Forecasting functional implications of global changes in riparian plant communities

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Riparian ecosystems support mosaics of terrestrial and aquatic plant species that enhance regional biodiversity and provide important ecosystem services to humans. Species composition and the distribution of functional traits – traits that define species in terms of their ecological roles – within riparian plant communities are rapidly changing in response to various global change drivers. Here, we present a conceptual framework illustrating how changes in dependent wildlife communities and ecosystem processes can be predicted by examining shifts in riparian plant functional trait diversity and redundancy (overlap). Three widespread examples of altered riparian plant composition are: shifts in the dominance of deciduous and coniferous species; increases in drought-tolerant species; and the increasing global distribution of plantation and crop species. Changes in the diversity and distribution of critical plant functional traits influence terrestrial and aquatic food webs, organic matter production and processing, nutrient cycling, water quality, and water availability. Effective conservation efforts and riparian ecosystems management require matching of plant functional trait diversity and redundancy with tolerance to environmental changes in all biomes.

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Riparian networks link terrestrial (upland and lowland) and aquatic ecosystems (wetlands, lakes, streams, rivers, and floodplains), forming integrated landscapes that extend from mountains to coasts and across continents. The characteristics of riparian ecosystems greatly influence the patterns and processes in these linked terrestrial and aquatic systems (Naiman *et al.* 2005). Native riparian zones are ecologically diverse and functionally dynamic features of landscapes (Naiman *et al.* 2005). The plant assemblages in riparian ecosystems have distinct compositions relative to upland communities, which explains how they enhance regional biodiversity (Sabo *et al.* 2005). High riparian biodiversity is maintained through complex relationships between aquatic and terrestrial organisms, system geomorphology, biogeochemistry, and disturbances (McClain *et al.* 2003).

In a nutshell:

- Understanding species functional traits is critical to forecasting how environmental changes will affect biodiversity and ecosystem functioning
- Global shifts in riparian plant traits include changes in phenology, increases in drought-tolerant generalists, and genetically modified plantation and crop species
- Non-native and invasive species can reduce or enhance functional trait diversity and overlap
- More research is needed to identify shifts in riparian plant communities outside of North America and Europe and to assess the effects of these changes on ecosystem function
- Riparian management should focus on maintaining functional traits that ensure resilience to environmental changes in ecosystems

Riparian plant assemblages possess dynamic functional traits that support terrestrial and aquatic ecological structure and function (Figure 1; Ellison *et al.* 2005). Traits associated with plant morphology, production, physiology, defense, and adaptation to pulsed environmental stressors (eg flooding, drought) distinguish the functional role of riparian plants from their upland counterparts (Tuckett *et al.* 2010). These traits, in turn, influence groundwater and surface water hydrology through plant evapotranspiration rates; organic matter availability through leaf and wood litter inputs to soil and aquatic communities; soil fertility through root leachates and the activity of microbial root symbionts; and the composition of dependent wildlife communities (Figure 1; Ellison *et al.* 2005; Naiman *et al.* 2005).

Many riparian plant traits are associated with valuable ecosystem services (MA 2005), including water purification through the removal of contaminants, water availability via groundwater recharge, flood protection provided by dense woody stems and natural levees, food and fiber production, and recreation (Figure 1; Naiman *et al.* 2005). Riparian zones are also vital migration corridors for wildlife (Hudgens and Haddad 2003). Anthropogenic influences have greatly altered riparian ecosystems, so that they are now widely recognized as systems of conservation concern (Christensen *et al.* 1996; Perry *et al.*

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2011). We argue that chronic environmental stressors are causing widespread shifts in the composition and abundance of riparian vegetation, with implications for genetic and species diversity, as well as functional (ie trait) diversity from local to global scales (Stromberg *et al.* 2007; Merritt and Poff 2010). Examples of such shifts include (1) declines in historically dominant riparian species and replacement with new dominants (eg Ellison *et al.* 2005; Friedman *et al.* 2005) and (2) changes in riparian plant functional trait distributions as a result of species declines, introductions, and hybridizations (eg Graça *et al.* 2002; Vanden Broeck *et al.* 2005). Changes to riparian plant community composition can lead to altered diversity and redundancy of plant functional traits (Díaz and Cabido 2001; Richardson *et al.* 2007) or to intraspecific genetic variation (Whitham *et al.* 2006; Bailey *et al.* 2009).

The loss of once-redundant functional traits or the gain of novel functional traits can alter the structure and functioning of terrestrial and aquatic consumer communities as well as rates of key ecosystem processes (Panel 1; eg Ellison *et al.* 2005; Richardson *et al.* 2007; Ford and Vose 2007). The direction and magnitude of changes to ecosystem structure and functioning across the aquatic–terrestrial interface could be predicted based on functional trait differences within or among species. Changes will be greatest where there are large functional trait differences between the riparian plant species that are declining versus those that are increasing in abundance, or where changes result in the loss of formerly dominant riparian plant traits (Panel 1). Riparian species are often specialists, and global changes are contributing to worldwide declines in specialist taxa (Poff *et al.* 2007; Clavel *et al.* 2011). Shifts toward dominance by generalist species may decrease compositional and functional heterogeneity in riparian ecosystems. For example, the replacement of native deciduous forests by non-native *Eucalyptus* species in Europe has decreased the heterogeneity of litter inputs to soils and streams, shifted the timing of litter inputs from fall to summer, reduced seasonal light variability beneath the forest canopy, and lowered surface- and groundwater levels through evapotranspiration (Graça *et al.* 2002). Conversely, the introduction of species with novel or rare functional traits may enhance functional trait diversity, as observed in some western US riparian forests with low to moderate abundance of *Elaeagnus angustifolia* (Russian olive), a nitrogen (N_2)-fixing non-native (Follstad Shah *et al.* 2010).

Here, we present a conceptual framework (Panel 1) and three case studies that document changes in riparian plant composition at landscape and intercontinental scales: (1) shifts in the proportion of deciduous and coniferous taxa in northern latitudes, (2) increases in drought-tolerant taxa in arid and semi-arid regions, and (3) the global distribution of plantation and crop taxa worldwide (Figure 2, a–c). Altered functional trait diversity is common to all these case studies, with implications for faunal diversity, food web structure, and ecosystem processes; these include rates of transpiration, organic matter decomposition mediated by differences in litter quantity and quality, and primary and secondary productivity (WebTables 1–3). These case studies focus on broadly distributed, well-studied riparian plant communities that serve to illustrate some of the major changes in ecosystem structure and function occurring in response to species introductions and changes in global climate and land use.

Global shifts in riparian plant composition

Shifts in deciduous and conifer species

Populations of conifer species are generally declining throughout the Northern Hemisphere (Figure 2a; Allen *et al.* 2010), affecting upland as well as riparian ecosystems. These declines are attributed to multiple, interacting environmental stressors, such as forest harvesting, climate-induced drought and fire, pests, and pathogens (WebTable 1; Ellison *et al.* 2005; van Mantgem *et al.* 2009). In North America, three broad-scale examples of conifer declines include *Pinus edulis* (piñon pine), *Pseudotsuga menziesii* (Douglas-fir), and *Tsuga canadensis* (eastern hemlock). Conifer mortality in western North America is linked to drought and biotic stress (eg mountain pine beetle) in species like *P edulis*, *Pinus ponderosa* (ponderosa pine), *Pinus contorta* (lodgepole pine), *Pinus sylvestris* (Scots pine), and *Pinus flexilis* (limber pine) (van Mantgem *et al.* 2009). Declines are further attributed to intensive harvesting of *P menziesii* in some areas along the Pacific Coast. In eastern North America, declines in *T canadensis* in predominantly deciduous forests have occurred rapidly due to the insect pest *Adelges tsugae* (hemlock woolly adelgid) (Figure 3, a and b; Ellison *et al.* 2005). Reductions in functional traits unique to conifers (eg year-round canopy cover and year-round inputs of slowly decomposing leaf material) have had varying impacts on dependent aquatic and terrestrial communities and ecosystem processes (WebTable 1).

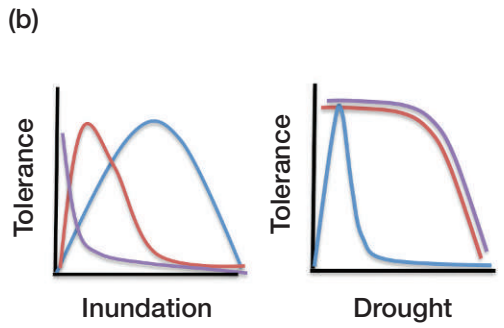
Although drought- and pest-induced conifer declines are widespread, conifers are expanding in other regions of the world as a result of climate-induced changes in species ranges and land-management practices that either select for or target specific conifer species. North American grasslands have been shifted toward shrublands as some conifers have moved into higher latitudes (eg *Picea mariana*, black spruce) or encroached into grasslands (eg *P menzeisii*) due to rising temperatures and the use of fire suppression regimes (Frelich and Reich 2010; Jones *et al.* 2010; Ratajcazk *et al.* 2012). Drought-induced diebacks of high-latitude hardwoods (Frelich and Reich 2010; Allen *et al.* 2010) and the spread of plantations (eg *P menziesii* along the Pacific Coast of North America, *Pinus taeda* [loblolly pine] and *Pinus elliottii* [slash pine] in the southern US, and *P sylvestris* and *Pinus nigra* [European black pine] in Europe) have further increased the proportion of conifers and their associated traits in

Panel 1. Framework to assess shifts in riparian functional traits on dependent communities

The functional implications of shifts in riparian plants can be assessed by categorizing the key traits of increasing and decreasing plant species, their tolerance to environmental conditions, and their contributions to dependent communities and ecosystem processes. In scenario 1 (historic condition), riparian plant composition is dominated by species X. Scenarios 2–4 show variations in the historic condition: in scenario 2, species X and Y co-dominate; in scenario 3, species Y dominates; and in scenario 4, species Y and Z co-dominate. Species X is a deciduous tree with high leaf production, high leaf litter carbon:nitrogen (C:N) ratio but low lignin content, high water use, and no fruit production. Species X also forms mycorrhizal associations to facilitate nutrient acquisition, and while tolerant of moderate flood inundation, it has low tolerance to drought. In contrast, species Y is a deciduous shrub with lower leaf production, lower leaf C:N ratio due to its N-fixation capacity, and higher lignin content than species X. Water use is similar between the two species. Species Y is less tolerant of flood inundation but more tolerant of drought as compared with species X. Species Y produces fruit around its seed, which supports a greater abundance of mammals relative to species X (scenarios 2–4). However, cavity-dwelling birds (eg owls and woodpeckers) and beaver (*Castor* spp) are absent from riparian forests dominated by species Y (scenario 3) because of its small stem diameter. Growth of aquatic and terrestrial macroinvertebrates is diminished (denoted by the difference in size of the Tipulid cranefly larvae) in riverine corridors dominated by species Y due to its high lignin content, despite its high N content (scenarios 2–4). Species Z is similar to species X with respect to plant growth form (ie tree), leaf production and chemistry, lack of fruit production, and ability to form mycorrhizal associations. However, species X has higher water use (higher evapotranspiration rates), whereas species Z is intolerant of flood inundation but highly tolerant of drought. The structure of dependent wildlife communities is maintained or somewhat enhanced where species Z is present, as it is functionally similar to species X in terms of structural plant traits. Whole-ecosystem process rates are highest where species X and Y (scenario 2) or species Y and Z (scenario 4) co-dominate relative to historic conditions (scenario 1). Annual rates of net primary production and evapotranspiration are reduced where species Y is dominant, due to its lower rate of leaf production, and species Y increases leaf litter breakdown rates because of higher foliar N (scenario 3). This hypothetical conceptual framework can be applied to our second global case study (*Increases in drought-tolerant species in semi-arid to arid regions*); here, trait shifts from *Populus* spp (analog to species X) to *Elaeagnus angustifolia* (analog to species Y) are mitigated to some extent by *Ulmus pumila* (analog to species Z). See text for details.

(a)

Key traits	Species X	Species Y	Species Z
Growth form	Tree	Shrub	Tree
Leaf production	High	Medium	High
Leaf litter C:N	High	Medium	High
Leaf lignin	Low	High	Low
Fruit production	No	Yes	No
Water use	High	High	Medium
Nutrient acquisition	Mycorrhizal association	N fixer symbiosis	Mycorrhizal association



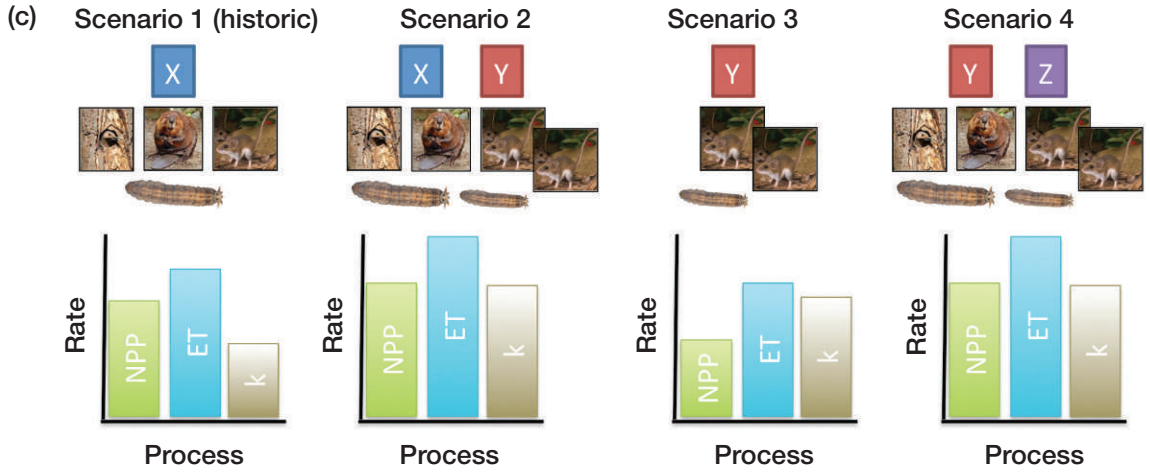


Figure 1. Conceptual framework showing how shifting dominance of three hypothetical species may alter riparian community structure and ecosystem function through differences in functional traits and tolerance to environmental factors. (a) Table of key functional traits of three hypothetical species (X, Y, and Z). (b) Relative tolerance to flood inundation and drought among the three hypothetical species. (c) Four scenarios of species shifts with subsequent effects on dependent wildlife and ecosystem processes. NPP = net primary production, ET = evapotranspiration, k = decay coefficient of leaf litter breakdown.

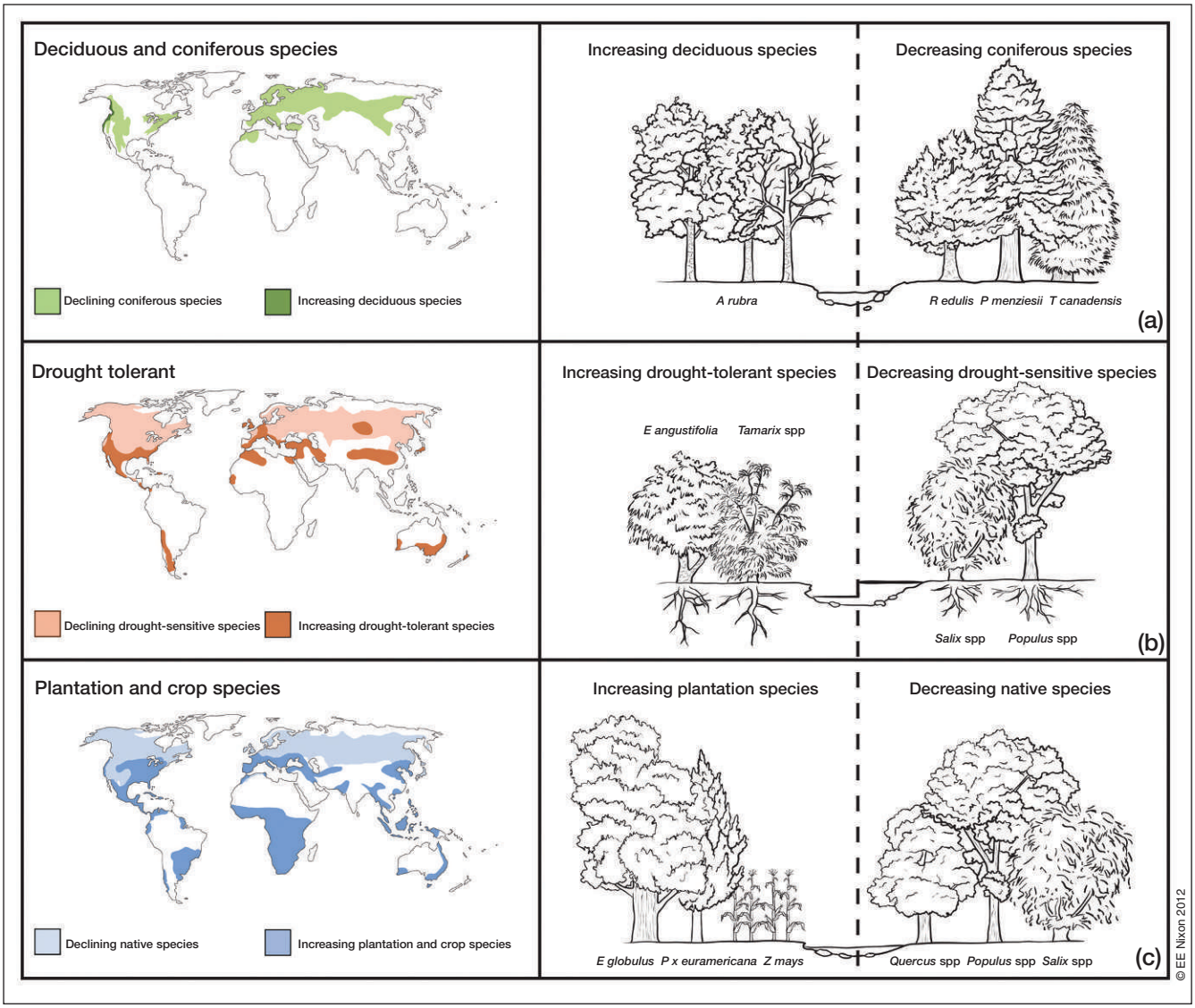


Figure 2. *Three global examples of broad-scale changes in riparian plant species composition: (a) shifts in coniferous and deciduous tree species, (b) increases in drought-tolerant species, and (c) global distribution of plantation and crop species. Distribution of increasing and decreasing tree species for each of the three examples are shown separately on each map. (a)* Pinus *and* Tsuga *species are declining throughout the Northern Hemisphere. These species are being replaced by deciduous species, such as* Alnus *spp, in North America. (b)* Populus *and* Salix *species are declining throughout the Northern Hemisphere, whereas drought-tolerant species such as* Tamarix *spp (native to Eurasia) and* Elaeagnus angustifolia *(native from the Middle East to central Asia) are gaining in North America, Europe, South America, Asia, and North Africa.* Acer negundo *(native to North America) is increasing in Europe, and* Salix *(native to Europe) is invading Australia and New Zealand. (c)* Populus *and* Salix *species are declining throughout the Northern Hemisphere, with the exception of* Populus *hybrids grown in plantations in North America and Europe. Native riparian vegetation throughout North America, Europe, Asia, Australia, and South America are declining as land is used for plantation and crop species, such as* Eucalyptus *spp and* Zea mays*, which are being planted globally. Illustrations of increasing and decreasing species emphasize how shifts in plant species composition have structural and functional consequences for riparian and adjacent aquatic ecosystems. Sources for tree species distribution maps are listed in WebPanel 1.*

these regions (WebTable 1). In managed forests, category of landownership can influence plant age demography as well as density. For example, large conifers are expected to dominate late successional forests in riparian reserves on public lands, whereas riparian areas on private lands owned by logging companies will undergo short rotation harvesting (every 40–50 years) followed by high-density conifer replanting (Johnson *et al.* 2007). Extensive conifer reforestation in some regions (eg southern US, Europe, China) may offset global increases in conifer mortality to some extent (van Mantgem *et al.* 2009; Allen *et al.* 2010).

Increases in drought-tolerant species in semi-arid to arid regions

Water scarcity due to river regulation, increasing human water-use demands, and changes in climate has enabled

the invasion and expansion of drought-tolerant taxa in riparian ecosystems in semi-arid to arid regions around the world (Richardson *et al.* 2007; Merritt and Poff 2010; Perry *et al.* 2011). A well-studied example is the observed decline of Salicaceae, a family of plants that includes obligate and facultative phreatophytic species (plants that obtain water from a permanent ground supply or directly from the water table) of the genera *Salix* (willow) and *Populus* (cottonwood, poplar). In both North America and Europe, many species of Salicaceae are being replaced by both native and non-native, drought-tolerant species (Figure 2b; Friedman *et al.* 2005; Bottollier-Curtet *et al.* 2011). A notable exception to the decline in Salicaceae is the introduction of non-native *Populus* spp in European plantations and the invasion of *Salix* spp in areas of Australia, New Zealand, and South Africa (Figure 2b; WebTable 2; Read and Barmuta 1999). Shifts in the presence or absence of traits unique to Salicaceae influence dependent community structure and ecosystem processes across the aquatic–terrestrial interface (WebTable 2).

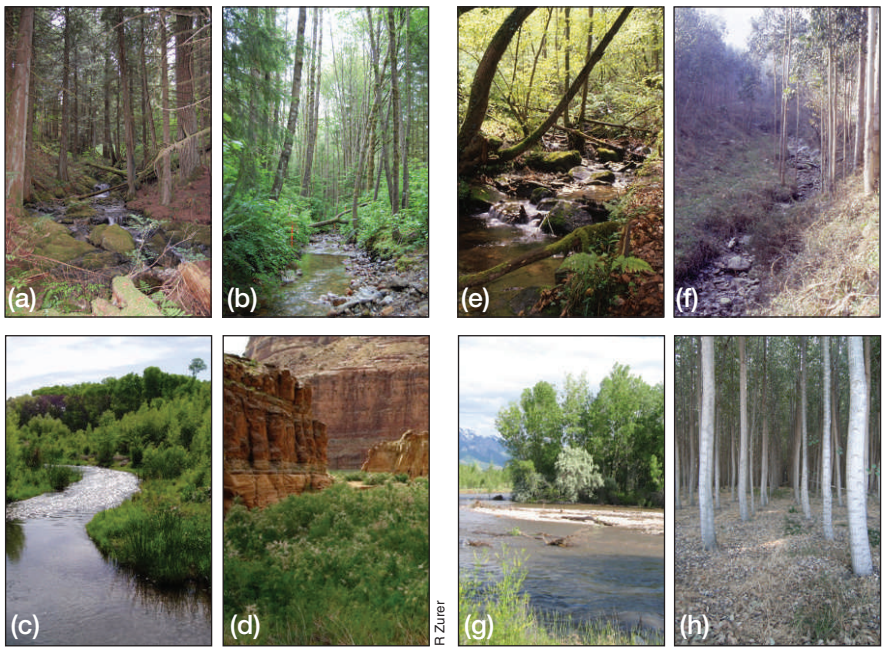


Figure 3. *Examples of changes in riparian plant composition. Streams with conifer cover (a) have more shading and more stable hydrology than streams where conifers are declining and deciduous species (eg* Alnus*; [b]) are gaining. Native riparian forests (eg those dominated by* Populus *and* Salix *species [c and g] or* Quercus *and* Alnus *species [e]) are more diverse in terms of the number of species and structural attributes than introduced, drought-tolerant species (eg* Tamarix*; [d]) that often form monotypic stands, or (f)* Eucalyptus *or (h)* Populus *plantations.*

The establishment and spread of Eurasian *Tamarix* spp (salt cedar, tamarisk) and *E angustifolia* occurs globally, but the invasive dominance of these species is best documented in North America (Figure 2b). These species are the most commonly occurring plants in riparian corridors of the western US after native *Salix* and *Populus* species (Figure 2b; Figure 3c, d, and g; Friedman *et al.* 2005). Ecological niche modeling predicts that large areas of the Canadian prairies are also susceptible to invasion by *Tamarix* spp (Lindgren *et al.* 2010). *Tamarix* spp and *E angustifolia* are facultative phreatophytes with drought-tolerant traits. *Tamarix* spp have reduced susceptibility to drought as compared with *Populus* spp and *Salix* spp (Glenn and Nagler 2005). *E angustifolia* has reflective, silvery foliage, a relatively thick cuticle, and sunken stomata – traits that help to reduce leaf temperature and transpiration in dry, warm climates (Katz and Shafroth 2003). *E angustifolia* is also associated with N_2-fixing bacteria within nodules on its roots (Katz and Shafroth 2003). The establishment and spread of *Tamarix* and *E angustifolia* is of less concern in Europe than in North America. Other drought-tolerant species, such as *Acer negundo* (American boxelder), however, have replaced native phreatophytes along European rivers where flow regulation and groundwater pumping restrict recruitment of Salicaceae, especially *Salix alba* (white willow; Bottollier-Curtet *et al.* 2011).

Ulmus pumila (Siberian elm) is another drought-tolerant species that has been introduced to riparian forests throughout North America (USDA NRCS 2012), although its occurrence in the western US is much less frequent relative to *Tamarix* and *E angustifolia* (Friedman *et al.* 2005). It persists, often alongside *Tamarix* and *E angustifolia*, in riparian areas too xeric for the Salicaceae. Yet *U pumila* and *Populus* species have similar structural traits (eg large canopy and basal area, high leaf production, high leaf litter C:N ratio but low lignin content). It is probably these similarities that allow some dependent wildlife species to persevere in areas where *Populus* species have been lost while *U pumila* has become established (Panel 1).

Increasing global distribution of plantation and crop plant species

Humans have drastically altered riparian environments for the production of food, biofuel crops, and plantations for wood and wood-derived products. Approximately 50% of the world's arable land is now used for livestock grazing and crops (Tilman *et al.* 2001). Crop species used for food, fuel, or industrial purposes are often grown in monoculture and possess low genetic variability, unlike native riparian vegetation (MA 2005). Worldwide,

approximately 1.4 billion hectares of land are currently being used to cultivate as few as 70 crop species (MA 2005); these are often grown in floodplains to take advantage of the close proximity of water.

Demand for plant-based products to provide shelter, fuel, and food for the 9–10 billion people projected by the middle of this century will increase crop-plant species production. Conversion of more land to crops and plantations will cause native plant species diversity to decline globally (Figure 2c; Tilman *et al.* 2001). For example, *Eucalyptus globulus* (Tasmanian blue gum; Figure 3f), a common plantation species that is grown for pulp and paper production, has drastically reduced land cover of native riparian vegetation (eg *Alnus*, *Populus*, *Salix*, *Quercus* species; Figure 3e) across the Iberian Peninsula (mainly northwest Spain and north-central Portugal; Graça *et al.* 2002) and has outcompeted other native *Eucalyptus* species in Australia (Figure 2c; WebTable 3; Potts and Dungey 2004). Two-thirds of all *E globulus* plantations are now centered in these regions (Potts and Dungey 2004). Plantations of *Populus x euramericana*, a hybrid between native *Populus nigra* (black poplar) and introduced *Populus deltoides* (eastern cottonwood), also occur widely across the floodplains of western Europe. In many of these areas, *P x euramericana* is now more abundant than the native *P nigra* (Vanden Broeck *et al.* 2004). Similarly, hybrids between native *Populus trichocarpa* (black cottonwood) and *P deltoides* or *P nigra* are now common in plantations along riparian corridors of rivers in the northwestern US (Figure 3h), where *P trichocarpa* forests were historically dominant (Hibbs *et al.* 2003). Hybridization and gene flow between domesticated species and local populations of congeners (eg from *Populus* hybrids to native *Populus* populations) lead to biotic homogenization (Vanden Broeck *et al.* 2005). Crops and plantations generally reduce functional trait diversity, with negative impacts on dependent communities (WebTable 3).

Functional effects of changing riparian plant composition

The resilience of riparian ecosystem functioning is dependent on the diversity and redundancy of plant traits (Panel 1; sensu Díaz and Cabido 2001). Functional redundancy ensures that multiple species have traits that support ecosystem functioning, whereas higher functional diversity within communities supports more ecosystem processes and a wider range of variation in key ecosystem processes (Díaz and Cabido 2001; Richardson *et al.* 2007). Regions with lower riparian plant diversity (ie lower taxonomic, phylogenetic, and genetic diversity) likely have less functional diversity and redundancy than regions with higher riparian plant diversity (Díaz and Cabido 2001; Sabo *et al.* 2005). Communities with few species encompass a limited number of functional traits. In more diverse communities, different species may share similar traits but differ with regards to their tolerance to environmental factors (Panel 1). Differences in environmental tolerance allow one species to persist or even flourish in the face of environmental change while another species with similar traits declines (Tuckett *et al.* 2010). Under such circumstances, functional trait redundancy increases the likelihood of maintaining ecosystem processes (Díaz and Cabido 2001).

The expansion of *Alnus* spp in conifer forests along the Pacific Coast of North America and the introduction of *E angustifolia* to the western US are examples of the balance between functional redundancy and functional dominance. In both cases, low densities of these N_2-fixers increase both plant species diversity and plant functional trait diversity or redundancy, as N_2-fixation is absent or rare among other riparian plant species in these areas. In contrast, where *Alnus* spp or *E angustifolia* (ie N_2-fixing species) dominate riparian communities, soil and surface water N concentrations increase (Compton *et al.* 2003; Follstad Shah *et al.* 2010), with variable impacts on the biodiversity of terrestrial and aquatic communities and subsequent rates of organic matter processing (Katz and Shafroth 2003; Moline and Poff 2008; Kominoski *et al.* 2011).

Altered biodiversity and functional trait redundancy

Global shifts in riparian plant composition have the potential to reduce biodiversity and functional trait redundancy in a variety of ways. First, the loss of unique and endemic riparian plants decreases regional diversity (Sabo *et al.* 2005). Second, local extirpations of individual species with unique traits reduce the number and composition of plant traits within the community. For example, conifer die-offs in the Appalachian Mountains of the eastern US result in a loss of perennial canopy cover and trees of large diameter. This results in higher and more seasonal rates of evapotranspiration as well as more seasonally variable hydrology, a decline in populations of cavity-dwelling fauna, and increased light availability, leading to increased biomass of understory plants and periphyton (WebTable 1; Ellison *et al.* 2005; Ford and Vose 2007). Third, introduced riparian plants (eg *Tamarix* and *Elaeagnus* in the US; *Salix* in Australia, New Zealand, and South Africa), crops, and plantations reduce biodiversity by forming near-to-complete monospecific stands (Figure 3, c–h; Di Tomaso 1998; Graça *et al.* 2002; Katz and Shafroth 2003). These changes are often associated with reduced functional trait diversity (eg reduced structural heterogeneity to support a variety of breeding or nesting sites and refugia) that results in reduced faunal diversity (Read and Barmuta 1999; Greenwood *et al.* 2004). However, non-native riparian plants do help to maintain wildlife populations in some cases, by providing novel habitat or resources or by replacing traits that would otherwise have been lost through declines in historical dominants (Panel 1; Davis *et al.* 2011). Fourth, reductions in rapidly hybridizing native riparian tree species (eg *Populus*) may

limit intraspecific genetic variation in functional traits (Whitham *et al.* 2006; Bailey *et al.* 2009), which can also influence the structure of riparian vegetation (Figure 4; LeRoy *et al.* 2006; Lojewski *et al.* 2009) and consumer communities in terrestrial and aquatic environments (LeRoy *et al.* 2006; Bailey *et al.* 2009).

Figure 4. *Variable decay in* Populus *spp and hybrids based on condensed tannin content. Leaves are shown after stream incubation of 28 days. Leaf cross types are (from left to right)* Populus angustifolia*, backcross hybrids (2),* F_1 *hybrid, and* Populus fremontii*. Decay rates are fastest for* P fremontii *and slowest for* P angustifolia*, which have the lowest and highest concentrations of condensed tannins, respectively. Image from LeRoy* et al. *(2006).*

Modified food webs and organic matter processing

Changes in riparian plant composition and functional traits can have bottom-up effects on consumer structure and function. These same changes can also affect rates of decomposition through altered timing, quantity, and quality of detrital inputs. Temperate zone conifers shed lower quality litter throughout the year, whereas broadleaf deciduous taxa, such as *Populus* and *Alnus* spp, provide a seasonal pulse of higher quality litter. *Eucalyptus* also sheds lower quality litter throughout the year relative to native riparian European plants, which decreases richness and abundance of stream consumers (Gonçalves and Canhoto 2009; Larrañaga *et al.* 2009) and can depress rates of decomposition in deciduous forest streams (Canhoto and Graça 1999; see also Gonçalves and Canhoto 2009). Compared to streams and forests dominated by conifers and *Eucalyptus*, differences in leaf phenology, production, and quality result in a higher biomass of microbes and invertebrates in streams and forests dominated by deciduous *Populus* and *Alnus* (Bärlocher and Graça 2002; Naiman *et al.* 2005). Foliar plant nutrient content of native and non-native N_2-fixing litter (eg *Alnus* spp, *E angustifolia*) can also increase riparian and stream N availability (Compton *et al.* 2003; Follstad Shah *et al.* 2010), which may increase rates of decomposition (Harner *et al.* 2009; Kominoski *et al.* 2011; but see Mineau *et al.* 2012). The presence of non-native *Salix* spp in riparian zones in Australia and New Zealand results in faster in-stream leaf litter breakdown rates relative to those seen in native *Eucalyptus* forests (Read and Barmuta 1999), but also results in diminished macroinvertebrate richness and abundance in both terrestrial and aquatic habitats, despite the greater litter inputs (Read and Barmuta 1999; Greenwood *et al.* 2004). Natural genetic variation within and among *Populus* species and hybrids results in differences in N levels, foliar-condensed tannin content, and N-cycling (Schweitzer *et al.* 2004; Fischer *et al.* 2010). Decomposition rates of *Populus* litter in both aquatic and terrestrial habitats are slower when there are greater concentrations of condensed tannins (Figure 4; LeRoy *et al.* 2006) or higher condensed tannin:N ratios (Schweitzer *et al.* 2004).

A globally relevant area of continued research is the ecosystem impacts of genetic modifications of plant traits. Little is known about how native species and plantation hybrids or genetically modified species differ in their effects on ecosystem function. Griffiths *et al.* (2009) found that *Zea mays* (maize) genetically modified to express *Bacillus thuringiensis* (Bt) toxins decomposed in streams faster than non-Bt litter, whereas Swan *et al.* (2009) observed no effect or the opposite effect. Axelsson *et al.* (2011) also found no effect of Bt-modification on leaf-litter decay rates of *Populus* plantation hybrids, but genetically modified leaves did support greater aquatic consumer abundance relative to unmodified leaves.

Altered hydrologic regimes

Watershed climate and hydrologic patterns are influenced in part by riparian plant composition through variations in plant transpiration rates, water infiltration, and water storage (Dahm *et al.* 2002; Ellison *et al.* 2005). For example, loss of *T canadensis* in eastern US forests is expected to lower air and soil humidity (Ellison *et al.* 2005), but will also reduce total riparian forest evapotranspiration both annually and seasonally, leading to altered watershed hydrology (Ford and Vose 2007). *Tamarix* stands can sustain or even elevate rates of evapotranspiration during drought (Cleverly *et al.* 2006), although rates of transpiration by *Tamarix* can be similar to other riparian species growing under the same climatic conditions (Dahm *et al.* 2002; Nagler *et al.* 2005). Sustained evapotranspiration lowers surface- and groundwater availability (Cleverly *et al.* 2006) and can reduce the water infiltration capacity of soils. For example, water levels in European streams draining monoculture plantations of *E globulus* are generally lower and more susceptible to storms than streams draining native forests because *E*

globulus increases evapotranspiration rates and soil hydrophobicity relative to native forests (Canhoto and Laranjeira 2007).

Conclusions

Riparian forests are dynamic structural and functional ecotones between upland and aquatic habitats, and functional trait redundancy is essential to support the high regional biodiversity, exchange of cross-ecosystem subsidies, and valuable ecosystem services characteristic of riparian areas (Baxter *et al.* 2005; Naiman *et al.* 2005; Sabo *et al.* 2005). Riparian plants have wide inter- and intraspecific variation in structural and functional traits that enable them to exist in these variable and dynamic environments. Changes in riparian species composition that alter the number of functionally redundant traits represented in the community can therefore have cascading effects on dependent communities and ecosystem processes (Panel 1). Riparian plant community composition is changing in response to global changes in climate (eg increased temperature, altered precipitation, hydrology), outbreaks of pests and pathogens, altered land use (eg conversion to agriculture), habitat fragmentation, unsustainable human water use, and biotic homogenization (Poff *et al.* 2007). Many alterations to riparian plant communities will persist and dramatically increase, as human population growth and demand for plant-based resources and water coincide with changes in global climate (Tilman *et al.* 2001; Richardson *et al.* 2007; Sabo *et al.* 2010).

Conservation and management decisions should be guided by scientific understanding of specific system alterations and ecological responses, with the goals of preserving riparian biodiversity, functional trait diversity, and functional trait redundancy (Cadotte *et al.* 2011). The effects caused by shifts in plant species assemblages can be predicted using known riparian plant functional traits (Figure 1) and their impacts on dependent terrestrial and aquatic communities and ecosystem functions (Panel 1). The greatest functional changes to aquatic and terrestrial ecosystems should occur where shifts in riparian plant composition substantively alter functional trait diversity and redundancy (eg scenario 3, Panel 1). This conceptual framework (Panel 1) can be used by natural resource managers to prioritize conservation measures for riparian plant communities with high functional trait diversity and redundancy, and therefore resilience to a variety of environmental factors (eg scenario 4, Panel 1). Such communities are more likely to persist under global change than communities composed of species with similar environmental tolerances and thus with low functional diversity and redundancy (eg scenarios 1 and 3, Panel 1). Riparian restoration efforts can also be designed for increased resiliency by considering functional trait diversity and redundancy when restoring the environmental conditions favorable for key species re-establishment.

We have identified several areas for future investigation, including the need to: (1) use experimental manipulation and modeling to identify plant functional traits that have the greatest influence on dependent aquatic and terrestrial communities and ecosystem processes; (2) assess whether the redundancy of key traits is functionally equivalent among species; (3) model different scenarios of change in riparian plant functional trait diversity and redundancy to better quantify expected community and ecosystem responses to global stressors in regions with known or expected shifts in riparian plant composition; (4) better understand the spatial (eg local to river network) and temporal (eg years to centuries) scales at which effects of changes in riparian plant functional traits are perpetuated; and (5) expand understanding of functional trait shifts in riparian ecosystems beyond temperate ecoregions of the Northern Hemisphere. Riparian ecosystems are prevented from functioning naturally because of human land use along waterways, and the damages that ensue are likely to increase as humans continue to change genetic, species, and functional trait diversity and as riparian zones are increasingly influenced by global changes. Future work will require a combination of new empirical studies as well as advanced spatial and phylogenetic modeling to strategically manage regions where rapid land-use changes overlap with alterations to genetic, species, and functional trait diversity.

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