

CHAPTER 2

Designing restoration programs based on understanding the drivers of ecological change

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Overview of concepts

Introduction

The activities of conservation planning and biological control of invasive species are both continuing to evolve, requiring greater collaboration between these disciplines to achieve mutual goals pertaining to invasive species management (Chapter 1). Invasive species can be a factor contributing to ecological degradation (Simberloff, 2011; Kumschick et al., 2015). Even reserves in relatively intact ecosystems in remote regions can be threatened by exotic species invasions. Often this impact is not recognized until after the invasive species has become too abundant and widespread for eradication or even containment (e.g., Herms and McCullough, 2014). Long term, such pervasive invader populations are usually prohibitively expensive to suppress using conventional chemical and mechanical methods, especially as the infested area increases to tens or hundreds of thousands of hectares. Development of an effective biological control program is a potential alternative for managing an invasive pest, but biological control frequently must be integrated into the broader conservation plans of the local ecosystem because invasive species, particularly invasive plants, are rarely the only factor contributing to ecological degradation, as we will illustrate. Even where an invasive species is the leading cause of ecological degradation, its control alone may not accomplish restoration goals, and additional measures may be necessary (Chapter 3). Moreover, funding for conservation is limited, necessitating a

strategic approach and a clear vision of what the intended end goal will be for the restoration.

In this chapter, we briefly review the conservation planning process, focusing on the roles invasive species play in ecological change. We pay particular attention to how to determine if an invasive species rises to the level of threat that warrants development of a biological control program, which we illustrate with a representative case study – the restoration of Connecticut River floodplain forests in the northeastern United States. A lack of integration into a wider restoration planning process has sometimes resulted in criticism of past biological control programs. For example, biological control of purple loosestrife (*Lythrum salicaria* L.) is one of the most widespread biological control programs for weeds in North America (Wilson et al., 2009), yet the necessity of controlling this invader has been questioned by some ecologists (Anderson, 1995) – although some of these concerns have since been rebutted (Blossey et al., 2001). More notably, in another case, a lack of integration of the biological control of saltcedar (*Tamarix* species) into a wider plan for the ecological restoration of riparian communities in the southwestern United States has resulted in controversy among various interest groups (see Chapter 4; or Dudley and Bean, 2012). Saltcedar is a widespread invader of riparian areas along southwestern rivers with well known, large negative ecological impacts, but on some rivers it has also become one of the few remaining riparian tree species (Tracy and DeLoach, 1999; Sher and Quigley, 2013). The release of a highly effective biological control agent for

saltcedar, without also taking action to increase recruitment of native floodplain tree species like willows (*Salix*) and cottonwoods (*Populus*), may have resulted in a loss of some marginal nesting habitat for the federally listed endangered southwestern willow flycatcher (*Empidonax traillii extimus* Phillips) (Finch et al., 2002; Smith and Finch, 2014). On some southwestern rivers, modifying operations at dams to restore a more natural flood regime downstream, alone or in combination with saltcedar biological control, may be more effective at restoring floodplain function, including natural recruitment of the native riparian trees that the flycatcher prefers for nesting (Cooper et al., 2003; Richard and Julien, 2003; Shafroth et al., 2005; Ahlers and Moore, 2009; Hultine et al., 2009; Merritt and Poff, 2010; Dudley and Bean, 2012). These examples show how important it is to evaluate the factors that are influencing ecosystem function and degradation before irreversible actions are taken. The mere high dominance by an invasive species is not necessarily equivalent to degradation of ecological function. Therefore, it is necessary to rank invasive species not just against each other for control priority, but also to rank their control against other conservation actions that may have a greater positive impact. It is critical to think holistically about how the system functions before designing a plan of action.

Ecological restoration planning process

The motivations for carrying out ecological restoration are diverse and depend on the stakeholders’ values. These motivations can include anything from landscape aesthetics and protection of endangered species to conservation of ecosystem services. The first step in the planning process is to achieve a consensus among stakeholders on what aspects of the ecosystem are valued, as well as what outcomes are desired for the restoration activity. This goal-setting process is subjective, and it is important to achieve a consensus among stakeholders early to avoid conflicts later, when program momentum may be significant, making change difficult or costly (Chapter 12). Next, one needs to understand the threats that have led to past declines in the aspects of the ecosystem where restoration is desired. Specifically, one needs to develop an understanding of system change with the best science available at the time, being aware that our knowledge of the system is usually incomplete. Consequently, it is important to be explicit about one’s assumptions of what is driving change in the system

because they could be incorrect (Wilkinson et al., 2005), and scientists should seek to test such assumptions to guide restoration in an adaptive management framework (Westgate et al., 2013).

Invasive species and system change

High abundance of invasive species in wildlands is often associated with dramatic ecosystem alterations, such as eutrophication of soil or water bodies (Green and Galatowitsch, 2002; Perry et al., 2004; Silliman and Bertness, 2004; Kercher et al., 2007), overgrazing (Knight et al., 2009; HilleRisLambers et al., 2010; Dornbush and Hahn, 2013), and altered disturbance regimes such as fire and flooding (Cooper et al., 2003; Katz and Shafroth, 2003; Keeley, 2006; MacDougall and Turkington, 2007; Stromberg et al., 2007; Merritt and Poff, 2010; Metz et al., 2013; Greet et al., 2013; Schmiedel and Tackenberg, 2013; Terwei et al., 2013; Reynolds et al., 2014). However, it is not always immediately obvious to what degree non-native species invasions are the cause or the consequence of the ecological change, or both. Determining the answer to this question is crucial to deciding if the most effective strategy is more likely to be restoring the physical environment and key ecological processes or starting a biological control program, or if both may be necessary.

MacDougal and Turkington (2005) defined invasive species that thrive on ecological change, such as altered ecosystem properties or a shift in disturbance regimes, as passengers (see Figure 2.1). Owing to their high density in degraded ecosystems, passengers appear more damaging than they actually are. If the ecosystem

		Invader causes ecological change	
		No	Yes
Invasion is a consequence of ecological change	No	Pedestrian	Driver
	Yes	Passenger	Back-seat driver

Figure 2.1 A chart to classify the ecological role of an invasive species on the spectrum from invasion being a consequence of ecological change to invasion being the cause of ecological change.

stressor that has allowed the passenger to proliferate is removed, one would expect passenger populations to decline. MacDougal and Turkington (2007) argued, for example, that the *Poa pratensis* L. invasion of Garry oak (*Quercus garryana* Douglas ex Hook.) savannas in British Columbia was a consequence of fire suppression. The failure of native vegetation to respond to *Poa* removal indicated that *Poa* was not the cause of change, only associated with it. Follow-up experiments found that restoration of fire to these ecosystems reduced invader abundance and promoted native species' recovery (MacDougal and Turkington, 2007).

Exceptions to the autogenous recovery of native populations following removal of the ecosystem stressor include situations where there are strong feedbacks between biotic factors and the physical environment (Suding et al., 2004). Specifically, once an invasive species is dominant, it might change the environment in ways that would favor its continued dominance even after the factor promoting its initial establishment was removed. For example, marsh disturbances such as ditching create microsites with better soil aeration where invasive common reed (*Phragmites australis* [Cav.] Trin. ex Steud.) can establish (Bart and Hartman, 2003; Chambers et al., 2003; Lathrop et al., 2003; Silliman and Bertness, 2004). Once established, *Phragmites* can transfer air within a clone via its hollow stalks, enabling it to spread to the rest of the marsh, forming large monospecific patches (Bart and Hartman, 2000; Lathrop et al., 2003). In another example, native deer herbivory was shown to accelerate forest invasion of garlic mustard (*Alliaria petiolata* [M. Bieb.] Cavara & Grande), Japanese barberry (*Berberis thunbergii* DC), and Japanese stiltgrass (*Microstegium vimineum* [Trin.] A. Camus), but was not as important as canopy disturbance or propagule pressure in explaining different levels of invasive weed abundance (Eschtruth and Battles, 2009). Once these invasive, non-native forest understory plants became abundant, propagule pressure would remain high even if canopy disturbance and deer herbivory were reduced. In such cases, restoration success would require both reducing the ecosystem stressor that had led to ecological degradation and suppressing the invasive species to reduce propagule pressure. Similarly, native plant propagules may be too scarce for native plants to recolonize on their own even after deer and invasive plant populations have been reduced, thus necessitating native plant seed addition or planting

(Tanentzap et al., 2009, 2011, 2013; Collard et al., 2010; Royo et al., 2010; Dornbush and Hahn, 2013). Holistic restoration approaches are especially important in urban and suburban areas, where there are usually multiple interacting stressors including invasive plants (Sauer, 1998).

In contrast to ecological passengers, MacDougal and Turkington (2005) defined drivers as invasive species that are both able to proliferate unaided by external ecological change and cause considerable damage. An example of an invasive driver is the fungal pathogen *Cryphonectria parasitica* (Murrill) Barr, the causal agent of chestnut blight. This fungus was accidentally introduced from Asia into North America, where it killed virtually all mature American chestnut (*Castanea dentata* [Marshall] Borkh.), the tree that once dominated many eastern North American forests (Braun, 1950). Attempts at biological control of the chestnut blight fungal pathogen with viruses were successful in Europe but not in eastern North America (Anagnostakis, 2001; Milgroom and Cortesi, 2004). Current efforts at restoring American chestnut are instead focused on breeding blight-resistant hybrids (Jacobs, 2007; Anagnostakis, 2012). Other examples of pure drivers of ecological change are the cottony cushion scale (*Icerya purchasi* Maskell), a phloem-sucking insect that caused many native plant populations in the Galápagos Islands to decline (Chapter 10), and laurel wilt, a disease caused by an invasive fungus vectored by the non-native redbay ambrosia beetle (*Xyleborus glabratus* Eichhoff), which is causing extensive mortality of redbay (*Persea borbonia* [L.] Spreng.) in the southeastern United States (Spiegel and Leege, 2013). Clearly, drivers are the most threatening invasive species and thus should receive a high priority on lists of candidate invaders for developing control programs.

Although originally set up as a dichotomy, the distinction between drivers and passengers is more accurately thought of as a spectrum, with many invasive species being intermediate cases where their proliferation has benefited from wider ecosystem change, but their high abundance also affects the ecosystem. Bauer (2012) has called these intermediate cases back-seat drivers, and his review suggests that most invasive plant species are back-seat drivers. Berman et al. (2013) proposed that invasive non-native ants in New Caledonia are back-seat drivers whose initial invasion is associated with disturbance, such as forest clearing, but which subsequently also harms native ant communities. Similarly, experimental

manipulations have shown that invasion by the red imported fire ant (*Solenopsis invicta* Buren.) in the south-eastern United States is driven by disturbance (King and Tschinkel, 2008). Many studies have documented large impacts by non-native fire ants on native ants and other native arthropods through competition and predation (Porter and Savignano, 1990; Gotelli and Arnett, 2000; Wojcik et al., 2001; Sanders et al., 2003). Decapitating flies in the genus *Pseudacteon* (e.g., *P. tricuspis* Borgmeier) were imported from Argentina and released as biological control agents of the red imported fire ant because the type of disturbance that promotes fire ant invasion has become unavoidable in much of the landscape, resulting in substantial damage to crops, livestock, human health, electrical equipment, and wildlife (Porter et al., 2004). Thus, where system changes that have enabled invasion by a back-seat driver are irreversible, there may be a sufficiently compelling argument for developing a biological control program.

Finally, there are non-native species whose establishment is not associated with significant ecological change either as a cause or consequence. We have labeled these species as pedestrians in Figure 2.1 to highlight the difference in pace of change. It is important to remember that the categories in Figure 2.1 are not immutable; many of today's invasive driver species were pedestrians receiving little notice during the first century of colonization in their new range (Kowarik et al., 1995; Crooks, 2005). With the right ecological or evolutionary changes, species can quickly switch between these categories. Moreover, local context matters; an invasive species that acts like a back-seat driver or passenger in one area may act like a driver in another part of its invaded range or in a different habitat (Wilson and Pinno, 2013). Therefore, in cases where there are no obvious large impacts by an invader in a particular ecosystem, further study elsewhere may be necessary to make a well informed assessment of their overall impact in the invaded range.

Ranking invasive species for classical biological control

Central to ranking ecological threats for remediation is a consensus on what level of impact is sufficient to require conservation action. For example, The Nature Conservancy's conservation planning process ranks threats (both biotic and abiotic) according to scope, severity, and irreversibility (also referred to as permanence). With

respect to an invasive species, scope could be the area or percentage of a habitat likely to become threatened by the invader over the coming decade. Severity could be thought of as the level of damage to native biota in the invaded area that can reasonably be expected from the threat given the continuation of current circumstances and trends. Severity is the seriousness of the impact. For example, an insect pest invasion that causes high mortality of its tree host would be considered a more severe threat than one that only reduced the tree's growth rate. Irreversibility (or permanence) is the degree to which the effects of a threat cannot be reversed by restoration. For instance, the effects of most damaging non-native species, once they become widespread, are difficult to reverse. Therefore preventing invaders from establishing, through early detection and elimination of incipient populations, generally receives high priority in conservation planning.

To help answer the question of how severe the threat posed by an invasive species needs to be to warrant the development of a biological control agent, given the costs and risks involved, we suggest using the following ranking, keeping in mind that ranking will vary depending on conservation goals and context, particularly stakeholder values. Invasive species that change community composition by taking up space and resources but do not destroy native biota should receive a low rank, especially if they are largely passengers of other ecological changes. Many non-native plants fall into this category. A more severe threat is posed by invasive species that cause a high rate of mortality in an important native species such as one of the following types: a community dominant, an endangered species, an ecosystem engineer, or an economically important species. Perhaps the most severe threat is posed by invasive species that have large undesirable impacts on ecosystem function. Such changes in ecosystem function include altered disturbance regimes, such as increases in fire intensity and frequency, large persistent changes in ecosystem properties like soil chemistry through salinization or nitrogen fixation, reductions in ecosystem services like drinking water supply through dramatic increases in transpiration, and qualitative changes in vegetation structure like conversion of forest to scrubland or grassland or vice versa.

Ranking of invasive species for control can be complicated if a species has both positive and negative ecological impacts. Consider the case of common reed (*P. australis*)

invading North American marshes. This reed results in an almost two-thirds decrease in native plant species richness (Silliman and Bertness, 2004); however, its presence has also been shown to increase tidal marsh soil accretion rates, increasing resilience to sea level rise and storm surges (Rooth and Stevenson, 2000; Rooth et al., 2003). Imposing a hierarchy on different types of impacts can help in making decisions regarding invasive species whose effects are both positive and negative. In the case of common reed (*Phragmites*) it was decided that loss of native plant and bird diversity was sufficient reason to embark on a biological control program (Tewksbury et al., 2002; Blossey, 2003). Crucial to a well informed decision-making process is quantifying the ecological impacts of an invader and understanding the causal mechanisms driving invasions before embarking on expensive control measures, biological or otherwise. Such an approach has not yet been widely adopted owing to a lack of relevant research results available to conservation managers.

To help guide the assessment of potential targets for developing a classical biological control program, we developed a decision tree (Figure 2.2). The first step in the process is to determine if the invasion is caused by some independent ecosystem change, such as eutrophication, overgrazing, or altered disturbance regime. If so, addressing this other stressor may be more important than attempting to control the invasive species directly. Next, one should assess the level of impact the invader is having. Given limited resources for conservation, control efforts should focus on the invaders with the most severe impacts. These first two steps need not necessarily involve lengthy scientific investigations. For example, in the case of the invasion of the emerald ash borer (*Agrilus planipennis* Fairmaire) in Michigan, it was immediately obvious that the pest was able to invade relatively unaltered ash forests and had severe impacts through causing high rates of mortality of a commercially and ecologically

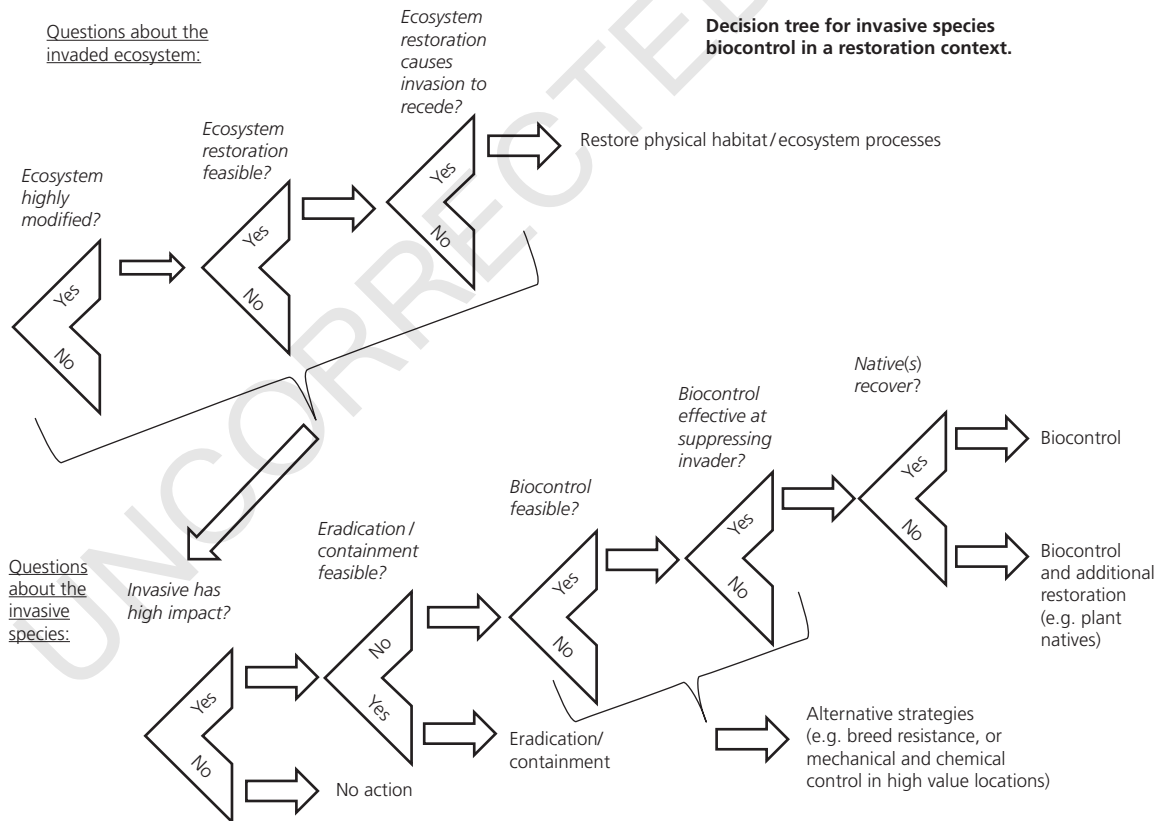


Figure 2.2 Decision tree to assist in determining the strategy that is likely to be most effective at restoring an ecosystem.

important tree species. Given those facts, an eradication/containment program was implemented. After this effort failed due to the sometimes large dispersal distances by adult emerald ash borers, a biological control program was initiated (Herms and McCullough, 2014). Biological control, however, is not always feasible or successful. For instance, control of an insect vector of a systemic disease is unlikely to reduce the vector's abundance sufficiently to prevent disease transmission (e.g., Fuester et al., 2014). In such cases an alternative conservation strategy, for example breeding disease-resistant varieties, may be more successful. Even where biological control is successful at suppressing invader populations, populations of native species may not recover satisfactorily and additional restoration actions such as planting native plants or reducing herbivory may be necessary (Lake et al., 2014).

Despite the potential challenges, conservation managers are increasingly looking to biological control as a more sustainable solution to invasive species management because conventional mechanical and chemical control needs a high level of investment indefinitely. A further advantage of biological over chemical and mechanical control is that it does not stop at the property line of participating landowners, thus avoiding a major source of re-invasion. A growing trend is to focus mechanical and chemical invasive species control on sites of exceptionally high conservation value (e.g., eagle nest tree threatened by invasive vines) or preserve locations with high public visibility where the desire is to keep them as a natural history museum (e.g., nature centers with an environmental education mission) to reduce costs. Thus, for invasive species that are already widespread, developing an effective biological control program may be the only potentially feasible way to suppress the invader's population and its damage over the long term and at geographic scales larger than a few hundred hectares. Given this realization, we would argue that conservation organizations and especially state and federal agencies should increasingly shift conservation resources used for mechanical and chemical invasive species control in the past towards developing more classical biological control programs for the most serious invasive insect and plant species in the future (Van Driesche et al., 2010; Martin and Blossey, 2013).

Designing a restoration plan using Connecticut River floodplain forests as a model

Aquatic habitats, riparian areas, and wetlands are the focus of much restoration work because of their disproportionate importance to ecosystem services (Costanza et al., 1997; Zedler and Kercher, 2005; Moreno-Mateos et al., 2012). These habitats are disturbed by floods and human activities, and they accumulate water, energy, sediments, nutrients, pollutants, seeds, and other propagules from the rest of the watershed, making them prone to invasion (Zedler and Kercher, 2004; Richardson et al., 2007; Catford and Jansson, 2014). A high abundance of invasive plants is, for example, a common cause of failure in wetland mitigation (Minkin and Ladd, 2003).

The Connecticut River was identified as a conservation priority through a regional "conservation action planning" (CAP) initiative convened by The Nature Conservancy (TNC) in New England in the 1990s. The Connecticut is New England's longest river, supporting extensive biodiversity and acting as a migration corridor for diadromous fish and birds. Its water constitutes 70% of the freshwater inflow to Long Island Sound and its watershed provides the drinking water supply for Boston, Springfield, Hartford, and many smaller cities and towns. The Connecticut River tidal wetlands and estuary were recognized at the 1994 Ramsar Convention as a wetland area of international importance. Its floodplains contain some of the region's most fertile agricultural soils and provide natural flood protection for downstream cities. Instead of addressing the needs of individual species, CAP recommend focusing on the processes and habitats that maintain the health of this critical ecosystem (Nislow et al., 2010).

Floodplain forests, low-lying forested areas along rivers that flood periodically, are considered one of the rarest and most threatened natural community types in New England. They provide valuable habitat for wildlife as well as absorbing flood waters, sediments, and pollutants. Many invasive species thrive in such nutrient-rich sites with a history of agricultural use, making the restoration planning for Connecticut River floodplain forests a good example for discussion of issues relevant to invasive species management. In this case study, we will examine the drivers of ecosystem change in the New England's floodplain forests, focusing on the role of

invasive non-native species and what are likely to be effective restoration strategies. Rather than taking the perspective of biological control scientists or even invasive species biologists, we are taking the perspective of the conservation planner where invasive species control may or may not be a priority conservation strategy, depending on the relative importance of other threats to this ecosystem. Application of the decision tree (Figure 2.2) led to contrasting strategies for restoration and invasive species management for different invasive species groups and types of floodplain forest habitats, as described below.

Restoring physical processes to suppress invasive plants

The most important process affecting floodplain forests is flooding (Junk et al., 1989). Flooding and associated sediment movement not only govern species composition but also shape the morphology of the river channel and floodplain (Hupp, 2000). A study of vegetation composition in relation to flood regime at 103 floodplain forest sites located throughout the Connecticut River watershed found that the abundance of both native upland trees and exotic invasive shrubs declined with increasing flooding, whereas the abundance of native floodplain tree species increased (Marks et al., 2014). Flood-intolerant invasive plants that were increasingly suppressed with increasing flood duration include *Acer platanoides* L., *Aegopodium podagraria* L., *Ailanthus altissima* (Mill.) Swingle, *A. petiolata*, *B. thunbergii*, *Celastrus orbiculatus* Thunb., *Cynanchum louiseae* Kartesz & Gandhi, *Elaeagnus umbellata* Thunb., *Euonymus alatus* [Thunb.] Siebold, *Frangula alnus* Mill., *Lonicera morrowii* A. Gray, *Rhamnus cathartica* L., and *Rosa multiflora* Thunb.

In contrast to the invasive shrubs and trees, a few non-native herbaceous species were found to be able to tolerate extended flooding. These included *Fallopia japonica* [Houtt.] Ronse Decr., *Fallopia* × *bohemica*, *Lysimachia nummularia* L., *L. salicaria*, *Microstegium vimineum* [Trin.] A. Camus., *Phalaris arundinacea* L., and *P. australis*. Three of these species (*L. salicaria*, *P. arundinacea*, and *P. australis*) are shade-intolerant marsh species and thus not a threat to floodplain forests. At floodplain forest sites where restoration of extended flooding can be accomplished, it is likely that problems with invasive plants can be effectively reduced.

Succession is the process of change in ecological communities after disturbance and as such provides a useful guide for restoration (Whisenant, 2005). In floodplains,

succession is initiated by the formation of new bars, which frequently happens during a large flood event. Pioneer species such as willows (*Salix*) colonize these bars. Growing pioneer trees and shrubs stabilize the bars and promote the accretion of more sediment, thereby improving conditions for colonization by late successional floodplain forest species that are both less flood tolerant and more shade tolerant (Dietz, 1952; Shelford, 1954; Lindsey et al., 1961; Hosner and Minckler, 1963; Johnson et al., 1976; Nanson and Beach, 1977; Bertoldi et al., 2009; Meitzen, 2009; Gurnell et al., 2012). Relatively few invasive species currently occur in these pioneer bar habitats on the Connecticut River because flooding is typically too severe and sediment accretion rates are high (Marks et al., 2014). Another factor promoting native dominance on bars is that native floodplain pioneers like *Salix nigra* Marshall, *Populus deltoides* Bartram ex Marshall, and *Acer saccharinum* L. produce their seeds in spring and are wind and water dispersed, an ideal strategy to reach fresh sediment seed beds as flood waters from the spring freshet recede (Mahoney and Rood, 1998), in contrast to most invasive shrubs and woody vines, whose bird-dispersed seeds occur in the fall. Thus, in un-channelized rivers the dynamics of lateral channel migration and bar formation create habitats that are relatively resistant to invasion by the existing suite of bird-dispersed, invasive shrubs in northeastern North America. It is crucial to maintain these physical processes to protect this habitat. Specifically, it is critical to avoid bank hardening and to sustain natural flood and sediment-transportation regimes as much as possible (Shankman, 1993; Schnitzler, 1995; Fierke and Kauffman, 2005; Leyer, 2006).

The exception to this natural invasion resistance of river bars is Japanese knotweed (collectively, *F. japonica*, *F. sachalinensis* [F. Schmidt ex Maxim.] Ronse Decr. and their hybrid, *F.* × *bohemica*), which readily colonizes bars and riverbanks especially on high-gradient rivers where flooding is naturally brief and scour from high flows moves knotweed rhizomes, which can re-sprout after being deposited on downstream bars. Japanese stiltgrass (*M. vimineum*) invasion may similarly benefit from water dispersal of seeds in riparian areas (Eschtruth and Battles, 2011). Japanese knotweed can reach a very high level of dominance in this habitat, which interferes with recruitment of trees and other native plants (Figure 2.3) (Urgenson et al., 2012). Thus, Japanese



Figure 2.3 Forlorn TNC intern standing surrounded by Japanese knotweed in a high-gradient river floodplain forest on the Green River in Massachusetts, June 23, 2009. Photo credit, Christian Marks.

knotweed not only transforms the understory of floodplain forests on high-gradient rivers but can eventually also reduce riparian forest cover by preventing tree seedling recruitment. A lack of riparian trees, with their extensive root systems, increases bank erosion (Secor et al., 2013). This ecological impact of Japanese knotweed was one of the motivations behind an international program (USA, Canada, and the UK) to attempt to develop an effective biological control project against Japanese knotweeds (Shaw et al., 2009; Grevstad et al., 2013). The first agent, the psyllid *Aphalara itadori* Shinji, in this project is currently under review in North America and being field-tested in England.

Assessing ecological impact of invasive species

Selection of species for control should ideally be based on quantitative evidence of their impact. While failure of native species to reproduce (as discussed above for Japanese knotweed's effect on riparian tree seedlings) is critical, so are higher mortality rates caused by effects of invasive species. Invasive vines and lianas are able to directly cause mortality of native plants and are thus of particular concern (Forseth and Innis, 2004; Hough-Goldstein et al., 2012; Center et al., 2013). The invasive liana oriental bittersweet (*C. orbiculatus*) causes

severe damage including mortality of mature trees in extensively invaded floodplain forests in Connecticut and Massachusetts among other states (Figure 2.4). However, severe impacts by *C. orbiculatus* are largely restricted to forest edges, canopy gaps, and heavily disturbed areas like old fields (McNab and Loftis, 2002; Kuhman et al., 2010; Pavlovic and Leicht-Young, 2011), which make up a relatively small part of the overall floodplain forest area and thus could be misleading as to the invader's true impact. However, a study of tree mortality in 103 Connecticut River floodplain forests estimated that 0.3% of floodplain forest trees were destroyed annually by oriental bittersweet (Marks and Canham, 2015). For mature trees where self-thinning is no longer an important cause of mortality (i.e., diameter at breast height [dbh] = 60 cm), lianas were second only to storms as a cause of floodplain tree mortality. Most of the liana-induced mortality of mature trees was due to invasive *C. orbiculatus* (43%) and native *Vitis riparia* Michx. and *V. labrusca* L. (35%), or a combination of *Celastrus* and *Vitis* (22%). By contrast, other abundant native lianas such as *Toxicodendron radicans* [L.] Kuntze and *Parthenocissus quinquefolia* [L.] Planch. do not appear to cause significant tree mortality.

Celastrus orbiculatus is dominant in the herb layer of Connecticut River floodplain forests and about eight



Figure 2.4 Connecticut River floodplain forest breaking down under a heavy load of invasive oriental bitter-sweet and turning into a weedy vine thicket, West Springfield, Massachusetts, March 15, 2013. Photo credit, Christian Marks.

times more frequent than native *Vitis* species (Marks et al., 2014), and it is therefore going to affect tree recruitment and old field succession more often. *Celastrus orbiculatus* can become so dominant in the herb and shrub layer of forest openings that it prevents tree sapling recruitment. Similarly, researchers have observed that *C. orbiculatus* can arrest or even reverse succession in old fields (McNab and Meeker, 1987; Fike and Niering, 1999). Therefore the impact of *C. orbiculatus*-caused tree mortality may be cumulative, unlike other sources of mortality that result in only temporary forest canopy gaps. The Connecticut River floodplain forest mortality study estimated that floodplain forest canopy area is currently destroyed by *C. orbiculatus* at a rate of 0.2% per year (Marks and Canham, 2015). If left unchecked for decades, the cumulative loss of forest canopy area owing to *C. orbiculatus* could be comparable to the potential future impact of emerald ash borer. *Fraxinus* made up 7.4% of the floodplain forest canopy in the study. At a constant rate of 0.2% per year, it would take just 39 years for *C. orbiculatus* to destroy a comparable 7.4% of the canopy. Thus, although it moves more slowly than an insect pest or pathogen, the cumulative impact of this invasive liana may be just as severe.

While chemical/mechanical control programs against invasive vines can be mounted quickly, they are costly and difficult to sustain. Volunteers at the Silvio O. Conte

National Wildlife Refuge along the Connecticut River helped us quantify the time needed for mechanical control of oriental bitter-sweet vines in two contexts. Along a heavily invaded floodplain forest edge, it took 115 man-hours/hectare (47 hours/acre) to cut bitter-sweet vines. In contrast, in a nearby old floodplain field dominated by cottonwood saplings that were starting to break down under smothering bitter-sweet vines, it took 435 man-hours/hectare (176 hours/acre) to cut bitter-sweet. The old field area was much harder to work in because the saplings were dense and there were many small vines, compared to fewer larger vines at the edge of the mature forest. These large labor costs would make it prohibitively expensive to control bitter-sweet at the landscape scale by conventional means and pose a financial burden even for restoration of individual floodplain forest sites if they are heavily infested. The development of an effective classical biological control agent is thus the only potentially financially viable means of reducing the impact of oriental bitter-sweet at the landscape scale. Trees falling into roads and onto power lines also have economic impacts, directly via cleanup costs and indirectly via power outages and blocked roads. Given the destructive potential of exotic vines and lianas (Forseth and Innis, 2004; Hough-Goldstein et al., 2012; Center et al., 2013), they should be ranked highly, not only in setting priorities for biological control but also in terms of the need for

greater regulatory restrictions on the introduction of new plant species from overseas.

Eradication and containment of a serious invader

Another potentially serious threat to floodplain forests is the Asian longhorned beetle (ALB) (*Anoplophora glabripennis* Motschulsky), which preferentially attacks species of *Acer* and *Populus*, common floodplain forest dominants on the Connecticut and many other northern US rivers. Repeated attack by ALB leads to tree mortality within a few years and the potential for damage in urban forests is large (Nowak et al., 2001). The threat to native forests, while still unknown, is potentially even larger. The eradication effort against ALB led by the USDA Forest Service has been focused mostly on urban areas, including one in Worcester, Massachusetts, at the edge of the Connecticut River watershed. This eradication program is an example of the early detection and rapid response approach to invasive species control that, if successful, would make a biological control program for ALB unnecessary. However, should ALB eradication fail in even one infested area and natural forests become extensively invaded, biological control would be a potentially feasible way to reduce the damage.

Biological control and breeding host resistance against pests and pathogens

Before the spread of Dutch elm disease (DED), American elm (*Ulmus americana* L.) was co-dominant with silver maple (*A. saccharinum*) in the canopies of floodplain forests on many northern rivers in the United States, including the Connecticut River (Nichols, 1916; Telford, 1926; Curtis, 1959). American elm was also the largest tree species in Massachusetts (Emerson, 1887). Even today, American elm is the most widespread and the second most abundant floodplain tree species in the Connecticut River watershed (Marks et al., 2014), but it now rarely lives long enough to reach the forest canopy (Figure 2.5). Green ash (*Fraxinus pennsylvanica* Marshall), which has a similar level of flood and shade tolerance as American elm, has to some degree replaced it in the southern part of the Connecticut River watershed, but green ash is now also threatened by emerald ash borer, which reached the Connecticut River watershed in Connecticut in 2013. Observations from formerly ash-dominated forest stands in the Great Lakes states where the emerald ash borer invasion began suggest that green ash might persist as an understory tree species, like American elm, because it reproduces early and seedlings are generally not attacked by emerald ash borer (Wagner and Todd, 2015). The reduction in floodplain forest

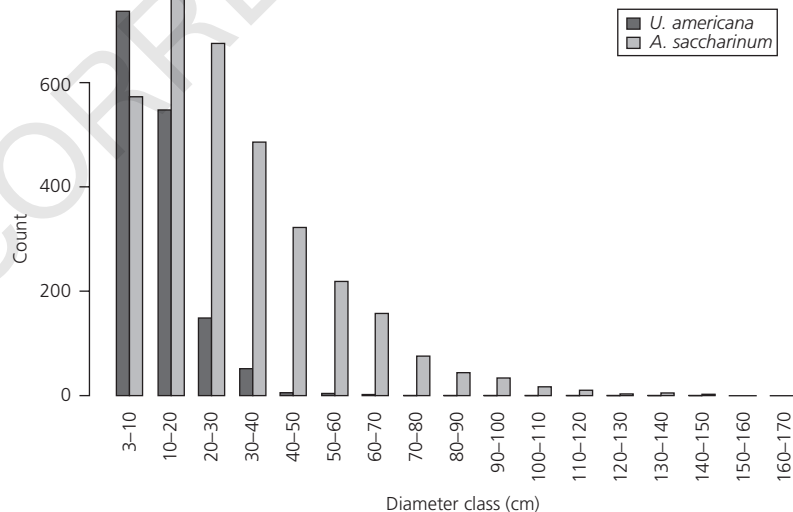


Figure 2.5 Tree size distribution for American elm (*U. americana*) and silver maple (*A. saccharinum*), the two most common tree species in Connecticut River floodplain forests when surveyed in 2008 to 2011. Note the rapid reduction of elms beyond 20 cm and absence over 60 cm dbh, in contrast to silver maple, likely due to Dutch elm disease. Unpublished data of Christian Marks.

stature associated with Dutch elm disease and emerald ash borer may have implications for bird species that prefer nesting or foraging in the upper canopy of riparian forests (Knutson and Klaas, 1998).

Given their destructiveness to ecologically and economically valuable trees, biological control has been considered for both Dutch elm disease and emerald ash borer. The more recently arrived emerald ash borer is the subject of an active biological control program and new parasitoids are still being released (Chapter 10). Although biological control of the bark beetles that spread DED and the deployment of hypovirulent strains of the fungus that causes DED were explored, neither of these biological control approaches were successful at reducing American elm mortality (Brasier, 2000; Fuester et al., 2014). Subsequent efforts at restoring American elm have instead focused on selecting surviving American elms for greater disease tolerance (Heybroek, 2000; Mittempergher and Santini, 2004; Townsend et al., 2005). While breeding of resistant elm varieties was initially done for use of elms in urban areas, programs are now underway to re-introduce highly disease-tolerant cultivars of native American elms into riparian habitats including Connecticut River floodplain forests (Slavicek et al., 2005; Slavicek and Marks, 2011; Knight et al., 2012). Although emerald ash borer causes high rates of mortality in the three native ashes of the region (*F. pennsylvanica*, *Fraxinus nigra* Marshall and *Fraxinus americana* L.) (Rebek et al., 2008; Knight et al., 2013), a few individuals appear to have some host resistance to the borer, and breeding native ash trees for greater host resistance is being explored as a restoration strategy to complement the biological control program (Koch et al., 2011).

Holistic ecological restoration and invasive species management

Rich, high-floodplain terraces typically have more invasive plants than other floodplain forest communities. High terraces are prone to non-native plant invasion, in part because soils are very fertile and floods are infrequent and of short duration, and because they have suffered from more intense disturbance by human activities, especially the historic clearance of native forest to create cropland. In our floodplain field work, we observed that many invasive woody plants (e.g., *R. multiflora*) had their greatest abundances in former agricultural land, as was also observed in other studies (McDonald et al., 2008; Mosher

et al., 2009; Kuhman et al., 2010, 2011). One exception to this general pattern that we observed in Connecticut River floodplain forests is Norway maple (*A. platanoides*), which does invade closed-canopy forests with deep shade in the understory, albeit slowly because of limited dispersal ability (Martin et al., 2010). These findings suggest that changes in land management could reduce the abundance of many but not all invasive plants species. In New England that would mean avoiding severe disturbances (like logging) in protected forests (Lee and Thompson, 2012), but this may conflict with other conservation goals, like creation of early successional habitat needed for certain declining animal species.

The invasive shrubs that we frequently encounter in abundance on high terraces in the Connecticut River floodplains include Japanese barberry (*B. thunbergii*), winged-euonymus or burning bush (*E. alatus*), Morrow's honeysuckle (*L. morrowii*), glossy buckthorn or alder buckthorn (*F. alnus*), multiflora rose (*R. multiflora*), and occasionally also autumn-olive (*E. umbellata*), Amur honeysuckle (*Lonicera maackii* [Rupr.] Herder), common buckthorn (*R. cathartica*), and Japanese wineberry (*Rubus phoenicolasius* Maxim.). It is not immediately obvious if these invasive shrubs have substantial ecological impacts on floodplain forests in New England beyond altering understory composition. For instance, our field data showed that there are still plenty of native tree seedlings to fill canopy gaps in floodplain forests even where there is a high abundance of non-native shrubs in the understory. The most concerning evidence of a negative impact by these invasive shrubs is on native insect herbivore communities and their predators. Native specialist as well as generalist Lepidoptera and arthropods fare poorly on non-native plants (Burghardt et al., 2010; Tallamy et al., 2010; van Hengstum et al., 2014). Thus, non-native plant invasions have consequences for higher trophic levels, such as birds that critically depend on insects as a source of protein for raising nestlings (Tallamy, 2004). This impact is substantial even where most trees are native and exotic invasive plants are largely restricted to the understory (Burghardt et al., 2009). While berries from invasive shrubs can provide an ample fall food source for migrating songbirds (Gleditsch and Carlo, 2011), that does not compensate for the decrease of insect prey during the nesting season. It seems fair to conclude from the evidence available that in New England forests the impacts of these invasive shrubs detract from the

forests' ecological value but are not so disruptive as to cause transformative change, such as preventing forest regeneration.

Nutrient-rich forests with ample moisture like high-terrace floodplains, coves, and seeps are noted for their exceptional native plant species richness and as such are attractive for conservation in the region, but restoration of the native herb and shrub layer community may require more action than just control of invasive plants. For example, years of mechanical control of Japanese barberry on some TNC forest reserves in Connecticut resulted in relatively bare areas with some re-sprouting and re-invasion by barberry but little recruitment of native plants. The lack of recruitment of desired native plants may be due to a lack of native seed (Drayton and Primack, 2012), intense browsing by native deer (Knight et al., 2009; Collard et al., 2010; Royo et al., 2010; Tanentzap et al., 2011; Dávalos et al., 2014; Nuttle et al., 2014), or even effects of non-native earthworms on the leaf litter layer and the soil seed bank (Frelich et al., 2006; Hale et al., 2006; Nuzzo et al., 2009; Fisichelli et al., 2013). Successful restoration of rich high-terrace floodplain forests in particular locations will require determination of the causes of degradation so that those causes can be addressed, in conjunction with any potential invasive species control.

Biological control agents from other regions

Although some of the invasive plants discussed here may not reach the level of impact in Connecticut River floodplain forests to warrant a biological control program, they may have more transformative impacts in other ecosystem types or in other regions. For example, common buckthorn (*R. cathartica*) can transform the structure of forests in the midwestern United States and adjacent Canada where soils and climate are more suitable for buckthorn (Archibold et al., 1997; Knight et al., 2007; Mascaro and Schnitzer, 2007). Many insects from buckthorn's native range in Europe were tested as biological control insects for common (*R. cathartica*) or glossy buckthorn (*F. alnus*) by the Minnesota Department of Natural Resources and CABI (Gassmann et al., 2010), but none were host specific and sufficiently damaging to buckthorns, and the biological control program for buckthorns was discontinued after 11 years of research.

Sometimes biological control also happens on its own owing to biotic resistance from native organisms in the invader area. The invasive tree-of-heaven, *A. altissima*, is susceptible to a presumed-native North American soil-borne vascular wilt fungus *Verticillium nonalfalfae* Inderb., which is now being explored as a potential biological control agent for interstate movement within the United States (Schall and Davis, 2009a, b; Harris et al., 2013; Kassin et al., 2014; Snyder et al., 2014). Similarly, the invasive multiflora rose (*R. multiflora*) is highly damaged by rose rosette disease, a viral pathogen native to the Rocky Mountains that is gradually spreading eastward and may eventually suppress non-native roses along the Connecticut River, as has already happened in the midwestern states (Epstein et al., 1997; Epstein and Hill, 1999; Amrine, 2002; Jesse et al., 2006; Banasiak and Meiners, 2009; Jesse et al., 2010). In addition, a chalcid wasp (*Megastigmus aculeatus* var. *nigroflavus* Hoffmeyer) that is specialized to attack the seeds of *R. multiflora* was accidentally introduced into North America from its native range in Asia (Amrine, 2002). Thus it makes sense for limited conservation resources in a given region to focus on the most serious invaders, knowing that a few of the locally less serious invaders may eventually also come under biological control because of developments in other regions.

Conclusion for Connecticut River watershed case study

The first priority of a conservation strategy should be to restore, as much as is economically feasible, the physical processes that control community composition and ecosystem functions over the long term. Where physical processes like disturbance regimes and nutrient levels are relatively unaltered, generally fewer exotic plant species have invaded; where physical processes have been dramatically altered, invasive plant control alone is unlikely to achieve ecological restoration. Consistent with this view, TNC has made restoration of physical processes a primary focus for its Connecticut River Program. In particular TNC is collaborating with owners of large dams to modify operations for greater ecological benefit (Warner et al., 2014), as well as to protect and reforest floodplain land to give the river the space it needs for geomorphic processes to unfold in uninhibited fashion. However, some invasive species are able to invade and do substantial damage even where physical

processes are intact. These species make compelling cases for classical biological control, particularly where invasion causes transformative ecological change. Specific examples where a biological control program could be justified by ecological impacts to Connecticut River floodplain forests include emerald ash borer, Japanese knotweed, and oriental bittersweet.

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