportunity for and direct costs of invasion control for invasive plants needs to be incorporated into existing forest growth and yield models or individual-based forest yield models, such as the Forest Service's Forest Vegetation Simulator (FVS) model.

By combining structured demography (integral projection models) with spatial spread models in discrete time, detailed projections of population growth and spread, as well as sensitivities and elasticities associated with both growth and spread, can be determined. Such models may allow us to predict the most and least sensitive stages of growth and spread of invasive plants and determine how variation at the different growth stages contributes to the spread of that plant (Jongejans et al. 2011).

Invasion simulations of a single invasive species into a food web indicate that food webs with the most species but the least connections among those species are the most likely to be invaded (Romanuk et al. 2009). Additional ecological network simulations that involve multiple invasive species introductions are needed to understand how invasional melt-downs occur. Do they become part of an existing stable ecological network or do they form a new highly connected network?

Invasions are primarily human-mediated, and consequently any success at managing invasive plants will require including a human dimension. Large global datasets that include information on population growth and environmental change may be integrated with economic costs of invasions to develop decision models. Terra Populus, developed by the Minnesota Population Center at the University of Minnesota, may be one such model. Terra Populus combines census and survey data (from the Integrated Public Use Microdata Series) with data on agricultural acreage and yields (Global Landscapes Initiative) and data from the Global Land Cover 2000 and WorldClim datasets. Other large data sets including the Global Invasive Species Database (ISSG 2017), Forest Service Forest Inventory and Analysis invasive plant data, USDA Natural Resources Conservation Service PLANTS database, and/or the Global Compendium of Weeds (HEAR 2017) may also be integrated in decision models incorporating human dimensions, population growth, and environmental change.

7.6.5 Data System Design

Advancements in computer hardware and software have expedited more sophisticated designs for data management and data systems needed in pest management programs. System design is the process of defining the architecture, components, modules, interfaces, and data for a system to achieve desired objectives. Data system designs include requirements for input and output, data storage and processing, and system control. Reliable data on pests and pest management are necessary for building reliable models, performing accurate analyses, developing effective policies, and making good management decisions. Data systems are needed for database management, integration of quantitative and spatial data, analytical algorithms, and decision-support tools. Data input and delivery may occur in real time through a network, and output and decisions may be delivered through web servers. Advancement of new technologies in remote sensing and spatially linked data loggers will expedite development of more sophisticated database and data processing systems.

7.6.6 Key Findings

- Major advances have been made in providing molecular tools for identification and detection of invasive pests.
- Improved chemistries and delivery tools have been developed and evaluated for pesticides used to control invasive pests.

7.6.7 Key Information Needs

- Development of new rearing, release, and recovery methods for natural enemies used in biological control programs, along with tools and models for evaluating their efficacy
- Traditional and transgenic breeding tools for developing resistant hosts
- Development of new high-technology tools such as three-dimensional printing and nanoreplication of insect decoy traps, mobile applications for tracking biological control releases, remote sensing using unmanned aerial vehicles (drones), and invasion simulation and dispersal models
- Improved detection tools for fast and accurate identification of new invasive species and broad-scale monitoring of invasive tree pathogens
- DNA barcoding to distinguish look-alike native and non-native invasive congeners and to identify species more reliably
- Models that include competing and/or facilitative co-occurring plants, herbivores, pathogens, and symbionts and that predict how they may or may not co-migrate in response to a changing environment
- Further investigation into the use of new management tools including novel genetic manipulations and cytoplasmic male sterility of plants
- Invasive species databases that link with global population, land use, and global climate change global databases

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