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8 Restoration of Landscapes and Habitats Affected by Established Invasive Species

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8.1 Introduction

Preventing invasions of aquatic and terrestrial habitats is the preferred and most cost-effective approach to address the invasive species threat (see Chap. 6). However, when prevention efforts fail, invasive species can become widespread and deeply embedded in native ecosystems, causing severe impacts (see Chaps. 2, 3, and 4). In such cases, invader control (see Chap. 7) accompanied by restoration facilitates recovery of native species and prevents reinvasion (e.g., Pearson et al. 2016). Here, we summarize the current state of restoration science and highlight critical information gaps that must be overcome to advance ecosystem restoration in terrestrial and aquatic systems affected by invasive plants, insects, diseases, and vertebrates.

Restoration objectives and associated management strategies vary by the type of invader, the extent of its impacts, characteristics of the affected site, and the value of the affected system in terms of its biological diversity, uniqueness, or the ecosystem services it provides to humans. Accordingly, objectives may range from classic ecosystem restoration strategies intended to fully restore a system to its pre-invasion state (ecological restoration) to more pragmatic strategies such as redirecting invasion trajectories toward desirable ecosystem services (functional restoration), despite deviations from historic composition and function, as in the case of "novel ecosystems" that have been severely transformed by multiple invaders (Forest Service Manual 2016; Hobbs et al. 2009). The decision to expend time and resources to attempt to fully restore a particular system (versus lesser restoration goals) is determined by assessing ecological, economic, and societal values of the recipient ecosystem; susceptibility to reinvasion by the same or other invaders; availability of effective restoration tools or tactics; and the defined management objectives (see example Chap. 7, Box 7.1). Several inputs are required for developing effective management and restoration strategies for affected ecosystems (see Chap. 7, Box 7.2). Generally, invasive species must be controlled to some degree in order for ecosystem restoration to be successful (see Chap. 7). Control efforts may occur prior to or in conjunction with initiation of the restoration process or may require implementation on a recurring basis for continued suppression of the invasive population, since invasive species are rarely eradicated (Myers et al. 2000). In general, ecosystem restoration efforts should emphasize ecosystem function, resilience, and resistance to future invasions in order to ensure long-term successes (Forest Service Manual 2016).

The degree and type of restoration effort depend on which native system components are affected and to what extent. Passive restoration occurs when native systems naturally recover following suppression or removal of the invasive species. For example, passive recovery may occur following control of terrestrial invertebrate or vertebrate invaders that harm native fauna allowing recovery and the subsequent return of vagile animals to formerly invaded areas, reestablishing functional populations once the invader is removed. However, this is commonly not the case for plants which

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often fail to reestablish following control of target pests for a variety of reasons (Pearson et al. 2016) including seed limitation (Seabloom et al. 2003) and various legacy effects (Magnoli et al. 2013). Hence, restoration is often an active process requiring an array of management strategies including reintroduction of propagules and/or nutrient or soil treatments to facilitate plant recovery. In aquatic systems, restocking native fish populations may be necessary following the use of chemicals like rotenone that kills both native and invasive fish in isolated water bodies.

Successful restoration requires an understanding of what makes an ecosystem resistant to invasion, what levels of genetic diversity enhance restoration efforts, and how to accelerate the search for and development of genetic resistance to insects and pathogens. Summarizing past activities and learning from past successes and failures is critical in directing future efforts, and such information can help enlist public and cooperator support for future restoration projects. Below, we discuss the nuances associated with restoration efforts in a variety of terrestrial and aquatic communities.

8.2 Restoration of Forests and Grasslands Affected by Invasive Plants

Understanding how a plant community has been degraded is key to its restoration. Systems may gradually degrade in a predictable linear fashion with change in the environmental conditions, producing a change in plant species composition and function that is proportional to the environmental change. Or, systems may be seemingly resilient to environmental changes, until a critical threshold is reached, at which point an unpredicted and rapid change occurs. In such cases, if one understands the trigger or driver of the sudden change, removal of the driver may reverse the change. Alternatively, some systems may respond to the same environmental change by reaching multiple stable states, termed hysteresis (Suding and Hobbs 2009). The restoration pathway could be very different from that which led to the degraded state (Beisner et al. 2003), making this possibly the most challenging type of restoration. Recent literature reviews examining the efficacy of weed management (all types, including herbicide, mechanical, and biocontrol, with herbicide being the most common) indicate that weed control alone often does not promote full system recovery (Kettenring and Adams 2011; Pearson et al. 2016; Reid et al. 2009). Lack of success may be caused by failing to address the type of system degradation. For example, deer (Cervidae) browse may have been at such a duration and extent that removal of deer and invasive plants does not result in full recovery of native species diversity (Royo et al. 2010). Similarly, removing invasive aquatic plants from a riparian system is only a temporary solution, if underlying nutrient loading of the system is not addressed (Lotze et al. 2006).

Active restoration may be required following invasive plant control and may include (1) initial reintroduction of the desired species or (2) use of a predictable successional trajectory to eventually reach the final desired species composition. The more degraded the site, the more likely option two will be necessary (Chazdon 2008). It is important to first assess the need for active restoration by evaluating the native seedbank's likelihood that passive recovery (spontaneous succession) may occur after the invader is removed (Holl and Aide 2011; Tropek et al. 2010).

For grasslands dominated by annual grasses in the Western United States, management and restoration emphasize resilience to both wildfire and species invasions. In these semiarid ecosystems, resilience and invasion resistance are strongly associated with soil moisture and temperature regimes (Chambers et al. 2014, 2017). Coates et al. (2016) found that areas with low resistance and resilience to cheatgrass (*Bromus tectorum*) could be targeted for using wildfire suppression efforts to avoid domination by cheatgrass due to fire.

An important obstacle to actively restoring native plant communities is secondary invasion by non-target invasive weeds following control of the target invader (Dickens et al. 2016; Pearson et al. 2016). System recovery is more likely to occur if the risk of secondary invaders is anticipated and managed in conjunction with control of the primary target weed. Restoration may also require recovery of the initial soil conditions because some plant invaders may alter original soil conditions by adding allelopathic compounds (Grove et al. 2012; Lankau et al. 2014; Suseela et al. 2016) or changing soil pH and/or nutrient levels (Castro-Diez et al. 2012; Liao et al. 2008), soil microbial composition (Middleton and Bever 2012), or other ecosystem properties in ways that either inhibit native plant recovery or facilitate invasion by exotic plants (Kardol and Wardle 2010; Suding et al. 2004; Symstad 2004; Yelenik et al. 2004). Amending degraded soil is especially important if changes in soil condition triggered a threshold response.

An overabundance of herbivores (DiTommaso et al. 2014; see also next section on vertebrates) and non-sustainable forestry practices (Haeussler et al. 2002; Puettmann 2011) are examples of drivers that have led to depletion of native seed banks, making some sites less resilient to disturbance and more susceptible to rapid secondary invasions. Consequently, gaps created in these types of systems by such target invaders are not able to recover passively upon removal of the invader and should be filled as quickly as possible with native plants or transitional non-invasive exotic species. Establishing a rich native plant community can increase a system's resistance to reinvasion (Maron and Marler 2007; Pokorney et al. 2005), with the caveat that richer plant communities are also

often the most vulnerable to invasion (Huebner and Tobin 2006; Stohlgren et al. 2003). Thus, increasing native species richness alone may not prevent invasion at resource-rich sites (Davis et al. 2000). A better strategy may be to actively plant aggressive, early successional native species that are more likely to outcompete non-native invasive plants (Funk et al. 2008), especially if present in high enough numbers. Once these early successional native species are established, mid- to late-successional native species can be added, possibly allowing a predictable successional trajectory to then take its course. Succession ecology provides a useful framework for approaches that rapidly fill the "invader gap" and move the system toward a native stable-state community (Cox and Anderson 2004; Sheley et al. 2006). However, movement toward a native stable-state community is only possible if existing undesirable drivers are addressed. In highly degraded sites, arrested novel communities may need to be accepted, but such communities, theoretically, could be managed to maximize native species richness and abundance and to deliver particular ecosystem services (Hobbs et al. 2009; Suding et al. 2004; Tognetti et al. 2010).

Failure to reseed native species is often a major obstacle to restoration (Firn et al. 2010; Hulet et al. 2010), especially for mid- to late-successional seres (Prach and Walker 2011). Plants from local and diverse seed sources are most likely to be successfully established in a restoration site. Seed source distance from the restoration site is an important consideration, and it is equally important to base seed source over an environmental gradient. Doing so increases diversity and may enable the species to adapt more quickly in a degraded environment (Johnson et al. 2010) and adapt to changes in climate (Havens et al. 2015). One method for ensuring native species survival over a relatively broad environmental gradient is to develop provisional seed zones, because they incorporate species-specific information concerning fitness in different environments and could be of great value when selecting species for restoration (Bower et al. 2014). Provisional seed zones have been developed for a few species, but these need further testing to assess their effectiveness (Bower et al. 2014; Johnson et al. 2013) even if they are deemed locally suitable (Tischew et al. 2011). An unintended outcome of using commercially produced native seed mixes obtained from different parts of an environmental gradient for restoration has been the introduction of non-site-specific genotypes which can negatively alter the local genetic integrity of species (Dyer et al. 2016). This increases genetic heterozygosity at the site but may compromise local fitness.

Even in cases where restoration of the desired plant species composition appears successful, much remains unknown regarding the reestablishment of ecosystem processes (nutrient cycling and interactions with other trophic levels). Indeed, for restored systems that have been evaluated (which are few), current restoration practices have failed to recover the original level of ecosystem functions (Moreno-Mateos et al. 2012; Yelenik and Levine 2010).

Globally, there are growing environmental markets that pay for ecosystem services (PES) to fund restoration efforts (e.g., Florida Everglades, Costa Rican and Madagascan reforestation efforts, and China's conversion of sloping cropland to forest and pasture). A problem associated with PES is the question of long-term sustainability related to dependency on available funds. Depending on the source of the funds, restoration via PES may also skew the restoration approach toward certain services while neglecting others. If not adequately regulated, this approach could lead to promotion of restoration projects that fall short of the full suite of ecosystem functions that the site once provided (Bullock et al. 2011; Palmer and Filaso 2009).

8.2.1 Key Information Needs

1. Improvements in seeding technology (e.g., Madsen et al. 2014) and other revegetation approaches to promote system recovery following invasive plant control
2. Identification of protocols to prevent loss of genetic diversity while sustaining cost-effective production of native seeds for use in restoration
3. Understanding and incorporating ecosystem process and function as recovery targets into all restoration activities
4. Developing guidelines differentiating degraded systems that (1) are a linear and proportional response to an environmental change, (2) respond to environmental change only after a threshold is reached and associated with a trigger, and (3) can take several pathways leading to multiple stable states, many of which are distinctly unlike the system's original state
5. Evaluation of pay for ecosystem services (PES) as a means of funding more restoration projects, including the need for regulating such payments so that ecosystem services and plant compositions associated with the undisturbed site take priority
6. Formulation of an economic model that helps determine when costs of restoration are too great to warrant an attempt at restoration

8.3 Genetic Considerations for the Restoration of Forests Affected by Invasive Insects and Disease

Once an invasive insect or pathogen has been successfully established, high mortality of the host tree species populations can occur rapidly. In rare cases, this results in extirpation or extinction of a species. A striking example was the elimination of the American chestnut (*Castanea dentata*) as

a dominant species in eastern hardwood forests by chestnut blight, an invasive fungal disease from Asia caused by *Cryphonectria parasitica* (Paillet 2002). Chestnut blight arrived within a matter of decades after ink disease (caused by the invasive pathogen *Phytophthora cinnamomi*) had caused widespread death of American chestnut in lower elevations throughout the Southeastern United States (Anagnostakis 2002). More recently, emerald ash borer (*Agrilus planipennis*) threatens potential extinction of the North American ash (*Fraxinus* spp.) resource (see www.iucnredlist.org). Long-term monitoring revealed mortality rates of 99–100% of green (*Fraxinus pennsylvanica*) and white ash (*F. americana*) trees greater than 10 cm in diameter at breast height, within 5–7 years of infestation in stands throughout southwestern Michigan and northwestern Ohio (Gandhi et al. 2014; Knight et al. 2013). Dozens of forest tree species throughout the United States are currently under threat of widespread mortality due to invasive insects and pathogens (Table 8.1). Genetic conservation efforts are underway for some of these species (Knight et al. 2010; Mangold 2011; Sniezko et al. 2011).

Although management sometimes reduces the abundance of these destructive invasive species, complete eradication is seldom accomplished. Focus then turns to identifying sources of resistance and enriching genetic resistance in native populations of the affected host tree species (Waring and O'Hara 2005). In natural ecosystems, genetically diverse populations of tree species, through a long-term co-evolutionary history with insects or pathogens, develop an array of resistance alleles that may involve the interactions of multiple genes or a smaller number of genes of large effect (Budde et al. 2016; Ennos 2015). When a non-native insect or pathogen is introduced, existing plant resistance mechanisms developed for defense against native pests and pathogens may offer some benefit. Allelic variation in genes directed against existing native threats may provide some protection against invasive insects and pathogens, but the degree of effectiveness can vary. These evolutionary variants are likely to be uncommon because, in the absence of the invasive species, they confer little or no selective advantage to trees that possess them. As a result of the huge amount of standing genetic variation found in the large effective population sizes of most obligate outcrossing forest tree species, response to an invasive insect or pathogen can range from entire populations that die quickly, to individual trees that remain symptom-free, to those that are less affected and therefore able to survive longer, to species that are no more susceptible to the invader than its original host was (Budde et al. 2016; Ennos 2015, Sniezko et al. 2014; Telford et al. 2015). Genetic variants that confer a level of resistance to invasive species may have evolved in response to different selection pressures, served a different function before the introduction of the invasive species, or form part of the gene network directed against a related species.

As susceptible trees succumb to an invasive insect or pathogen, gaps are created that provide opportunities for regeneration to occur under the continued high selection pressure from the invasive species. This can result in dramatic shifts in allele frequencies that favor survival or confer resistance. This process of natural selection can, over many generations, lead to passive restoration of species and ecosystems that have been impacted by invasive insects and diseases. The generation time for tree species can take decades; thus, the slow process of natural selection leading to the development of resistance may not take place within an acceptable time frame for forest managers. Successful natural regeneration of a self-sustaining population is dependent on several factors. First and most importantly, there must be a level of genetic resistance among the surviving members of the population. The type and complexity of resistance is also a factor; for example, single gene resistance can sometimes be rapidly overcome by pathogens, while resistance conferred by many genes is generally more durable (Sniezko et al. 2014). The frequency and geographic distribution of resistant individuals plays an important role as well. If resistance is present at low frequency in the population, as is often the case without a shared co-evolutionary history, the surviving trees may be scattered over large areas, limiting their opportunities for reproduction. Tree species that have prolific seed production along with long-distance pollen and seed dispersal would be favored to overcome such obstacles. Not surprisingly, evidence indicating the possible occurrence of natural selection for resistance has been reported in natural populations of two such species, American elm (*Ulmus americana*), which has been heavily affected by Dutch elm disease (*Ophiostoma ulmi* and *Ophiostoma novo-ulmi*), and European ash (*Fraxinus excelsior*), which is threatened by ash dieback disease (caused by the fungal pathogen *Hymenoscyphus fraxineus*). Elm seedlings from regional seed collections, conducted in 1959 and again in 1981, were inoculated to assess tolerance to Dutch elm disease (Smalley and Guries 1993). This study revealed an increase in the frequency of tolerance in seed collected from trees that had experienced a longer exposure time to Dutch elm disease (Smalley and Guries 1993). Similarly, a progeny test of 320 open-pollinated European ash families from seed collected from Lithuania and seven additional European countries across a southern gradient found that families from regions with the longest history of ash dieback disease had the highest survival rates and lowest incidence of disease damage (Pliūra et al. 2011). These examples indicate that potential for resistance exists and, if warranted, natural selection could be accelerated or supplemented through breeding programs.

In some cases, mortality caused by invasive insects and diseases is so extensive it severely reduces genetic diversity

Table 8.1 Forest tree breeding programs for development of resistance to invasive insects and diseases in the United States

Host tree species		Invasive species			
Common name	Scientific name	Common name	Scientific name	Organization(s)	Status of breeding program
American x Chinese chestnut hybrids	*Castanea dentata X Castanea mollissima*	Chestnut blight	*Cryphonectria parasitica*	The American Chestnut Foundation, Connecticut Agricultural Experiment Station, USDA Forest Service NRS	Breeding program for resistance
American x Chinese chestnut hybrids	*Castanea dentata X Castanea mollissima*	Ink rot disease	*Phytophthora cinnamomi*	The American Chestnut Foundation, Clemson University	Resistance detected in genetic/provenance trials
Butternut	*Juglans cinerea*	Butternut canker	*Sirococcus clavigignenti-juglandacearum*	USDA Forest Service ORSO and NRS; University of Tennessee	Evidence for genetic variation in resistance in seedling or clone screens
Butternut x Japanese walnut hybrids	*Juglans cinerea X Juglans ailantifolia*	Butternut canker	*Sirococcus clavigignenti-juglandacearum*	USDA Forest Service NRS, University of Tennessee	Evidence for genetic variation in resistance in seedling or clone screens
Tanoak	*Notholithocarpus densiflorus*	Sudden oak death	*Phytophthora ramorum*	USDA Forest Service DGRC, University of California at Berkeley, Oregon State University	Efforts to identify resistance initiated
Whitebark pine	*Pinus albicaulis*	White pine blister rust	*Cronartium ribicola*	USDA Forest Service DGRC, RMRS, and CDA	Resistant planting stock deployed
Rocky mountain bristlecone pine	*Pinus aristata*	White pine blister rust	*Cronartium ribicola*	USDA Forest Service DGRC, PSWRS, RMRS	Evidence for genetic variation in resistance in seedling or clone screens
Foxtail pine	*Pinus balfouriana*	White pine blister rust	*Cronartium ribicola*	USDA Forest Service DGRC, R5 Placerville	Efforts to identify resistance initiated
Limber pine	*Pinus flexilis*	White pine blister rust	*Cronartium ribicola*	USDA Forest Service DGRC, PSWRS, RMRS	Evidence for genetic variation in resistance in seedling or clone screens
Sugar pine	*Pinus lambertiana*	White pine blister rust	*Cronartium ribicola*	USDA Forest Service DGRC and R5 Placerville	Resistant planting stock deployed
Great Basin bristlecone pine	*Pinus longaeva*	White pine blister rust	*Cronartium ribicola*	USDA Forest Service DGRC, PSWRS and RMRS	Evidence for genetic variation in resistance in seedling or clone screens
Western white pine	*Pinus monticola*	White pine blister rust	*Cronartium ribicola*	USDA Forest Service DGRC, CDA, R5 Placerville	Resistant planting stock deployed
Southwestern white pine	*Pinus strobiformis*	White pine blister rust	*Cronartium ribicola*	USDA Forest Service DGRC, PSWRS, CDA	Evidence for genetic variation in resistance in seedling or clone screens
Eastern white pine	*Pinus strobus*	White pine blister rust	*Cronartium ribicola*	USDA Forest Service ORSO and DGRC; University of Minnesota	Resistant planting stock deployed
Port-Orford-cedar	*Chamaecyparis lawsoniana*	Root rot	*Phytophthora lateralis*	USDA Forest Service DGRC	Resistant planting stock deployed
Port-Orford-cedar	*Chamaecyparis lawsoniana*	Stigmina foliage blight	*Pseudocercospora thujina*	USDA Forest Service DGRC	Resistance detected in genetic/provenance trials
American elm	*Ulmus americana*	Dutch elm disease	*Ophiostoma novo-ulmi*	USDA Forest Service NRS, University of Minnesota	Evidence for genetic variation in resistance in seedling or clone screens

(continued)

Table 8.1 (continued)

Host tree species		Invasive species			
Common name	Scientific name	Common name	Scientific name	Organization(s)	Status of breeding program
Oak species	*Quercus* spp.	Sudden oak death	*Phytophthora ramorum*	USDA Forest Service PSWRS	Evidence for genetic variation in resistance in seedling or clone screens
Green ash	*Fraxinus pennsylvanica*	Emerald ash borer	*Agrilus planipennis*	USDA Forest Service NRS	Evidence for genetic variation in resistance in seedling or clone screens
White ash	*Fraxinus americana*	Emerald ash borer	*Agrilus planipennis*	USDA Forest Service NRS	Evidence for genetic variation in resistance in seedling or clone screens
Black ash x Manchurian ash hybrids	*Fraxinus nigra X Fraxinus mandshurica*	Emerald ash borer	*Agrilus planipennis*	USDA Forest Service NRS	Evidence for genetic variation in resistance in seedling or clone screens
American beech	*Fagus grandifolia*	Beech scale (beech bark disease)	*Cryptococcus fagisuga*	USDA Forest Service NRS	Resistant planting stock deployed
Fir species	*Abies* spp.	Balsam woolly adelgid	*Adelges piceae*	North Carolina State University	Evidence for genetic variation in resistance in seedling or clone screens
Eastern hemlock	*Tsuga canadensis*	Hemlock woolly adelgid	*Adelges tsugae*	University of Rhode Island, North Carolina State University	Evidence for genetic variation in resistance in seedling or clone screens
Carolina hemlock hybrids	*Tsuga caroliniana X Tsuga* spp.	Hemlock woolly adelgid	*Adelges tsugae*	US National Arboretum	Evidence for genetic variation in resistance in seedling or clone screens
Redbay	*Persea borbonia*	Laurel wilt	*Raffaelea lauricola*	University of Florida	Evidence for genetic variation in resistance in seedling or clone screens
Koa	*Acacia koa*	Koa wilt	*Fusarium oxysporum*	Hawaii Agriculture Research Center, USDA Forest Service DGRC	Resistant planting stock deployed
Ōhi‘a	*Metrosideros polymorpha*	Rapid ‘Ōhi‘a Death	*Ceratocystis huliohia Ceratocystis lukuohia*	University of Hawaii, USDA ARS, USDA Forest Service PWRS, DGRC and Region 5 Forest Health Protection	Efforts to identify resistance initiated

Abbreviations: *NRS* Northern Research Station, *ORSO* Oconto River Seed Orchard, *DGRC* Dorena Genetic Resource Center, *RMRS* Rocky Mountain Research Station, *CDA* Couer D'Alene Nursery, USFS, *PSWRS* Pacific Southwest Research Station, *R5 Placerville* USDA Forest Service Region 5 Genetics program at Placerville nursery

of affected populations. This can lead to inbreeding depression and a catastrophic loss of essential allelic variants, resulting in a loss of fitness in the next generation. The few surviving trees may be resistant to the disease or insect, but their progeny may be more vulnerable to secondary threats (native pests, other invasive insects, pathogens, or abiotic stresses such as drought and fire) because the resistance alleles have been lost. Even in situations where recovery is possible, the species' distribution or density is likely to have been drastically reduced. The remaining genetic diversity may be insufficient to allow adaptation to new threats, including adaptation to a potentially changing climate. Despite indications of natural selection in American elm for Dutch elm disease resistance and in European ash for resistance to ash dieback, both are facing new threats. Recent outbreaks of elm yellows (*Candidatus Phytoplasma ulmi*) have been documented in the United States, and although emerald ash borer is native to Far Eastern Russia, it has now become established in Western Russia (Moscow) where it is poised to spread throughout Europe (Herath et al. 2010;

Orlova-Bienkowskaja 2014; Sherald 2009). The loss of genetic diversity in these species has likely made them even more vulnerable to new threats, as will be the case for North American ash trees that survive emerald ash borer, should ash dieback ever invade the United States. Black ash (*Fraxinus nigra*) is reported to be highly susceptible to ash dieback, and green ash is reported to be moderately susceptible (Drenkhan and Hanso 2010; Gross and Sieber 2016).

Silviculture can be used to favor and support regeneration of forest species impacted by invasive insects and diseases with the goal of retaining or increasing genetic diversity and increasing population-level resistance (Waring and O'Hara 2005). Natural selection can be accelerated by careful selection and removal of diseased or infested trees, with the goal of eliminating susceptible alleles from the gene pool while retaining genetic diversity. A test comparing seedling progeny from parent trees from an unmanaged stand of American beech (*Fagus grandifolia*) with seedling progeny from parent trees in a stand where single tree selection and removal of trees with symptoms of beech bark disease had been performed 12 years earlier indicated that there was a 50% increase in the number of beech bark disease-resistant seedlings from the managed stand compared to seedlings from the unmanaged stand (Koch 2010; Koch et al. 2010). Despite these promising results, residual stands ravaged by invasive insects and diseases frequently consist of a small number of widely dispersed surviving individuals that are unable to recover naturally. In these situations, the process of stand recovery can be accelerated through breeding remaining resistant individuals to retain genetic diversity and adaptive capacity and to harness and even improve upon the combinations of genes that proved advantageous to their survival.

8.3.1 Breeding Resistance to Invasive Forest Pathogens

The most enduring and successful efforts at breeding for resistance against an invasive pathogen attacking forest trees have focused on the fungus *Cronartium ribicola*, the cause of white pine blister rust, which has been in the United States since 1898 (Kinloch 2003; Sniezko et al. 2014). All nine species of white pine (*Pinus* spp.) native to the United States are susceptible to blister rust, and all except *P. longaeva* (Great Basin bristlecone pine) have been infected in their native range (Sniezko et al. 2011; Tomback and Achuff 2010). Infection levels as high as 70 to 100% have been reported in the northern range of whitebark (*P. flexilis*) and limber pine (*P. albicaulis*) (Kinloch 2003). Three species are vulnerable to extinction because of the negative effect of blister rust on regeneration (Tomback and Achuff 2010). Complete resistance conferred by a single dominant major gene has been identified in four of the white pine species (Kinloch 2000; Kinloch and Dupper 2002), and several types of partial or quantitative (controlled by multiple genes) resistance have been identified (Sniezko et al. 2014). The best approach and current focus for obtaining durable resistance is to breed for both complete and partial resistance in production populations (Sniezko et al. 2014). Assessment of genetic resistance is underway in all nine species, and more extensive efforts for breeding resistance are ongoing for several of the species (summarized in Table 8.1; see Fig. 8.1). Resistant seedlings are currently being deployed (as part of artificial regeneration strategies) for four of the species to date (Waring and Goodrich 2012), and substantial progress has been reported (see Box 8.1). Pathogens such a *C. ribicola* have the capacity for rapid evolution as they can complete many generations over the lifetime of their host tree. Field trials are monitoring the durability and stability of tree resistance over time, on a range of sites with varying risk of rust infection. Western white pine (*P. monticola*) and sugar pine (*P. lambertiana*) results are encouraging (Kinloch et al. 2012; Sniezko et al. 2012a, 2014). Efforts are underway to further increase the level of resistance in several of these species.

Box 8.1 On the Road to Success: Tangible Evidence of the Impact of Host Resistance

According to the International Union for Conservation of Nature's Red List of Threatened Species, the species status of Port-Orford-cedar (*Chamaecyparis lawsoniana*), listed as "vulnerable" in 2000, has been downgraded to "near threatened" as of 2013, with anticipation that it will be listed as a species of "least concern" within 10 years if current conservation actions, including planting resistant seedlings (see Fig. 8.2), are successful and maintained (Farjon 2013). The interagency, inter-regional genetic resistance program in Port-Orford-cedar is based at the USDA Forest Service Dorena Genetic Resource Center in the Pacific Northwest Region and has produced one of the most quickly implemented and effective resistance programs in forest trees.

In 2011, in another example, the US Fish and Wildlife Service determined that "the whitebark pine warrants protection under the Endangered Species Act" and was under imminent threat of high magnitude, assigning it a listing priority number (LPN) of 2 in 2011. In 2015, the LPN was reduced to eight (U.S. Fish and Wildlife Service 2015), a decision that was attributed, in part, to the identification and propagation of genetically resistant trees. This program is coordinated by USDA Forest Service efforts (see Table 8.1).

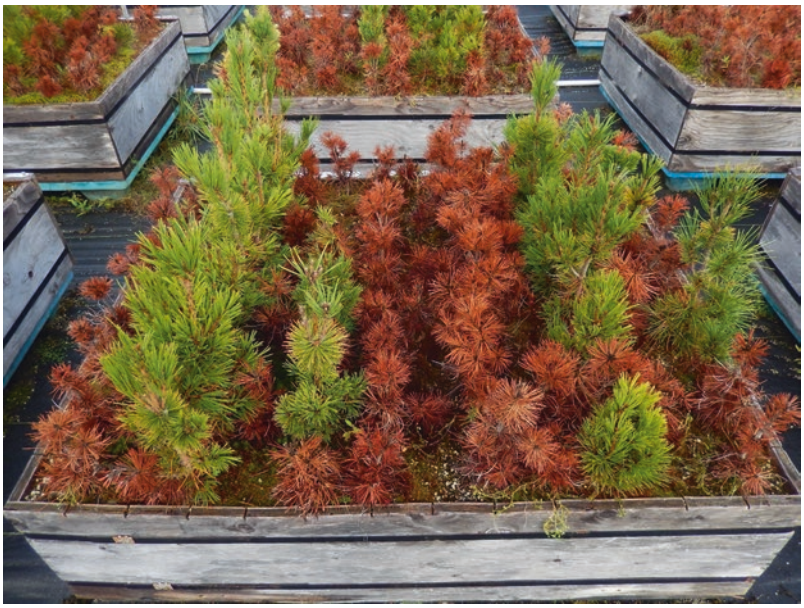

Fig. 8.1 Whitebark pine seedlings that have been inoculated with white pine blister rust at the USDA Forest Service Dorena Genetic Resource Center. Resistant seedlings are those that have remained green and healthy

Fig. 8.2 Restoration of Port-Orford-cedar. Volunteers and USDA Forest Service personnel plant 900 Port-Orford-cedar seedlings along Grayback Creek in southern Oregon to help restore a riparian area used by salmon and steelhead trout. The seedlings will be monitored to determine if resistance to root disease caused by *Phytophthora lateralis* is durable. Community groups involved with the planting include the Middle Rogue Steelheaders Trout Unlimited Chapter, Illinois Valley Watershed Council, The Nature Conservancy, Forestry Action Committee, and Southern Oregon Fly Fishers

The hybrid (interspecies) breeding approach exploits the original host tree resistance to the invasive insect or pathogen. Frequently, the original host species is related to the newly invaded tree species allowing hybridization. Butternut (*Juglans cinerea*), a native North American species that has experienced severe decline because of butternut canker (*Sirococcus clavigignenti-juglandacearum*), hybridizes naturally with Japanese walnut (*Juglans ailantifolia*) (Hoban et al. 2009). The Japanese walnut, which is resistant to butternut canker, was widely planted in the United States since it was introduced in the nineteenth century and has since naturalized in many areas (Hoban et al. 2012). As a result, hybrids of Japanese walnut and butternut, including advanced-generation hybrids, occur in natural populations and retain the pathogen resistance from the Japanese walnut lineage (Broders et al. 2015; Hoban et al. 2009). The lack of evidence for heritable resistance within native butternut populations, combined with the low number of surviving pure

butternut (the species is locally extinct throughout much of the former range), strongly suggests that it will be necessary to use hybrid breeding, with Japanese walnut as a source of resistance alleles, to achieve levels of resistance adequate for butternut restoration (LaBonte et al. 2015).

In examples like butternut, hybrid breeding may be the only option. Hybrid breeding programs are challenging because selection for resistance is not always sufficient and the program must also ensure that the ecosystem function and adaptive traits of the native species are retained. The chestnut blight resistance breeding program of The American Chestnut Foundation is among the most notable and long-standing hybrid breeding programs in the United States. Although there is no evidence of complete, single gene resistance to chestnut blight in either the American chestnut or other Asian species of chestnut, quantitative (multi-gene) resistance is present in the Chinese chestnut (*Castanea mollissima*). Very little information is available in the literature related to the presence of or testing for quantitative resistance in the American chestnut, possibly due to the early focus placed on the hybrid breeding approach (Budde et al. 2016). The American Chestnut Foundation program produced hybrids between American chestnut and Chinese chestnut and selected for blight resistance using several generations of backcrossing and intercrossing to retain desirable American traits (Hebard 2012). More recently, the program has also selected American chestnut for resistance to ink disease. Complete resistance to this pathogen has been identified in one of the hybrid breeding lines (Jeffers et al. 2012; Zhebentyayeva et al. 2013), but additional testing will be necessary to confirm this result. Significant resources have been directed to support using advanced-generation hybrids from The American Chestnut Foundation's program to develop and optimize artificial regeneration procedures for chestnut restoration (Clark et al. 2014). Although the first widespread tests of advanced-generation hybrids demonstrated promising levels of early seedling establishment, susceptibility to both ink disease and chestnut blight remains a significant issue (Clark et al. 2015; Pinchot et al. 2014). The American Chestnut Foundation program continues to pursue increasing the resistance to both pathogens.

Dutch elm disease, caused by the invasive pathogens *Ophiostoma ulmi* and *Ophiostoma novo-ulmi*, was first identified in Ohio in 1930 killing a tremendous number of American elm trees that were highly valued street trees for their beautiful arching canopies. Early efforts to identify resistance were focused mostly on developing cultivars by selection, propagation, and testing of large surviving elm trees or by screening large numbers of seedlings (Smalley and Guries 1993; Townsend and Douglass 2001). The cultivars that were developed were mostly used as landscape and nursery trees. Efforts to restore American elm in naturally forested areas focused initially on deploying five of these previously developed nursery cultivars and later were expanded to include progeny from a cross between two of the five cultivars (Slavicek et al. 2005). The long-term performance of these plantings may be problematic, as genetic diversity is limited and three of these cultivars are susceptible to elm yellows (Sinclair et al. 2001; Smalley and Guries 1993). Recently, efforts have been initiated to enhance adaptive capacity and expand genetic diversity through breeding (Slavicek and Knight 2013).

One of the most significant successes attributed to a forest tree resistance breeding is development of populations of Port-Orford-cedar (*Chamaecyparis lawsoniana*) that have genetic resistance to a root disease caused by *Phytophthora lateralis* (Sniezko et al. 2012b) (see Box 8.1). This program identified both single gene and multi-genic sources of resistance, delineated breeding zones, and established seed orchards. The program is now producing seed from several breeding zones (Sniezko et al. 2012b). Reforestation and restoration efforts using Port-Orford-cedar seed resistant to *P. lateralis* are now underway. Field trials to monitor the efficacy and durability of resistance have been established. The program's success will be decided over time as seed used in field trials is evaluated for restoration and reforestation efforts.

Laurel wilt is among the newest invasive diseases affecting trees in the United States. The disease is vectored by the redbay ambrosia beetle (*Xyleborus glabratus*), which introduces its fungal symbiont (*Raffaelea lauricola*) into the sapwood of host trees. The beetle was first detected in 2002 and, along with its fungal symbiont, was associated with extensive mortality of redbay (*Persea borbonia*) in 2003. The disease spreads rapidly within stands, and mortality levels greater than 90% have been reported within just a few years (Hughes et al. 2015). Since then, laurel wilt has been confirmed in eight southeastern states. Eight additional forest and landscape tree or shrub species (including two that are considered threatened or endangered) have been confirmed to be infected, and five additional species are vulnerable, based on results from artificial inoculation (Hughes et al. 2015). Researchers at the University of Florida identified and clonally propagated redbay trees that remained asymptomatic in heavily diseased natural areas (Hughes and Smith 2014). Field trials demonstrated tolerance in a few selected genotypes, and additional genotypes are being propagated for testing.

8.3.2 Breeding Resistance to Invasive Insects

Although laurel wilt is caused by an invasive pathogen vectored by an invasive insect, some invasive pathogens are vectored by native insects. The original vector for Dutch elm disease was the native elm bark beetle (*Hylurgopinus*

rufipes), but over time as non-native insect species entered the United States, the list of vectors of Dutch elm disease has grown (Jacobi et al. 2007; Lee et al. 2009). Control of these insect vectors, whether native or invasive, can be critical for managing the diseases they vector. Genetic traits of the host can play a pivotal role in control of insects associated with disease. For example, the correlation between early flushing and reduced susceptibility to Dutch elm disease in both American and European elm may be due to a mismatch between the period of maximum host susceptibility and timing of beetle emergence in the spring, thus allowing the trees to escape infection (Ghelardini and Santini 2009). In the case of beech bark disease, breeding has focused on selecting for resistance to the beech scale insect (*Cryptococcus fagisuga*). Although this scale insect is not a vector of the fungal species (*Neonectria ditissima*, *N. faginata*) that cause the disease, its feeding activity creates many entry points for the fungal spores (Ehrlich 1934). In the absence of scale infestation, species of *Neonectria* alone have not been associated with the high tree mortality levels characteristic of beech bark disease. Effective techniques to screen for resistance to the scale insect in the field, in potted seedlings, or in grafts have been developed (Koch and Carey 2014), as have efficient methods to propagate resistant beech trees (Carey et al. 2013). Genetic studies have confirmed that resistance to the scale insect is heritable, and regional seed orchards of grafted resistant American beech trees are being established (Koch and Heyd 2013; Koch et al. 2010). Unfortunately, the American beech now appears to be threatened by another potentially invasive pest causing what is currently referred to as beech leaf disease (Pogacnik and Macy 2016). Research is being conducted to follow up on the identification of a foliar nematode as a possible causal agent of this disease. The nematode appears to be closely related to the recently reported *Litylenchus crenatae*, found in *Fagus crenata*, a beech species native to Japan (Carta 2018; Kanzaki et al. 2019). In addition to confirmation of the causal agent of this disease, continued monitoring will be needed to fully understand what the long-term, landscape-scale impacts will be, but current information is pointing to what could quite possibly be a devastating and wide-ranging impact to American beech, particularly given the stress it is already enduring due to beech bark disease.

Other invasive insect species cause significant damage and mortality directly as a consequence of completing their life cycle on or within specific tree hosts. Emerald ash borer and hemlock woolly adelgid (*Adelges tsugae*) are currently among the most significant threats to forests in the Eastern United States. Efforts are underway to identify and breed for resistance to these invasive species (Table 8.1). Genetic variation in the susceptibility of green ash to emerald ash borer was first observed in natural stands where, despite long-term emerald ash borer infestation resulting in the death of over 95% of the ash, occasional surviving trees were identified (Knight et al. 2012a). Bioassay experiments performed on grafted replicates of some of these green ash trees have confirmed that the increased level of resistance observed in select trees is due to multiple types of host defense responses, including mortality of early instar larvae, larvae with significantly lower weights, and reduced adult feeding on foliage (Koch et al. 2015) (Fig. 8.3). Although additional field testing and genetic studies are needed, these results indicate that there is potential for developing of a successful emerald ash borer resistance breeding program.

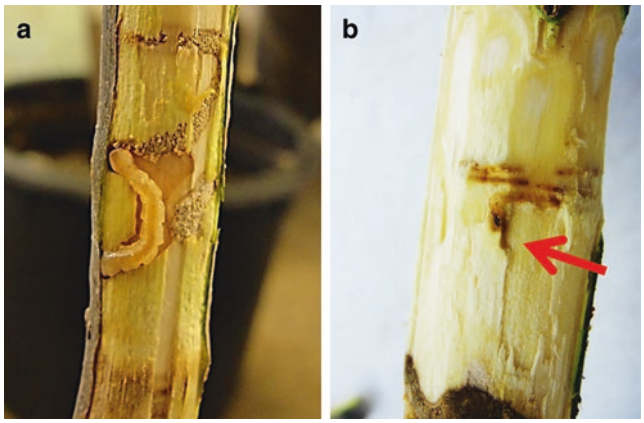

Fig. 8.3 Results of emerald ash borer egg bioassay. The larva in *panel A* has successfully developed to a late instar on this susceptible green ash tree, while the larva in *panel B* has been killed by defense responses mounted by the tree, indicating resistance

A citizen science approach was used to identify eastern hemlock trees (*Tsuga canadensis*) that survived in areas heavily infested by hemlock woolly adelgid (Ingwell and Preisser 2010). Rooted cuttings of some surviving trees were compared to susceptible controls and hemlock woolly adelgid-resistant western hemlock (*Tsuga heterophylla*) using an artificial infestation technique. Results showed that, although there was no difference between the initial establishment of hemlock woolly adelgid sistens (winter generation) on resistant versus susceptible eastern hemlock cuttings, significantly lower adult sistens were produced on the resistant genotype (Ingwell and Preisser 2010). Current efforts are focused on optimizing the inoculation technique to develop an efficient screen for resistance as a first step toward developing a breeding program (Powers et al. 2015).

8.3.3 Deployment of Resistant Planting Stock or Alternative Non-host Species

The development of a resistance breeding program is only one facet involved in the process of restoration. In some cases, there may be no detectable host resistance within the species, and interspecies hybridization may not be success-

ful. In other cases, there may be evidence for resistance, but the threat to sensitive habitats warrants implementation of restoration activities before resistant planting stock is available. In such cases, proactive planting of alternative non-host species may be considered. For example, American elm cultivars and a full-sibling elm seedling family, along with oak (*Quercus* spp.) and sycamore (*Platanus occidentalis*) seedlings, were used in plantings to restore ash-dominated riparian forests at risk of high ecological impact due to near synchronous emerald ash borer-induced mortality of ash (Knight et al. 2012b; Nesbit et al. 2015). Similar approaches are being considered for northern black ash forests threatened by emerald ash borer. The destruction of black ash has the potential to cause a transition to non-forest conditions (Palik et al. 2012) and, subsequently, a significant rise in the water table (Slesak et al. 2014). Extensive analysis of emerald ash borer risk, potential impacts of climate change, and co-occurring species has been performed to identify potential candidate species for replacing black ash (Iverson et al. 2015).

Whether resistant hosts are developed through breeding, or non-host trees are used as an alternative to restore forest ecosystems affected by invasive species, the same basic steps are required. These include (1) seed production and collection; (2) mass propagation of planting stock in a nursery or greenhouse; (3) site preparation, which can vary significantly across sites; and 4) post-planting maintenance during the establishment phase, which may include occasional watering, weed removal, and herbivore control. Each step requires a significant investment in labor, with needs for specific skill sets, tools, facilities, and infrastructure (Campbell and Schlarbaum 2014). Applied nucleation is a promising strategy for cost-effective restoration of forests affected by invasive insects and diseases. This approach utilizes natural successional processes and is based on planting trees in irregularly spaced clusters, which serve as the focal point of propagule establishment and provide islands of habitat that attract birds and mammals, which then aid in seed dispersal. Recent reports indicate that this approach reduces the need for management activities (such as watering, fertilization, and invasive plant removal) and, consequently, is a lower-cost alternative to a regularly spaced plantation design for facilitation of forest recovery and restoration (Corbin and Holl 2012; Corbin et al. 2016).

8.3.4 Key Information Needs: Toward Developing Capacity for Solutions

Recent literature reviews suggest that host resistance, forest genetics, and tree improvement may be the most effective approaches for retaining and restoring resilience in our forests under the continuous threat of invasive insects and diseases (Budde et al. 2016; Ennos 2015; Telford et al. 2015; Wheeler et al. 2015). Resistance breeding programs can provide real solutions to invasive insects and diseases within reasonable time periods, especially when supported by the necessary infrastructure and skills. Such programs have a long record of success in crops, fruit and nut trees, and forest trees. A resistance breeding approach does not require the use of genetically modified organisms (GMOs) produced through transgenic or gene editing technologies, although established breeding programs can, under certain circumstances, successfully incorporate these techniques to develop strategies to accelerate breeding (see Chap. 9). GMOs or even gene-edited plants are not always widely accepted by the public, and despite assertions that GMOs provide sustainable solutions more quickly or more cost-effectively than a well-designed and executed breeding program, there is no evidence available to support this because there are currently no GMO forest trees that have been approved for planting in natural forests. Use of genetic engineering to produce a plant with resistance can have application in plantation and crop forestry, but a tree genetically modified for resistance represents a single genotype and lacks the genetic diversity to achieve the resilience needed for ecosystem restoration. For utilization in ecosystem restoration, a GMO would have to be integrated with a breeding program to incorporate genetic diversity and adaptive capacity, an approach that The American Chestnut Foundation intends to pursue, should they successfully obtain regulatory approval (Steiner et al. 2017). Therefore, the use of GMOs would not negate or reduce the need for traditional breeding programs. Unfortunately, the demand for forest genetics and tree improvement programs to address invasive insect and disease problems comes at a time when the infrastructure and expertise required for such programs has been declining for two decades (Campbell and Schlarbaum 2014; Wheeler et al. 2015). In addition to basic infrastructure, expertise in forest tree breeding and forest tree genetics is essential for implementing cost-effective breeding programs. Tree breeding requires the development and the disciplined execution of long-term plans based on (1) a solid understanding of the desired phenotype and the genetic basis for the phenotype (Groβkinsky et al. 2015; Zivy et al. 2015), (2) screening and development of breeding populations, (3) maintenance of local adaptation and genetic diversity, and (4) testing and deployment of the resistant trees. Even in a situation where resistance breeding strategies have succeeded in developing resistant trees, the lack of necessary infrastructure (seed orchards to produce improved seed, nurseries to mass produce planting stock) for carrying out restoration may prevent effective deployment of such resistance. Effective long-term planning also requires (1) strategies for germplasm conservation; (2) an understanding of the long-term interaction of the invasive pathogen or insect on the standing genetic varia-

tion of the host species across the landscape (e.g., would natural selection and natural regeneration be sufficient for recovery?); (3) validation of resistance and assessment of durability through long-term monitoring of field trials across different sites and environments; (4) assessment of the different types of resistance and the distribution and frequency of such resistance within a species; (5) an understanding of the dynamics of the disease triangle (host, pest/pathogen, and environment) across the native range of the host, including the environments in which most people interact with trees (streets, parks, urban woodlands, arboreta, tree plantation, and highly fragmented natural forests); and (6) development of updated seed zones, taking into consideration predicted environmental changes due to climate change.

8.4 Restoration of Forests and Grasslands Affected by Invasive Vertebrates

The incursion of invasive vertebrates in terrestrial ecosystems can impact both native plants and wildlife (see Chap. 2). From a restoration perspective, the first step in restoring systems affected by invasive vertebrates is to suppress populations of the target invader to a level sufficient to reduce their impacts, thus allowing restoration to proceed (see Chap. 7). However, frequently restoration activities must begin in concert with control of the invasive vertebrate, and, in some cases, it may be necessary to suppress several invasive vertebrates and/or plants simultaneously or in a specific sequence in order to avoid releasing other invaders from suppression (Bergstrom et al. 2009; Chapuis et al. 2004; Morrison 2007; Zavaleta et al. 2001). For example, on sub-Antarctic Macquarie Island, extirpation of feral cat (*Felis catus*) populations resulted in an increase in exotic rabbit (*Oryctolagus cuniculus*) populations which devastated certain native vegetation communities and released exotic plants like annual bluegrass (*Poa annua*) (Bergstrom et al. 2009). Control of invasive vertebrate predators can also threaten native vertebrates if strategies are not carefully executed, such as the control of feral pigs (*Sus scrofa*) on the Channel Islands that resulted in increased predation by golden eagles (*Aquila chrysaetos*) on the endangered island fox (*Urocyon littoralis*) (Morrison 2007; Roemer et al. 2001). Invasive vertebrate herbivores, such as feral hogs, goats, and horses, can directly harm native plants and cause disturbances that can facilitate plant invasions (Campbell and Donlan 2005). The resulting plant invaders may frequently persist or they may increase, along with other invasive plant species, following control of invasive vertebrate herbivores (Chapuis et al. 2004; Morrison 2007). Hence, weed control (see Chap. 7) and vegetation restoration practices described elsewhere in this chapter (Sect. 8.2) should be implemented in conjunction with control of invasive vertebrate herbivores. In more extreme cases involving vertebrates that act as ecosystem engineers (see Chap. 2), such as nutria (*Myocastor coypus*), which disrupt waterways (Carter and Leonard 2002), physical restoration of the hydrology of the system may be required before vegetation and other system components can recover.

Reductions in invasive vertebrate populations may facilitate natural recovery of vagile native fauna. For example, reducing populations of invasive cavity nesting birds such as starlings (*Sturnus vulgaris*) provides cavities that can be utilized by native cavity nesters (e.g., Smith 2005), and reductions of invasive predator populations permit native prey populations to recover as in New Zealand where rat (*Rattus* spp.) control is critical for bird conservation (Moorhouse et al. 2003). However, in cases where the affected native species is rare or threatened, it may be necessary to reintroduce the species or subsidize their populations initially, applying traditional wildlife management approaches (Mills 2012). The presence of multiple invasive vertebrates can greatly complicate management and restoration because invaders can develop strong interactions with native vertebrates and other invasive vertebrates (Zavaleta et al. 2001). In such cases, control of any one target invader can initiate complex outcomes with extreme unintended side effects (Bergstrom et al. 2009; Zavaleta et al. 2001). In the case of multiple invasive species, particularly at multiple trophic levels, it may be necessary to implement integrated management strategies that address each invader separately to protect against intended outcomes (Zavaleta et al. 2001).

8.4.1 Key Information Needs

Restoration of native communities affected by exotic vertebrates requires better understanding of the impacts that vertebrate invaders have on different native taxa so that control efforts can be planned in ways that mitigate unintended consequences associated with releasing secondary invaders (Bergstrom et al. 2009; Zavaleta et al. 2001); in addition, follow-up restoration efforts can be carefully directed to recover system components that may not recover without assistance. While it is recognized that impacts of vertebrate pests on plant communities may require active restoration efforts (see above), research is needed to document the extent to which other taxa may or may not recover naturally following activities to control vertebrate pests.

8.5 Restoration of Aquatic Habitats Invaded by Aquatic Species

In many aquatic ecosystems, restoration of native-only communities is not feasible. The few and often non-selective, broad-spectrum strategies available for species removal—

generally mechanical removal by netting or electrofishing or chemical removal using piscicides—preclude their widespread application. Furthermore, the frequent and often long-range movements that are characteristic of some non-native species make them resistant to eradication. Even the process of removing species from relatively simple habitats can require near-impossible efforts (Pacas and Taylor 2015), and long-term success is contingent on preventing reinvasion. In flowing water systems, this generally consists of using artificial barrier to prevent movement, a tactic that is accompanied by its own suite of problems (Fausch et al. 2009). In some cases, the objective has been to control but not eradicate non-native species, and native species have occasionally rebounded (Propst et al. 2015). However, "control fatigue" sometimes sets in if there is an erosion of funds or management focus, resulting in the rapid reestablishment of non-native species populations (Meyer et al. 2006). A further impediment to applying control measures is the substantial societal resistance to removal of non-native species that are prized for recreation, food, or outdoor-related economic activity. Fresh water for municipal, agricultural, and industrial use constitutes a fundamental ecosystem service. Diverse uses of fresh water provided by many federal lands add enormous complexity to management efforts to reduce non-native species in favor of native ones.

Within the subset of habitats where non-native species removal is feasible and undertaken, opportunities exist for restoring native species. Recolonization by native species may be rapid and begin immediately following removal of non-native species (i.e., within days or weeks). In fluvial aquatic ecosystems, passive restoration of native animal species following removal of non-native species typically relies on downstream drift of organisms originating from untreated, upstream reaches. This is a standard strategy for addressing aquatic insects in streams and is often used as a measure of ecosystem recovery (e.g., Kjærstad et al. 2015). Upstream migration by native taxa from areas downstream of treated reaches is rarely feasible; these locations are often the sources of the invading non-native taxa, and the installation of structures that prevent recolonization by invasive species similarly constrains native taxa (Fausch et al. 2009). In standing water, amphibians have successfully recolonized mountain lakes following removal of introduced fish (Knapp et al. 2007). However, for many native taxa, passive recolonization is not feasible due to their limited mobility, few local sources of potential re-colonists, or lack of access to restored habitats (Knapp and Sarnelle 2008).

Despite the often poor probability of recolonizing native aquatic species, active restoration continues to be a standard practice. This is not unexpected, because management of aquatic species, particularly fishes, has a 150-year tradition of fostering the introduction and spread of species of value to society. Some hatchery facilities are dedicated solely to the production of rare native species for use in conservation programs (e.g., Dexter National Fish Hatchery, NM), whereas others are responsible for maintaining local stocks of conservation value. The establishment of broodstocks of native species that are used for restoration has evolved substantially, particularly with respect to maintaining genetic diversity both in the hatchery and in recipient populations (Fisch et al. 2015). This continues to be an ongoing challenge, because even a single generation of hatchery domestication results in some degree of artificial selection (Christie et al. 2016). Introductions of native species may involve any or all age classes, from sexually mature adults to fertilized embryos, and programs can rely on translocations of wild individuals instead of hatchery products. Also, local populations of native species are sometimes salvaged from an area before treatment to remove non-native species and transferred off-site to nearby water bodies or hatcheries until treatment is completed. As an aside, many hatchery facilities now propagate non-native fish that are sterile; these fish are widely introduced to promote recreational fishing, and though they may have ecosystem effects, these effects are expected to be minimal because these fish are unable to establish reproducing populations or cause hybridization.

The decision involving where to practice aquatic species restoration is rather arbitrary and is often dictated by convenience or opportunity. Efforts to prioritize conservation actions have been underway for decades, including sophisticated approaches that (1) weigh a host of variables to identify sites that are critical to the survival of a species or are representative of rare or at-risk habitats (Groves 2003), (2) rank the value and vulnerability of individual populations, stocks, or species (McElhany et al. 2000), or (3) integrate the two (Fausch et al. 2009). According to Wenger et al. (2011), aquatic habitats are highly dynamic and climate change is likely to drive future changes, including the distribution of native and non-native species. The development of massive bio-geo databases, coupled with tools to perform synthetic analyses, now permits a further step: the site-specific, probabilistic assessment of occupancy by native species in light of both climate change and non-native species invasions (e.g., for bull trout (*Salvelinus confluentus*) and cutthroat trout (*Oncorhynchus clarkii lewisi*) in the Northwestern United States) (Isaak et al. 2015). Many taxa, however, must await assembly of existing data, deployment of new species surveillance techniques (e.g., eDNA sampling) (McKelvey et al. 2016; Thomsen et al. 2012), and, for the myriad lesser known species, a better understanding of their ecology.

8.5.1 Key Information Needs

The preceding text touched on the critical areas of research that are needed or underway. Barring an unlikely consensus

in the way societies view the introduction and redistribution of non-native aquatic species—from an unavoidable consequence of global commerce, a positive addition to biodiversity, or an ecological menace—the issues associated with non-native species invasions are likely to continue. Moreover, their ecological idiosyncrasies and ability to rapidly adapt to new environments may necessitate employing individualized control measures against the non-native species, perhaps while managing targeted native species to ensure they persist. Consequently, and perhaps regrettably, the need and scope for new tactics, strategies, and understanding is likely to continue to grow.

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