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# Plant roots steer resilience to perturbation of river floodplains

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## Key Points:

- We develop a mechanistic model for river floodplain equilibrium states and their response to changing flow regime
- Temporal irreversibility to reversible conditions is shown to originate from plant root adaptation to the new regime
- We use a worldwide common example of water impoundment to quantify long-term floodplain dynamics.

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## Abstract

Freshwater ecosystems along river floodplains host among the greatest biodiversity on Earth and are known to respond to anthropic pressure. For water impounded systems, resilience to changes in the natural flow regime is believed to be bi-directional. Whether such resilience prevents the system from returning to pristine conditions after the flow regime changes reverse is as yet unclear, though widely documented. In this work we show that temporal irreversibility of river floodplains to recover their status may be explained by the dynamics of riparian water-tolerant plant roots. Our model is a quantitative tool that will benefit scientists and practitioners in predicting the impact of changing flow regimes on long-term river floodplain dynamics.

## Plain Language Summary

Catchment impoundment and the withdrawal of flowing water from mountain torrents and rivers for human needs are practices that modify the mean discharge and variability of natural streams. The long-term impact includes changes to floodplain morphology and the compositions of terrestrial and aquatic biodiversity. Vegetation encroachment is then widely observed on floodplains where water is not a limiting factor for plants to grow. The extent to which such alterations are reversible is an important object of this study, and has important implications for water management strategies when hydraulic structures reach the end of either their physical life or their economic benefit. We develop a comprehensive theoretical model that reveals the important role of plant roots in these processes. The model is applied to impoundment of the River Maggia in Switzerland. It is found that natural conditions before dam construction might not be fully restored by simply removing the dam. Our approach offers an important step towards improving natural water management schemes and optimal dam regulation strategies in the face of human and climatic hydrological changes.

## 1 Introduction

River impoundment is a water management practice used worldwide that primarily affects the river natural flow regime. Often exacerbated by a lack of sustainable management actions, alterations to the flow regime provide a major source of anthropic pressure on freshwater ecosystems (Stella & Bendix, 2019). The process first affects the river-

47 ine geomorphic asset and may later change the ecologic integrity of related biota com-  
48 munities (Bunn & Arthington, 2002; Poff et al., 1997; Rosenberg et al., 2000; Tullios et  
49 al., 2004). In the long term, floodplain and riparian zones gradually lose their functional,  
50 societal, and economic values (E. Wohl et al., 2005). About 48% of all world river sys-  
51 tems are regulated nowadays, and this proportion is forecast to rise to 93% by 2030 (Grill  
52 et al., 2015). Urgency measures have now become an inherent part of the biodiversity  
53 strategy program (EC, 2020). Commencement of dam operations typically causes down-  
54 ward shifts in mean streamflow and corresponding river stages, the disappearance of mod-  
55 erate flooding events, and sediment flow interruption. When sediment inflow is interrupted  
56 by a dam, the altered sediment-carrying capacity of the river leads to incision and en-  
57 trenchment of the channel, thus promoting disconnection between the channel and the  
58 floodplain (E. E. Wohl, 2004). River hydrograph attributes (Trush et al., 2000) are also  
59 important in controlling the development of juvenile vegetation (Kui et al., 2017; Stella  
60 et al., 2006). Following a downward shift in water table perhaps enhanced by channel  
61 incision, plant roots may travel deeper in soil in order to track soil moisture even at higher  
62 elevation differences (Smith, 2007; Pasquale et al., 2012). Such an hydrotropic response  
63 also reshapes the vertical root density distribution of riparian plants (Gorla et al., 2015).  
64 Hence, a frequently observed transient floodplain response to hydrologic regime shift be-  
65 gins with intense riparian vegetation establishment and encroachment causing river chan-  
66 nel narrowing (Choi et al., 2005; Gordon & Meentemeyer, 2006; Allred & Schmidt, 1999;  
67 Molnar et al., 2008; Stella et al., 2003). From a dynamical system perspective, such eco-  
68 geomorphic transformations occur as a ‘transient phase’ that may last for decades (Petts,  
69 1987), before the riverine ecosystem adjusts to a new dynamic equilibrium (Petts, 1984).  
70 According to Petts (1987), the ‘transient phase’ depends on several factors including chan-  
71 nel type, mobility of sediment and channel boundaries, biota species adaptation, etc. The  
72 degree of reversibility of the transformation processes upon restoring pristine hydrologic  
73 conditions is largely unknown (Molnar et al., 2008; Perona, Camporeale, et al., 2009; Tul-  
74 los et al., 2009).

75 Ecosystem shifts following perturbation have often been ascribed to catastrophe-  
76 like dynamics. A tipping point (i.e., bifurcation) towards new stable equilibria occurs  
77 when some key system parameter acting as the system driver reaches a critical value (Scheffer  
78 et al., 2001). A key feature of such catastrophic transitions is their hysteretic behaviour  
79 and irreversibility when the system driver conditions are reversed. It is therefore tempt-

80 ing to draw ideas from catastrophe theory to explain the effect of river impoundment  
81 on freshwater ecosystems. However, May (1977) observed that ecosystem dynamics may  
82 possess multiple stable equilibrium points and Zahler and Sussmann (1977) pointed out  
83 that irreversibility may not necessarily be a consequence of catastrophic transitions. Our  
84 present work expands on this idea.

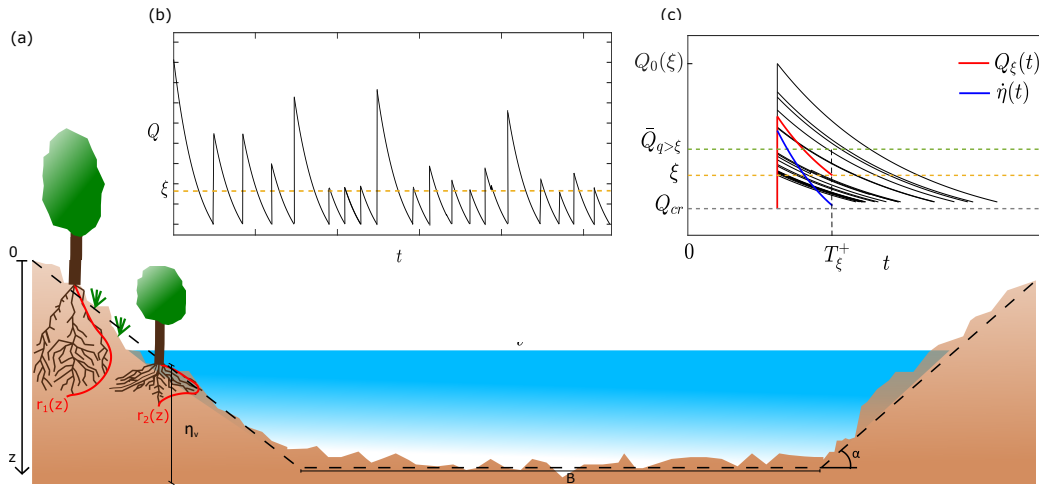
85 Ecomorphodynamics systems theory has elegantly explained how different fluvial  
86 styles can be the result of a triad process involving water, sediment and vegetation dy-  
87 namics (Bärenbold et al., 2016; Bertagni et al., 2018; Caponi & Siviglia, 2018). A means  
88 by which to unravel information and thus quantify the extent and reversibility of flood-  
89 plain changes to hydrological perturbations is offered by modelling the response of ri-  
90 parian plants and their root systems to perturbation. The analytical tractability of spa-  
91 tial mathematical models inevitably requires simplification even without explicitly con-  
92 sidering the dynamics of root adaptation (Bertagni et al., 2018; Caponi et al., 2019). How-  
93 ever, further steps in this direction can be achieved by focusing on point rather than dis-  
94 tributed spatial resolution. This is sufficient to show how resistance to uprooting responds  
95 to a changing flow regime and to what extent the process is reversible.

96 In this work, we develop a comprehensive model that accounts for the evolution  
97 of plant uprooting by flow after impoundment, and describes the (stable) equilibrium  
98 states of the floodplain system at a point. The complex dynamics of river floodplain re-  
99 sponse to perturbation are thus reduced to that of a dynamical system represented by  
100 a suitable state variable. In particular, we investigate the existence of novel stable equi-  
101 librium states for perturbed riverine corridors and discuss their possible irreversibility.  
102 The model is applied to a typical example of dam impoundment, which is common world-  
103 wide and is known to lead to intense riparian vegetation encroachment with consequent  
104 river narrowing (Molnar et al., 2008; Perona, Molnar, et al., 2009).

## 105 **2 Riparian processes and model formulation**

106 Figure 1a indicates how roots of phreatophytic vegetation tend to adapt to water  
107 table fluctuations. At high elevations above the phreatic surface, the plant root biomass  
108 distribution locates preferentially deep into the soil. Conversely, at lower elevations close  
109 to the phreatic surface the root biomass distribution is shallow and highly developed near  
110 the soil surface (Tron et al., 2015). Therefore, a vertical (down)shift in the water table

111 may not necessarily hinder the growth of phreatophytic species, but instead affect their  
 112 rooting depth and vertical distribution (Gorla et al., 2015). In turn, the anchorage depth  
 113 of roots influences the ability of a plant to withstand erosion processes and its survival  
 114 probability to uprooting by flow (Docker & Hubble, 2008; Pasquale et al., 2014; Simon  
 115 & Collison, 2002). Here, we combine stochastic and deterministic approaches of ripar-  
 116 ian vegetation dynamics into a comprehensive and almost entirely analytical framework.  
 117 Accordingly, we use the probability of plant uprooting by flow,  $P_\tau$  as a proxy variable  
 118 to represent the statistical state of the floodplain at a given time. Hence, it is implic-  
 119 itly assumed that vegetation mortality is solely caused by flow-induced uprooting; other  
 120 mechanisms such as plant burial have not been considered because their effect may also  
 121 favor vegetation survival (Kui & Stella, 2016; Politti et al., 2018). Plant uprooting prob-  
 122 ability depends on: plant elevation with respect to riverbed elevation; the representa-  
 123 tive mean flow erosion event at the riverbed elevation; and the critical scour depth for  
 124 the plant (Perona & Crouzy, 2018). Both latter quantities depend on the statistical prop-  
 125 erties of the river discharge (and water levels), which obviously differ between pre- and  
 126 post-impoundment periods. We now proceed toward assembling all processes in the model.



**Figure 1.** Sketch of the modeling framework. a) Illustration of the river section and its trapezoidal idealization (black dashed line) with riverbanks inclined at angle  $\alpha$  with respect to the riverbed. The two plants located on the riverbanks display different root biomass profiles, which may be represented analytically as  $r_1(z)$  and  $r_2(z)$  where  $z$  is the depth below the soil surface using the model proposed by Tron et al. (2014). b) Synthetic hydrologic signal of the flow discharge (CPP);  $\xi$  demarks the prescribed threshold when implementing Peak Over Threshold Theory. c) Sequence of events that lie above the threshold  $\xi$ . The statistical average of all the events is the mean reference event (red line). The blue line represents the bed erosion rate (modified from Calvani et al. (2019)).

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## 2.1 Probability distribution of time to uprooting

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Perona and Crouzy (2018) modelled plant uprooting by flow as a result of stochastic erosion dynamics requiring a time interval  $T$  to scour the bed to the critical depth leading to plant collapse. They obtained the following analytical expression for the probability density function (pdf) of the elapsed time  $T$  to uprooting  $p_\tau$  for flow erosion events of generic shape and plant critical rooting depth:

$$p_\tau(T) = \frac{L_e}{2\sqrt{\pi G(T)^3}} e^{\left(-\frac{(L_e - V(T))^2}{4G(T)}\right)} \left[ \frac{g_t(T)}{2} + e^{\left(\frac{(L_e + V(T))^2}{4G(T)}\right)} W(T) \right] \quad (1)$$

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where  $g_t(T)$  describes the noise affecting the erosion process at time  $t = T$ ,  $G(T) = \frac{1}{2} \int_0^T g_t(\tau) d\tau$ ,  $V(T) = \int_0^T \dot{\eta}(\tau) d\tau$ ,  $W(T) = \sqrt{\pi} \text{Erfc} \left[ \frac{L_e + V(T)}{2\sqrt{G(T)}} \right] \left( \dot{\eta}(T) \sqrt{G(T)} - \frac{g_t(T)}{2} \frac{V(T)}{\sqrt{G(T)}} \right)$ , and  $\tau$  is the dummy variable of integration.  $L_e$  is the scouring depth that determines uprooting, and  $\dot{\eta}(t)$  is the erosion rate event corresponding to the plant elevation. Values of  $L_e$  and  $\dot{\eta}(t)$  are assessed in sections 2.4 and 2.5. The following expression for  $g_t$  is obtained assuming that erosion may be represented by a Ornstein-Uhlenbeck stochastic flow process, in which the flow velocity profile is logarithmic and fluctuations acting on sediment particles follow Einstein's diffusion theory (for more details, see the mathematical derivation of equation (8) in the Supporting Information (SI)):

$$g_t = 8.5 D_{50} u_* \quad (2)$$

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where  $D_{50}$  is the median grain size of the sediment, and  $u_*$  is the shear velocity.

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## 2.2 Water discharge and groundwater level dynamics

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Variability in both the water discharge and groundwater levels is addressed using a Compound Poisson process (CPP) (Ridolfi et al., 2011), comprising white shot-noise random positive pulses followed by deterministic decays (Figure 1b). Hence, the pdf of flow discharge is given by:

$$p(Q) = \frac{\gamma_d^{-\beta_d}}{\Gamma[\beta_d]} e^{-Q/\gamma_d} Q^{\beta_d-1}, \quad (3)$$

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where  $Q$  is the flow rate,  $\Gamma[\cdot]$  is the Gamma function (Abramowitz & Stegun, 1948),  $\gamma_d$  is the mean amplitude of the pulses and  $\beta_d$  is the product between the mean frequency of the jumps,  $\lambda_d$ , and the deterministic exponential decay rate,  $\tau_d$  (see, also SI). Next, we use normal flow conditions to obtain the corresponding water level at each cross sec-

152 tion of interest. Likewise, we assume that water stage follows a CPP with parameters  
 153  $\gamma_l$  and  $\beta_l$  that are fitted to the empirical pdf of water level (see also SI) and synchronously  
 154 drive the dynamics of the phreatic water table in the soil Tron et al. (2014).

### 155 **2.3 Grain size distribution**

156 The bed erosion rate and root profile require input values for  $D_{50}$ ,  $D_{10}$ , and  $D_{90}$ ,  
 157 which are respectively the median, the tenth, and the ninetieth percentiles of the sed-  
 158 iment size distribution. To account for the sediment retention capacity of the dam and  
 159 the reduction in bed mobility downstream, a shift in sediment size between pre- and post-  
 160 dam periods was included in the modelling framework (Yang et al., 2014). Thus, we did  
 161 not explicitly model sediment sorting and bed armoring processes; instead, we empir-  
 162 ically modelled sediment size increase in the post-dam period.

### 163 **2.4 Root profile and scour depth**

164 According to Perona and Crouzy (2018), the probability of uprooting depends on  
 165 the scouring depth,  $L_e = L_0 - L_c$ , which is the difference between the effective root-  
 166 ing length and the critical rooting length leading to uprooting. We obtain  $L_e$  by com-  
 167 bining the model proposed by Tron et al. (2014) for the vertical root profile,  $r(z)$ , where  
 168  $z$  is distance below the riverbed level, with that by Bau' et al. (2019) for the critical root-  
 169 ing length,  $L_c$ . As shown in the SI,  $L_e$  can be obtained by solving the following integral:

$$L_{e,t} = a_m \int_0^{L_e} r(z) dz \quad (4)$$

170 where  $L_{e,t}$  indicates the flow-exposed total rooting length due to scour, and  $a_m$  is a pro-  
 171 portionality constant that links  $L_{e,t}$  to its corresponding root biomass, here expressed  
 172 through the integral of  $r(z)$ . The mathematical derivation of equation 4 and further de-  
 173 tails of the parameters  $L_{e,t}$  and  $a_m$  are given in the Supporting Information.

### 174 **2.5 Reference mean event and bed erosion rate**

175 Estimation of the probability of uprooting requires knowledge of the temporal evo-  
 176 lution of a reference mean erosion event above a given threshold. For simplicity, we as-  
 177 sume the threshold  $\xi$  for onset erosion coincides with the discharge that just starts to  
 178 inundate the plant at its elevation,  $\eta_v$  (see Figure 1). Thereby, erosion (and therefore



179 potential uprooting) at a given location can only occur for flood events whose stage reaches  
 180 or exceeds the bed elevation at that location, i.e. for values that lie above  $\xi$ . To deter-  
 181 mine the reference flow event we therefore use the mean of all such events obtained an-  
 182 alytically from Calvani et al. (2019),

$$Q_\xi(t) = Q_0(\xi)e^{-t/\tau_1} \quad (5)$$

183 where  $Q_0$  is the mean of all peak events exceeding the threshold  $\xi$ , and  $\tau_1$  is the inte-  
 184 gral temporal scale of the reference mean event. The reference mean event (red line in  
 185 Figure 1c) ceases at  $T_\xi^+$ , which is the up-crossing period of the signal.

186 From the reference mean discharge event, we then obtain the reference bed erosion  
 187 event associated with the reference flow event as per Calvani et al. (2019):

$$\dot{\eta}(t) = \frac{1}{(1 - \lambda_g)\Delta X} \alpha_{BL} \left( \frac{\left(\frac{Q_\xi(t)}{A\sqrt{SK_s}}\right)^{3/2} S}{D_{50}\left(\frac{\rho_g - \rho_w}{\rho_w}\right)} - \tau_{cr}^* \right)^b D_{50} \sqrt{\frac{\rho_g - \rho_w}{\rho_w}} g D_{50}, \quad (6)$$

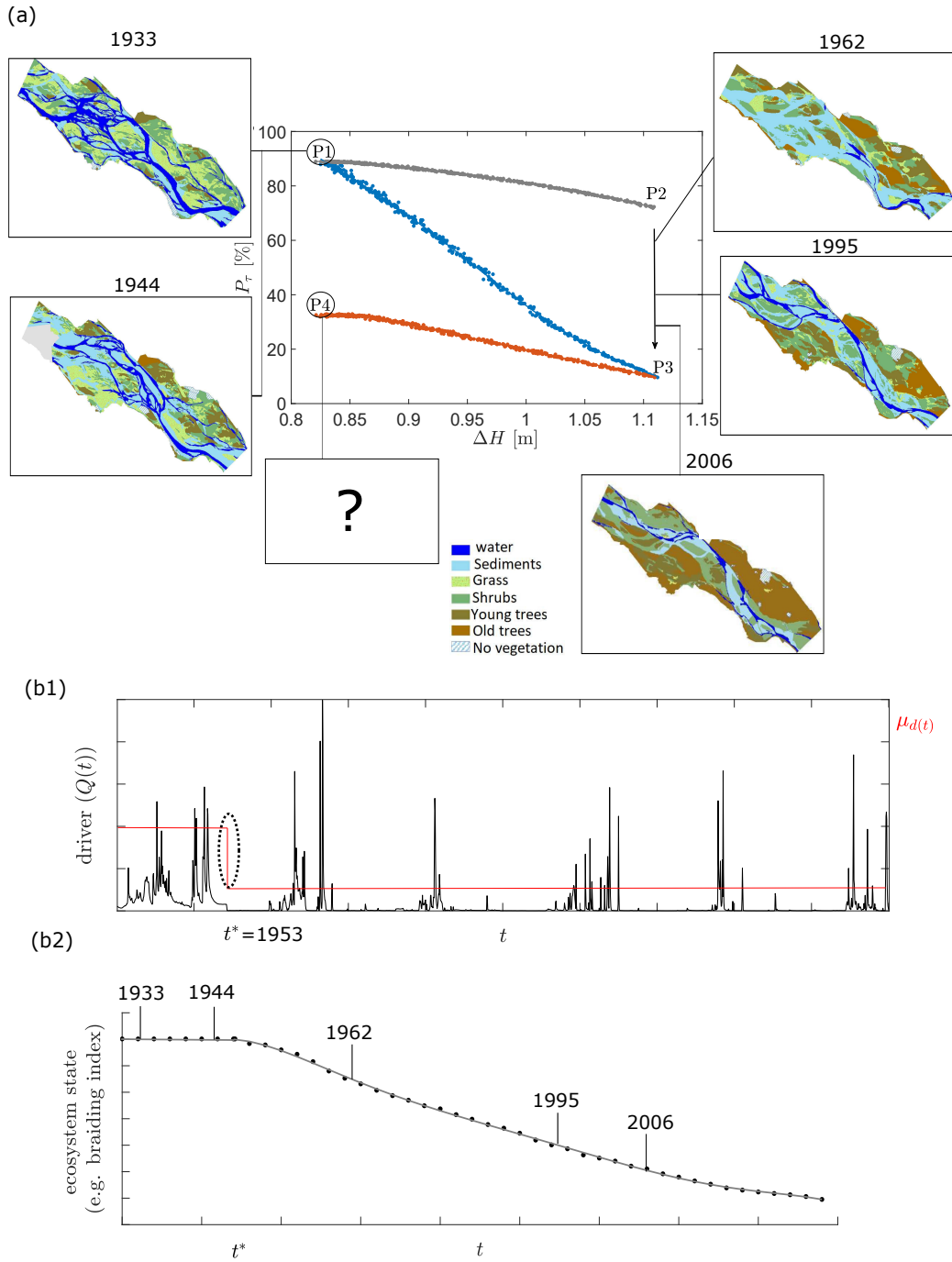
188 where  $\lambda_g$  is the sediment porosity,  $\Delta X$  is the erosion length scale,  $\alpha_{BL}$  is the coefficient  
 189 in the bed-load transport formula,  $A$  is the wet cross-sectional area of the river,  $K_s$  the  
 190 Strickler coefficient of the sediment,  $g$  the acceleration due to gravity,  $\rho_g$  is the density  
 191 of the sediment,  $\tau_{cr}^*$  is the critical Shields parameter, and  $b$  is the exponent in the sed-  
 192 iment transport formula. Equation 6 applies to a point in a generic river section and has  
 193 been obtained by combining the 1D-Exner equation for conditions of net bed erosion (e.g.  
 194 negligible sediment inflow at the point) with a Meyer-Peter and Müller type sediment  
 195 transport relationship. The mean erosion event is depicted by the blue line in Figure 1c.

### 196 **3 Results from model application to an actual case study**

197 The model is applied to the case study of the river Maggia, as it flows through the  
 198 Valle Maggia in Tessin, Switzerland. After impoundment by dams commenced in 1953,  
 199 the river discharge experienced a severe hydrologic shift, which triggered vegetation en-  
 200 croachment and gradual channel narrowing (Ruf et al., 2007; Molnar et al., 2008; Per-  
 201 ona, Molnar, et al., 2009). The SI provides a description of relevant data and the cal-  
 202 culation of all model parameters. Note that dam impoundment led to a decrease in  $\tau_d$   
 203 (from 3.31 to 1.60 d) and  $\lambda_d$  (from 0.22 to 0.05 d<sup>-1</sup>), and to an increase in  $\gamma_d$  (from 23  
 204 to 50 m<sup>3</sup>/s). The product  $\gamma_d \lambda_d \tau_d$  gives the mean flow discharge of the CPP signal  $\mu_d$ .

205 The values obtained for  $\mu_d$  coincide with mean values of the actual hydrographs, which  
 206 are  $16.5 \text{ m}^3/\text{s}$  and  $4 \text{ m}^3/\text{s}$  for the periods 1933-1953 and 1954-2007, respectively. A ta-  
 207 ble listing values assigned to the parameters in the equations presented in Section 2 has  
 208 been included in the SI. Apart from data retrieved from the literature and previous stud-  
 209 ies of the Maggia Valley, values of several parameters (related to plant properties and  
 210 geometry) had to be estimated owing to lack of information. The model satisfactorily  
 211 represents the expected behaviour of the hydrograph, as shown in Figure 2b. During the  
 212 post-dam period only the highest river discharge peaks characterise the hydrograph, un-  
 213 like for the pre-dam period. These peaks correspond to a CPP having higher intensity,  
 214 lower frequency, and lower temporal correlation. The probability of uprooting  $P_\tau$  was  
 215 calculated by numerically integrating Eq.(1) over the duration of the erosion event, and  
 216 plotting the result as a function of increasing  $\Delta H$  (i.e. the difference between plant riverbed  
 217 elevation and mean water stage for increasing hydrograph (down)shifts). Hence,  $\Delta H$  rep-  
 218 represents the driver in terms of hypothetical hydrologic shift severity caused by impound-  
 219 ment.

220 Figure 2a shows the location of the stable statistical equilibrium states (blue points)  
 221 of the river floodplain state (represented by  $P_\tau$ ) for increasing  $\Delta H$ . Pre-dam conditions  
 222 are represented by the point P1, indicating that plants had more than 90% probability  
 223 of being uprooted by the reference mean erosion event of the pre-dam hydrograph. The  
 224 colour-rendered aerial photographs (1933, 1944, colour legend in Figure caption) show  
 225 the floodplain morphology before dams started to operate. Dam operation produced a  
 226 vertical downshift in mean discharge (and water stages) (see Figure 2b), i.e. a sudden  
 227 increase of  $\Delta H$  brought the system to the ‘out-of-equilibrium’ point P2, where plants  
 228 still had the root architecture of pristine conditions, but were suddenly exposed to post-  
 229 dam erosion event scenarios. In this case, the probability of uprooting remained high and  
 230 the image from 1962 shows a floodplain almost without water but with a high braiding  
 231 index. In the post-dam period (point P2), plant roots started to adapt to the lower wa-  
 232 ter table conditions by deepening root biomass and consequentially reducing the prob-  
 233 ability of uprooting. This process was gradual, and it took several years for the flood-  
 234 plain system to reach the point P3 (see images 1995 and 2006), which represents the new  
 235 stable equilibrium for the post-dam hydrological conditions. The same reasoning can be  
 236 repeated for hypothetical milder shifts of the driver, i.e.  $\Delta H$ , thus obtaining the blue  
 237 sequence of stable equilibrium states joining points P1 and P3. The process of discon-



**Figure 2.** a) Uprooting probability,  $P_\tau$ , plotted against  $\Delta H$ , for plant elevation,  $\eta_v = 1.2$  m. The insets show the morphological evolution of the river floodplain in 1933, 1944, 1962, 1995, and 2006. b1) Time series of the driver (flow discharge). Note that the value represented for the mean flow rate,  $\mu_d$ , is offset for illustrative purposes. b2) Time series of the ecosystem state (braiding index). The years illustrated are intended to recall the evolution of the spatial distribution shown in the subplots in Figure a).

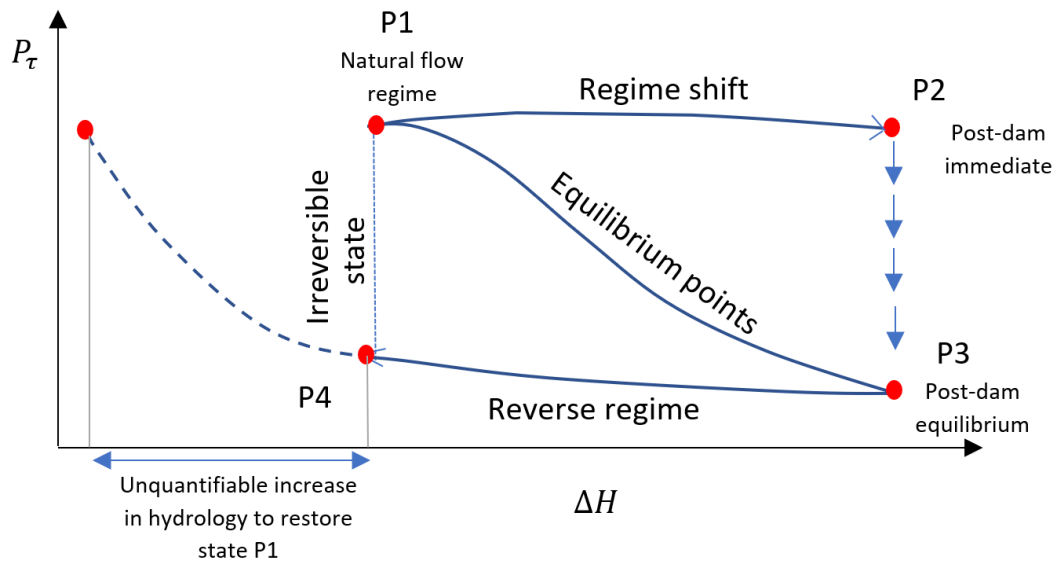
238 nection between the floodplain and the main channel due to channel incision was not con-  
239 sidered here and might lead to two opposite scenarios. For vegetation species able to track  
240 the lowering of the water table, their root biomass may deepen further in soil and the  
241 probability of plant uprooting by flooding events would further decrease. On the con-  
242 trary, vegetation species with low adaptation capability would possibly die and slowly  
243 lead to a non-vegetated system, which is not object of this study. Hence, the first sce-  
244 nario necessarily implies that the value of  $P_r$  in the post-dam period may change when  
245 considering the ability of different plant species to adapt to extreme and sudden drought  
246 conditions. This indirectly explains plant speciation and invasion by species that toler-  
247 ate and/or favor the new conditions.

248 For a system in state P3, hypothetical dam removal and return to the natural flow  
249 regime would imply a sudden reduction in  $\Delta H$  to its original value. The system would  
250 thus jump to the point P4. Notwithstanding that flow erosion events at point P4 are more  
251 frequent and have the same erosion capacity as those at point P1, the deep root system  
252 prevents recovery of the original probability of uprooting, thus explaining the tendency  
253 of the floodplain to maintain its current narrow morphology.

254 Given that the model describes only the stable equilibrium points of the system,  
255 it is nevertheless instructive to consider the expected dynamics throughout the time do-  
256 main (Figure 2b2). Up to time  $t^*$  the system state is at point P1. The state then jumps  
257 from P2 to P3 at  $t = t^*$ , following the hydrologic shift of the driver. From point P2 on-  
258 ward, the probability of uprooting declines, presenting a temporal picture as to how the  
259 system states transition from state P2 to P3. The time lapse over which the curve de-  
260 creases represents the ‘relaxation time’ of the system (in other words, the time required  
261 by the ecosystem state to adapt to the new equilibrium). A sensitivity analysis concern-  
262 ing the most relevant input parameters is enclosed in the Supporting Information. An  
263 important result of the sensitivity analysis emerges when the grain size distribution is  
264 maintained constant between pre- and post-dam periods. This preserves the retention  
265 capacity of the soil and hence the zone favorable for root growth. For a plant elevation  
266 equal to 1.2 m, this results in a value of uprooting probability at the stable equilibrium  
267 point P3 that is four times higher than that in Figure 2a). Maintaining sediment con-  
268 tinuity in the post-dam period would thus help vegetation control.

#### 269 4 Discussions, implications and conclusions

270 The proposed model has shed light on the type of transitions and temporal irre-  
 271 versibility that potentially affect a river floodplain following hydrological regime shifts.  
 272 Figure 3 summarizes this process. The curve between P1 and P3 represents the statis-  
 273 tical (stable) equilibrium points at which the probability of uprooting follows the pro-  
 274 gressive adjustment of the root system to the imposed hydrological conditions. In other  
 275 words, this curve represents a succession of steady states resulting from a quasi-static  
 276 change in hydrologic conditions. Hence, this segment of the curve can be compared to  
 277 quasi-static transformations occurring in thermodynamics, where the system always re-  
 278 mains at equilibrium. The inability of the system to recover its pristine conditions, e.g.  
 279 such as returning from point  $P_4$  to point  $P_1$  may be ascribed to the development of deep  
 280 roots as they track the changing water table conditions. However, the model does not  
 281 explain the dynamical origin of such irreversibility, causing  $P_4$  to also be a stable equi-  
 282 librium point. This picture appears plausible for water tolerant plants, such as riparian  
 283 plants. Their roots may tolerate long periods under soil saturated conditions. Hence, in  
 284 returning to the original natural flow regime, new deep roots would no longer form, and  
 285 existing roots might not die off but instead persist in the soil for the entire life time of  
 286 the plant. Conversely, plant species not tolerating submersed conditions would simply  
 287 die off and be replaced by others, thus delaying the return to pristine conditions (tem-  
 288 porary irreversibility) for which  $P_4$  would be out-of-equilibrium.



**Figure 3.** Detailed sketch of the different regime transitions of the ecosystem state.

289 Similar dynamics have also been documented in the literature, but have never been  
 290 modeled quantitatively. For instance, Auble et al. (2007) found that vegetation recov-  
 291 ery following removal of a dam is complex and does not follow a reversal response, lead-  
 292 ing to the necessity for river restoration intervention. Hence, if dams were to be removed,  
 293 vegetation coverage and community would not be much affected, leading to a long-term  
 294 impact on vegetation succession, especially in systems with low sediment transport (Hobbs  
 295 et al., 2009). The removal of invasive species that often colonise terraces and benches  
 296 of dammed rivers is extremely complex (Foley et al., 2017), making the process of rein-  
 297 troduction of native species difficult to achieve (Orr & Stanley, 2006; Tullos et al., 2016).  
 298 For instance, the vegetation response following dam removal on the Souhegan River in  
 299 Merrimack (USA) merely consisted of changes to certain herbaceous plants growing clos-  
 300 est to the river channel and in the off-channel wetland (Lisius et al., 2018). Furthermore,  
 301 intensive establishment of mature vegetation during the post-dam period would increase  
 302 riverbank stability, thus also making it difficult for the river morphology to re-establish  
 303 its natural pattern (Shafroth et al., 2002). This was also documented by Pearson et al.  
 304 (2011), who stated that the process of morphological recovery of the Souhegan River has  
 305 been influenced by the segmentation of alluvial and non-alluvial sections that had been  
 306 marked by establishment of vegetation on the channel banks during impoundment. Again  
 307 this, in some measure, is satisfactorily explained by the reduced probability of uproot-  
 308 ing by flow caused by plant root hydrotropic response. Shafroth et al. (2002) also sug-  
 309 gested that the persistent occurrence of transient phases after dam construction has a  
 310 determinant impact on the life duration of mature vegetation (e.g. forest), which could  
 311 persist for even more than a century. In practice, mature vegetation cannot easily be re-  
 312 moved by flow erosion processes and return to point P1 may only happen for erosion events  
 313 of very large return periods or by mechanical action (e.g., restoration). At this point we  
 314 speculate that a reasonable model representing such an out-of-equilibrium system dy-  
 315 namics could have the form

$$\frac{dP_\tau}{dt} = f_1(P_\tau) - f_2(1 - P_\tau), \quad (7)$$

316 where  $f_1(P_\tau)$  represents the positive tendency of the system to reduce the root biomass,  
 317 which would facilitate uprooting. Conversely,  $f_2(1 - P_\tau)$ , represents the tendency of the  
 318 system to modify and increase the root biomass in order to decrease the uprooting prob-  
 319 ability, thus favoring plant survival. Clearly, as  $P_\tau$  depends on the parameter  $\Delta H$ , then

320 the (likely nonlinear) form of  $f_1$  and  $f_2$  should be such that the equation  $f_1(P_\tau) - f_2(1 -$   
321  $P_\tau) = 0$  describes all the equilibrium points (stable and unstable). The fact that the  
322 stable equilibrium points of our model joining  $P_1$  and  $P_3$  all lie on a continuous curve  
323 suggests that non-reversibility may be ascribed to the presence of other stable equilib-  
324 rium points (e.g.,  $P_4$ ) for the general ecosystem dynamics (May, 1977) rather than to  
325 a catastrophic-like mechanism. Such multiple points would represent the capability of  
326 water tolerant plants to develop and maintain alive deep roots that tolerate anoxia when  
327 conditions are reversed.

328 Our sensitivity analysis (see SI) has also shown that the effective particle size of  
329 fine sediment plays an important role in uprooting probability. Hence, replenishment of  
330 fine sediment could offer a potential way of maintaining the uprooting percentages for  
331 post-dam conditions at levels closer to those for pre-dam conditions. Such a goal could  
332 be achieved for instance by inducing artificial floods, a well-established technique used  
333 to reduce river morphological changes after dam impoundment. In the present applica-  
334 tion, artificial flooding should be controlled to ensure that the increase in frequency of  
335 peak events would bound the erosion rate so as to hinder river narrowing and incision,  
336 and stream-bank erosion (Stähly et al., 2019). This strategy could also be adopted to  
337 reduce the accumulation of fine sediment upstream of a dam, whose presence consider-  
338 ably limits the storage capacity of the associated reservoir. The input of fine sediment  
339 would not only benefit the shape of the river but also its biodiversity, thus preventing  
340 the riparian system from drifting to alternative states (Arheimer et al., 2018). The ar-  
341 tificial flooding strategy appears to be promising in terms of effectiveness. This is also  
342 confirmed by results obtained by Perona, Camporeale, et al. (2009), who used a lumped  
343 model to predict that adding an artificial disturbance each year would lead to increases  
344 of 10% in both sediment and water area in the Maggia River reach considered herein.

345 To conclude, plant root profile can affect riparian ecosystem resilience to pressures  
346 such as hydrological alterations and flow erosion processes. Our results suggest that ini-  
347 tial state conditions may only be restored after impoundment through the occurrence  
348 of an hydrologic event of a much larger return period or by the clearance of riparian veg-  
349 etation through deforestation and river restoration. This novel combined method can  
350 identify and complement dam regulation strategies and promote sustainable solutions  
351 to preserve terrestrial and aquatic ecosystems before planetary boundaries are reached  
352 (Steffen et al., 2015).

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No new data has been used for this research. Part of the data used to implement the model is available in the following in-text data citation reference: Ruf (2007). The aerial images illustrated in Figure 2a) can be found online on Mendeley Data (<http://dx.doi.org/10.17632/czjwgb9jpb8.1>).

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