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BIODIVERSITY RESEARCH

Riparian vegetation: degradation, alien plant invasions, and restoration prospects

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ABSTRACT

Rivers are conduits for materials and energy; this, the frequent and intense disturbances that these systems experience, and their narrow, linear nature, create problems for conservation of biodiversity and ecosystem functioning in the face of increasing human influence. In most parts of the world, riparian zones are highly modified. Changes caused by alien plants — or environmental changes that facilitate shifts in dominance creating novel ecosystems — are often important agents of perturbation in these systems. Many restoration projects are underway. Objective frameworks based on an understanding of biogeographical processes at different spatial scales (reach, segment, catchment), the specific relationships between invasive plants and resilience and ecosystem functioning, and realistic endpoints are needed to guide sustainable restoration initiatives. This paper examines the biogeography and the determinants of composition and structure of riparian vegetation in temperate and subtropical regions and conceptualizes the components of resilience in these systems. We consider changes to structure and functioning caused by, or associated with, alien plant invasions, in particular those that lead to breached abiotic- or biotic thresholds. These pose challenges when formulating restoration programmes. Pervasive and escalating human-mediated changes to multiple factors and at a range of scales in riparian environments demand innovative and pragmatic approaches to restoration. The application of a new framework accommodating such complexity is demonstrated with reference to a hypothetical riparian ecosystem under three scenarios: (1) system unaffected by invasive plants; (2) system initially uninvaded, but with flood-generated incursion of alien plants and escalating invasion-driven alteration; and (3) system affected by both invasions and engineering interventions. The scheme has been used to derive a decision-making framework for restoring riparian zones in South Africa and could guide similar initiatives in other parts of the world.

Keywords

Biogeographical processes, biological invasions, conservation biogeography, emerging ecosystems, exotic species, invasive alien species, resilience, restoration.

INTRODUCTION

Riparian zones (the fringes of rivers or streams) are the interface between aquatic and terrestrial ecosystems. They are affected by fluvial processes such as flooding and deposition of alluvial soil, and typically support a distinctive flora that differs in structure and function from adjacent terrestrial vegetation (Gregory *et al.*, 1991; Naiman *et al.*, 1993, 2005; Tang & Montgomery, 1995; Prach *et al.*, 1996; Naiman & Décamps, 1997). Riparian vegetation fulfils or influences various important ecological functions in relation to aquatic habitats, including the provision of food, moderation of stream water temperature via evapotranspiration and shading, providing a buffer zone that filters sediments and controls nutrients, and stabilization of stream banks (Barling & Moore, 1994; Hood & Naiman, 2000). It also provides a corridor for the movement of biota (Naiman & Décamps, 1997) and serves many important roles for humans (Kemper, 2001). Ewel *et al.* (2001) coined the term 'critical transition zones' for ecosystems such as riparian zones that serve as conduits for substantial fluxes of materials and energy from one adjacent, clearly defined ecosystem to another. Such ecosystems, usually forming small parts of the landscape, are often the focus of intensive human activity, and present numerous challenges for managers. They also pose interesting questions for conservation biogeographers.

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Many types of human-mediated disturbances, occurring at (and driven by processes that occur at) scales from local to global, influence riparian ecosystems (see Appendix S1 in Supplementary Material). The immediate hydrological alterations caused by dams and the regulation of flows alter river channel form and the composition and extent of riparian habitat (Dudgeon, 1992; Jansson *et al*., 2000; Nilsson & Berggren, 2000; Merritt & Wohl, 2002; Nilsson & Svedmark, 2002; Shafroth *et al*., 2002). Land use immediately adjacent to the river (e.g. cultivation of crops) may increase sediment deposition and eutrophication (Ferrar *et al*., 1988; Hancock *et al*., 1996; Kentula, 1997; Patten, 1998). Logging (Hancock *et al*., 1996; MacNally *et al*., 2001; Apan *et al*., 2002; Iwata *et al*., 2003), grazing and trampling (Mathooko & Kariuki, 2000; Meeson *et al*., 2002), water extraction (Stromberg *et al*., 1996; Patten, 1998; Meeson *et al*., 2002; An *et al*., 2003), and recreation (Washitani, 2001) also affect riparian zones. Such disturbances often occur in concert with, or act as triggers for, the proliferation of alien plants. The diversity and abundance of alien plants have increased in riparian zones throughout the world. As occurs with any major change in plant species composition, increased abundance of alien plants may drive radical alterations in structure and functioning, or may have little influence, depending on the circumstances. Plant invasions may also manifest as a symptom of such changes.

Although riparian ecosystems have been heavily modified for centuries (Décamps *et al*., 1988; Washitani, 2001), generalized frameworks for their management are scarce (but see Wissmar & Beschta, 1998; Middleton, 1999; Webb & Erskine, 2003; Holmes *et al*., 2005). Most publications dealing with management/restoration of riparian zones are reach-specific local studies (Gore & Shields, 1995; Stanford *et al*., 1996; Sweeney *et al*., 2002). It is our contention that improved management of riparian systems demands the explicit and integrated consideration of crucial processes at a range of spatial and temporal scales. This paper (1) describes how changing environmental conditions in riparian ecosystems affect invasibility, and (2) provides a conceptual framework for managing/restoring riparian zones based on generalities relating to key ecological processes and the components of resilience in these systems, especially those potentially affected by alien plant invasions.

BIOGEOGRAPHY OF RIPARIAN VEGETATION

The type of vegetation in a riparian zone is determined by the regional climate, the regional pool of species, and the hydrological, geomorphological, and disturbance regime (Naiman *et al*., 1993; Décamps *et al*., 1995; Shafroth *et al*., 2002; Cooper *et al*., 2003). In most parts of the world, riparian vegetation is dominated by woody plants, and may be classified on the basis of structure as shrubland, woodland, or forest vegetation. Herbaceous species dominate where climate, hydrogeomorphology, or disturbance regime is unfavourable for woody species, e.g. in areas that are too cold (at high latitudes and altitudes), too waterlogged, or that burn too frequently to permit shrub and tree persistence. Hydrology, especially the degree of seasonal drought, is important for determining whether shrubland or woodland vegetation develops in riparian zones in arid areas.

Characteristic plants in riparian assemblages are mainly specialists that exploit the water resources associated with frequently disturbed watercourses. Such species typically are resilient under frequent and intense disturbance. Specific morphological adaptations include those related to withstanding flooding, sediment deposition, physical abrasion, and stem breakage (Naiman *et al*., 1998). These constraints act as an ecological filter to select those species able to establish and persist, often resulting in plant assemblages that are distinctive from adjacent terrestrial vegetation (Ellenberg, 1988). This is particularly evident in regions where water is limiting for all or part of the year.

Stream classification systems have been developed to assist in conceptualizing the various features of rivers at different scales (Rosgen, 1994). Most classifications are hierarchical, underscoring the importance of the surrounding catchment in determining the structure and dynamics of streams (Frissell *et al*., 1986). A geomorphological model is often used as a first stage of classification. For example, a hierarchical geomorphological model for South African rivers spans the following scales in order of decreasing size: catchment, segment, geomorphological zone, reach, morphological unit, and hydraulic biotope (Wadeson, 1999). The catchment (also termed drainage basin or watershed) contributes water and sediment to the specified stream system; a segment is a major branch of the system. The geomorphological zone is a stream segment flowing through a single bedrock type; a reach is a length of stream segment lying between breaks in, for example, channel slope; a morphological unit is the basic structure comprising the channel morphology, such as a pool, riffle, or run; and a hydraulic biotope is a patch within the morphological unit with homogeneous substrate, water depth, and velocity.

DETERMINANTS OF RIPARIAN VEGETATION COMPOSITION AND STRUCTURE

General principles

Rivers and streams are dynamic, non-equilibrium ecosystems subject to frequent disturbance events that have a strong influence on the biotic characteristics of riparian assemblages (Naiman & Décamps, 1997). Fluvial and hydrological processes are the principal determinants of plant distribution patterns in riparian corridors within particular biogeographical regions (Hupp & Osterkamp, 1996; Stromberg *et al*., 1996). New habitat for plant colonization is provided by the fluvial erosion–deposition process, while hydrology influences the vegetation through floods, droughts, and water table fluctuations. Riparian vegetation in many rivers has been characterized by vertical and lateral gradients, reflecting the strong influence of flooding and water availability on species distributions (Van Coller *et al*., 2000). Many riparian plant assemblages, especially those along high-order streams, change continuously. Flooding may physically uproot or damage individuals and inundate areas, causing death or reduced growth. Bank collapse can remove entire plant assemblages, while deposited sediments provide new habitat for colonization.

Availability of water from the water table is a major limiting resource to riparian plant species in arid and semiarid areas, and it influences establishment, growth, and survival, particularly of woody riparian species that are rooted in the water table (Rood & Mahoney, 1990; Smith *et al.*, 1991; Ellery *et al.*, 1993; Auble *et al.*, 1994). Where floodplain sediments are coarse and highly permeable, fluctuations in the groundwater table of the riparian zone are directly associated with fluctuations in the river water levels (Mackenzie *et al.*, 1999). Prolonged drought or flow reductions relating to diversions, impoundments, or ground water pumping can lead to a lowering of riparian water tables and ultimately mortality in riparian trees (Auble *et al.*, 1994).

Life-history strategies determine whether, where, and when a riparian plant species may colonize a site. In many regions, the relative importance of sexual vs. vegetative reproduction and seed banks vs. seed dispersal in recruitment dynamics is poorly known for riparian ecosystems. Opportunities for recruitment occur mostly after floods, either in the form of new sediment deposition or in smaller gaps opened up in the riparian vegetation due to flood damage. Dispersal of propagules in water (hydrochory) is important in structuring the flora and maintaining high species richness in riparian ecosystems (Nilsson *et al.*, 1991; Johansson *et al.*, 1996). River corridors are also important for plant dispersal via vertebrates and wind (Gregory *et al.*, 1991; Johansson *et al.*, 1996; Charalambidou & Santamaría, 2002; Imbert & Lefevre, 2003), and dispersal of many riparian species may involve an initial wind-mediated phase with a secondary hydrochorous stage (BarratSegretain, 1996; Howell & Benson, 2000). The final location of water-borne propagules is determined by at least two interacting factors: the hydrological regime during seed release and transport, and the channel morphology and hydraulics (Merritt & Wohl, 2002). Alterations to either factor can affect whether propagules reach safe sites for establishment; species with more specific habitat requirements for establishment will be least resilient to such changes.

To successfully recruit from seed in the post-flood environment, either the reproductive phenology must correspond to the flooding season, so that seeds are dispersed into a favourable germination environment (Mackenzie *et al.*, 1999), or else the species requires a propagule bank, such as a persistent soil-stored seed bank (Leck, 1989) that may be triggered to germinate following the flood (or rain) event. Surprisingly, little attention has been paid to seed banks in riparian areas (Prach & Straškrabová, 1996; Goodson *et al.*, 2001; Richter & Stromberg, 2005), but a few studies suggest that soil seed banks are generally less well developed in riparian than in terrestrial ecosystems (Schneider & Sharitz, 1988; Manders, 1990; Kalliola *et al.*, 1991).

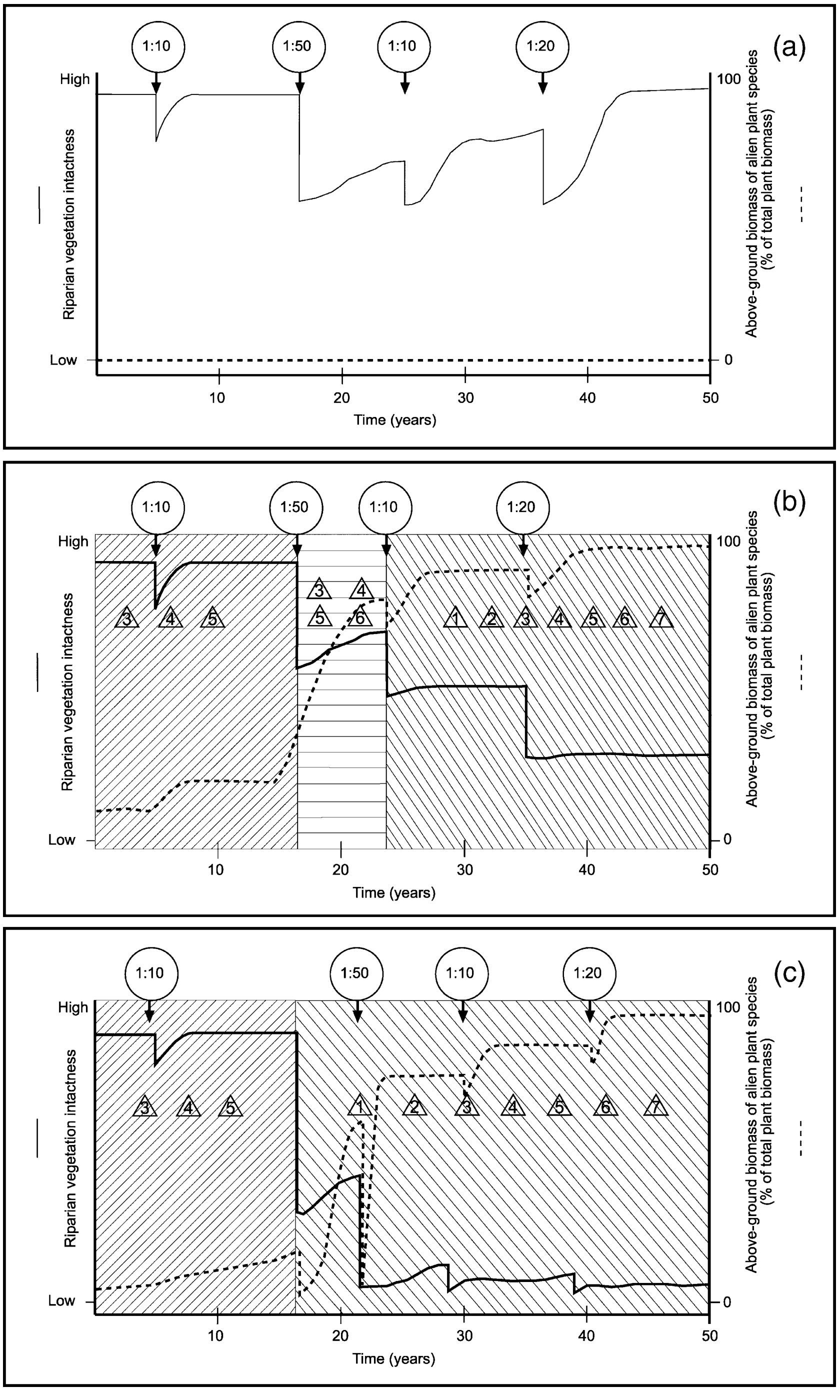
Establishment includes germination, seedling establishment, and growth to maturity. Specific microsites defined by soil moisture levels, light conditions, temperature fluctuations, or other environmental conditions (e.g. fire) often are required before the seeds of a particular species will germinate, and these requirements can limit the distribution of a species in the landscape (Gross, 1984; van der Valk, 1992). Many riparian plant species require bare, wet surfaces that may be generated by large floods, or by channel migration, channel abandonment, and riverbank erosion (Kalliola *et al.*, 1991; Scott *et al.*, 1997). The post-germination fate of the seedlings also explains much of the variation in species distributions (van der Valk, 1992). In riparian areas, seedlings with shallow and poorly developed root structures are very sensitive to drought, water logging, and scouring (Woolfrey & Ladd, 2001; Rood *et al.*, 2003). In more humid areas, establishment success depends on the maintenance of low water levels during germination and seedling establishment (Streng *et al.*, 1989), whereas in semiarid areas establishment sites are often more abundant, but water availability and the rate of decline of the water table limit establishment (MacKenzie *et al.*, 1999).

Later-successional species do not require large openings for germination, and their recruitment may be uncoupled to flood events. Life-history characteristics such as adaptations for vertebrate dispersal and the ability to germinate in the shade of established vegetation are attributes of such species.

Establishment of new (alien) plant species

River ecosystems are highly prone to invasion by alien plants, largely because of their dynamic hydrology and because rivers act as conduits for the efficient dispersal of propagules (Thébaud & Debussche, 1991; Pyšek & Prach, 1993, 1994; Planty-Tabacchi *et al.*, 1996). A theoretical framework of fluctuating resources as determinants of community invasibility (Davis *et al.*, 2000) suggests that timing of the event and permutations resulting from currents and changes in water levels are important mediators of success for immigrants. Periodic high water levels make space for new species by removing vegetation and by increasing resource levels by making nutrients and light available. Declining water levels also expose soil, making space and resources available to plants. Even if subsequent rises in the water level kill plants that had established, if the new species had set seed, the low water level disturbance could have initiated the vegetational change. A single hydrological event can change invasion dynamics (Davis & Pelsor, 2001; Box 1). However, the effect of water level fluctuations can be only predicted when considered in tandem with phenological events such as timing of seed production and release; this is especially relevant for species not exhibiting long-term dormancy.

Plant invasions are increased directly or indirectly by many types of human-mediated disturbances to rivers and riparian zones (see Appendix S1). Once introduced and established in a catchment, many alien plants can exploit opportunities provided both by natural flood events and by anthropogenic disturbances. As most rivers flow through human settlements, there are multiple opportunities for the introduction of alien propagules into the riparian zone. Rivers thus function as 'conveyor belts' rapidly moving propagules, often along with pollutants and large sediment loads, to sites made highly receptive by many types of human-driven modification. Many examples indicate that altered dynamics of riparian ecosystems trigger the establishment and spread of invasive alien plants (Cowie & Werner, 1993; Décamps *et al.*, 1995; Wissmar & Beschta, 1998; Hood & Naiman, 2000; Tickner *et al.*, 2001; Washitani, 2001; Cooper *et al.*, 2003). Since many alien plants are early seral species that thrive in the low-competition environments created by disturbance, invasions in riparian areas are often positively associated with the level of disturbance



Box 1 Schematic representation of changes in vegetation intactness in a hypothetical riparian ecosystem over 50 years. In the three scenarios (a, b, c) the system experiences four flood events: 1-in-10-years floods at years 5 and 25; a 1-in-20-years flood at year 36; and a 1-in-50-years flood at year 17. Panel (a) shows a riparian ecosystem unaffected by invasive alien plants. The system shows a high degree of resilience, with a quick return to pre-flood intactness of structure and functioning following the 1-in-50-years flood. Panel (b) depicts an ecosystem with a low representation of invasive alien species at time 0. Each successive flood event promotes further establishment and proliferation of alien plants, with an escalating effect on system intactness and resilience. After 50 years, the riparian community comprises only invasive alien plants and is severely compromised in terms of resilience and functioning. A biotic threshold induced by the invasive species occurs at year 20, and an abiotic threshold is induced at year 25. Panel (c) shows the combined effects of an engineering intervention (e.g. road or bridge construction) and invasion of alien plants. The massive human-induced disturbance at year 11 causes a substantial reduction in biomass of native species and impairs functioning; it also stimulates rapid proliferation of invasive species which benefit further from each ensuing flood event. The human-induced abiotic threshold caused by the engineering event and the biotic threshold caused by the rapid expansion of invasive species typify the rapid changes of many riparian systems driven by invasion together with other forms of stress or disturbance.

Shadings in Panels (b) and (c) indicate where fundamentally different management options are available — potential interventions for the different zones are indicated by triangles (numbers denote options described in Table 2).

(Planty-Tabacchi *et al.*, 1996). Conversely, if the natural disturbance regime of the river is damped, for example through artificial flow regulation and flood attenuation, the recruitment of indigenous species may be negatively affected (Scott *et al.*, 1997), potentially paving the way for incursion by late-seral species, both alien and native (Johnson, 1998; Lesica & Miles, 1999; Shafroth *et al.*, 2002). Riparian habitats are also important foci of some alien species for the subsequent invasion of adjacent terrestrial landscapes (e.g. *Heracleum mantegazzianum* in the Czech Republic; Pyšek *et al.*, 2007). They also provide a conduit for the dispersal of alien species through otherwise hostile landscapes (Pyšek & Prach, 1995; Stohlgren *et al.*, 1998).

Once established, positive feedback mechanisms can promote the spread of certain plant species at the expense of others via habitat alteration and may result in the development of extensive, dense thickets of alien vegetation in riparian zones (Box 1, panels b & c). Propagule pressure may be the proximate reason for some species becoming invasive, since massive propagule supply ensures population-level resilience, facilitating proliferation and spread (see Appendix S1).

FUNCTIONS AND VALUES OF RIPARIAN VEGETATION

General principles

Plants influence many properties of riparian ecosystems (Tabacchi *et al*., 2000). Through the process of evapotranspiration, riparian plants influence stream flow rates, ground water levels, and local climates. Rates of evapotranspiration and of groundwater use vary widely between plant species depending on factors such as rooting depth, leaf area, and ability to regulate stomatal conductance (Scott *et al*., 2000; Dahm *et al*., 2002). Plants also influence the vertical patterns of moisture throughout the soil profile, with root architecture being one of the factors that influences zones of water uptake and patterns of 'hydraulic redistribution' of soil water (Burgess *et al*., 2001; Hultine *et al*., 2004). Plant species that develop large or dense woody stems can reduce the velocity of flood water and thus increase rates of local groundwater recharge, thereby influencing yet another aspect of the hydrological cycle. Plants directly and indirectly mediate many nutrient cycling processes, and, for example, can reduce levels of nitrogen and other minerals from stream or ground water (Schade *et al*., 2001). Plants influence many properties of soils, such as salinity, organic matter, and C:N ratios, depending on their rate of litter production and on the chemical composition of the litter. With respect to stream geomorphology, plants influence rates of sedimentation (depending in part on the amount of biomass present in low strata) and resistance of soils to erosion during flood events (depending in part on root density). Plants that seasonally develop fine, dry fuel loads increase the probability of fire spread in riparian corridors (Brooks *et al*., 2004). Of course, plants also are fundamental in sustaining higher trophic levels in terrestrial and adjacent aquatic ecosystems. In addition to providing sources of food for granivores and herbivorous/detrital insects, birds, and mammals, they provide cover and nesting sites for many types of animals.

Riparian ecosystems are noted for having high levels of plant diversity, and as these levels of diversity change, ecosystem functions may change in a predictable way. Clear relationships between plant species diversity and ecosystem function have been quantified for only a few processes (e.g. productivity, decomposition rates). Key questions remain regarding relationships between plant species diversity (or plant functional type diversity) and many riparian ecosystem processes and functions including streambank stabilization rate, water purification, and various aspects of the hydrological cycle. For those functions that have been studied, results suggest that the functions decline when species numbers decline to very low levels (Hooper *et al*., 2005).

Many of the conditions created by vegetation-influenced processes – such as stabilized stream banks, clean water, diverse animal assemblages, and recharged water tables — are valued by humans, and the corresponding processes that create them have been described as ecosystem functions or ecosystem services (Hooper *et al*., 2005). When a valued condition declines, the ecosystem often is considered to be 'degraded'. For example, if phreatophytic trees (deep-rooted species that obtain a significant portion of their water needs from the zone of saturation) have increased in abundance, leading to increased net evapotranspiration losses and reduced stream flows, the ecosystem might be considered 'degraded' by those who value perennial stream flow. Typically, however, as riparian vegetation changes, a suite of functions change, and not always in tandem. Some ecosystem functions are negatively correlated, and not all desired functions can be 'maximized' at any given site (Findlay *et al*., 2002). For example, in the case of the phreatophytic trees, in addition to influencing hydrological functions, they also could increase habitat for birds, which could be perceived as a positive change by ornithologists. Thus, assessments of degradation and management response are deeply steeped in public perceptions and values.

Any change in composition of the plant assemblage will bring about some change in ecosystem function. However, it is the dominant species that are most influential, and thus the greatest functional changes will occur if the abundance of these species changes. The greater the difference in morphology, growth rate, and other traits between the previously and currently dominant species (irrespective of whether the new dominant is native or alien), the greater will be the change in function. Often, such major changes in growth form or life-history traits of the dominant species are precipitated by changes in the bottom-up (resource levels) or top-down (herbivory) processes that shape plant assemblages. Thus, for example, partial stream dewatering could lead to shifts in species dominance from shallow to deep-rooted phreatophytes, intensive grazing by livestock could lead to shifts from perennial grass species to trees or shrubs, nutrient depletion below dam-reservoir systems could lead to increased representation of nitrogen-fixing plant species, and nutrient enrichment associated with agriculture could lead to increased abundance of eutrophilic species.

Ecosystem function and alien species

Because major changes in plant species composition are often driven by alterations in physical ecosystem processes, it can be difficult to determine causes of the change and to 'ascribe blame'. Is the cause of some functional change due to the newly dominant species the proximate factors that allowed it to ascend to dominance, or some interaction between the two? The question, 'Are invasive species the drivers or passengers of change in degraded ecosystems?' (MacDougall & Turkington, 2005) is a non-trivial issue that merits careful consideration when formulating restoration plans. Separating 'cause' and 'symptom' is, in some cases, a considerable challenge in the context of alien species and ecosystem degradation.

Certain plant species alter the composition and structure of the vegetation and those that replace indigenous vegetation over substantial areas (termed 'transformers'; see Richardson *et al*., 2000) can change ecosystem function (Table 1). For example, the increased biomass of dense stands of invasive *Acacia mearnsii* or *Eucalyptus* species in riparian zones results in increased water use by the vegetation (Le Maitre *et al*., 2002; Dye & Jarmain, 2004). This in turn alters the hydrology of the catchment, causing stream reductions of up to 100% in afforested catchments in South Africa's grassland biome (Van Lill *et al*., 1989).

Table 1 Conceptual framework for restoration of riparian vegetation influenced by alien plant invasions, indicating potential interventions at different spatial scales. Large river floodplains are not considered. Factors are conceptualized in Appendix S1 in Supplementary Material

<table>
<tr><th>Factors increasing susceptibility to invasion</th><th>Catchment</th><th>Segment</th><th>Reach</th></tr>
<tr><td rowspan="2">Altered sediment dynamics</td><td>Water release from impoundments to promote natural deposition/erosion patterns</td><td colspan="2">Restructure river channel</td></tr>
<tr><td></td><td></td><td>Modify channel roughness to promote natural deposition/erosion patterns</td></tr>
<tr><td>Altered dispersal regimes (longitudinal)</td><td>Water release in relation to dispersal characteristics of key native species</td><td></td><td></td></tr>
<tr><td rowspan="2">Reduced propagule pressure (native plant species)</td><td></td><td colspan="2">Create foci of indigenous species to increase propagule supply downstream</td></tr>
<tr><td></td><td></td><td>Introduce propagules of key native species</td></tr>
<tr><td rowspan="2">Increased propagule pressure (alien plant species)</td><td>Initiate alien-clearing operations high in first-order streams, then work downstream</td><td></td><td>Ensure adequate provision for follow-up control of alien recruitment</td></tr>
<tr><td colspan="3">Explore options for reducing seed production via biological control</td></tr>
<tr><td>Increased availability of safe sites</td><td></td><td></td><td>Manage local disturbance regime (e.g. grazing, human access, fire)</td></tr>
<tr><td rowspan="2">Increased edge effects</td><td>Promote appropriate land-use practices</td><td colspan="2">Create corridors to link intact patches</td></tr>
<tr><td></td><td></td><td>Create buffer zones around intact patches</td></tr>
<tr><td rowspan="3">Altered composition and structure</td><td colspan="3">Initiate alien clearing high in first-order streams, then work downstream</td></tr>
<tr><td></td><td colspan="2">Manage grazing and fire regimes</td></tr>
<tr><td></td><td></td><td>Provide natural recruitment triggers and/or propagules</td></tr>
<tr><td rowspan="4">Altered competitive hierarchies</td><td>Water release from impoundments to promote natural deposition/erosion patterns</td><td colspan="2">Remove alien species</td></tr>
<tr><td colspan="3">Control point sources of pollution</td></tr>
<tr><td>Control water extraction levels</td><td colspan="2"></td></tr>
<tr><td></td><td colspan="2">Manage grazing and fire regimes</td></tr>
</table>

Alien *Tamarix* trees have replaced native vegetation in large areas of the arid western USA (Friedman *et al*., 2005). These trees have been attributed with altering and degrading many riparian ecosystems by consuming large quantities of water, reducing the width of river channels, salinizing soil, and modifying wildlife habitats (Zavaleta *et al*., 2001). However, many of the functional changes attributed to *Tamarix* may instead be attributable to the altered fluvial landscape that simultaneously allowed *Tamarix* to dominate and riparian stands to attain high density (Shafroth *et al*., 2005). For example, recent studies indicate that water use (evapotranspiration rates) by *Tamarix* is similar to that of native riparian trees and shrubs (Nagler *et al*., 2003; Glenn & Nagler, 2005). However, ecosystem-level leaf area and water use can be elevated in reaches below flow-regulating dams. Altered flood timing associated with flow regulation can create prime habitat for *Tamarix*, while the reduced frequency of flood scour allows it to attain high stand density. Thus it often is the species that 'takes the blame'. Similarly, although widely attributed with increasing soil salinity, this plant–environment interaction has only recently been examined scientifically. While *Tamarix* is certainly well adapted to grow on soils that have become salinized through natural actions or cultural actions such as river regulation and flood suppression, the evidence is less strong that the species routinely salinizes soils. On free-flowing river reaches, where floods routinely mobilize ions, salts do not accumulate in *Tamarix* soils at greater rates than in soils of other vegetation types (Bagstad *et al*., 2006).

Can alien plant species cause declines in diversity? The broadly accepted connection between invasive species and diversity declines (Slobodkin, 2001) has only recently been subjected to rigorous scrutiny. One study in wetlands found that introduced plant species were not associated with declines in plant species diversity (Houlahan & Findlay, 2004). Rather, plant diversity in the wetlands was low when a highly dominant species was present, whether native or alien (see also Hejda & Pyšek, 2006). Studies in riparian corridors have found plant species diversity to be similar in patches dominated by native and alien trees alike (Bagstad *et al*., 2006) and have found positive correlations between native and alien species richness (Stohlgren *et al*., 1999). These studies are consistent with a general finding that introduced plant species seldom cause extirpations through the process of competitive exclusion (Davis, 2003), although there are lag effects that have not yet played out, as there are for extinctions relating to habitat loss and fragmentation (Helm *et al*., 2006). The implication is that effort may, in some cases, be more appropriately directed towards managing for the landscape-scale processes that maintain high levels of plant species diversity, such as intermediate levels of disturbance, particular levels of resources, and a high degree of temporal and spatial heterogeneity (Brooks *et al*., 2004; Sarr *et al*., 2005). For example, flood suppression and water stabilization below regulating dams, sharp increases or decreases in water or nutrients, or changes in light quantity stemming from increases or decreases in overstorey cover all could cause declines in riparian-zone plant species diversity.

Given that hydro-geomorphological processes clearly influence the structure of riparian plant assemblages and that these in turn affect the hydrology and fluvial geomorphology of rivers, surprisingly little attention has been paid to the interactions between invasions and these physical processes (Tickner *et al*., 2001). Invasion may change the character of riparian ecosystems and channel morphology. For example, following invasion of riparian zones by the alien shrub *Sesbania punicea* in South Africa, thickets of this species trap sediments, increasing available habitat for further expansion of this and other alien species (Hoffmann & Moran, 1988). A similar process occurs following invasion by *Tamarix ramosissima* in North America, where tamarisk thickets increased the hydraulic roughness to trap and stabilize transported sediments and cause channel aggradation. Eventually, this process leads to a narrowing of river channels during high flows and builds stable floodplains and riverbanks (Zavaleta, 2000; Tickner *et al*., 2001; Zavaleta *et al*., 2001).

Other alien species alter vegetation flammability. For example, spread of the alien shrub *Chromolaena odorata* in South Africa leads to more frequent fires that cause mortality of the indigenous riparian vegetation (Macdonald & Frame, 1988). Invasion of riparian zones by the reed *Arundo donax* greatly increases the frequency of fire that drives the proliferation of the species (Brooks *et al*., 2004).

RESILIENCE IN RIPARIAN VEGETATION

General principles

Resilience is the ability of an ecosystem to return to its former state following a disturbance or stress (Wali, 1999), or the time required to return to its former state (Mitchell *et al*., 2000). The term is often used vaguely, without defining the properties of the ecosystem that could be measured to determine the degree of resilience, or the level of deviation from an acceptable (or reference) level. Here, we consider resilience in terms of structural/functional composition. Because riparian zones are so dynamic, resilience is difficult to conceptualize in these systems since components are always recovering from disturbance. Most riparian species are inherently resilient under frequent and intense disturbance, but different growth forms or guilds respond differently to particular disturbance events. Annuals and other short-lived herbaceous species may recover through seedling recruitment, whereas woody species and clonal herbaceous perennials may recover vegetatively by resprouting from damaged stems or from branches that become lodged and rooted in sediments downstream. Sedell *et al*. (1990) identified linkages between the floodplain and channel (i.e. lateral linkages), upstream and downstream and upstream river sections (i.e. longitudinal linkages), and river bed and channel (i.e. vertical linkage) as crucial elements of resilience in riverine systems. Refuges from the frequent disturbances are the source of recolonization for places recovering from disturbance. For example, in a major flood event, riverine habitats nearest the main channel will experience the greatest force of the storm discharge and, consequently, the greatest loss to plant and animal populations. If floodplains are still connected to main channels, these floodplain environments are critical locations for both escape from major flood impacts and a source of colonists' post-disturbance. Human-impacted rivers may have reduced resilience because of diminished linkages from levees and floodplain filling (lost lateral linkages), dams (lost longitudinal linkages), and hard-surfaced channels (lost vertical linkages).

The rate of recovery in riparian ecosystems is dependent on the intensity and frequency of disturbance events. Brinson (1990) proposed a conceptual model for three different scales of disturbance events. Thus: (1) *short-term*: annual floods that determine the short-term patterns of seed germination and seedling establishment; (2) *intermediate*: medium power, intermediate frequency floods that determine the patterns of ecosystem structure that persist for $10–10^2$ years; and (3) *long-term*: high-power, low frequency floods that create large geographical features that persist for $10^2–10^3$ years. Thus, a 1-in-50-years flood may alter riparian vegetation structure for a period of one to several decades.

In some regions, riparian vegetation may also be affected by the prevailing disturbance regimes in neighbouring terrestrial assemblages. Fire and grazing, as in the case of medium-power floods, remove above-ground vegetation. Survival strategies such as the ability to resprout from protected buds, or to recruit rapidly from a propagule bank, confer resilience to individual plant species following these disturbances. However, the structure and composition of assemblages may change as certain species recover better than others under a particular set of conditions. Terrestrial plant species colonize the riparian zone to some extent, and are common in the drier parts of the floodplain of semiarid region rivers, but are limited by the extent of their morphological adaptations to floods and seasonally waterlogged conditions.

Critically, the high frequency of disturbance events in riparian zones means that there are many opportunities for the resilience of plant communities to be compromised. For example, an untimely fire or heavy grazing could delay recovery following a medium frequency flood event. It has been proposed that ecosystems that are naturally subject to moderate to extreme abiotic regimes, including riparian ecosystems, have a greater tendency to display alternative stable states that may be resilient to restoration management interventions (Didham *et al.*, 2005).

Resilience and alien species

The issue of resilience and alien species can be viewed from several perspectives. In some cases, alien species do not appreciably alter resilience. In others, the arrival, establishment, persistence, and proliferation of alien species clearly reduce resilience. Consider one ecosystem attribute — that of species composition. Frequent low-power floods provide many opportunities for the reshuffling of species composition, including the incursion of new species (Pyšek & Prach, 1993; Décamps *et al.*, 1995; Henderson, 1998; Stohlgren *et al.*, 1998; Richardson, 2001). If resilience is strictly defined as the return to some exact species composition, then the presence of the new species would reduce resilience. Additionally, some alien species can alter the trajectory of succession, leading to the creation of ecosystems that differ markedly from those that occurred at the site previously. Again, resilience is reduced.

The establishment of an alien plant species could also be viewed as a type of resilience. For example, consider the ecosystem function of primary productivity. Soil nutrient levels and primary productivity have declined in some riparian ecosystems because of anthropogenic actions. For example, dam construction can trap fine sediments and flood-borne nutrients in reservoirs leading to below-dam changes, while intensive livestock grazing can result in erosion of upper soil horizons. Some of the alien (and native) species that have increased in riparian zones, such as *Prosopis* spp. (now widespread in many parts of the world) and *Elaeagnus angustifolia* (now abundant in North America), harbour nitrogen-fixing symbionts. This symbiosis may confer a competitive advantage to plant species in nutrient-depleted ecosystems. The establishment of these plants, and their role in increasing primary productivity and soil fertility, could be viewed as a type of ecosystem resilience. Another example can be found in highly modified riparian ecosystems where the environmental tolerance ranges of some native plant species (for factors such as soil salinity, moisture, or anoxia) have been exceeded. In such areas, the influx of alien species that can tolerate the new environments could be seen as a type of resilience that puts community attributes (such as species diversity) and ecosystem attributes (such as primary productivity) on a trajectory towards pre-impact levels.

CRITICAL ISSUES FOR RESTORING RIPARIAN ZONES AFTER ALIEN INVASION

Ecological restoration aims to repair human-mediated changes to the diversity and dynamics of ecosystems (Jackson *et al.*, 1995). It usually involves reconstructing an ecosystem to return it to some previous condition, and usually entails the re-establishment of species, assemblages, structure, and ecological functions that prevailed in the system previously (van Diggelen *et al.*, 2001). Complete ecological restoration generally is impossible at the landscape scale because of land-use (and water use) conflicts and costs (van Diggelen *et al.*, 2001). In riparian ecosystems it may be feasible to restore segments of the riparian corridor, but restoring the river's catchment area, which potentially has a large effect on the hydrological and fluvial processes, is usually not possible. Thus, the scale of and potential for restoration of the riparian zone is constrained by the condition of the catchment area. This makes it critical to have a detailed understanding of the temporal and spatial dynamics of the catchment landscape, including past natural and human-induced changes (Wissmar & Beschta, 1998) (Table 2). The complex interactions between biotic factors and the physical environment in riparian zones define thresholds that delineate options for intervention at a variety of spatial scales. Effective restoration therefore demands careful consideration of alternative states and positive feedbacks (Suding *et al.*, 2004). The most realistic approaches for riparian restoration are either to work within the limitations posed by the catchment, focusing on reach-scale restorations (Moerke & Lamberti, 2004), or to work in those catchments where goals are still achievable and/or where priority for conservation is high.

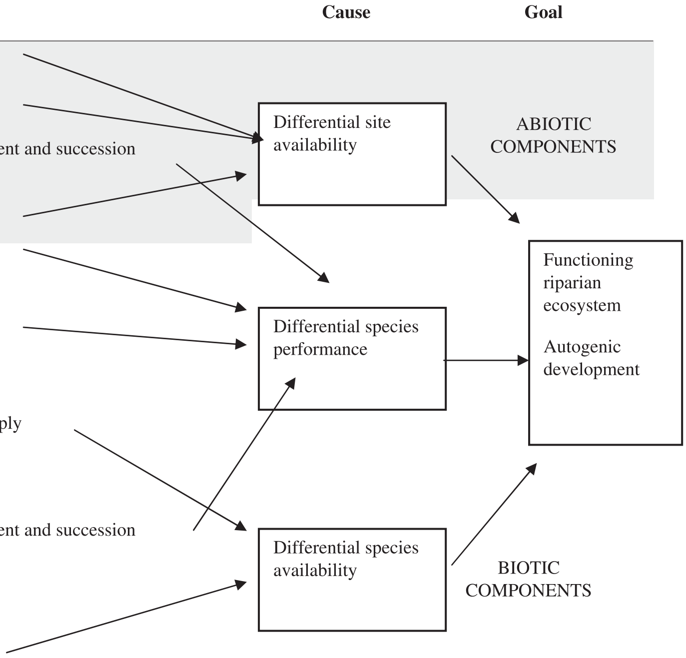
The conceptual model developed by Whisenant (1999) that invokes biotic and abiotic thresholds (see also Hobbs & Harris, 2001) is useful in the context of riparian ecosystems that are both influenced by invasions and are highly susceptible to invasion by alien plants. Where the inputs of physical energy, in the form of water or wind movement, are dominating forces in structuring an ecosystem, as in riparian zones (Planty-Tabacchi *et al.*, 1996; Shafroth *et al.*, 2002), manipulating the abiotic components must be pivotal considerations in ecosystem repair (Ehrenfeld, 2000). The primary variables driving the distribution and abundance of biota in flood-prone rivers are usually abiotic (Stanford *et al.*, 1996). For example, damming and diversions of rivers have caused the decline of many aquatic and riparian species and altered structure and function of many ecosystems (Rood *et al.*, 2003). Restoring such areas requires the hydrological regime (flood frequency and intensity) of the river to be restored first (Vaselaar, 1997; Patten *et al.*, 2001; Rood *et al.*, 2003) since floods and sediment routing are critical for the creation of appropriate sites for colonization by riparian species (Wissmar & Beschta, 1998). Reinstating water and sediment flows can also directly affect the relative performance of native and alien species (Sher *et al.*, 2000; Levine & Stromberg, 2001).

Biotic components such as vegetation structure and composition are the appropriate focus of repair targets in situations where hydrological and geomorphological functioning can support the intended assemblage of species (Hobbs & Harris, 2001) or where this has been, or can be, restored. Riparian zones that are patchily invaded, or have only recently become densely invaded by alien plants, potentially may be restored to their historic, catchment-scale species composition through biotic manipulations alone — by removal of the invasive species (Holmes & Richardson, 1999).

In practice, restoration needs to involve the setting of sequential, multistep goals (Palmer *et al.*, 1997). In riparian situations, clear physical and biotic goals must be based on sufficient baseline data, but a major limitation is that reference systems for defining restoration goals are globally rare (e.g. Rosgen, 1994; Prins *et al.*, 2005). In reality, aiming for a return to some historic

Table 2 A framework depicting the main management actions potentially available for facilitating the restoration of riparian plant communities affected by alien plant invasions. Scheme based partly on ideas expressed by Whisenant (1999). Shaded areas involve manipulation of abiotic components; the rest relate to biotic components

Management action	Spatial scale	Process implicated
1. Manipulate flow regime	Catchment	Fluvial dynamics
2. Stabilize stream banks	Reach	Fluvial dynamics Seedling establishment and succession
3. Clear alien stand	Catchment to reach	Fluvial dynamics Plant competition
4. Control regenerating aliens	Catchment to reach	Plant competition
5. Introduce biological control	Catchment to reach	Alien propagule supply
6. Manipulate disturbance regime (e.g. fire, grazing)	Segment to reach	Seedling establishment and succession
7. Seeding or planting	Segment to reach	Propagule supply



condition is usually inappropriate, untenable, and futile. First, most riparian ecosystems have a long history of use by humans, and have been extensively transformed over centuries, often rendering it impossible to know the historic species composition.

An alternative approach to management/restoration of riparian ecosystems emerges if one accepts that riparian ecosystems are open and dynamic, and that humans are a crucial part of the ecosystem. Under this view, management/restoration does not aim to recreate any historic species assemblage but to restore those processes that provide a desired riparian ecosystem structure and function. If ecosystems are viewed as open and dynamic, re-creation of some historic condition becomes an exercise in nostalgia. If humans are viewed as part of the ecosystem, then plant species accidentally or intentionally introduced by humans become just another species in the ecosystem. The native/alien dichotomy could be counter-productive in restoration practices, leading to an overemphasis on structure and composition over function. The emphasis on removal of aliens as a restoration approach has been criticized as being essentially a gardening exercise (Tredici, 2004).

There are many instances where a small number of highly influential alien plant species are clearly fundamental stressors and disruptors of ecosystem functioning (Holmes *et al.*, 2005). In such cases concerted efforts to remove these species (or reduce their density), prevent or reduce the risk of them re-invading, and re-establish species that are more conducive to the desired functions, are appropriate and tenable. Such operations need to be conducted with due cognizance of the components of resilience and the determinants of abiotic and biotic thresholds. For example, where dense alien thickets have been present for a long time, and/or have altered the fluvial–geomorphological processes of the river (the alien-induced abiotic threshold in Box 1, panel c), a more natural erosion–sedimentation cycle may be a fundamental prerequisite following alien clearance before indigenous riparian vegetation may be restored. As long as the hydrological and geomorphological processes of the river catchment have not been impaired, for instance through widespread soil cultivation and erosion or increased abundance of alien plants, the historic rates and ranges of abiotic processes may return following alien plant clearance in the riparian zones. It is important to note, however, that the commitment to clearing is a long-term one that requires acute attention to follow-up control. Short-term projects lacking social or political will are unlikely to succeed. Further, complete removal of alien species may be more damaging in some situations than killing them standing (e.g. by ringbarking), or even leaving them untreated. Riverbank stabilization measures may be required in situations where indigenous species have been eliminated and their recruitment is predicted to be slow. However, stabilization should not be done where it is suspected that the alien thickets have caused increased sediment deposition and channel aggradation (Tickner *et al.*, 2001), as the first step of restoration should be to remove these sediments, and allow the river to return to a more natural geomorphology.

In summary, it is crucial to assess which abiotic and biotic thresholds (see examples in Box 1) have been crossed in invaded riparian zones, and to ascertain whether the removal of the invasive species alone is sufficient to stop further changes that are deemed undesirable and promote the recovery of natural vegetation in the riparian zone. Such assessments should be done within the context of the catchment area and the limitations imposed by any human-induced changes to fluvial and hydrological processes. It is prohibitively expensive to consider restoring, using plant re-introduction techniques, entire riparian corridors. It is almost always more appropriate to consider a set of minimum interventions for achieving various alternative restoration goals or trajectories. Successful small-scale restorations of river reaches have been conducted, for example the restoration of riparian forest via bare root and containerized plants (Sweeney *et al*., 2002). The planting or sowing of indigenous riparian species should accelerate recovery of riparian vegetation in highly altered riparian zones, for example following the clearance of dense and extensive thickets of alien plants, as the propagule pressure of native species is likely to be below the threshold needed to drive reassembly of the community without human intervention. Riparian vegetation refugia may be scarce and soil-stored seed banks depleted. Therefore, the recolonization of riparian zones via suitable indigenous species dispersing into the area will be slow and the probability of re-establishment of the alien species, or incursion of other alien species, will be high. In highly altered rivers, the creation of nodes of indigenous riparian vegetation (Galatowitsch & Richardson, 2005) is likely to be an important method in promoting the long-term restoration of riparian zones.

Spontaneous or directed succession (Luken, 1990), a convenient restoration tool in some human-modified habitats (e.g. Prach *et al*., 2001), may be less efficient in riparian zones because of their dynamic nature and the continuous propagule pressure from alien species. When considering spontaneous succession as a restoration tool, the settings of the specific project must be considered and scientific knowledge integrated into the restoration programme (Prach *et al*., 2001).

For many river reaches globally, such as those in urban areas, natural riverine processes cannot be restored because the economic costs are too high or the social and political will are not present. In many cities, the floodplains of rivers have been converted to housing or industrial areas, restricting the river bed to a small channel; although the levees can be set back to some degree, the historic floodplains cannot realistically be reclaimed by the river. Large human settlements are sustained in arid regions by massive and extensive dam and reservoir systems and water distribution structures; although the flow pattern of below-dam rivers can be naturalized to some degree (Rood *et al*., 2003), many dams are a permanent feature of the present landscape. Rivers by their nature reflect their watershed, and urbanized rivers are often vegetated by a mixture of the historically dominant species and a wide variety of introduced species, including agricultural and horticultural plants and other cultivars. In such highly modified rivers, it is perhaps advisable to let plant communities 'self assemble' with species (alien or native) that are adapted to these novel conditions. Removal of alien plants from rivers in urban landscapes and other situations with pervasive human influence is, in almost every case, futile and potentially counter-productive with respect to maintaining ecosystem function. Efforts to remove the imprint of humans from the landscape also may be counter-productive with respect to human–nature interactions. There may be value, instead, in accepting and appreciating the fact that rivers reflect their watersheds, whether dominated by people or not. In such cases, we suggest that the focus should be on maintaining river health and key ecosystem services, but working with novel ecosystems (Hobbs *et al*., 2006) that are best adapted to these novel conditions. There are many valid motivations for restoring riparian ecosystems (see general discussion in Clewell & Aronson, 2006). Irrespective of the motivation, restoration must be planned with due cognizance of biogeographical processes at different spatial scales, facets of resilience and ecosystem functioning, and realistic endpoints.

The concepts expressed in this paper have been used to define an objective decision-making framework for restoring riparian zones affected by invasive alien plants in South Africa (Holmes *et al*., 2005), and could guide such initiatives elsewhere.

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SUPPLEMENTARY MATERIAL

The following material is available for this article:

Appendix S1 Human-mediated changes to riparian vegetation that potentially lead to degradation, with special emphasis on changes potentially promoting the establishment, proliferation and spread of invasive alien plant species. Large river floodplains are not considered.

This material is available as part of the online article from:
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