6 Invasive Species and the Resiliency of a Riparian Environment

James M. Dyer and C. Mark Cowell

CONTENTS

6.1	Introduction		87
6.2	What Contributes to Successful Invasion?		88
6.3	Crull's Island		88
	6.3.1	Invasive Species on Crull's Island	89
		Site Characteristics of Crull's Island	
	6.3.3	Changing Vegetation Patterns on Crull's Island	
		6.3.3.1 Floodplain	
		6.3.3.2 Terrace	
	6.3.4	Altered Abiotic Gradients and Competitive Relationships	
		Management Concerns	
Acknowledgment			
References			100

6.1 INTRODUCTION

Research into exotic species invasions has focused on both the life-history traits of the invaders and the site qualities that may make ecosystems prone to invasion. Successful invasion of an ecosystem is typically a result of conducive combinations of species and site characteristics (Alpert et al. 2000). Crull's Island, PA, aggressively colonized by two invasive species following the construction of an upstream dam, illustrates this interaction well. The island is used as a case study to highlight the dynamics of a highly *invasible* system. The process of invasion is discussed within the context of resiliency theory. Originally posited for ecological systems (Holling 1973), resiliency theory has been extended to address linked ecological and social systems (e.g., Carpenter et al. 2005; Walker et al. 2002). Although a few studies have applied the framework of resiliency theory to investigations of exotic species (e.g., Forys and Allen 2002), little has been done regarding invasive plants. Our examination of Crull's Island highlights the

many dilemmas associated with natural area management in the eastern United States, where extensive human modification of landscape processes has combined with introduction of nonnative species to fundamentally alter the functioning of the region's ecosystems.

6.2 WHAT CONTRIBUTES TO SUCCESSFUL INVASION?

Invasive species tend to share many characteristics: the ability to disperse long distances to new sites; the ability to establish readily in areas modified by human activities; the ability to outcompete native species and spread rapidly from their initial point of establishment; and the tendency to be difficult to eradicate once established. One example of a *species-focused* explanation of invasiveness is the empty niche hypothesis, which proposes that exotic species become invasive because they are able to access resources in the community that native species do not utilize (Hierro et al. 2005).

On the other hand, alteration of the natural disturbance regime, which is often critical for the establishment of invasive species, provides an example of a *site-focused* explanation of invasiveness. Disturbance alters both resource availability and competitive interactions, and changes to the disturbance regime may favor exotic species with adaptive traits not present within the native community (explaining why exotics are often seen to create persistent monotypic stands; Prieur-Richard and Lavorel 2000).

6.3 CRULL'S ISLAND

Dozens of islands are situated in the Allegheny River of northwestern Pennsylvania; seven located between Warren and Tionesta (Figure 6.1) were designated the "Allegheny Islands Wilderness" by the U.S. Forest Service in 1984. The largest (39 ha) of these wilderness islands is Crull's Island (41° 49′ N, 79° 16′ W), which possesses some of the best examples of riverine forest in Pennsylvania (Smith 1989). The Forest Service also designated Crull's Island as a research natural area in 1988, and in accordance with its wilderness designation, only recreation, education, and research activities are permitted on the island.

Crull's Island, formed from glacial outwash and alluvial deposits, is overlain by loam and sandy loam soils (Cerutti 1985). Topographically, the island is composed of a terrace <3 m above the river banks, which is surrounded by a floodplain 1–110 m wide. A steep slope separates the terrace and floodplain in most areas, though on the upstream side of the island there is a more gradual transition, with an intermediate upper floodplain surface (Figure 6.2). The region is characterized by a humid continental climate, with mild summers and year-round precipitation. The island is situated in the Northern hardwoods–hemlock forest region, near the boundary with the Mesophytic region (Dyer 2006).

Crull's Island has a long history of agricultural land use. The island was originally purchased by the Crull family, who were farming most of it by the midnineteenth century (Babbitt 1855). Cultivation and livestock grazing continued on the island into the early twentieth century (Crull 1996, personal communication).

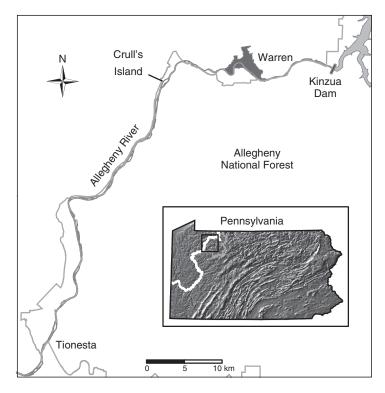


FIGURE 6.1 Location of Crull's Island. Inset map shows location of study area in Pennsylvania with respect to the Allegheny River and the Allegheny National Forest.

6.3.1 INVASIVE SPECIES ON CRULL'S ISLAND

Crull's Island has been colonized by two problematic species with multiple *invasive* traits, the first being Japanese knotweed (*Polygonum cuspidatum*). Japanese

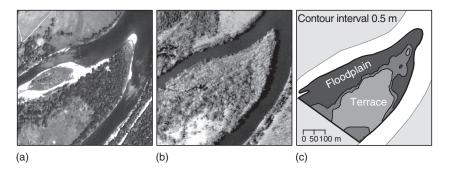


FIGURE 6.2 Vegetation and topography of Crull's Island: (a) 1939 USDA aerial photograph, (b) Present-day USGS digital orthophoto, (c) Contours and primary geomorphic surfaces. The upper floodplain, intermediate between the terrace and lower elevation floodplain, is evident at the head of the island.

knotweed is a shade-tolerant, rhizomatous perennial, 1-3 m in height. Although herbaceous, its erect stems can develop bamboo-like woody stems, explaining another of its common names, Mexican bamboo. In the United States, it is most frequently referred to as P. cuspidatum, whereas in the United Kingdom it is more commonly called *Fallopia japonica (Reynoutria japonica* is another synonym; Bram and McNair 2004). Introduced as an ornamental in the nineteenth century from its native East Asia, Japanese knotweed is considered invasive in both Europe and the United States, especially in New England and the Midwestern United States. It threatens native species, reducing both plant species diversity as well as habitat diversity (Weston et al. 2005). Although it does not seem capable of regeneration from seed in Europe (in contrast to the United States), it has demonstrated long-distance dispersal from points of introduction in both the United States and Europe (Beerling et al. 1994; Bram and McNair 2004; Hulme 2003). New colonization events can occur through the spread of rhizomes in soil transported by humans, and especially through rhizome dispersal by rivers (Pyšek and Prach 1993; Weston et al. 2005).

Japanese knotweed is most widespread on stream banks, in disturbed sites such as roadsides, as well as on the edges of, and within, open woodlands. It attains highest abundance in high light environments, and once established it is able to form dense patches. The dense clumps, dense canopy, and accumulation of stem litter exclude most other plants once Japanese knotweed establishes. It may also possess allelopathic properties. Japanese knotweed can spread via rhizomes, which can be >2 m in depth, and extend 15–20 m in length. Because of its extensive rhizomes, Japanese knotweed is very difficult if not impossible to control once established. Pulling, cutting, burning, and herbicide treatments have not proven entirely successful. Cutting may actually increase stem density and facilitate spread, and herbicide application is often problematic in riparian environments (i.e., adjacent to streams and rivers; Beerling et al. 1994; Bram and McNair 2004; Weston et al. 2005).

The second problematic species with multiple invasive traits on Crull's Island is reed canary grass (*Phalaris arundinacea*). Reed canary grass is a C3 grass that grows to a height of 1–2 m. Although native to both North America and Europe, European cultivars were introduced into the United States in the mid-nineteenth century. While the native variety was not considered aggressive, current populations may be hybrids and are considered invasive (Lindig-Cisneros and Zedler 2002). Despite the invasive potential of these cultivars, they continue to be planted for forage, stream bank erosion control, ditch stabilization, and phytoremediation (Gifford et al. 2002; Lavergne and Molofsky 2004). Reed canary grass seems to be able to occupy sites where native species perform poorly, and once established, it progressively displaces native species, especially in riparian environments (Apfelbaum and Sam 1987; Miller and Zedler 2003).

Reed canary grass is a prolific seeder, but can also spread from rhizomes or branch fragments. Once established, it spreads quickly through rhizomes to form dense stands (Gifford et al. 2002; Lavergne and Molofsky 2004; Lindig-Cisneros and Zedler 2002). Early-season growth is concentrated above ground, preempting the establishment of other species. Subsequent growth occurs below ground, favoring vegetative spread into adjacent plant canopies (Adams and Galatowitsch 2005).

In addition, reed canary grass exhibits seed dormancy, so that it becomes an important component of the seed bank (Lavergne and Molofsky 2004).

A facultative wetland species, reed canary grass, is also found in riparian areas and some upland sites, and outcompetes native species under a wide range of moisture conditions from flooding to drought. It requires high light, and germinates best in moist to waterlogged soils following disturbance (Lavergne and Molofsky 2004; Lindig-Cisneros and Zedler 2002; Miller and Zedler 2003). Vegetative spread can be altered by changes in water depth, as well as frequency or duration of high water levels (Lavergne and Molofsky 2004). Herbicides have not been effective in treating reed canary grass, since the plant quickly reestablishes from seed and rhizomes (Perry and Galatowitsch 2004). As with other invasive species, control is difficult, and the best strategy would be to prevent the initial establishment. Disturbed areas seem most vulnerable to invasion, especially if sites have experienced multiple or interacting disturbances (Kercher and Zedler 2004). In riparian settings, downstream sites are at increased risk of invasion following initial establishment of both reed canary grass and Japanese knotweed.

Japanese knotweed and reed canary grass possess many typically invasive lifehistory traits. Both are capable of long-distance dispersal and readily colonize disturbed sites. Once established, they form dense stands, are able to spread vegetatively into new areas, and are very difficult to eradicate. Thus, positive feedbacks are established; even if a colonized site (such as Crull's Island) is returned to its preinvasion conditions, it is unlikely that these exotic species would relinquish their dominance.

6.3.2 SITE CHARACTERISTICS OF CRULL'S ISLAND

Successful invasion often results when exotic species traits interact with particular site characteristics (Alpert et al. 2000). Crull's Island has a number of properties making it prone to successful invasion, due to its riparian setting and the fact that it has been substantially influenced by human activity (Cowell and Dyer 2002).

Multiple traits of riparian areas in general confer vulnerability to invasion by exotic species, and wetland invasions are among the most aggressive of natural ecosystems in North America (Lavoie et al. 2003). The river itself serves as an agent of dispersal for rhizomes and seeds, and typically riparian areas contain many exposed banks, islands, and bars where new species might colonize. Additionally, riparian areas are subject to frequent disturbance through flooding, which removes biomass, frees up space, reduces competition, and results in high light levels. Many riparian settings experience favorable growing conditions for colonists: high moisture levels and frequent nutrient inputs. Once established, an invasive species can spread laterally from its point of introduction (Pyšek and Prach 1993; Tickner et al. 2001).

These *natural* characteristics which make riparian areas inherently invasible may be compounded by human activities, which can alter normal disturbance regimes and habitat conditions. For instance, riparian areas experience a high degree of land use change. Furthermore, alteration of a river's flow regime through human activities such as channelization or damming (which occurred upstream from Crull's Island) can result in changes to water table depths of riparian sites, soil moisture fluctuations, frequency of inundation, and changes in erosion and deposition of sediment. Such dramatic changes to the disturbance regime and habitat conditions at riparian sites make them especially vulnerable to exotic species invasion.

The hydrologic regime generated by dammed rivers is often associated with reduced species diversity (Nilsson and Berggren 2000). A fundamental effect of many dams is a reduction in the variability of stream flow, with fewer large floods leading to greater stability in riparian habitats (Naiman et al. 1993). The principal impact of dams on vegetation is often the maturation of riparian communities to late successional stages (Johnson 1994; Marston et al. 1995; Miller et al. 1995). Little analysis of the downstream impacts of dams on eastern U.S. deciduous forests exists, although Barnes (1997) and Knutson and Klaas (1998) demonstrate that forests along regulated rivers in Wisconsin and Minnesota have shifted in structure and composition from their presettlement condition. Upstream damming has significantly altered the hydrologic regime of Crull's Island.

In the nineteenth and twentieth centuries, the Allegheny River in the vicinity of Crull's Island experienced at least five major flooding events (>1900 m³/s). In 1965, Kinzua Dam was constructed 25 km upstream of Crull's Island to limit such flooding along the Allegheny River, particularly in urban areas such as Pittsburgh. The influence of dam construction on the geomorphology (and subsequently the vegetation) of Crull's Island has been dramatic. Prior to dam construction, highest flows affecting Crull's Island would occur in spring (mean maximum discharge = $1269 \text{ m}^3/\text{s}$), associated with spring rains and snowmelt. Flows would gradually decrease until their summer minima (mean minimum discharge = $12 \text{ m}^3/\text{s}$). Construction of the dam moderated annual extremes; now, mean maximum flow = $688 \text{ m}^3/\text{s}$ and mean minimum discharge = $29 \text{ m}^3/\text{s}$. The highest recorded flow since dam construction occurred in 1972; the recurrence interval associated with this flow level had a recurrence interval <2 years before dam construction (Figure 6.3; Cowell and Stoudt 2002).

6.3.3 CHANGING VEGETATION PATTERNS ON CRULL'S ISLAND

Riparian areas are naturally *patchy*, with spatial patterns in species assemblages reflecting the geomorphic features of the floodplain and terraces (Hupp and Oster-kamp 1985, 1996). This pattern is driven by the decline in flood frequency and stream power away from the active channel, producing variation in the extent of erosive scouring and mechanical damage, the duration of anaerobic conditions, and the distribution of alluvial sediments (Hack and Goodlett 1960; Hupp 1986). Thus, disturbance and environmental conditions vary spatially and temporally in riparian settings, accommodating a variety of life-history strategies. Previously, we identified patches on Crull's Island in context of their historical development, especially with respect to construction of Kinzua Dam upstream (see Cowell and Dyer 2002 for details of the sampling methodology). Here, we focus specifically on the establishment and colonization of invasive species on the island.

Two distinctive plant associations—floodplain and terrace—segregate along the first axis of a Nonmetric Multidimensional Scaling (NMS) ordination. The segregation

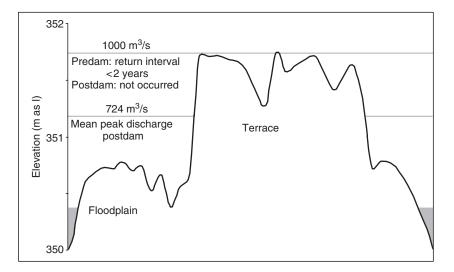


FIGURE 6.3 Elevation profile across a survey transect (vertical exaggeration is \sim 50×), showing pre and postdam discharge levels relative to floodplain and terrace of Crull's Island.

of these low-elevation floodplain sites and higher elevation terrace sites likely results from flooding-related impacts on the island's vegetation. The frequently inundated floodplain sites also had higher levels of base cations such as calcium and magnesium, and contained more silt than higher elevation terrace sites. Although vegetation patches are discernible on the island related to natural geomorphic settings, distinctive human imprints are observed within each patch.

6.3.3.1 Floodplain

Floodplain sites are dominated by sycamore (*Platanus occidentalis*) and silver maple (*Acer saccharinum*), and to a lesser extent American elm (*Ulmus americana*) and white ash (*Fraxinus americana*) in the smaller size classes (Figure 6.4). Although compositionally similar, two distinct patches are noted within the floodplain. Essentially, the lowest elevation sites included in the floodplain were largely bare before dam construction (Figure 6.2), and most individuals established in the decade following dam construction in 1965. In contrast, on the *upper floodplain*, many trees date back to the late nineteenth century, suggesting that predam scouring-associated mortality was not as frequent here as on the lower floodplain. The other especially notable difference between the upper and lower floodplain is the presence of invasive species: Japanese knotweed and reed canary grass are the dominant herbaceous species occurring on the lower floodplain.

Before the construction of Kinzua Dam, Crull's Island provided a classic example of vegetation mediated by the natural disturbance regime of its riparian setting. Flood events created early successional habitat by removing biomass, freeing up resources, and modifying substrate through scouring and deposition (Bendix and Hupp 2000; White and Jentsch 2001). Flow regulation via Kinzua

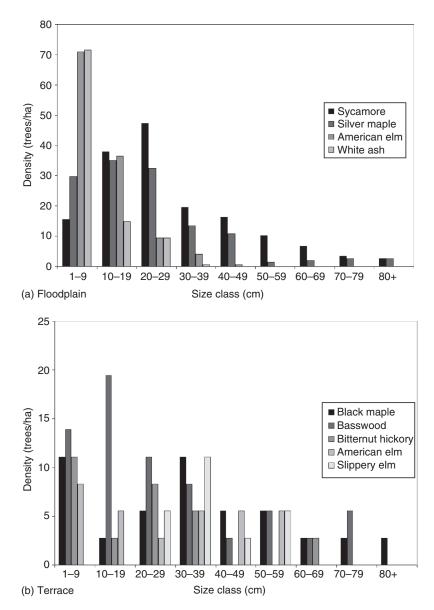


FIGURE 6.4 Size-class distribution for the two primary geomorphic surfaces on Crull's Island: the floodplain, and the older, mature forest of the terrace. Note the scale difference in the *y*-axes. Within the floodplain, tree density is higher on the younger, lower floodplain (349 trees/ha) compared with that on the older, higher floodplain surface (244 trees/ha).

Dam has caused an increase in the mean flow and the termination of the powerful flood events with the ability to destroy biomass and scour existing sites. Following dam construction, no early successional patches have been established on the island, and the lower floodplain has been colonized. Concomitant to this decrease in

disturbance events has been the increased stress of anaerobic soil conditions associated with flood events of longer duration. Although the cohort of sycamore, silver maple, and other floodplain species that have established after flow regulation will likely maintain its dominance for decades, it is unlikely to be self-replacing in the absence of newly scoured sites. These early successional riparian species are intolerant of shade, and their establishment is tied to open sites created by flood disturbance. Reed canary grass and especially Japanese knotweed, however, are well suited to this modified environment.

6.3.3.2 Terrace

In contrast to the floodplain, forested areas of the higher elevation terrace are characterized by upland tree species. Like the floodplain, however, two distinctive patches are discernible within the terrace resulting from anthropogenic influences. The oldest trees of the terrace date to the period 1870–1890, corroborating historical accounts that agriculture was discontinued on this part of the island following a massive flood in 1865 (Crull 1996, personal communication). Forest in this part of the island is represented by trees in a range of size classes (suggesting continual establishment), especially black maple (*A. nigrum*) and basswood (*Tilia americana*), as well as American elm, slippery elm (*U. rubra*), and bitternut hickory (*Carya cordiformis*; Figure 6.4).

The highest ground on the terrace remained cultivated or pastured until around 1930, however. In terms of woody species, this area today contains mostly hawthorns (*Crataegus* sp.), which are able to establish in active pasture owing to their defensive thorns (Stover and Marks 1998). By and large, the hawthorns that are present today are visible on a 1939 air photo; succession has not proceeded within this pasture with the cessation of grazing, and a distinctive boundary still is evident between the maple–basswood terrace forest and the old field with its scattered hawthorns (Figure 6.2). The old field is still dominated by reed canary grass, which was likely planted for forage in the late nineteenth or early twentieth century. Not only is this invasive species precluding the establishment of other species, it also seems to be spreading into the adjacent forested area. As mature elm trees at the forest edge died, likely due to the arrival of Dutch elm disease in the 1970s (Stout 1999, personal communication), adjacent trees responded with increased growth rates; however, recruitment of juveniles into the newly opened site is not occurring. Instead, reed canary grass is expanding at the expense of the forest community.

On the higher island terrace, the older maple–basswood dominated forest does seem capable of gap-phase regeneration. All size classes seem to be represented in this stand, and as gaps are created upon the death of larger individuals, smaller trees are able to ascend into the canopy (Oliver and Larson 1996). On the terrace old field, however, succession to forest is not occurring, and reed canary grass maintains its dominance on the site. In addition, it encroaches into the adjacent forest stand.

6.3.4 Altered Abiotic Gradients and Competitive Relationships

Grime (2001) has characterized habitats on the basis of two primary gradients: productivity and disturbance intensity. These gradients form two sides of a triangle,

and habitats occurring at the vertices of this triangle favor species with three distinctive life-history strategies. *Ruderals* are generally short-lived with high fecundity, and occur in productive sites that are subject to frequent disturbance. *Stress tolerators* occur in sites with infrequent disturbance but low productivity. *Competitors* are able to rapidly monopolize resources on productive sites, but are precluded by frequent disturbance. (These three strategies represent the extremes of life-history strategies; intermediate strategies [e.g., *competitive ruderal, stress-tolerant competitor*] are observed in habitats experiencing intermediate levels of disturbance and stress.) Both reed canary grass and Japanese knotweed would be considered competitors (Grime 2001), a strategy type apparently absent within the native community on Crull's Island with its frequent disturbance.

Human modification of the riparian environment on Crull's Island has significantly altered habitats of both terrace and floodplain environments. These changes create conditions favorable to novel life-history strategies according to Grime's (2001) categorization. A competitive ruderal life-history strategy, characterized by a long period of vegetative growth in this mesic, highly productive, nutrient-rich habitat, would have been favored on the floodplain prior to dam construction. Frequent flooding and associated scouring would have precluded dominance by competitors. The cessation of annual flooding after dam construction stabilized areas of the floodplain, however. Without frequent disturbance, the competitors reed canary grass and Japanese knotweed have been able to thrive at the expense of many resident species.

In contrast to the floodplain, the dominant human modification of the terrace involved land use change. A stress-tolerant competitor strategy, evidenced by later stages of forest succession compared with the floodplain with its recurring flooding, would be favored on this highly productive (but infrequently disturbed) environment. A permanent shift in vegetation composition has occurred with clearing of forest for agriculture and the introduction of the competitor reed canary grass.

Through alteration of the disturbance regime and abiotic gradients on Crull's Island, competitive relationships have changed, and nonnative species have been able to establish. The modified environment (e.g., cessation of scouring, but longer duration flood events) has created novel conditions (e.g., low light, anaerobic soil conditions on the floodplain) that the pool of native species does not seem able to exploit.

6.3.5 MANAGEMENT CONCERNS

The Ecological Society of America recently published policy and management recommendations dealing with invasive species (Lodge et al. 2006). These guidelines call for the strengthening of government authority and interagency coordination in the management of invasive species; they also elucidate the critical importance of intensive monitoring for known invasive species, and the importance of early control and eradication when populations are still localized. Of course, given the ability of invasive species to spread from their points of introduction, the policy recommendations also address the prevention of initial introductions, and the screening of nonnative organisms for their invasiveness risk. A practical application of determining traits of species or sites that foster successful invasion is to identify and protect especially vulnerable ecological systems. For many sites where invasive species already dominate the native community, restoration to some earlier desired state is impractical in terms of available resources, costs, and potential for success. However, for many systems with perceived high ecological value, the control of exotic species invasion may be a high priority for management. For these systems, it is therefore useful to think about managing for natural integrity.

Crull's Island is the largest of several islands in Pennsylvania, federally designated as wilderness area. The wilderness designation attempts to address the trend of shrinking riparian forest habitat, a community type that has experienced dramatic declines in the eastern United States since Euro-American settlement. However, this chapter has highlighted the habitat changes on Crull's Island caused by dam construction as well as the introduction of exotic species with novel life-history traits. Viewed in the framework of resiliency theory, these changes seem to be steering Crull's Island to a new stable state, posing serious management concerns.

The outcome of succession following a disturbance event can be influenced by the nature of the disturbance event as well as predisturbance ecosystem conditions. However, resiliency theory acknowledges the fact that many ecological systems are observed to return to a *stable state* following disturbance (Mayer and Rietkerk 2004), with species composition, interactions, and ecosystem processes similar to predisturbance conditions. Conceptually, the landscape can be described as a series of basins representing stable ecosystem states. Under a given set of environmental conditions, a ball would come to rest at a point within a basin, and tend to return to this original state if perturbed. However, if the perturbation were severe enough, the ball might be pushed into another basin, coming to rest in a new stable state (Scheffer et al. 2001).

In ecological systems, resiliency refers to the level of disturbance a system can experience before shifting to a new stable state, characterized by a different set of dominant species. Species interactions create internal feedbacks that maintain the biotic and abiotic conditions of this new state; thus, an *alternative stable state* is attained (Holling 1973; Mayer and Rietkerk 2004). Because of these internal feedbacks, the longer the system exists in a particular state, the harder it is to *push* it back to a previous state (Mayer and Rietkerk 2004).

Examples frequently cited in treatments of resiliency and alternate stable states include the dramatic shift from clear to turbid lake conditions following humaninduced eutrophication, or the conversion of grassland to woodland associated with a change in grazing intensity (e.g., Folke et al. 2004). These examples illustrate potential unexpected characteristics of a system shifting from one stable state to another. First is the possibility of nonlinear behavior of the change; environmental conditions may change gradually (e.g., an increase in nutrient loading to a lake) until a threshold is crossed, resulting in a rapid change of state. The existence of a critical threshold is often not known until it is crossed. (Note that nonlinear behavior— crossing a threshold in response to changing conditions—does not mean presence of alternate stable states.) Alternative stable states imply that for a given set of conditions, two or more persistent states must be possible (Mayer and Rietkerk 2004). A second characteristic associated with these state changes is that, owing to feedbacks in the new state, merely changing conditions to *preshift* conditions may not be sufficient to change the system back to its original state (Mayer and Rietkerk 2004; Scheffer et al. 2001). In addition, human activity may affect system feedbacks (for example, by altering disturbance regimes or species relationships), which may reduce resiliency. The depth to the basin is made shallower, such that smaller perturbations can lead to an alternate stable state (Folke et al. 2004).

Elton (1958) suggested that high species richness conferred resistance to invasion, because fewer empty niches would be available for exotics to exploit in diverse communities. Although evidence for this hypothesis is equivocal (Richardson and Pyšek (2006) conclude that abiotic factors promoting high native species richness will also promote high exotic species richness), Allen et al. (2005) argue that system resilience is driven not by species identities within a system, but by the functions those species provide. If the same functional groups are represented in the invasive species that displace native species, system resilience may not necessarily be lost (Forys and Allen 2002; Prieur-Richard and Lavorel 2000). However, the introduction of an exotic species representing a new functional group (such as the nitrogenfixing *Myrica faya* in Hawaii; Vitousek et al. 1987) can dramatically alter ecosystem interactions, and make the system more likely to shift to a new stable state (Folke et al. 2004).

On Crull's Island, it would appear that the invasive species represent a new functional group—the competitor strategists (Grime 2001). Reed canary grass and Japanese knotweed possess adaptive traits that enable them to be superior competitors when compared with native species. Once established, these species are able to aggressively maintain a site and spread into adjacent areas. Thus, internal feedbacks are established, which would make returning this system to its preshift condition extremely difficult without major inputs; merely restoring the predam flood regime may be insufficient to return the island to its previous state. Moreover, floods large enough to disturb the floodplain forest on Crull's Island are unlikely to be permitted due to their adverse economic impact.

Resilience can be defined as the ability of an ecological system to maintain its abiotic conditions and dominant species (and their interactions) when subjected to internal change and external disturbance (Cumming et al. 2005). On Crull's Island, human modification (land use change, altered flow regime, introduction of exotic species) has clearly acted as a driver, i.e., a force pushing the system from one basin of stability to another. The establishment of the invasive species reed canary grass and Japanese knotweed indicates that system resiliency is exceeded, leading to a shift to a new stable state on the island. Changes to plant species composition are ongoing, as riparian forest is replaced by monotypic stands of invasive species. Because of the superior competitive ability of these species once they become established, the state change will likely be irreversible without aggressive and continual management intervention. The changes in community composition call into question the notion that the forest of this wilderness island is an old-growth riparian community preserved from the effects of human influence (ANF 1996; Smith 1989; Wiegman and Lutz 1988). Although direct manipulation of the vegetation on Crull's Island is not permitted due to its wilderness designation (ANF 1996), the perception that the island's vegetation is a "natural community" with "no direct management needed to maintain the present ecological conditions" (Wiegman and Lutz 1988, p. 13) should be addressed.

Cronon (1996, 2003) has argued that "the time has come to rethink wilderness" since very few places are "untrammeled by man," but instead are experiencing a "rewilding" following past human activities. Although it is true that no place is free of human influence, especially in areas such as the eastern United States with very few pristine environments, we are nevertheless forced to address issues of ecosystem resilience in the face of aggressive invasive species. Vale (2005) has noted that creation of wilderness areas represents a protectionist impulse, and wilderness may be seen as a desired land use. To this end, it may be valid to think in terms of the need for more aggressive management in at least some wilderness areas. In the case of Crull's Island, the present system represents an obvious human imprint. It is not wilderness simply in the sense of free from human influence; it also fails in its goal to protect the riparian forest habitat. Biological diversity is of increasing concern today in the face of widespread extinction. Protected areas provide refugia of diversity as well as opportunities for visitor experience, enjoyment, and education. Biological diversity is a valued trait of many of our natural areas, yet it is threatened by invasive species (such as garlic mustard, purple loosestrife, and a host of others in addition to Japanese knotweed and reed canary grass) that have the potential to develop monotypic stands. In many areas, the inputs required to control invasive species exceed our ability to provide those inputs. Some areas, however, especially those with high intrinsic natural value, or representative of a threatened habitat type, may be considered a high priority for invasive species control regardless of wilderness designation. In the eastern United States, riparian areas like Crull's Island can be considered a high-priority conservation target. The extent of riparian forest has decreased by more than 80% due to floodplain development (Noss et al. 1995), and further declines in riparian biodiversity may be anticipated from increased modification of fluvial processes. Because of the historic loss of riparian habitat, restoration efforts may be required, shifting these systems back to some desired condition. Given the inherent variability in ecosystems, the benchmark used for the target of restoration efforts is debatable, though it is often sought to maintain the system within its natural range of variability (Sprugel 1991). Unfortunately, resiliency theory suggests that shifting from one stable state to another can be a nonlinear process, requiring a larger amount of time, effort, and resources (Mayer and Rietkerk 2004). Within this context, invasive species represent a major problem in natural areas where their establishment tips the system to a new steady state.

Control of natural disturbance to manage for a more consistent and predictable discharge has resulted in reduced resilience in this Allegheny River riparian ecosystem. Such unintended management consequences support the adoption of *natural disturbance-based management* approaches, which seek to emulate those processes that maintain habitat heterogeneity, both spatially and temporally, and thereby maintain ecosystem resilience (Drever et al. 2006). Given the difficulties with ecosystem restoration, when restoration involves moving the system out of one steady-state basin into another, it is obviously most advantageous to keep

change from occurring in the first place. To prevent systems from undergoing undesirable state shifts, we have two routes: we can maintain system resilience (keep the sides of our stability basin steep), or we can control the perturbations that might trigger a state change (pushing the ball into a different stability basin). Variables that govern system resiliency, such as land use or soil properties, often change gradually and can be readily monitored; in contrast, events that trigger state shifts, such as the establishment of an invasive species, are often difficult to predict and control (Scheffer et al. 2001). For all practical purposes, successful colonization by invasive species may lead to a change of state that is irreversible. Not only must we consider exotic species invasions in terms of economic impacts, or as extinction threats to particular native species, but as a potential threat to entire ecosystems.

ACKNOWLEDGMENT

We thank Mary Dyer for many constructive comments on the manuscript.

REFERENCES

- Adams, C.R. and Galatowitsch, S.M., *Phalaris arundinacea* (reed canary grass): Rapid growth and growth pattern in conditions approximating newly restored wetlands, *Ecoscience*, 12, 569, 2005.
- Allegheny National Forest (ANF), Allegheny National Wild and Scenic River: River Management Plan, USDA Forest Service, Warren, PA, 1996.
- Allen, C.R., Gunderson, L., and Johnson, A.R., The use of discontinuities and functional groups to assess relative resilience in complex systems, *Ecosystems*, 8, 958, 2005.
- Alpert, P., Bone, E., and Holzapfel, C., Invasiveness, invisibility and the role of environmental stress in the spread of non-native plants, *Perspect. Plant Ecol. Evol. Syst.*, 3, 52, 2000.
- Apfelbaum, S.I. and Sams, C.E., Ecology and control of reed canary grass (*Phalaris arun-dinaceae L.*), *Nat. Area. J.*, 7, 69, 1987.
- Babbitt, E.L., The Allegheny Pilot, 1st ed., Babbitt, Freeport, PA, 1855.
- Barnes, W.J., Vegetation dynamics on the floodplain of the lower Chippewa River in Wisconsin, J. Torrey Bot. Soc., 124, 189, 1997.
- Beerling, D.J., Bailey, J.P., and Conolly, A.P., *Fallopia japonica* (Houtt.) Ronse Decraene (*Reynoutria japonica* Houtt.; *Polygonum cuspidatum* Sieb. & Zucc.), *J. Ecol.*, 82, 959, 1994.
- Bendix, J. and Hupp, C.R., Hydrological and geomorphological impacts on riparian plant communities, *Hydrol. Process.*, 14, 2977, 2000.
- Bram, M.R. and McNair, J.N., Seed germinability and its seasonal onset of Japanese knotweed (*Polygonum cuspidatum*), *Weed Sci.*, 52, 759, 2004.
- Carpenter, S.R., Westley, F., and Turner, M.G., Surrogates for resilience of social-ecological systems, *Ecosystems*, 8, 941, 2005.
- Cerutti, J.R., Soil Survey of Warren and Forest Counties, Pennsylvania, USDA Soil Conservation Service, Washington, DC, 1985.
- Cowell, C.M. and Dyer, J.M., Vegetation development in a modified riparian environment: Human imprints on an Allegheny River Wilderness. *Ann. Assoc. Am. Geogr.*, 92, 189, 2002.

- Cowell, C.M. and Stoudt, R.T., Dam-induced modifications to upper Allegheny River streamflow patterns and their biodiversity implications, *J. Am. Water Resour. Assoc.*, 38, 187, 2002.
- Cronon, W., The trouble with wilderness or, getting back to the wrong nature, *Environ. Hist.*, 1, 7, 1996.
- Cronon, W., The riddle of the Apostle Islands: How do you manage a wilderness full of human stories? *Orion*, 22, 36, 2003.
- Cumming, G.S., Barnes, G., Perz, S., Schmink, M., Sieving, K.E., Southworth, J., Binford, M., Holt, R.D., Stickler, C., and Van Holt, T., An exploratory framework for the empirical measurement of resilience, *Ecosystems*, 8, 975, 2005.
- Drever, C.R., Peterson, G., Messier, C., Bergeron, Y., and Flannigan, M., Can forest management based on natural disturbance maintain ecological resilience? *Can. J. For. Res.*, 36, 2285, 2006.
- Dyer, J.M., Revisiting the deciduous forests of eastern North America, *Bioscience*, 56, 341, 2006.
- Elton, C.S., *The Ecology of Invasion by Animals and Plants*, Methuen, London, 1958, Chapter 6.
- Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., and Holling, C.S., Regime shifts, resilience, and biodiversity in ecosystem management, *Annu. Rev. Ecol. Evol. Syst.*, 35, 557, 2004.
- Forys, E.A. and Allen, C.R., Functional group change within and across scales following invasions and extinctions in the Everglades ecosystem, *Ecosystems*, 5, 339, 2002.
- Gifford, A.L.S., Ferdy, J.B., and Molofsky, J., Genetic composition and morphological variation among populations of the invasive grass, *Phalaris arundinacea, Can. J. Bot.*, 80, 779, 2002.
- Grime, J.P., *Plant Strategies, Vegetation Processes, and Ecosystem Properties*, 2nd ed., Wiley, Chichester, UK, 2001, Chapters 1 and 2.
- Hack, J.T. and Goodlett, J.C., *Geomorphology and Forest Ecology of a Mountain Region in the Central Appalachians*, Geological Survey Professional Paper 347, U.S. Government Printing Office, Washington, DC, 1960.
- Hierro, J.L., Maron, J.L., and Callaway, R.M., A biogeographical approach to plant invasions: The importance of studying exotics in their introduced and native range, *J. Ecol.*, 93, 5, 2005.
- Holling, C.S., Resilience and stability in ecological systems, Annu. Rev. Ecol. Syst., 4, 1, 1973.
- Hulme, P.E., Biological invasions: Winning the science battles but losing the conservation war? *Oryx*, 37, 178, 2003.
- Hupp, C.R., Upstream variation in bottomland vegetation patterns, northwestern Virginia, *B. Torrey Bot. Club*, 113, 421, 1986.
- Hupp, C.R. and Osterkamp, W.R., Bottomland vegetation distribution along Passage Creek, Virginia, in relationship to fluvial landforms, *Ecology*, 66, 670, 1985.
- Hupp, C.R. and Osterkamp, W.R., Riparian vegetation and fluvial geomorphic processes, *Geomorphology*, 14, 277, 1996.
- Johnson, W.C., Woodland expansion in the Platte River, Nebraska: Patterns and causes, Ecol. Monogr., 64, 45, 1994.
- Kercher, S.M. and Zedler, J.B., Multiple disturbances accelerate invasion of reed canary grass (*Phalaris arundinacea* L.) in a mesocosm study, *Oecologia*, 138, 455, 2004.
- Knutson, M.G. and Klaas, E.W., Floodplain forest loss and changes in forest community composition and structure in the upper Mississippi River: A wildlife habitat at risk, *Nat. Area. J.*, 18, 138, 1998.
- Lavergne, S. and Molofsky, J., Reed canary grass (*Phalaris arundinacea*) as a biological model in the study of plant invasions, *Crit. Rev. Plant Sci.*, 23, 415, 2004.

- Lavoie, C., Jean, M., Delisle, F., and Létourneau, G., Exotic plant species of the St. Lawrence River wetlands: A spatial and historical analysis, *J. Biogeogr.*, 30, 537, 2003.
- Lindig-Cisneros, R. and Zedler, J.B., *Phalaris arundinacea* seedling establishment: Effects of canopy complexity in fen, mesocosm, and restoration experiments, *Can. J. Bot.*, 80, 617, 2002.
- Lodge, D.M., Williams, S., MacIsaac, H.J., et al., Biological invasions: Recommendations for U.S. policy and management, *Ecol. Appl.*, 16, 2035, 2006.
- Marston, R.A., Girel, J., Pautou, G., Piegay, H., Bravard, J.P., and Arneson, C., Channel metamorphosis, floodplain disturbance, and vegetation development: Ain River, France, *Geomorphology*, 13, 121, 1995.
- Mayer, A.L. and Rietkerk, M., The dynamic regime concept for ecosystem management and restoration, *Bioscience*, 54, 1013, 2004.
- Miller, J.R., Schulz, T.T., Hobbs, N.T., Wilson, K.R., Schrupp, D.L., and Baker, W.L., Changes in the landscape structure of a southeastern Wyoming riparian zone following shifts in stream dynamics, *Biol. Conserv.*, 72, 371, 1995.
- Miller, R.C. and Zedler, J.B., Responses of native and invasive wetland plants to hydroperiod and water depth, *Plant Ecol.*, 167, 57, 2003.
- Naiman, R.J., Décamps, H., and Pollock, M., The role of riparian corridors in maintaining regional biodiversity, *Ecol. Appl.*, 3, 209, 1993.
- Nilsson, C. and Berggren, K., Alteration of riparian ecosystems caused by river regulation, *Bioscience*, 50, 783, 2000.
- Noss, R.F., LaRoe, E.T., and Scott, J.M., Endangered ecosystems of the United States: A preliminary assessment of loss and degradation, Biological Report 28, U.S. Department of Interior, National Biological Service, Washington, DC, 1995.
- Oliver, C.D. and Larson, B.C., Forest Stand Dynamics, McGraw Hill, New York, 1996.
- Perry, L.G. and Galatowitsch, S.M., The influence of light availability on competition between *Phalaris arundinaceae* and a native wetland sedge, *Plant Ecol.*, 170, 73, 2004.
- Prieur-Richard, A.H. and Lavorel, S., Invasions: The perspective of diverse plant communities, Aust. Ecol., 25, 1, 2000.
- Pyšek, P. and Prach, K., Plant invasions and the role of riparian habitats: A comparison of four species alien to central Europe, J. Biogeogr., 20, 413, 1993.
- Richardson, D.M. and Pyšek, P., Plant invasions: Merging the concepts of species invasiveness and community invisibility, *Prog. Phys. Geogr.*, 30, 409, 2006.
- Scheffer, M.S., Carpenter, S.R., Foley, J.A., Folke, C., and Walker, B., Catastrophic shifts in ecosystems, *Nature*, 413, 591, 2001.
- Smith, T.L., An overview of old-growth forest in Pennsylvania, Nat. Area. J., 9, 40, 1989.
- Sprugel, D.S., Disturbance, equilibrium, and environmental variability: What is "natural" vegetation in a changing environment? *Biol. Conserv.*, 58, 1, 1991.
- Stover, M.E. and Marks, P.L., Successional vegetation on abandoned cultivated and pastured land in Tompkins County, New York, J. Torrey Bot. Soc., 125, 150, 1998.
- Tickner, D.P., Angold, P.G., Gurnell, A.M., and Mountford, J.O., Riparian plant invasions: Hydrogeomorphological control and ecological impacts, *Prog. Phys. Geog.*, 25, 22, 2001.
- Vale, T.R., The American Wilderness: Reflections on Nature Protection in the United States, University of Virginia Press, Charlottesville, VA, 2005, Chapter 10.
- Vitousek, P.M., Walker, L.R., Whiteaker, L.D., Mueller-Dombois, D., and Matson, P.A., Biological invasion by *Myrica faya* alters ecosystem development in Hawaii, *Science*, 238, 802, 1987.
- Walker, B.S., Carpenter, S., Anderies, J., Abel, N., Cumming, G.S., Janssen, M., Lebel, L., Norberg, J., Peterson, G.D., and Pritchard, R., Resilience management in socialecological systems: A working hypothesis for a participatory approach, *Conserv. Ecol.*, 6, 14, 2002 [online]. Available at http://www.ecologyandsociety.org/vol6/ iss1/art14/print.pdf.

- Weston, L.A., Barney, J.N., and DiTommaso, A., A review of the biology and ecology of three invasive perennials in New York State: Japanese knotweed (*Polygonum cuspidatum*), mugwort (*Artemisia vulgaris*) and pale swallow-wort (*Vincetoxicum rossicum*), *Plant Soil*, 277, 53, 2005.
- White, P.S. and Jentsch, A., The search for generality in studies of disturbance and ecosystem dynamics, *Prog. Bot.*, 62, 399, 2001.
- Wiegman, P.G. and Lutz, K.A., *Establishment Record for the Crull's Island Research Natural Area within the Allegheny National Forest, Warren County, Pennsylvania*, USDA Forest Service, Warren, PA, 1988.