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Guidelines on ecological thresholds for temperature, water level fluctuations and nutrient loading in European riparian wetlands, suitable for adaptive management

Abstract

Ecological thresholds represent the point at which an ecological process or parameter changes abruptly in response to relatively small changes in a driving force. Although the non-linear nature of ecological dynamics is widely recognised, the concept of threshold responses have only recently received warranted attention in conservation and management.

In this report we synthesise current knowledge on ecological thresholds and alternative stable states and review numerous examples of threshold responses in riparian ecosystems. The review shows that changes in the hydrologic regime often represent the trigger that causes abrupt ecological transitions. Conversely, clear threshold responses to variations in temperature and nutrients appeared less common.

We then discuss the implications of threshold relationships for the management of riparian wetlands. Critical steps needed to embody thresholds models in adaptive management include the assessment of wetlands predisposition to thresholds responses, and the adaptation of monitoring schemes to facilitate the statistical identification of non-linear relationships

Monitoring is a key component of adaptive management, and the development of large observational EU platforms is expected to deliver a wealth of data that should be used to gather empirical evidence of thresholds dynamics and to develop a predictive framework for the prevention of undesired ecosystem shifts.

Ecological thresholds – Concepts and examples

An ecological threshold can be defined as the point at which an ecological process or parameter (e.g. biomass production, species presence) change abruptly, or where small changes in a driving force (e.g. temperature) produce dramatic changes in the ecosystem. Both the scientific and popular literature are rich in examples of rapid and even catastrophic ecosystem changes in response to what initially appeared as insignificant alterations of the environment. Indeed, conservation biologists and ecosystem managers have increasingly recognised the non-linear and complex nature of ecosystem dynamics (Scheffer and Carpenter 2003, Suding and Hobbs 2009). However, even if the notion of ecosystem instability has been known for decades (May 1977), theoretical development and practical applications in conservation science have only recently received warranted attention (Groffman et al. 2006). The concept of ecological thresholds is intimately linked to that of ecosystems' alternative stable states. The state of an ecosystem refers to its structure and function, including its populations and communities as well as their relationship with each other and with the environment. Therefore alternative states represent different combination of ecosystem states (e.g. assemblage of species, productivity) and environmental conditions that may stably persist at certain spatial and temporal scales (Suding et al. 2004). The stability of these alternative states depends on feedback mechanisms among its component organisms and the environment. In this perspective ecosystems are seen as "valley of stability" where the depth of the valley represents its "resistance" to change, while the steepness of the valley represents the ecosystems' "resilience", that is the speed at which it would return to its original state after disturbance (Figure 1). Given enough energy (e.g. an environmental driver), the system can be "pushed over the hill" (threshold) into another valley or state.

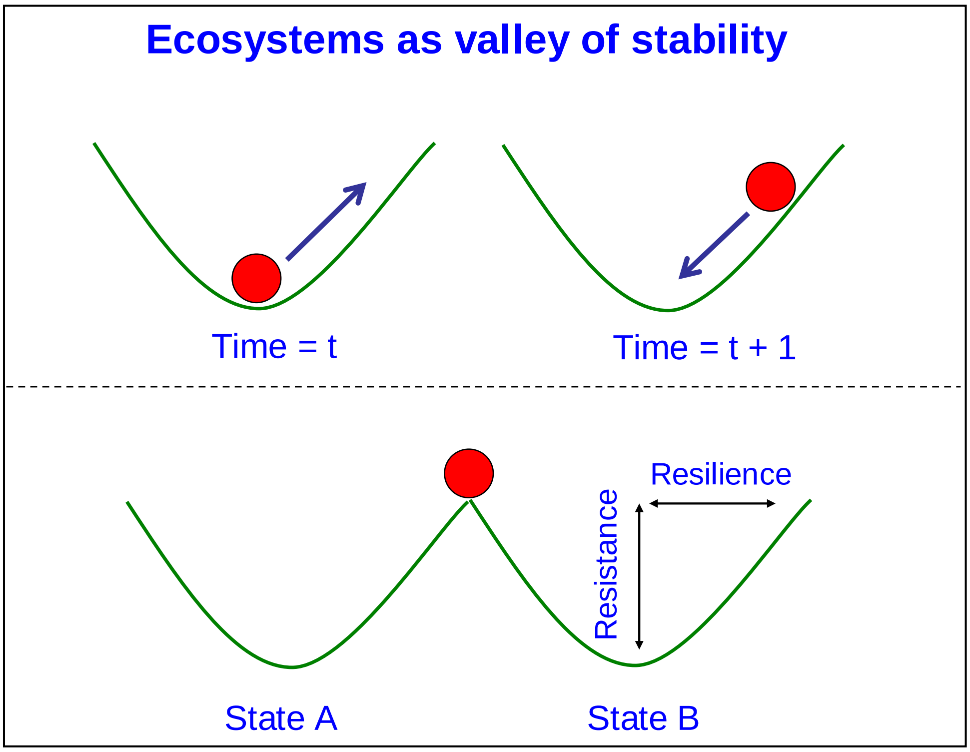

Figure 1. Schematic representation of ecosystems as valley of stability. The depth of the valley represents the ecosystem's resistance, which is the energy that is needed to move it to another state. The steepness of the valley sides represents the ecosystem's resilience, or the speed at which it returns to its initial state after perturbation. The upper panel shows a hypothetical resilient ecosystem that returns to its initial state after being "pushed" up. The lower panel represents an ecosystem at a threshold level between state A and B (redrawn after Groffman et al. 2006).

The graphical representation of Figure 1 provides an intuitive definition of thresholds. However, the non-linear nature of threshold dynamics is better understood by idealised functions as in Figure 2.

Figure 2 shows three hypothetical relationships between an ecosystem state variable and an environmental stressor. In the first example (Figure 2a) this relation is linear, whereas the following examples (Figure 2b, 2c) show a non-linear (abrupt change) response. This figure is also useful to introduce the important concepts of reversibility and hysteresis.

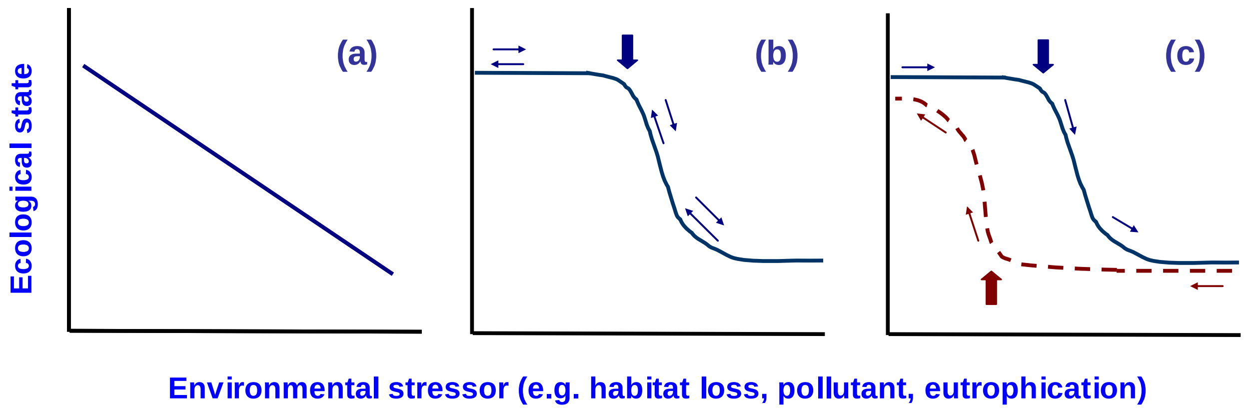

Figure 2. Hypothetical trajectories of change in the ecosystem state as a function of changes in environmental conditions, or anthropogenic disturbance. Ecological state indicates ecosystems' property such as species diversity, biomass production, or some desired ecosystem service. In (a) the response is linear showing no threshold behaviour. In (b) the ecosystem shows a dramatic response only when a specific threshold is reached (thick blue arrow). In this model the change is reversible and will follow the same path; ecosystem will restore to the original state once historic (pre-disturbance) conditions are re-established. In (c) the ecosystem shows a hysteretic response, where the trajectories of change and recovery follow different paths. This response model has important implications for restoration ecology, because the environmental threshold at which the original change occurred is different from that needed to restore the system (thick red arrow). That is, re-establishing pre-disturbance conditions is not enough to promote ecosystem recovery.

In fact, any discussion on ecosystem shift in environmental management ultimately raises questions about its reversibility. Reversible thresholds occur when ecosystems are able to return to the original ecological state once the "right" environmental conditions are met. For example, in some cases eutrophic lakes maintained in a turbid state by anthropogenic phosphorus inputs can reverse to a clear water state once nutrients inputs are reduced (Carpenter et al. 1999). Similarly, degraded kettle-hole landscapes and their associated communities appear able to recover to historic conditions (i.e. pre-disturbance) if the natural flooding regime is re-established (Mitsch and Wilson 1996). These examples would be graphically represented by Figure 2b, where the trajectory of change and recovery follow similar paths.

In some instance, however, the recovery of ecosystems to the original state follows a different trajectory compared to the one taken in the initial state change. This is called a hysteretic response and is graphically represented by Figure 2c. In these circumstances, re-establishing historic abiotic conditions is not enough to promote ecosystem recovery. Examples of this kind of response are typical of some semi-arid rangeland ecosystems where excessive grazing has promoted a shift in plant communities from drought-tolerant grasses to woody species; simply reducing grazing pressure to historic conditions does not restore grasslands (Van de Koppel et al. 1997). On the same theme, reducing acid deposition in some catchments affected by acid rain may not restore stream acid neutralising capacity, because acid deposition has changed soil chemical properties that ultimately controlled stream water chemistry (Driscoll et al. 2001). The reversibility (or lack of) ecosystem changes therefore depends on internal feedbacks that tend to maintain the ecosystem in the altered state. In these circumstances, more active hand-on management strategies might be needed to disrupt such internal feedbacks and promote ecological recovery (Suding and Hobbs 2009).

In an environmental management perspective it is useful to identify three types of thresholds: i) ecosystem state shift, ii) critical loads and iii) external factor thresholds (Groffman et al. 2006).

Ecosystem shifts occur when small changes in a driver cause massive and often surprising changes in the ecosystem. One classic example was the shift in the estuary ecosystem of Florida Bay from a clear water state, dominated by rooted aquatic vegetation, to a turbid state dominated by phytoplankton (Gunderson and Holling 2002). The key driving forces in this case were a combination of human derived nutrients input combined with drought and salinity.

The second type, analysis of critical loads, aims at identifying the quantity of pollutant or disturbance that an ecosystem can assimilate before significant ecological changes occur. These thresholds analyses are often used by environmental authorities to set legal limits to anthropogenic pollutants inputs. Analysis of ecosystem shifts and critical load thresholds are obviously interrelated, for example where critical loads from pollutants are the actual cause of dramatic ecosystem changes.

A third application of the threshold concept in ecology regards those instances where extrinsic factors constraint and regulate the structure and functioning of ecosystems. For example, river systems are ultimately regulated by larger scale catchment geomorphology and hydrologic regimes. Physical thresholds are common in rivers where the mobilisation of streambed particles is initiated only at certain flow velocity and shear stress levels (Bertoldi et al. 2010). An even more obvious threshold occurs when water level rises and spills over the banks inundating lateral floodplains. Modification of these thresholds by human activities can affect riverine ecosystems severely (see below). Recent studies in urban ecology suggest that there is a non-linear relationship between the amount of impervious surface (i.e. artificial structures such as roads, parking lots, etc) and many indices of aquatic ecosystem health, indicating that there might be a thresholds value of impervious surface after which ecological consequences are evident (Paul and Meyer 2001, King and Baker 2010).

Although our understanding of threshold responses and non-linear behaviours of ecosystems is growing, our ability to identify specific examples of multiple states in ecosystems and to effectively quantify thresholds for practical applications in environmental conservation and management is very limited (Groffman et al. 2006, Dodds et al. 2010). Clearly, this is due to the complex nature of ecosystems and to the multiple and interacting forces that regulate them. However, adaptive management (where management options are constantly re-evaluated based on evidence) would certainly benefit from an identification of thresholds in key drivers or the identification of those ecosystems that are more prone to regime shifts. Similarly, restoration ecology would be a far easier process if the feedback mechanisms that often maintain the system in a degraded state could be specified and eventually disrupted to promote recovery.

In the next sections we briefly introduce riparian wetlands ecosystems, their main characteristics and the derived societal benefits. We then provide a brief review of cases where non-linear or thresholds responses were observed; although regime shifts and threshold behaviour have been more frequently observed in lotic ecosystems, we argue that riparian wetland are no exception and that flow regime and riparian organisms are often linked in non-linear fashion. Finally, we discuss the implications of thresholds responses for the management and restoration of riparian wetlands.

Glossary	
Threshold	Point where even small changes in environmental conditions will lead to large changes in the ecosystem
Alternative stable state	Alternative combinations of ecosystem states and environmental conditions that may persist at a particular spatial extent and temporal scale
Feedback	Mechanisms (often biotic) within the ecosystem that tend to either amplify (positive feedback) or dampen (negative feedback) the response of the ecosystem to environmental change
Ecological resistance	Amount of change, or disturbance that an ecosystem can sustain before significant changes in the processes that regulate the system occur
Ecological resilience	The speed at which an ecosystem returns to its former state after it has been disturbed and displaced from that state
Hysteresis	Describe the situation in alternative stable states where the pathway of degradation differs from recovery

Riparian wetlands

Riparian wetlands are defined as semi-terrestrial zones that separate the aquatic and the terrestrial ecosystems. The exact location, length and shape of riparian zones certainly depends on the spatial and temporal scale of observation; however, the definition of riparian wetlands as transitional zones is clear enough (Strayer and Findlay 2010). Riparian wetlands are among the most threatened ecosystems due to intensive human modification, and yet they support high biodiversity that is enhanced by high habitat complexity and connectivity (Robinson et al. 2002, Tockner et al. 2010). Because of their transitional nature, riparian wetlands are strongly regulated by the hydrologic regime and represent optimal dissipaters of physical energy from waves breaking. This property has important functions for biogeochemical processes and biodiversity maintenance. Also, riparian wetlands receive and process large amounts of organic matter of both aquatic and terrestrial origin thus representing hot-spots of nutrient cycling. In brief, they represent areas where "interactions with the land have a strong influence on ecological processes and structures in the water, and vice versa" (Strayer and Findlay 2010). From a conservation and management perspective, riparian wetlands have numerous functions and provide a wide range of important ecosystem services and goods (Table 1).

Table 1. Examples of major ecosystem functions, associated processes and ecosystem goods provided by freshwater riparian wetlands. The table only list some of the most important functions (adapted from Capon et al. 2013).

Ecosystem function	**Ecosystem process**	**Ecosystem services / Goods**
Gas regulation	Role in biogeochemical cycles	Sink for green-house gases and harmful solutes
Climate regulation	Influence of riparian canopy cover	Regulation of local and in-stream temperature
Disturbance prevention	Buffering of environmental disturbances	Flood mitigation, bank protection
Nutrient regulation / Waste control	Role of riparian soils and organisms in nutrients processing	Pollution control / detoxification
Energy transfer	Food webs as transfer of energy between aquatic and terrestrial zones	Maintenance of productive systems
Propagule dispersal / Corridor	Role of wind, flooding and organisms as propagule dispersal and corridors	Maintenance of meta-populations, seed-bank
Refuge provision	Role of buffer areas as refuge habitats	Maintenance of aquatic and terrestrial species
Food production	Production of edible resources	Hunting, gathering, farming, aquaculture
Recreation	Provision of landscape with aesthetic/artistic/recreational values	Camping, fishing, bird watching, artistic activities.

Thresholds in wetland ecosystems

In this section we review some of the observed threshold responses in freshwater riparian ecosystems. Note that because of the functional link between riparian and aquatic systems, especially in river floodplains, the same threshold responses often apply to both systems.

As previously mentioned, water regime is the master variable that regulates riparian ecosystems and often represents the main driver of threshold behaviours and state shift.

The so called “recruitment box” model initially proposed by Mahoney & Rood (1998) is a clear example of threshold response governed by water level changes. The model describes the range of water levels (upper and lower limits) and timing (seasons) at which the seedlings of different cottonwood species are most likely to become successfully established. The model also identifies a threshold in the rate of decline of the stream water level below which the survival of the cottonwood seedlings is hindered (Table 2). Similar findings were obtained experimentally by Amlin & Rood (2002), who also observed higher sensitivity of *Salix* seedlings compared to *Populus* seedlings to the rate of water table decline.

Similar studies were also motivated in the US by the increasing spread of drought tolerant *Tamarix* species along rivers in western US and Mexico. In these regions, groundwater depletion and damming has lead to a progressive shift in the composition of riparian plant communities from native cottonwoods and willows to the invasive *Tamarix.* In Europe, where *Tamarix* species are autochthonous and co-occur with other *Populus* and *Salix* species, the identification of important hydrological thresholds that determine the success of one species over the other is key for protecting riparian areas from further degradation. Gonzalez et al. (2012) were able to quantify thresholds in key hydrological variables (water table depth, flood duration and frequency) that dictated the maintenance or collapse of mature populations of *Populus*, *Salix* and *Tamarix* (Table 2). Overall their results were consistent with other studies reporting that both *Populus* and *Salix* species cannot withstand water table levels deeper than 2 -3 meters below the surface, while *Tamarix* species appeared still lively at water table depths of more than 6 meters. However, Gonzales et al. (2012) also recommended that controlling maximum groundwater depth should be combined with optimal management of flood duration and frequency in order to saturate riparian soil and allow roots growth of target species.

Another obvious threshold response of riparian vegetation is associated with the shift in surface flow from permanent to intermittent. Permanent stream flow conditions allow for the development of very productive hydric perennial plants that provide optimal animal habitats and control bank erosion; the abundance of these plants often decline dramatically once flow become intermittent (Lite and Stromberg 2005, Stromberg et al. 2005). Stromberg et al. (2005) also observed that once flow became intermittent, floodplain vegetation showed instead a continuum response, where species richness and cover changed linearly as flow permanence declined.

The shift from permanent to intermittent flow clearly represents a major ecological threshold for the river system itself; as previously explained, riparian and lotic ecosystems are functionally linked and this is particularly evident in river floodplains. A classic threshold model in river geomorphology focuses on identifying the values in sediment supply, sediment calibre and discharge at which a single-thread straight or meandering river channel switches to a multi-thread braided channel (Bertoldi et al. 2010). Riparian vegetation in the floodplain is not only affected by this transition, but can directly influence the thresholds at which channel adjustments occur (Gurnell et al. 2009). For example, island development within braided channel depends on the supply and rapid growth of uprooted trees over exposed bars. Fast growing Salicaceae often play a major role in this process. Climate driven changes in the phenology and distribution of important riparian species can therefore indirectly influence channel forming processes.

In meandering river systems, the lateral migration of channels creates new wetlands ecosystems by initiating ecological succession. Simulation models suggested that the duration of flooding represent a critical threshold for the creation and maintenance of diverse riparian habitats in floodplains; river regulation that changes the duration of floods above the threshold would therefore lead to severe riparian degradation (Richter and Richter 2000).

On a similar theme, Hefferman (2008) observed that a positive feedback between vegetation and river channel stability is responsible for the formation of two alternative states in some desert streams. In this model, a density-dependent vegetation resistance to flooding determine whether the ecosystem will stabilise in i) a gravelbed-stream state in which low vegetation abundance is maintained by flood-induced mortality, or ii) a wetland state in which channel vegetation has reached a critical abundance that can withstand flooding. This study was one of the first to report the existence of alternative stable states in wetland ecosystems, and has important implication for riparian wetland management in arid regions. Recovery of desert riparian wetland will only occur if the restoration effort is able to overcome the feedbacks that maintain these systems in a gravelbed stream state.

The threshold dynamics discussed so far are mostly driven by non-linear responses of riparian vegetation to the hydrologic regime. However, as previously mentioned, riparian wetlands represent hot-spots of biogeochemical processes, which can also vary non-linearly along abiotic gradients. For example, Fenner et al. (2006) measured methane (CH_4) emission from wetland soils (peat) along a temperature gradient; they observed no significant emissions at temperatures below 6 ºC, while a strong increase in CH_4 emission was apparent above 6 ºC, eventually reaching a plateau at 15 ºC. Although their study focused on peat lands, similar effects could be expected in riparian wetlands, which are potential sources of greenhouse gases. Machefert et al. (2004), for instance, observed a threshold effect of rainfall where major rainfall events triggered a pulse of high nitrous oxide emissions (N_2O) from riparian wetlands in agricultural fields.

Recent research also suggests that the strength of the linkages between in-stream biogeochemical processes and the riparian environments vary non-linearly along the stream width gradient. Sakamaki and Richardson (2013) were able to identify a threshold of stream width over which the influence of riparian forests on in-stream organic matter properties (e.g. C/N, Chl *a*.) became negligible. Conversely, below the thresholds width of 7.6 m variation in organic matter properties correlated strongly with local riparian vegetation.

From these examples is evident that riparian and associated lotic ecosystems often show non-linear responses to environmental factors and that key thresholds values can often be identified. Nonetheless, applications of threshold concepts in riparian ecosystem management and validation of known thresholds in experiments or restoration efforts are unduly rare.
In the next section we highlight some of the implications that non-linear responses and ecosystem state shifts have for the management of riparian wetlands.

Table 2. Examples of threshold responses in riparian wetland ecosystems

Response variable	Main driver	Mechanism / Threshold	Reference
Cottonwood seedling recruitment	Water table; Stream stage decline rate.	Successful establishment occurs in riparian areas between 50 and 200 cm above base stage; stage decline rate should not exceed 2.5 cm per day.	(Mahoney and Rood 1998, Amlin and Rood 2002)
Mortality rates of *Populus*, *Salix* and *Tamarix* spp.	Water table; Flood frequency	Thresholds values for water table depth (WT), and flood frequency (FF) at which species show < 50% mortality. For *Salix alba* WT > - 1.2 m and FF > 5.4 events/year. For *Populus nigra* WT > - 2.18 m and FF > 3.8 events/year. For *Tamarix* spp. WT > - 2.96 m and FF > 2.5 events/year. For *Populus alba* WT > - 3.45 m and FF > 2 events/year.	(Gonzalez et al. 2012)
Abundance of riparian plants functional groups (hydric perennials *vs* mesic perennials)	Flow permanence	Shift in water flow from permanent to intermittent represents a critical threshold where the abundance of productive hydric plants decline significantly.	(Stromberg et al. 2005)
Abundance of *Populus, Salix* and *Tamarix*	Flow permanence	*P. fremontii* and *S. gooddingii* were dominant over the invasive *T. ramosissima* where surface flow was present > 76% of the time, inter-annual groundwater fluctuation was < 0.5 m, and average maximum depth to ground water was < 2.6 m.	(Lite and Stromberg 2005)
Initiation of lateral channel migration in the floodplain that would allow the persistence of diverse riparian vegetation at different successional stages.	Flood duration	Annual floods (at 125% bankfull discharge) with cumulative duration ≥ 15 days are needed to allow the persistence of riparian forest patch types in their natural range of abundance.	(Richter and Richter 2000)
Methane (CH_4) emission from peatland soils	Temperature	Significant methane emissions when temperature increases over 6 ºC	(Fenner et al. 2006)
Nitrous oxide (N_2O) from riparian wetland in agricultural fields	Precipitation; Nutrient supply	Rainfall events over 10mm triggered a pulse of N_2O emissions.	(Machefert et al. 2004)
In-stream fine particulate organic matter (FPOM)	River width	FPOM properties (C/N; Chl. *a*) correlated strongly with riparian forest features in streams narrower than 7.6m. Above this threshold width FPOM appeared unrelated to riparian vegetation.	(Sakamaki and Richardson 2013)

Implications of threshold responses for the management of riparian wetlands

There is growing evidence that threshold behaviours occur in many ecosystems including riparian wetlands. However, this does not mean that all non-linear responses are associated with specific thresholds and even where they occur the exact identification is challenging. Also, although the case studies discussed above provide quantitative guidelines for certain thresholds, these remain rather system-specific and their applicability across eco-regions remains untested. As Groffman et al. (2006) stated, the biggest limitation to the use of threshold concepts in environmental management is the lack of general principles on how to apply these concepts to different response variables (e.g. vegetation structure, biogeochemical processes) and in different ecosystem types. For example, in the case of riparian wetlands it is likely that wetlands in arid and temperate regions respond differently to similar abiotic drivers; even within the same catchment, wetlands in upland areas might show different sensitivity compared to those further downstream (Brinson 1993).

In order to incorporate the threshold concept in the management of riparian wetlands we should adapt current monitoring scheme so as to provide early warning signals that the system is approaching a threshold. Monitoring is a key component of adaptive management and we should take advantage of the growing body of statistical methods developed to investigate non-linear and threshold relationships (Table 3). Hence, key steps for embodying ecological thresholds into adaptive management and restoration of riparian wetlands include i) assessing their exposure and sensitivity to global change, ii) understanding what makes the ecosystem more or less prone to threshold responses and state shift and iii) adapting monitoring schemes to facilitate the statistical identification of non-linear relationships. Additionally, any restoration effort should keep in mind that the dynamics of degraded states often differ from those of pristine states, and that the trajectories of recovery may differ from those of degradation. Degraded ecosystems can be resilient to change because they often represent alternative stable states that are maintained by internal feedbacks (Suding et al. 2004)

Wetland exposure and sensitivity

Riparian wetlands are expected to be particularly exposed to climate-driven changes, being affected both directly, as well as indirectly from changes in the terrestrial and aquatic domain. Nonetheless, current knowledge of their specific sensitivity remains poor. Some authors suggested that riparian wetlands may be very vulnerable to climate-driven changes because of their high exposure and history of degradation. Others see riparian ecosystem as disturbance-mediated environments, which have evolved under high climatic variability and thus should be less sensitive to climate change (Capon et al. 2013). However, human modification of riparian habitats have often dampened or totally eliminated natural environmental variations, consequently affecting their resilience (Folke et al. 2004). Hydrologic regime, which is the master variable that regulates riparian ecosystems, is clearly sensitive to climatic change, which could lead to an increase in the magnitude, frequency and duration of floods and droughts events. Changes in precipitation will affect groundwater hydrology that, as we have seen before, is extremely significant for many riparian ecosystems. Also, climate-driven changes in sediment transport and deposition will affect physical and biogeochemical processes in riparian ecosystems. Temperature changes can also affect the phenology and distribution of many riparian species eventually disrupting important trophic interactions between the aquatic and terrestrial environment (Baxter et al. 2005). Climatic changes are also likely to promote increasing river regulation and water extraction, as well as vegetation clearing for agriculture and pasture, thus exacerbating the impact on riparian systems on a global scale. Also, somehow ironically, mitigations measure for CO_2 emission and the shift towards renewable energy such as plantation forestry and hydropower facilities may result in further threats to rivers and riparian ecosystems. Therefore, the positive feedback between climate-driven changes and direct anthropogenic alterations may impact riparian habitats and biodiversity at an accelerating pace.

Assessing predisposition to threshold responses

Understanding if, and to what extent, an ecosystem is susceptible to threshold responses and state shift is not a straightforward process; however some criteria can be identified to guide managers in the process.

Riparian wetlands can be seen as disturbance-mediated ecosystems, strongly regulated by variations in the hydrologic regime and thus naturally resilient to change. However, artificially regulated wetlands are more likely to be susceptible to threshold responses, having lost their natural capacity to adjust to environmental variations and recover from disturbance. Also, ecosystems that have lost or gained key functional groups may also show increasing likelihood of state shifts. Invasion of riparian habitats by *Tamarix* spp. in some western US catchments has changed the abiotic environment including riparian shading properties and nutrient processing (Stromberg et al. 2005, Suding and Hobbs 2009). Similarly, trout invasion can lead to increasing predation of aquatic invertebrates, and consequently reduce the flux of emerging adult insects into adjacent terrestrial systems with consequences for riparian consumers (Baxter et al. 2004, Epanchin et al. 2010). In particular, the loss or gain of species defined as "ecological engineers" can result in rapid alteration of the ecosystem. For example, excessive browsing by elks in the Yellowstone National Park strongly reduced the abundance of *Salix* spp. along rivers and indirectly impacted beavers' population. Beavers are effective ecological engineers, the loss of which severely altered river hydrology and further hindered the establishment of *Salix* spp. to the point that even decreasing browsing pressure could not restore riparian *Salix* spp. to the natural state (Wolf et al. 2007).

To generalise, thresholds responses are considered more likely to occur in systems characterised by i) strong species interactions where top-down and bottom-up effects can lead to dramatic changes, ii) presence of ecosystem engineers, and iii) where the available species pool is large potentially leading to "priority effects" where the first species to colonise (e.g. after a disturbance event) determine the trajectory of ecological succession.

The ecological connectivity of ecosystems also determines their resilience to disturbance by providing important propagule availability for re-establishing biodiversity. Isolated wetlands might have lost their natural "rebuilding capital" thus becoming more susceptible to rapid state shifts.

Environmental managers can therefore focus on these few criteria to evaluate the potential of ecosystems to show threshold behaviours. Identifying important internal feedbacks that maintain the system in a given state or the presence of strong biotic interactions and ecosystem engineers represent a key first step in the evidence needed by adaptive management and certainly deserve additional research effort.

Nonetheless, the potential for threshold responses is no guarantee that they will occur. Managers should take advantage of monitoring programmes and statistical tools to actually gather evidence of non-linear relationships in the system and to assess whether a state shift is approaching.

Adaptive management, monitoring and the identification of thresholds

Monitoring is a key component of adaptive management, and if properly designed it can provide evidence to guide managers about whether thresholds models are appropriate for the particular ecosystem. Monitoring data should allow specific pattern-based analyses in order to test whether thresholds relationships are occurring. For example, long-term data series can be used to assess abrupt transitions over time. Long term monitoring is particularly important in this case, because ecological state transitions can take years to occur even after rapid changes in the abiotic environment (Robinson and Uehlinger 2008). Moreover, field studies suggest that ecosystems undergoing a transition to an alternative state might show increased variation in many ecological parameters (Carpenter and Brock 2006). Long time-series therefore provide key data for these investigations. Similarly, spatial monitoring data can be used to assess if ecosystems show sharp spatial variation in certain parameters in the absence of associated variation in environmental characteristics (Andersen et al. 2009). This would suggest that the system has crossed an ecological threshold. Certainly more research is needed to verify the specific validity is these findings for riparian wetlands.

Adaptive management must be a learning process where different approaches should be evaluated in an experimental framework. Effort is needed to identify wetland-specific early warning indicators of approaching thresholds. For example, microbial based monitoring schemes have been developed in some waterbodies that are able to predict approaching eutrophication and algal bloom thresholds (Paerl et al. 2003).

Moreover, a variety of statistical tools and software (Table 3) have been developed to specifically tackle non-linear relationships and identify threshold responses. A sound data-base generated by monitoring could serve as the foundation for developing and testing threshold models in wetland ecosystems.

Table 3. Common statistical methods to identify thresholds and non-linear relationships (adapted from Dodds et al. 2010).

Method	**Description**
Piecewise regression	Determination of whether 2 relationships fit the data better than one
Non linear curve fitting	Fit non-linear user defined equations
Two-dimensional Kolmogorov–Smirnov test	A nonparametric test for changes in variance; predicts a threshold in the driver and the response variable
Quantile regressions	Detect changes in variance of one variable for different ranges of another variable
Regime shift detection	Find shifts in temporal data series
Threshold Indicator Taxa Analysis (TITAN)	Indicates changes in community structure across a Gradient
Significant zero crossing (SiZer)	Non-parametric approach based on derivatives and smoothing functions

Future directions

The scarcity of field applications of threshold models ecology is at odds with the growing theoretical advances. Certainly this has to do with the complexity of most analytical techniques and the perception that only exceptionally long data series can fulfil their requirements (Andersen et al. 2009). However, the development of observational platforms (e.g. the EU Water Framework Directive [WFD] monitoring system and the EU Biodiversity Observation Network [EU BON]) will deliver large datasets with great potentials even for the most complex analyses. The need to embody threshold responses in the management of ecosystems has become an urgent need considering how climate averages are expected to change smoothly and yet certain communities appear to respond abruptly (Deyoung et al. 2008). Future research should also aim at assessing how climate change may influence current threshold responses. For example, critical thresholds in river geomorphology describe the shift from single-thread to braided channels in terms of sediment supply and hydrology; however, pioneer riparian vegetation plays a key role in channel re-configuration and critical threshold values may thus change as vegetation respond to climatic variations (Gurnell et al. 2009).

Most of the analytical techniques mentioned in this report allow the identification of threshold only after these have been crossed, meaning that they are of little help in the prevention of abrupt changes in ecosystems. Nonetheless, the growing interest in the assessment of non-linear relationships and ecosystem shifts in response to environmental drivers should provide empirical evidence that can be used to develop predictive frameworks for specific ecosystems (Andersen et al. 2009).

Finally, ecologists and environmental managers should join forces to identify which are the internal feedbacks that enhance the resilience of degraded ecosystems. Disturbed and degraded systems often represent alternative stable states whose dynamics differ substantially from those of pristine systems. They are indeed novel ecosystems (Tockner et al. 2013). In these cases, thresholds models of reversibility and hysteresis (Fig. 2) are valuable to predict how the system will respond to restoration effort. A clear understanding of the dynamics of human modified systems is therefore indispensible for the future development of management and restoration strategies.

References

Amlin, N. M. and S. B. Rood. 2002. Comparative tolerances of riparian willows and cottonwoods to water-table decline. Wetlands **22**:338-346.

Andersen, T., J. Carstensen, E. Hernandez-Garcia, and C. M. Duarte. 2009. Ecological thresholds and regime shifts: approaches to identification. Trends in Ecology & Evolution **24**:49-57.

Baxter, C. V., K. D. Fausch, M. Murakami, and P. L. Chapman. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. Ecology **85**:2656-2663.

Baxter, C. V., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology **50**:201-220.

Bertoldi, W., L. Zanoni, and M. Tubino. 2010. Assessment of morphological changes induced by flow and flood pulses in a gravel bed braided river: The Tagliamento River (Italy). Geomorphology **114**:348-360.

Brinson, M. M. 1993. Changes in the functioning of wetlands along environmental gradients. Wetlands **13**:65-74.

Capon, S. J., L. E. Chambers, R. Mac Nally, R. J. Naiman, P. Davies, N. Marshall, J. Pittock, M. Reid, T. Capon, M. Douglas, J. Catford, D. S. Baldwin, M. Stewardson, J. Roberts, M. Parsons, and S. E. Williams. 2013. Riparian Ecosystems in the 21st Century: Hotspots for Climate Change Adaptation? Ecosystems **16**:359-381.

Carpenter, S. R. and W. A. Brock. 2006. Rising variance: a leading indicator of ecological transition. Ecology Letters **9**:308-315.

Carpenter, S. R., D. Ludwig, and W. A. Brock. 1999. Management of eutrophication for lakes subject to potentially irreversible change. Ecological Applications **9**:751-771.

Deyoung, B., M. Barange, G. Beaugrand, R. Harris, R. I. Perry, M. Scheffer, and F. Werner. 2008. Regime shifts in marine ecosystems: detection, prediction and management. Trends in Ecology & Evolution **23**:402-409.

Dodds, W. K., W. H. Clements, K. Gido, R. H. Hilderbrand, and R. S. King. 2010. Thresholds, breakpoints, and nonlinearity in freshwaters as related to management. Journal of the North American Benthological Society **29**:988-997.

Driscoll, C. T., G. B. Lawrence, A. J. Bulger, T. J. Butler, C. S. Cronan, C. Eagar, K. F. Lambert, G. E. Likens, J. L. Stoddard, and K. C. Weathers. 2001. Acidic deposition in the northeastern United States: Sources and inputs, ecosystem effects, and management strategies. Bioscience **51**:180-198.

Epanchin, P. N., R. A. Knapp, and S. P. Lawler. 2010. Nonnative trout impact an alpine-nesting bird by altering aquatic-insect subsidies. Ecology **91**:2406-2415.

Fenner, N., D. J. Dowrick, M. A. Lock, C. R. Rafarel, and C. Freeman. 2006. A novel approach to studying the effects of temperature on soil biogeochemistry using a thermal gradient bar. Soil Use and Management **22**:267-273.

Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology Evolution and Systematics **35**:557-581.

Gonzalez, E., M. Gonzalez-Sanchis, F. A. Comin, and E. Muller. 2012. Hydrologic thresholds for riparian forest conservation in a regulated large Mediterranean river. River Research and Applications **28**:71-80.

Groffman, P., J. Baron, T. Blett, A. Gold, I. Goodman, L. Gunderson, B. Levinson, M. Palmer, H. Paerl, G. Peterson, N. Poff, D. Rejeski, J. Reynolds, M. Turner, K. Weathers, and J. Wiens. 2006. Ecological thresholds: The key to successful environmental management or an important concept with no practical application? Ecosystems **9**:1-13.

Gunderson, L. and C. S. Holling. 2002. Panarchy: understanding transformations in human and natural systems. Island Press, Washington (DC).

Gurnell, A., N. Surian, and L. Zanoni. 2009. Multi-thread river channels: A perspective on changing European alpine river systems. Aquatic Sciences **71**:253-265.

Heffernan, J. B. 2008. Wetlands as an alternative stable state in desert streams. Ecology **89**:1261-1271.

King, R. S. and M. E. Baker. 2010. Considerations for analyzing ecological community thresholds in response to anthropogenic environmental gradients. Journal of the North American Benthological Society **29**:998-1008.

Lite, S. J. and J. C. Stromberg. 2005. Surface water and ground-water thresholds for maintaining Populus-Salix forests, San Pedro River, Arizona. Biological Conservation **125**:153-167.

Machefert, S. E., N. B. Dise, K. W. T. Goulding, and P. G. Whitehead. 2004. Nitrous Oxide Emissions from Two Riparian Ecosystems: Key Controlling Variables. Water, Air, & Soil Pollution: Focus **4**:427-436.

Mahoney, J. M. and S. B. Rood. 1998. Streamflow requirements for cottonwood seedling recruitment - An integrative model. Wetlands **18**:634-645.

May, R. M. 1977. Thresholds in breakpoints in ecosystems with a multiplicity of stable states. Nature **269**:471-477.

Mitsch, W. J. and R. F. Wilson. 1996. Improving the success of wetland creation and restoration with know-how, time, and self-design. Ecological Applications **6**:77-83.

Paerl, H. W., L. M. Valdes, J. L. Pinckney, M. F. Piehler, J. Dyble, and P. H. Moisander. 2003. Phytoplankton photopigments as indicators of estuarine and coastal eutrophication. Bioscience **53**:953-964.

Paul, M. J. and J. L. Meyer. 2001. Streams in the urban landscape. Annual Review of Ecology and Systematics **32**:333-365.

Richter, B. D. and H. E. Richter. 2000. Prescribing flood regimes to sustain riparian ecosystems along meandering rivers. Conservation Biology **14**:1467-1478.

Robinson, C. T., K. Tockner, and J. V. Ward. 2002. The fauna of dynamic riverine landscapes. Freshwater Biology **47**:661-677.

Robinson, C. T. and U. Uehlinger. 2008. Experimental floods cause ecosystem regime shift in a regulated river. Ecological Applications **18**:511-526.

Sakamaki, T. and J. S. Richardson. 2013. Nonlinear variation of stream-forest linkage along a stream-size gradient: an assessment using biogeochemical proxies of in-stream fine particulate organic matter. Journal of Applied Ecology **50**:1019-1027.

Scheffer, M. and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends in Ecology & Evolution **18**:648-656.

Strayer, D. L. and S. E. G. Findlay. 2010. Ecology of freshwater shore zones. Aquatic Sciences **72**:127-163.

Stromberg, J. C., K. J. Bagstad, J. M. Leenhouts, S. J. Lite, and E. Makings. 2005. Effects of stream flow intermittency on riparian vegetation of a semiarid region river (San Pedro River, Arizona). River Research and Applications **21**:925-938.

Suding, K. N., K. L. Gross, and G. R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. Trends in Ecology & Evolution **19**:46-53.

Suding, K. N. and R. J. Hobbs. 2009. Threshold models in restoration and conservation: a developing framework. Trends in Ecology & Evolution **24**:271-279.

Tockner, K., M. Pusch, D. Borchardt, and M. S. Lorang. 2010. Multiple stressors in coupled river-floodplain ecosystems. Freshwater Biology **55**:135-151.

Tockner, K., M. Pusch, J. Gessner, and C. Wolter. 2013. Domesticated ecosystems and novel communities: challenges for the management of large rivers. Ecohydrology & Hydrobiology **7**:167–174.

Van de Koppel, J., M. Rietkerk, and F. J. Weissing. 1997. Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. Trends in Ecology & Evolution **12**:352-356.

Wolf, E. C., D. J. Cooper, and N. T. Hobbs. 2007. Hydrologic regime and herbivory stabilize an alternative state in yellowstone national park. Ecological Applications **17**:1572-1587.