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Why do plants respond differently to hydropeaking disturbance? A functional approach

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ABSTRACT

Hydropeaking, which refers to large and rapid flow fluctuations caused by the turning on or off of hydro-turbines to generate electricity, is a topic of growing interest due to its impact on fluvial ecosystems. To date, most hydropeaking studies have focused on the impact of this hydropower operation mode on invertebrate and fish communities, but little attention has been paid to its impact on riverine communities and how functional traits may make plants resistant to hydropeaking. We determined how a set of 32 plant functional traits are expressed in 14 riverine species, and how such expression affects their capacity to cope with common sources of hydropeaking disturbance (i.e., inundation, water stress, and rapid water fluctuations linked to up-ramping and down-ramping hydropeaking operations). We categorized species as "resistant", "partially-resistant" or "vulnerable" based on the capacity of each trait to confer resistance to hydropeaking disturbances. Two indexes (i.e., "hydropeaking plant species resistance index" (HPPR) and "hydropeaking plant community resistance" index (HPCR)) were developed to rank our species based on their tolerance to hydropeaking and to determine which were the commonest "hydropeaking-resistant" traits within the plant community. Our results evidenced that coincidences in trait expression are common between species with similar growth forms. Grasses were the most resistant to inundation and water fluctuations, whereas trees and shrubs were so to water stress. In general, forbs were rather vulnerable to all the hydropeaking disturbances. The differences observed between the resistance expected and the obtained for several plant species illustrate the importance of our approach to fine-tune the diagnostics on plant species vulnerability to hydropeaking.. We believe this initiative will help river managers to detect suitable species to restore rivers affected by hydropower production.

1. Introduction

Hydropeaking (HP) is a hydropower generation technique that involves a frequent and rapid variation in flow over short periods of time, many times sub-daily, to respond to rapidly changing electrical demands and prices (Young et al., 2011). The use of HP to generate electricity translates into a strong alteration of river hydraulics (i.e., changes in water level, flow velocity, turbulence, bed shear stress). Such hydraulic changes can in turn modify river habitat conditions and create an unfavorable environment for fluvial organisms, including riverine plants. To date, the degradation of plant communities inhabiting river margins exposed to HP has received only minor attention (Gorla et al., 2015; Bejarano et al., 2018; Bejarano et al., 2020; Baladrón et al., 2022). This is unfortunate given the role of riverine plants in maintaining fluvial ecosystem functioning (Naiman and Decamps, 1997; Bejarano et al., 2018) and environmental river services.

Fluvial processes triggered by HP regimes (i.e., inundation, water flow restrictions, fast water currents and water quality changes) can jeopardize seed germination, establishment, growth, and long-term survival of riverine plants (see Baladrón et al., 2022). Inundation events during HP may keep riverine plants under submergence for long periods of time affecting key processes involved in photosynthesis (i.e., light interception and leaf gas exchange) and, eventually, leading to slow gas exchange, anoxia, and the accumulation of toxic compounds in the rhizosphere and plant tissues (e.g., Greenway et al., 2006). Conversely, rapid water-level fall (i.e., down-ramping) rates can have a strong impact on seed germination and plant survival; some operations may restrict water flow downstream a hydropower dam to the point that plants may experience high evapotranspiration rates and risk of desiccation, especially when soil moisture deficits occur over a prolonged

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period of time (Bejarano et al., 2018). In addition, fast currents during the up-ramping and the peaking operation stages can favor the erosion of river banks where riparian plants stand; on the other hand, during down-ramping stages, sediments transported in water are deposited, resulting in plants (especially those at the bottom of the river channel) being coated in silt, or partly to completely buried (Bejarano et al., 2018). Drag and lift mechanical forces induced by fast and turbulent water flow during phases of rapid rise in discharge may also cause physical injury, breakage and plant uprooting (e.g., Madsen et al., 2001). Finally, increasing turbidity and changes in water temperature, concentration of oxygen, suspended matter, nutrients, and pollutants have been associated with HP, with potentially important consequences for riverine plants (Weitkamp, 2008; Bornette and Puijalon, 2011; Riis et al., 2012).

The fluvial processes described above are common to riparian zones in general, implying that riparian plants have traits to cope with some levels of HP (Catford and Jansson, 2014). Functional traits, which can be defined as morphological, anatomical, biochemical, physiological and phenological features or mechanisms of resilience measurable at the individual level (Violle et al., 2007) can confer plants different degrees of resistance to environmental constraints (see Valladares et al., 2007) and modulate plant specieś responses to HP (Bejarano et al., 2018). But this is only in theory. The erratic and abrupt variations of flow under HP create habitats that are both frequently inundated and exposed (Bejarano et al., 2018). Such conditions may exceed plant resistance conferred by traits since it is very unlikely for plant species to develop functional strategies to cope simultaneously with flow regimes that combine long periods of flooding, frequent water level fluctuations, and intense drought events (Niinemets and Valladares, 2006; see Baladrón et al., 2022). Therefore, it is key to understand how the expression of multiples traits can help plants to withstand the ample variation of fluvial conditions imposed by HP, and which species are closer to meeting all the “hydropeaking-resistant” requirements (i.e., a combination of adaptations to submergence, drought and hydraulic mechanical forces (e.g., Maberly and Spence, 1989; Baladrón et al., 2022) to successfully complete their life cycle under HP disturbance. HP is gaining momentum worldwide due to its excellent capabilities for fast regulation with changing demand, and future energy scenarios may strongly rely on this renewable energy to supply power to industry and public consumption (see Forseth and Harby, 2014). The expected increase in the use of hydropower may result into a degradation of river resources, including its vegetation. In this regard, it is key to provide river managers with assessment frameworks aimed at analyzing the impact of existing or planned HP operations on riverine plants, ultimately guiding sustainable operations of HP plants and restoration of impacted rivers. To date, a systematic approach to assess riverine plant resistance to the most common disturbances triggered by HP operations (i.e., inundation, fast water drawdown and rapid water fluctuations) does not exist. To cover this knowledge gap, we present the first “hydropeaking-resistant” functional trait filtering method aimed at determining the vulnerability of single taxa and riverine plant communities to HP. The methodology includes two novel HP indices that are used to score and rank riverine plant species based on their functional traits, from the most resistant to HP, to the most vulnerable. Analyzing the impact of HP on plants from a trait-based perspective is more informative than predicting plantś response to HP according to “ecological affinities” (i.e., data that describe the general response of a species to an environmental variable, habitat, or resource (e.g., drought or flooding tolerance, soil moisture); Palmquist et al., 2017). This is true because plants share traits among different floristic regions (Díaz et al., 1998; Bejarano et al., 2016), whereas “ecological affinities” often integrate multiple traits, potentially obscuring the functional reasons why a riverine plant may perform better or worse in HP systems.

Fourteen riverine plants occupying distinct belts in free-flowing rivers depending on their flood tolerance (i.e., from higher to lower elevations on the riverbank: riparian trees, amphibious and aquatic species) were passed through our filtering method. We expected that the method will predict species resistance to HP based on their traits, and determine which traits contribute the most to preserve the integrity of the overall species community against HP. Specifically, we wanted to check whether species resistance predictions obtained with our trait-based method are in agreement with previous experimental results on plant performance under HP (see Baladrón et al., 2022; Fig. 1), and with the widespread expected responses according to species ecology and habitat requirements (e.g., preferences for water).

Additionally, we explored relationships and coincidences between trait expression (morphological or physiological attributes) and groups of plants with similar growth form to determine whether specific plant growth forms are more likely to be resistant to specific forms of HP disturbance. We expect to find more coincidences in the expression of “hydropeaking-resistant” traits between species belonging to the same growth form group than between species belonging to different groups. For instance, there is evidence that some sedges and forbs (e.g., *Comarum palustre*, *Calamagrostis purpurea*) share traits that confer strong resistance to submergence and water fluctuations (e.g., presence of aerenchyma tissue and radial O2-loss barriers to prevent oxygen diffusion outward from the plant; Manzur et al., 2015) and the ability to resprout after disturbance (e.g., Klimešová et al., 2018; Baladrón et al., 2022). This is in contrast to riparian plants (i.e., shrubs and trees growing on upper riverbank sections), which are particularly sensitive to unnatural highly fluctuating flows (Johansson and Nilsson, 2002). Conversely, riparian shrubs and trees are expected to present higher resiliency to dry conditions compared to other plant growth forms lacking woody tissues, thick leaves, and other traits helping plants to prevent hydraulic failure during drought (McDowell et al., 2008). We also expect that plant growth forms presenting a combination of adaptations to submergence and drought (e.g., amphibious plants such as *Carex acuta* and *Carex vesicaria*; Maberly and Spence, 1989) may counterbalance the negative effects of soil waterlogging and plant submergence during maximal water-level phases, but also minimize the risk of desiccation during phases of low water levels.

2. Materials and methods

2.1. Method overview

We selected three relevant hydrological alterations linked to HP (i.e., flooding, water stress drawdown, and water fluctuations) capable to impair plantś performance (e.g., germination, plant survival and growth rates, biomass production, metabolic processes; see Table 1).

Fourteen species commonly found along riparian areas (i.e., *Alnus incana* (Ai), *Agrostis capillaris* (Ac), *Betula pubescens* (Bp), *Calamagrostis purpurea* (Cpu), *Carex acuta* (Ca), *Carex vesicaria* (Cv), *Comarum palustre* (Cpa), *Filipendula ulmaria* (Fu), *Galium palustre* (Gp), *Ledum palustre* (Lp), and *Pinus sylvestris* (Ps), *Rosa majalis* (Rm), *Salix myrsinifolia* × *phylicifolia* (Smp) and *Viola palustris* (Vp)) and which represent a variation in traits were selected for trait-based characterization. The performance of these species under HP was previously studied by Baladrón et al. (2022) (Fig. 1), which allows for establishing a comparison between previous experimental results and the theoretical response of the species to HP based on their traits addressed here.

Attending to their potential capability to modulate species response to HP, 32 functional traits (19 morpho-anatomical and 13 physiological traits) and the different forms or “categories” in which a specific trait can be expressed (i.e., trait attributes) were obtained from Baladrón et al. (submitted), who performed a comprehensive literature review (see complete trait list in sub-section 2.4). A functional characterization of each species was performed and summarized under “radar-type” figures (see section 3.2.; Fig. 4). These characterizations constituted the theoretical basis to determine the degree of resistance to HP of each species.

Trait attributes assigned to each species were reclassed into three HP

Species	PGF	Habitat and Ecology	Performance under HP (Baladrón et al. 2022)		
			F	WF	WS
Alnus incana	Tree	*Tolerant of poor, wet soil (Hultén and Fries 1986); grows vigorously along creeks, rivers, and lake shores (Brisson et al. 2006).*			
Agrostis capillaris	*Grass*	*Very resistant to drought (Chytrý et al. 2021); more often found on dry ground than in moist places (Maczey 2016) but also can be abundant on poorly drained and damp soils nearby wetlands (Stace 1997).*	*na*	*na*	*na*
Betula pubescens	*Tree*	*Preference for well-drained soils, but can also survive on wet, poorly aerated soils; it grows nearby watercourses and areas with ponded water (Hultén and Fries 1986).*			
Calamagrostis purpurea	*Grass*	*Mainly on constantly moist or damp soils, but can tolerate water-saturated, badly aerated soils (Chytrý et al. 2021). Confined to wetlands, wet meadows, damp woodlands, marshes, mire margins and lakeshores (Conert 1998).*			*na*
Carex acuta	*Grass (sedge)*	*Grows on shallow water or wet ground at the edges of rivers, streams, canals, lakes and ponds, swamps, ditches and marshlands; tolerant to frequent flooding (Preston et al. 2002; Hultén and Fries 1986).*			*na*
Carex vesicaria	*Grass (sedge)*	*Wet habitats (e.g., where the water table lies close to or above the soil surface); it is found by lakes, rivers, streams, ponds, marshes, swamps, ditches, wet meadows and depressions (Preston et al. 2002).*			*na*
Comarum palustre	*Forb*	*Often growing in soaked, poorly aerated soils (Chytrý et al. 2021); present in wet marshes, fens, bogs and swamps (see Ertter 2012).*			*na*
Filipendula ulmaria	*Forb*	*Occupies wetter, peatier soils, especially in upland areas; characteristic of sites where water levels fluctuate, but absent from permanently waterlogged ground (Grime et al. 1988; Hultén and Fries 1986).*			
Galium palustre	*Forb*	*Often growing in soaked, poorly aerated soils (Chytrý et al. 2021). Present in wetland habitats, including wet meadows, swamps, marshes, fens, ditches, ponds and lakesides (Grime et al. 1988).*			
Ledum palustre	*Shrub*	*It grows nearby depression wetlands, but not in wet soil (e.g., upland areas not frequently submerged, soil surfaces usually above the water table (Chytrý et al. 2021).*	*na*	*na*	*na*
Pinus sylvestris	*Tree*	*Low flooding tolerance (Glenz et al. 2006); it survives in moist sites and wetlands, but its growth rate and vitality is strongly reduced in extensively moist conditions (Repo et al. 2016). Tolerates dry conditions (López Gonzalez 2001).*			
Rosa majalis	*Shrub*	*Preference for soils of average moisture, missing on wet soils; tolerant to occasional flood (Chytrý et al. 2021). Resistant to lack of moisture and droughts (Solomentseva et al. 2020).*	*na*	*na*	*na*
Salix myrsinifolia x phylicifolia	*Tree/shrub*	*Mainly on constantly moist or damp soils, but can tolerate water-saturated, badly aerated soils (Chytrý et al. 2021). Grows on damp rocky ground, riverbanks and lake shores (Hultén and Fries 1986).*			
Viola palustris	Forb	*Grows in humid surfaces (e.g., bogs, marshes, wet heaths and meadows), often soaked, poorly aerated soils (Chytrý et al. 2021; Hultén and Fries 1986).*			*na*

Fig. 1. Plant species selected for trait-based characterization. A general description of each taxon is provided, including plant growth form (PGF), their occurrence in habitats, main requirements for moisture and drought/flooding tolerance, and their performance under HP disturbance (F = Flooding; WF = Water fluctuations; WS = Water stress); see Baladrón et al. 2022). The term "na" indicates that information is not available for a given species.

categories: "resistant", "partially-resistant" and "vulnerable". Although plant resistance may either rely on avoidance or tolerance elements and mechanisms (i.e., avoidance refers to traits that help plants to resist adverse conditions by preventing the deleterious effects of these conditions whereas tolerance consists in traits that enable plants to endure adverse conditions (Fitter and Hay, 2002; Puijalon et al., 2011), we use the term "resistant" indistinctly to refer to plants capable either to avoid or tolerate HP disturbances. On the contrary, the term vulnerable will refer to plants without avoidance or tolerance elements and mechanisms to successfully counterbalance the negative effects of HP. Trait attributes conferring species a strong advantage under HP (e.g., well-developed adventitious roots to avoid anoxia under submergence) were coded as "resistant" (green color); when a trait attribute conferred to the species only a moderate resistance to HP, it was coded as "partially-resistant" (orange color). The capacity of moderately deep-rooted systems to access water under dry conditions is an example of a trait attribute "partially-resistant" to HP water stress; moderately deep-rooted plants can absorb more water from deeper soil layers than shallow-rooted plants, but less than plants with very deep roots. Finally, when a trait attribute did not provide protection to the species against HP disturbance (e.g., woody stems make plants vulnerable to mechanical forces associated with HP fast water-level fluctuations), it was coded as "vulnerable" (red color).

With the functional reclass, "traffic-light type" summary figures were generated to visualize the resistance or vulnerability of each species to flooding, water stress and water fluctuations. Individual resistances and

Table 1
Main consequences resulting from HP derived hydrological alterations affecting plant performance ().

Hydrological alterations	Changes triggered in the river environment	Consequences for vegetation
Flooding	Rapid light attenuation	Reduced biomass production, difficulties to regenerate plant organs (e.g., leaves and absorbing roots).
	Slow gas difussion	Photosynthesis and respiration impairment, inhibition of root formation and branching, limited growth of existing roots and mycorrhizae.
	Anoxia	Cell acidification, reactive oxygen species (ROS) generation, low ATP production (oxidative phosphorylation disruption), depletion of plant carbohydrate reserves, impairment of plant functions (e.g., stomatal opening, photosynthesis, water and mineral uptake, hormonal balance).
	Accumulation of toxic compounds	Impaired physiological and plant biochemical reactions, breakdown of cell membranes.
Water stress	Soil moisture deficits Water shortage causing water stress	Reduced growth and vigor, wilting, inhibition of seed germination
Water fluctuations	Increase in drag and lift mechanical forces	Physical injury, biomass loss, breakage and uprooting of plants, limited seed germination
	Erosion during up-ramping and peak flow stages	Loss of riparian substrate, plant uprooting, biomass loss due to impact of river substrate materials (e.g., sand, gravel, pebbles).
	Sediment deposition during receding discharge	Plants coated in silt or buried, soil surface clogging, limited seedling establishment and survival.

adapted from Bejarano et al. 2018

vulnerabilities conferred by the 32 traits were integrated using two indices: 1) an "HP plant resistance index" (HPPR) to determine the capacity of the 14 selected species to withstand HP, and 2) an "HP community resistance index" (HPCR) to assess the dominance of trait attributes conferring resistance, and therefore their contribution in protecting the plant community as a whole against HP (see index description in sub-sections 2.2. and 2.3).

Additionally, to measure trait attribute resemblance between plant species, we calculated a similarity coefficient index (i.e., counted the number of trait attribute coincidences between each pair of species and divided it by the total number of functional traits). To aid visualization, the resulting similarity coefficients (expressed as percentages) where gathered in a figure, and trait expression relationships between groups of plants with similar/ different growth forms were explored.

2.2. HP plant species resistance index (HPPR)

The purpose of HPPR was to assess the capacity of each plant to cope with flooding, water fluctuations, and water stress based of the expected degree of resistance conferred by each trait against each of the three HP disturbances. Species falling under each functional category would receive a score (i.e., resistant, partially-resistant, and vulnerable species received two, one and zero ranking points, respectively). Afterwards we combined all the individual trait ranking points and obtained a single score (HPPR, Eq. (1)).

$$\text{HPPR} = ((Ri/NT)\,\text{x}\,2) + ((Pi/NT)\,\text{x}\,1) + ((Vi/NT)\,\text{x}\,0) \tag{1}$$

where:Ri = number of traits conferring resistance against HPPi = number of traits conferring partial resistance against HPVi = number of traits conferring vulnerability against HPNT = total number of traits evaluated as resistant, partially-resistant, or vulnerable to HP

HPPR values ranged between 0 (extremely vulnerable to HP) and 2 (extremely resistant to HP); species that scored approximately 1 are expected to be partially-resistant to HP. HPPR values were calculated separately for each HP disturbance.

2.3. HP plant community resistance index (HPCR)

As opposed to HPPR, HPCR is aimed at assessing the contribution of each single trait to protect the integrity of the overall riverine plant community; the more common a "hydropeaking-resistant" trait is within the community, the more relevance it will have in protecting it against HP. To test the index, we have considered our 14 selected plants as a whole riverine plant community. HPCR follows the HPPR procedure: we combined the ranking points scored by each species for a given trait (e.g., scores of the 14 species for leaf cuticle thickness), and obtained a single value (HPCR, Eq. (2)).

$$\text{HPCR} = ((Ri/Nsp)\,\text{x}\,2) + ((Pi/Nsp)\,\text{x}\,1) + ((Vi/Nsp)\,\text{x}\,0) \tag{2}$$

where:Ri = number of times that a trait was expressed as "resistant" against HP within the plant communityPi = number of times that a trait was expressed as "partially-resistant" against HP within the plant communityVi = number of times that a trait was expressed as "vulnerable" against HP within the plant communityNsp = number of species within the plant community; each species will express a trait as capable to confer resistance, partial resistance or vulnerability against HP

HPCR values ranged between 0 (a functional trait that makes the community extremely vulnerable to HP) and 2 (a trait that confers the community an extremely high resistance to HP); traits that scored approximately 1 are expected to confer resistance to approximately half of the species in the plant community.

2.4. Selected traits and the advantages they confer against HP

The 32 functional traits were selected for their capacity to adapt plants to the stress imposed by submergence and soil waterlogging derived from flooding, mechanical forces exerted by flow discharges of high magnitude and rapid water fluctuations, and drought. These traits constitute morphological and physiological mechanisms and evolutionary adaptations that can potentially help predict the resistance/ vulnerability of riverine plants to HP. These traits were: Plant growth-form (PGF), Shoot growth-form (SGF), Woodiness (WD), Leaf cuticle thickness (LCT), Leaf shape (LSH), Leaf size (LSI), Leaf consistency (LCON), Leaf anatomy (LAN), Leaf mass per leaf area (LMA), Rooting depth (RDE), Root morphology (RMO), Shape reconfiguration (SHRE), Suberin barriers (SB), Below-ground organs (BGOs) and root mass allocation, Plant height (PHE), Leaf venation network (LVN), Presence of chloroplasts in epidermis (PCHE), Location of stomata (LSTO), Presence of trichomes (PTRI), Leaf persistence (LPER), Resprouting ability (RA), CO2 concentrating mechanisms (CO2-CM), Antioxidants mechanisms (AM), Presence of coleoptile (PCOL), Seed germination (SG), Stomatal control (STOC), Non-structural carbohydrates carbohydrates and flooding acclimation responses (NSC), Plant ventilation systems (PVS), Adventitious roots (ADV), Chloroplasts movement under changing light intensities (CHMOV), Corticular photosynthesis (COPH), Mycorrhizal symbioses (MS). All traits and their respective categories are summarized in Baladrón et al. (submitted).

2.5. Data management and results visualization

HPPR and HPCR scores (calculated for each species under each type of HP disturbance) were used to rank species based on their tolerance to flooding, water fluctuations, and water stress. A green-to-red gradient of colors was defined to easily visualize the degree of resistance of each species to disturbance, from the darkest green corresponding to the highest scores (i.e., the most resistant species), to the darkest red corresponding to the lowest scores (i.e., the most vulnerable species). The same criterion was used to visualize which were the most common "hydropeaking-resistant" traits within the plant community, and therefore which of them contributed the most in protecting its integrity against flooding, water fluctuations, and water stress resulting from HP (see Fig. 2).

3. Results

3.1. Relationships between trait attribute expression and plant growth form

By analyzing the classification of our 14 species under any of the trait attributes defined under each functional trait by Baladrón et al. (submitted), we found that the number of coincidences in trait attributes were higher between groups of plants with similar growth form. Forbs (Fu, Gp, Vp, Cpu and Cpa) and grasses (Ca, Cv and Ac) shared between 47% and 94% of trait attributes; tree species (Ps, Bp, Ai and Smp) expressed between 50% and 75% of the traits in the same fashion, and shrubs (Rm and Lp) did so in 50% of the traits. Trait attribute coincidences between shrubs and tree species ranged between 31% and 56%. On the other hand, coincidences between herbaceous species (i.e., forbs and grasses) and riparian plants (i.e., shrubs and trees) were more reduced ranging between 41% and 13%. The species that shared the highest amount of trait attributes were Ca and Cv (94%), Cpu and Ac (91%), Gp and Vp (81%), and Ai and Smp (75%); the lowest percentages of shared attributes were found between Ps and most herbaceous species, and between Lp and grasses. Ai and Ca (19%), and Lp and Cpu (16%) also shared a very limited number of trait attributes (Fig. 3). Trait attributes characterizing each of the 14 selected species are shown in Fig. 4.

3.2. Species resistance to HP disturbance

Three species (Ai, Ca, Smp) showed high (or moderately-high) resistance to the three HP disturbances evaluated. Seven species showed vulnerability to one source of disturbance (i.e., Cv, Ac, Cpu, Cpa and Gp to water stress; Lp and Ps to flooding). Two species may be compromised by two sources of disturbance (i.e., Bp may be vulnerable to flooding and water fluctuations, and Fu may be so to water fluctuations and water stress). The remaining two species (Vp and Rm) may not be capable to withstand any of the three disturbances analyzed (see Figs. 5, 6, 7 and 8).

Species that showed high or moderately-high resistance to flooding were Cv, Ca, Ac, Ai, Cpu, Cpa, Gp, Smp and Fu ($1.28 > HPPR > 1.03$). >50% of traits in Cv, Ca, Cpu and Ac were categorized as fully resistant to flooding. In several species (i.e., Ai, Smp, Cpa and Fu), the contribution of traits conferring partial-resistance to flooding compensated low percentages of resistant traits; in such cases, the combined number of resistant and partially-resistant traits was large enough to raise their HPPR above 1 ($1.21 > HPPR > 1.03$). Five species (Vp, Bp, Ps, Rm and Lp) where vulnerable or moderately-vulnerable to flooding ($0.97 > HPPR < 0.66$; between 45 and 55% of traits categorized as vulnerable). Moreover, approximately 50% of traits in Ps, Rm and Lp made these three plants highly vulnerable to flooding ($0.76 > HPPR > 0.66$) (Figs. 5 and 6).

Four species (Lp, Smp, Ps and Ai) showed a high resistance to water stress ($1.58 > HPPR > 1.28$). >50% of the traits in Lp, Smp and Ps were categorized as fully resistant to water stress. In three species (i.e., Bp, Rm and Ca), traits conferring partial-resistance to water stress contributed to raise their HPPR scores above 1 ($1.04 > HPPR > 1.00$). Seven species (Ac, Cv, Cpu, Gp, Fu, Vp, Cpa) were vulnerable to water stress ($0.96 > HPPR > 0.6400$; between 44 and 56% of traits categorized as vulnerable), with Vp and Cpa being the most vulnerable species ($0.67 > HPPR > 0.64$) (Figs. 5 and 7).

Species that showed high or moderately-high resistance to water

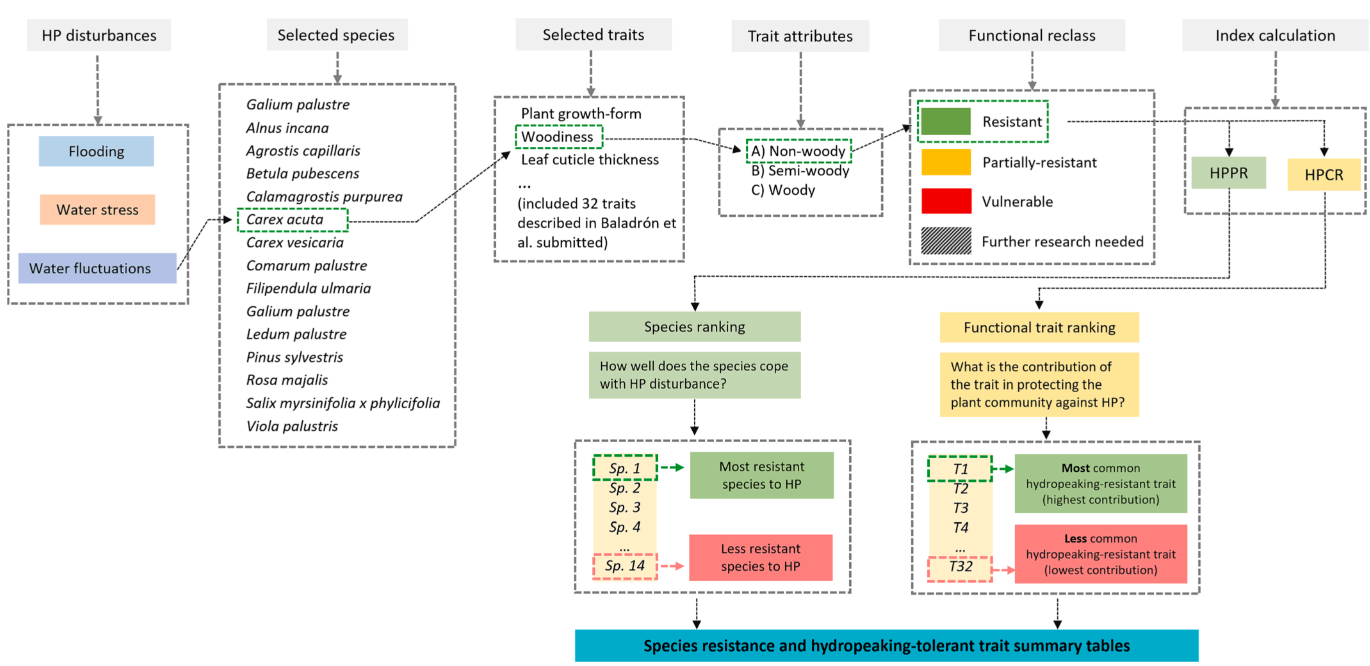

Fig. 2. Methods summary. Example of how species resistance and functional trait relevance for HP resistance were determined. *Carex acuta* (Ca) is evaluated for resistance to water-level fluctuations (WF) based on how flexible its organs are (Woodiness). Ca has non-woody tissues and therefore it can bend and reconfigure its shape with increasing flow velocity; as a result, Ca may not experience uprooting neither biomass loss due to WF, and can be classified as resistant to WF for the trait "Woodiness"). Trait attributes are reclassed as resistant = 2 points; partially resistant = 1 point; and vulnerable = 0 points. We incorporate all the values corresponding to the 32 selected traits (see Baladrón et al. submitted) into the calculation indexes (i.e., HPPR and HPCR); the scores obtained for the two indexes allow us establishing a HP species-resistance ranking and a "hydropeaking-resistant" trait ranking for the three sources of disturbance analyzed (i.e., flooding, water fluctuations and water stress).

	Ps	Bp	Fu	Ai	Ca	Cv	Gp	Vp	Lp	Cpu	Ac	Rm	Cpa	Smp
Ps		0.50	0.16	0.56	0.19	0.19	0.22	0.19	0.53	0.25	0.22	0.38	0.16	0.50
Bp			0.50	0.63	0.28	0.25	0.34	0.38	0.38	0.31	0.31	0.56	0.41	0.47
Fu				0.41	0.44	0.44	0.63	0.69	0.25	0.41	0.44	0.50	0.63	0.44
Ai					0.19	0.25	0.31	0.25	0.38	0.31	0.34	0.31	0.31	0.75
Ca						0.94	0.47	0.50	0.16	0.63	0.63	0.28	0.47	0.22
Cv							0.50	0.50	0.13	0.69	0.66	0.22	0.53	0.25
Gp								0.81	0.31	0.59	0.66	0.41	0.63	0.38
Vp									0.28	0.53	0.56	0.38	0.66	0.28
Lp										0.16	0.19	0.50	0.28	0.34
Cpu											0.91	0.31	0.53	0.28
Ac												0.28	0.50	0.34
Rm													0.38	0.41
Cpa														0.25
Smp														

Fig. 3. Proportion of trait attributes shared by the selected riverine species (expressed as per mil). The similarity between the two species is shown through a gradient of red, yellow, and green colors, from the darkest red corresponding to species that share a reduced number of attributes, to the darkest green assigned to species that have a large number of attributes in common.

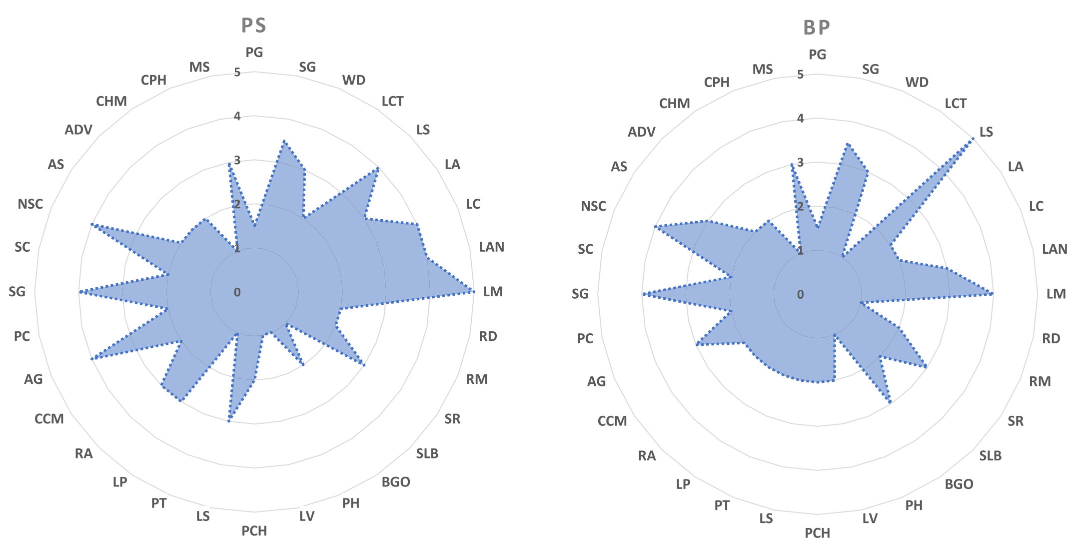

Fig. 4. Radar figures showing the "functional footprint" of each of the species considered in the study: *Pinus sylvestris* (Ps), *Betula pubescens* (Bp), *Filipendula ulmaria* (Fu), *Alnus incana* (Ai), *Galium palustre* (Gp), *Viola palustris* (Vp), *Carex acuta* (Ca), *Carex vesicaria* (Cv), *Ledum palustre* (Lp), *Calamagrostis purpurea* (Cpu), *Agrostis capillaris* (Ac), *Rosa majalis* (Rm), *Comarum palustre* (Cpa) and *Salix myrsinifolia* × *phylicifolia* (Smp). PGF, SGF, WD, LCT, LSH, LSI, LCON, LAN, LMA, RDE, RMO, SHRE, SB, BGOs, PHE, LVN, PCHE, LSTO, PTRI, LPER, RA, CO2-CCM, AM, PCOL, SG, STOC, NSC, PVS, ADV, CHMOV, COPH and MS represent the 32 traits analyzed in this study (see sub-section *2.4.*). Scores in the radar correspond to the trait attributes under which each species fall. Species with similar footprints are those with the greatest number of trait attributes coincidences. To aid visualization, traits PG and SG have been re-scaled dividing each category by 2, so scores corresponding to these traits can fit in a 0 to 5 scale (e.g., PG: category 1) Nano-phanerophyte = category 0.5 in the radar, 2) Micro-phanerophyte = category 1 in the radar; category 3) Meso-phanerophyte = category 1.5 in the radar, etc). Categories in the radar can be found in Baladrón et al. (submitted).

fluctuations were Ca, Cv, Ac, Cpu, Smp, Ai, Ps, Lp and Gp (1.37 > HPPR > 1.06). >50% of the traits in Ca, Cv, Ac and Cpu were categorized as fully resistant to water fluctuations. In four species (i.e., Smp, Ai, Ps, Lp), traits conferring partial-resistance to water fluctuations played a key role in raising the scores above 1 (1.22 > HPPR > 1.06), potentially helping these plants to better withstand the negative effects of water fluctuations. Five species (Fu, Vp, Cpa, Bp, Rm) were vulnerable to water fluctuations (0.95 > HPPR > 0.74); between 39 and 42% of the traits were categorized as vulnerable). Among these five, Bp and Rm were the most vulnerable (0.79 > HPPR > 0.74) (Figs. 5 and 8).

3.3. *Contribution of traits to plant community resistance against HP*

The traits that may provide resistance to most of the 14 selected

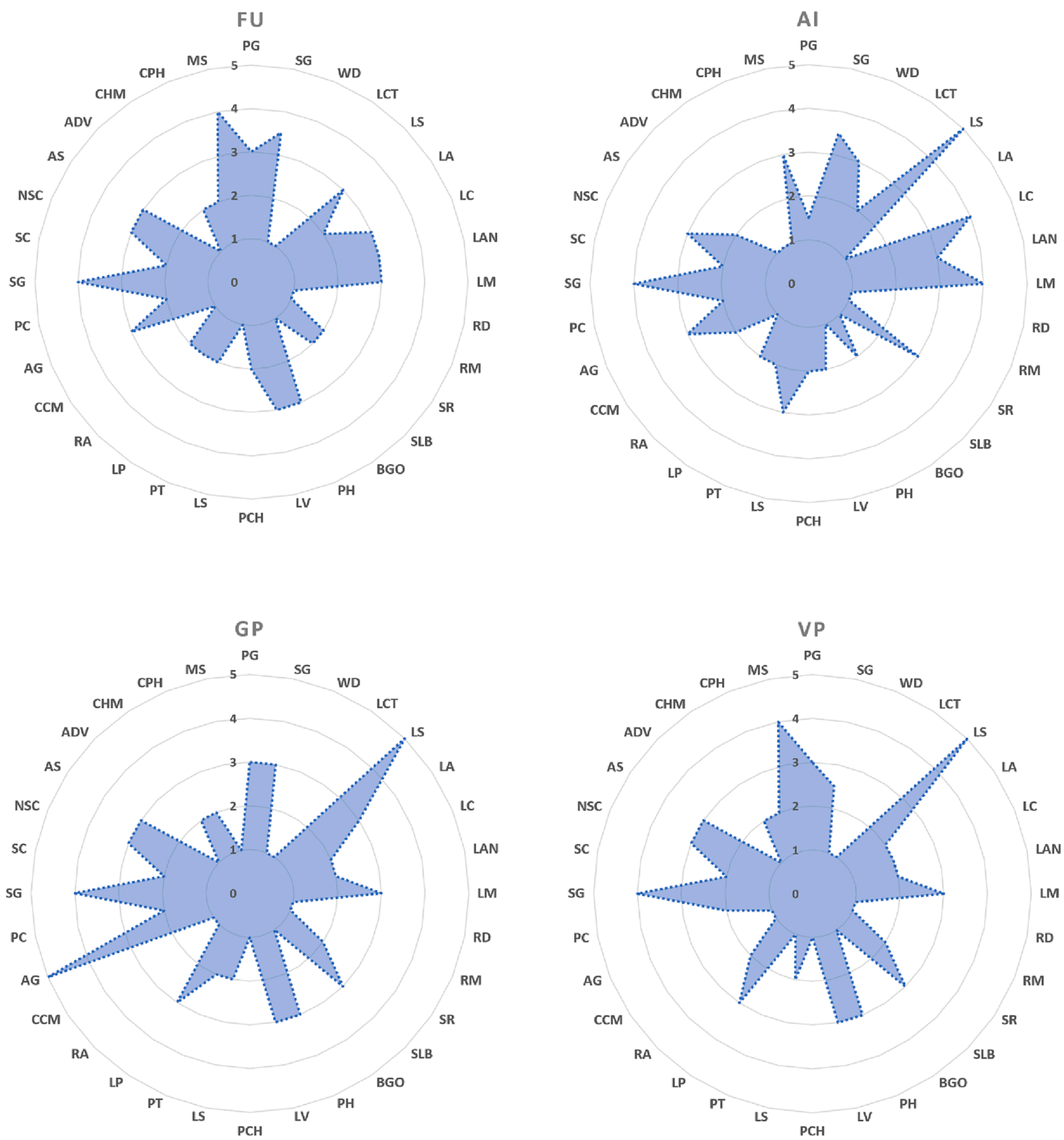

Fig. 4. (*continued*).

species against flooding, water fluctuations, and water stress are seed germination, plant growth form, shoot growth form, the presence of below ground organs and mass allocation, and leaf venation network. Other traits may potentially protect most of the species against one or two sources of HP disturbance, but not simultaneously against the three.

Ten morphological traits (shoot growth form, below ground organs and mass allocation, leaf mass per leaf area, leaf cuticle thickness, leaf anatomy, suberin/ lignin barriers, leaf consistency, leaf venation network, rooting depth, and plant growth form) and six physiological traits (i.e., seed germination, leaf persistence, stomatal control, resprouting ability, adventitious roots, and antioxidant generation mechanisms) offered resistance against flooding to>50% of the plant community (HPCR > 1.07). In contrast, four morphological (i.e., location of stomata, plant shape reconfiguration, plant height, and leaf shape) and five physiological traits (i.e., mycorrhizal symbioses, CO2 concentrating mechanisms, corticular photosynthesis, presence of coleoptile, and chloroplast movement under changing light intensities) may augment plant community vulnerability against flooding (HPCR < 0.71) (see Fig. 6).

Seven morphological traits (i.e., location of stomata, shoot growth form, below ground organs and mass allocation, plant growth form, leaf anatomy, leaf area, leaf venation network) and six physiological traits (i.e., seed germination, leaf persistence, stomatal control, resprouting ability, mycorrhizal symbiosis, antioxidants generations) offered resistance against water stress to>50% of the plant community (HPCR > 1.07). On the other hand, four morphological (i.e., leaf cuticle thickness, root morphology, leaf mass per leaf area, and leaf shape) and four physiological traits (i.e., CO2 concentrating mechanisms, corticular photosynthesis, presence of coleoptile, and chloroplast movement under changing light intensities) made most species in the plant community vulnerable against water stress (HPCR < 0.64) (see Fig. 7).

Six morphological traits (i.e., plant growth form, below ground organs and mass allocation, leaf mass per leaf area, shoot growth form, woodiness, leaf venation network) and four physiological traits (i.e., seed germination, leaf persistence, resprouting ability and stomatal control) offered resistance against water fluctuations to>50% of the plant community (HPCR > 1.07). In contrast, 4 morphological (i.e., plant height, leaf cuticle thickness, root morphology, leaf area) and 2 physiological traits (i.e., corticular photosynthesis, presence of coleoptile) can potentially increase plant community vulnerability against water fluctuations (HPCR < 0.64) (see Fig. 8).

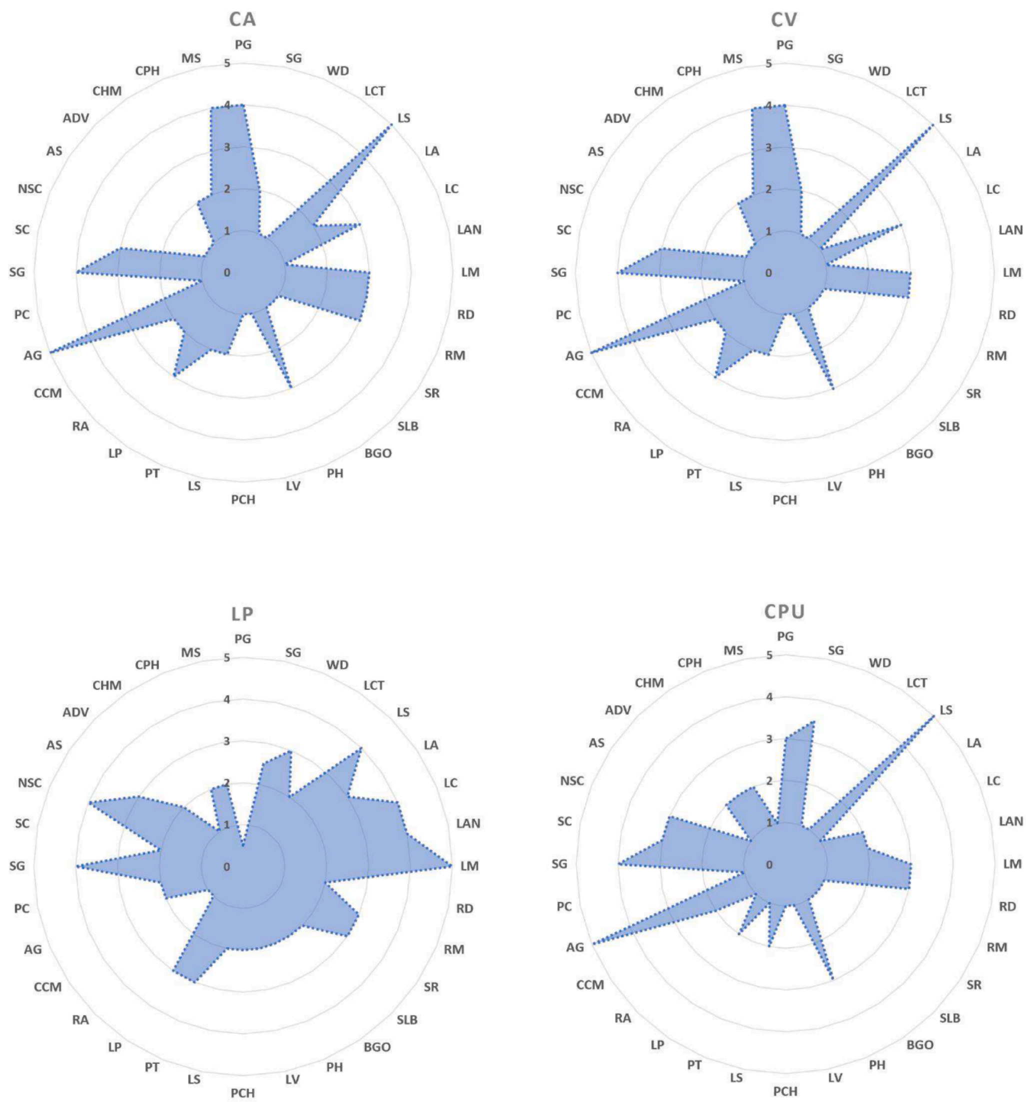

Fig. 4. (*continued*).

4. Discussion

Here we present a functional trait-based method to determine the potential resistance of riverine plants to hydropeaking (HP) and discuss its potential use and limitations for restoring rivers affected by HP. We assessed the resistance of a selection of 14 riverine plants to common HP disturbances (i.e., inundation, water fluctuations, and water stress). For this aim, the incorporation, standardization and interpretaion of plant species trait information available from multiple literature sources was required.

We found that plant resistance to HP predicted by our indices was not always lined up witth what it would be expected according to species ecology and habitat requirements. This was the case of forbs which, unexpectedly, showed a rather low resistance to water fluctuations. The four species that belong to this group (*Filipendula ulmaria*, *Galium palustre*, *Viola palustris*, *Comarum palustre*) present traits that confer resistance to the mechanical stress derived from HP, including flexible stems, leaves with vein topologies able to tolerate hydraulic system disruptions resulting from mechanical stress (i.e., loopings in second order veins of brochidodromous leaves; Sack and Scoffoni, 2013), plants with a small area exposed to the fluid (i.e., small growth forms such as hemicryptophytes (*Filipendula ulmaria*, *Galium palustre*, *Viola palustris*) and chamaephytes (*Comarum palustre*)); Speck, 2003; Puijalon et al., 2011), "low-cost" strategies for leaf production (i.e., plants with low leaf mass per area may minimize energy losses associated to leaf breakage during HP, as the energy invested by the plant in producing its leaves is small; see Poorter et al., 2009), and significant allocation of carbohydrate reserves in underground structures (i.e, if aboveground biomass loss occurs during HP, perennial herbs such as *Filipendula ulmaria*, *Galium palustre*, *Viola palustris* and *Comarum palustre* can restore it using carbohydrates accumulated in stolons, tubers and rhizomes; Klimešová and Klimeš, 2007; Clarke et al., 2013c). However, forbs also present multiple traits that may make them vulnerable to the mechanical stress imposed by HP. As opposed to taller plants such as trees and shrubs, forbs present overwintering (perennating) structures (i.e., buds, meristems, and leaves) located close to the ground (Raunkiær, 1934). Such structures may be submerged and injured by fast and turbulent water flow during phases of a rapid rise in discharge. Moreover, the rather papery consistency of forb leaves (i.e, thinner cuticles) may limit their capacity to resist the hydrodynamic forces exerted by HP flows (see Onoda et al., 2011). In addition, forbs have fibrous, laterally spread, shallow-roots, which, as opposed to taproots (present in *Pinus sylvestris*, *Carex acuta*, *Ledum palustre* or *Rosa majalis*), do not facilitate the necessary anchorage and mechanical stability (Pukkala et al., 1994; Bielak et al., 2014) to

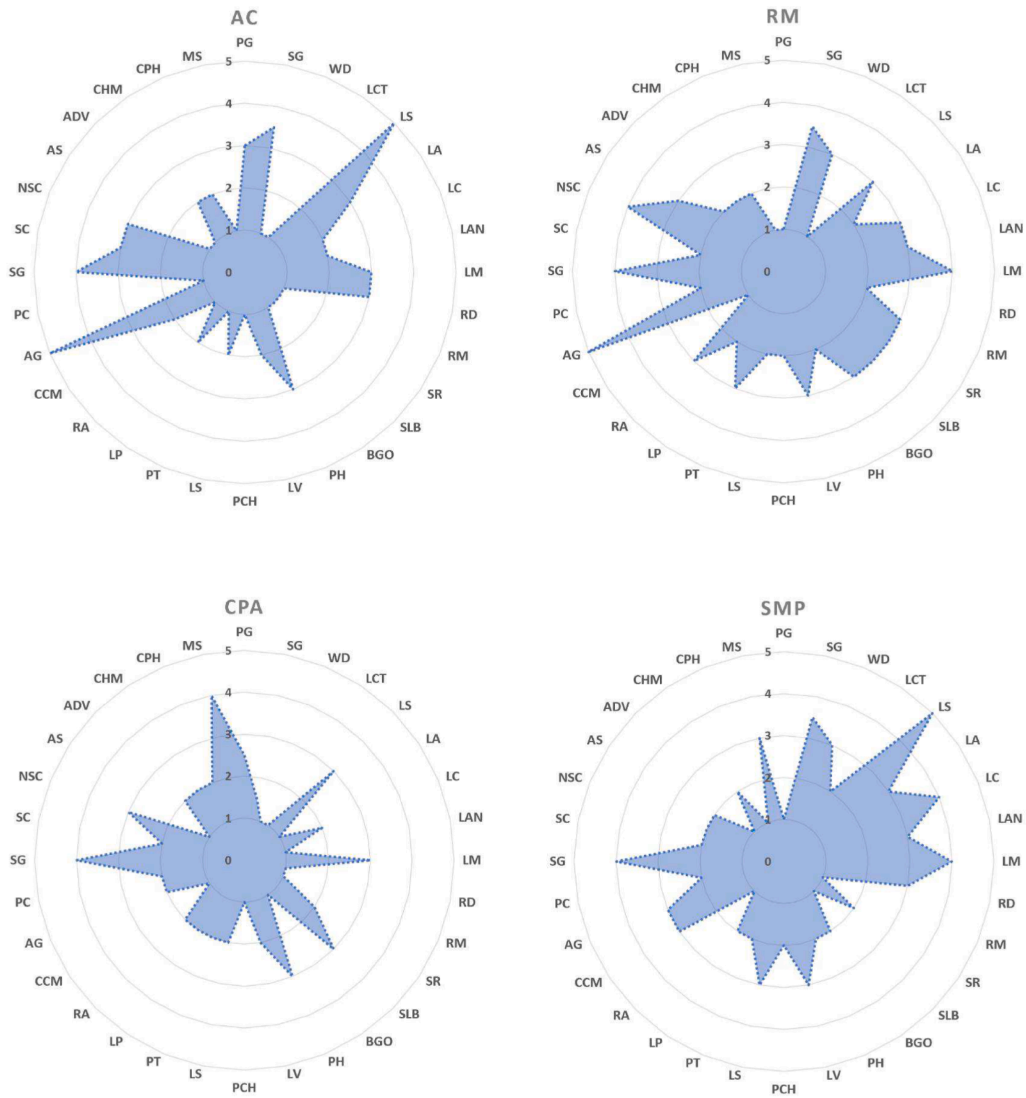

Fig. 4. (*continued*).

INUNDATION

Cv	Ca	Ac	Cpu	Ai	Cpa	Gp	Smp	Fu	Vp	Bp	Ps	Rm	Lp
1.28	1.24	1.24	1.21	1.21	1.07	1.03	1.03	1.03	0.97	0.93	0.76	0.72	0.66

WATER STRESS

Lp	Smp	Ps	Ai	Bp	Rm	Ca	Ac	Cv	Cpu	Gp	Fu	Vp	Cpa
1.58	1.44	1.36	1.28	1.04	1.00	1.00	0.96	0.88	0.84	0.79	0.72	0.67	0.64

WATER FLUCTUATIONS

Ca	Cv	Ac	Cpu	Smp	Ai	Ps	Lp	Gp	Fu	Vp	Cpa	Bp	Rm
1.37	1.33	1.28	1.22	1.22	1.11	1.06	1.06	1.06	0.95	0.95	0.94	0.79	0.74

+ Increasing resistance to disturbance −

Fig. 5. Species ranking based on resistance to flooding, water stress and water fluctuations. A color is assigned to each species based on its growth form: grass (green), forb (purple), shrub (yellow), and tree (brown).

FUNCTIONAL TRAIT	Cv	Ca	Ac	Ai	Cpu	Cpa	Gp	Smp	Fu	Vp	Bp	Ps	Rm	Lp		R	P	V	HPCR
Shoot growth-form (SGF)	R	R	R	R	R	R	V	R	R	V	R	R	R	V	T2	0.79	0.00	0.21	**1.57**
Below-ground organs and mass allocation (BGO)	R	R	R	P	R	R	R	P	R	R	V	P	V	P	T14	0.57	0.29	0.14	**1.43**
Leaf mass per leaf area (LMA)	R	R	R	P	R	R	R	P	R	R	P	V	P	V	T9	0.57	0.29	0.14	**1.43**
Leaf cuticle thickness (LCT)	R	R	R	V	R	R	R	V	R	R	R	V	R	V	T4	0.71	0.00	0.29	**1.43**
Leaf anatomy (LAN)	R	R	R	P	R	R	R	P	P	R	P	V	P	V	T8	0.50	0.36	0.14	**1.36**
Suberin/lignin barriers (SLB)	R	R	R	R	R	V	V	R	P	V	P	R	V	P	T13	0.50	0.21	0.29	**1.21**
Leaf consistency (LCON)	P	P	R	V	R	R	R	V	P	R	R	V	P	V	T7	0.43	0.29	0.29	**1.14**
Leaf venation network (LVN)	V	V	P	P	V	P	R	R	R	R	P	V	R	P	T16	0.36	0.36	0.29	**1.07**
Rooting depth (RDE)	V	V	V	R	V	R	R	V	R	R	R	P	P	P	T10	0.43	0.21	0.36	**1.07**
Plant growth-form (PGF)	R	R	V	R	V	V	R	P	V	V	R	R	P	P	T1	0.43	0.21	0.36	**1.07**
Presence of chloroplasts in epidermis (PCHE)	R	R	R	V	R	R	R	V	V	R	V	V	V	V	T17	0.50	0.00	0.50	**1.00**
Leaf area (LAR)	R	P	V	R	R	R	V	V	P	P	P	V	P	V	T6	0.29	0.36	0.36	**0.93**
Location of stomata (LSTO)	V	V	V	R	V	V	V	R	R	V	V	R	V	V	T18	0.29	0.00	0.71	**0.57**
Shape reconfiguration (SHRE)	R	R	R	V	R	V	V	V	V	V	V	V	V	V	T12	0.29	0.00	0.71	**0.57**
Plant height (PHE)	V	V	V	R	V	V	V	P	V	V	R	R	P	P	T15	0.21	0.21	0.57	**0.64**
Leaf shape (LSH)	V	V	V	V	V	R	V	V	R	V	V	V	R	V	T5	0.21	0.00	0.79	**0.43**
Woodiness (WD)															T3				
Presence of trichomes (PTRI)															T19				
Root morphology (RMO)															T11				
Seed germination (SG)	R	R	R	R	R	R	R	R	R	R	R	R	R	R	T25	1.00	0.00	0.00	**2.00**
Leaf persistence (LPER)	R	R	P	P	P	P	R	P	P	R	P	R	P	R	T20	0.43	0.57	0.00	**1.43**
Stomatal control (STOC)	R	R	R	P	R	P	P	P	P	P	P	P	P	P	T26	0.29	0.71	0.00	**1.29**
Resprouting ability (RA)	P	P	R	R	R	P	R	R	P	P	P	V	V	R	T21	0.43	0.43	0.14	**1.29**
Adventitious roots (ADV)	R	R	R	R	V	V	R	R	R	R	V	V	V	V	T29	0.57	0.00	0.43	**1.14**
Antioxidants generation (AG)	V	V	V	R	V	R	V	R	R	R	R	P	V	R	T23	0.50	0.07	0.43	**1.07**
Non-structural carbohydrates accumulation (NSC)	R	R	P	P	P	P	P	R	P	P	V	V	V	V	T27	0.21	0.50	0.29	**0.93**
Aerenchyma structures and root ventilation systems (AER)	R	R	R	P	R	R	V	P	V	V	V	P	V	V	T28	0.36	0.21	0.43	**0.93**
Mycorrhizal symbioses (MYCSYM)	V	V	R	V	R	V	R	V	V	V	V	V	R	R	T32	0.36	0.00	0.64	**0.71**
CO2 concentrating mechanisms (CO2-CM)	P	P	P	P	P	V	V	R	V	V	P	P	V	V	T22	0.07	0.50	0.43	**0.64**
Corticular photosynthesis (COPH)	V	V	V	R	V	V	V	R	V	V	R	R	V	V	T31	0.29	0.00	0.71	**0.57**
Presence of coleoptile (PCOL)	R	R	R	V	R	V	V	V	V	V	V	V	V	V	T24	0.29	0.00	0.71	**0.57**
Chloroplasts movement under changing light intensities (CHMOV)	V	V	V	R	V	V	V	V	V	V	V	V	V	R	T30	0.14	0.00	0.86	**0.29**

	Cv	Ca	Ac	Ai	Cpu	Cpa	Gp	Smp	Fu	Vp	Bp	Ps	Rm	Lp
R	0.59	0.55	0.55	0.45	0.55	0.45	0.48	0.38	0.38	0.41	0.31	0.28	0.21	0.21
P	0.10	0.14	0.14	0.31	0.10	0.17	0.07	0.28	0.28	0.14	0.31	0.21	0.31	0.24
V	0.31	0.31	0.31	0.24	0.34	0.38	0.45	0.34	0.34	0.45	0.38	0.52	0.48	0.55
HPPR	**1.28**	**1.24**	**1.24**	**1.21**	**1.21**	**1.07**	**1.03**	**1.03**	**1.03**	**0.97**	**0.93**	**0.76**	**0.72**	**0.66**

Fig. 6. Resistances and vulnerabilities of selected riverine plants to flooding, based on the expression of 32 functional traits. Percentages at the bottom correspond to the proportion of trait attributes that conferred resistance (R) (green scale), partial resistance (P) (yellow scale) or vulnerability (V) (red scale) to each species against flooding. Percentages on the right correspond to the resistance, partial-resistance and vulnerability conferred by each trait to the overall plant community (e.g., a resistance (R) equal to 0.7 means that 70% of the individuals expressed the trait in a fashion that conferred resistance against flooding).

cope with drag forces derived from HP, and uprooting may occur (Chaves et al., 2002; Bejarano et al., 2018). The lack of coleoptile (i.e., a structure that protects plant cotyledons from mechanical damages) and the absence of corticular photosynthesis (i.e., photosynthesis in bark tissues of woody plants) may also make forbs vulnerable to HP water fluctuations.

Specieś general knowledge on ecological and habitat requirements may lead to wrong or, at least, imprecise verdicts on their expected behaviour during wet or dry periods. By contrast, the HPPR index scores provide an objective measure of each species' resistance (or vulnerability) to each HP disturbance analyzed (i.e., flooding, water fluctuations, and water stress), allowing to rank species accordingly. For instance, although the literature on the ecology of species suggests that *Alnus incana* and *Betula pubescens* should respond similarly to floods (Frye and Grosse, 1992; Johansson and Nilsson, 2002; Schnitzler-Lenoble, 2007), these species HPPR scores differed from each other, highlighting a substantially higher capacity of *Alnus incana* to resist inundation events compared to *Betula pubescens*. *Filipendula ulmaria*, a taxon characteristic of sites where water levels fluctuate (Hultén and Fries, 1986; Grime, 1988) did not show a remarkably high HPPR score under inundation. *Rosa majalis*, a species acknowledged as fully resistant to drought (Solomentseva et al., 2020), may only be partially-resistant according to its HPPR score when measured for water stress. Discrepancies were also found for amphibious plants under water stress (e.g., *Carex acuta* and *Carex vesicaria*; Maberly and Spence, 1989); although these plants present multiple adaptations to drought (see Fig. 4), HPPR scores were rather low indicating that they may not fully minimize the risk of desiccation during phases of HP low water levels.

The scores we obtained for some of the species were lined up with the widespread expected responses according to species ecology and habitat requirements (e.g. preferences for water). Grasses, usually growing close to the water, were the most resistant species to flooding and water fluctuations, while trees and shrubs were in general more vulnerable. The high HP plant resistance index (HPPR) scores obtained by the amphibious *Carex acuta* and *Carex vesicaria* corroborate the high resistance to submergence of this genus reported by previous studies (Visser et al., 2000; Johansson and Nilsson, 2002; Edwards and Čížková, 2019; Bejarano et al., 2020). HPPR scores of *Calamagrostis purpurea*, a hygrophilous species occupying ground layers nearby wetlands, swamps and rivers (Štech et al., 2020; Chytrý et al., 2021), and *Agrostis capillaris*, a species abundant in wetlands and with preference for humid soils (Stace, 1997; Maczey, 2016; Chytrý et al., 2021) were also high, suggesting that these species should also easily thrive along riverbanks inundated during HP operations. Exclusive trait attributes of grasses (e.

FUNCTIONAL TRAIT	Lp	Smp	Ps	Ai	Bp	Rm	Ca	Ac	Cv	Cpu	Gp	Fu	Vp	Cpa		R	P	V	HPCR
Location of stomata (LSTO)	R	R	R	R	R	R	R	R	R	R	R	V	R	R	T18	0.93	0.00	0.07	**1.86**
Shoot growth-form (SGF)		R	R	R	R	R	R	R	R	R		R		V	T2	0.91	0.00	0.09	**1.82**
Below-ground organs and mass allocation (BGO)	P	P	P	P	V	V	R	R	R	R	R	R	R	R	T14	0.57	0.29	0.14	**1.43**
Plant growth-form (PGF)	R	R	R	R	R	R	V	P	V	P	P	P	P	P	T1	0.43	0.43	0.14	**1.29**
Leaf anatomy (LAN)	R	P	R	P	P	P	R	V	R	V	V	P	V	R	T8	0.36	0.36	0.29	**1.07**
Leaf area (LAR)	R	R	R	V	P	P	P	R	V	V	R	P	P	V	T6	0.36	0.36	0.29	**1.07**
Leaf venation network (LVN)	P	R	V	P	P	R	V	P	V	V	R	R	R	P	T16	0.36	0.36	0.29	**1.07**
Rooting depth (RDE)	P	R	P	V	V	P	R	R	R	R	V	V	V	V	T10	0.36	0.21	0.43	**0.93**
Woodiness (WD)	R	R	R	R	R	R	V	V	V	V	V	V	V	V	T3	0.43	0.00	0.57	**0.86**
Leaf consistency (LCON)	R	R	R	R	V	P	P	V	P	V	V	P	V	V	T7	0.29	0.29	0.43	**0.86**
Presence of trichomes (PTRI)	R	P	V	P	P	R	P	V	P	V	P	P	V	P	T19	0.14	0.57	0.29	**0.86**
Leaf cuticle thickness (LCT)	R	R	R	R	V	V	V	V	V	V	V	V	V	V	T4	0.29	0.00	0.71	**0.57**
Root morphology (RMO)	R	V	P	V	P	R	R	V	V	V	V	V	V	V	T11	0.21	0.14	0.64	**0.57**
Leaf mass per leaf area (LMA)	R	P	R	P	P	P	V	V	V	V	V	V	V	V	T9	0.14	0.29	0.57	**0.57**
Leaf shape (LSH)	R	V	R	V	V	V	V	V	V	V	V	V	V	V	T5	0.14	0.00	0.86	**0.29**
Shape reconfiguration (SHRE)															T12				
Suberin/lignin barriers (SLB)															T13				
Plant height (PHE)															T15				
Presence of chloroplasts in epidermis (PCHE)															T17				
Seed germination (SG)	R	R	R	R	R	R	R	R	R	R	R	R	R	R	T25	1.00	0.00	0.00	**2.00**
Leaf persistence (LPER)	R	P	R	P	P	P	R	P	R	P	R	P	R	P	T20	0.43	0.57	0.00	**1.43**
Stomatal control (STOC)	P	P	P	P	P	P	R	R	R	R	P	P	P	P	T26	0.29	0.71	0.00	**1.29**
Resprouting ability (RA)	R	R	V	R	P	V	P	R	P	R	R	P	P	P	T21	0.43	0.43	0.14	**1.29**
Mycorrhizal symbioses (MYCSYM)	R	R	R	R	R	R	V	R	V	R	R	V	V	V	T32	0.64	0.00	0.36	**1.29**
Antioxidants generation (AG)	R	R	P	R	R	V	V	V	V	V	V	R	R	R	T23	0.50	0.07	0.43	**1.07**
CO2 concentrating mechanisms (CO2-CM)	V	R	P	P	P	V	P	P	P	P	V	V	V	V	T22	0.07	0.50	0.43	**0.64**
Corticular photosynthesis (COPH)	V	R	R	R	R	V	V	V	V	V	V	V	V	V	T31	0.29	0.00	0.71	**0.57**
Presence of coleoptile (PCOL)	V	V	V	V	V	V	R	R	R	R	V	V	V	V	T24	0.29	0.00	0.71	**0.57**
Chloroplasts movement under changing light intensities (CHMOV)	R	V	V	R	V	V	V	V	V	V	V	V	V	V	T30	0.14	0.00	0.86	**0.29**
Non-structural carbohydrates accumulation (NSC)															T27				
Aerenchyma structures and root ventilation systems (AER)															T28				
Adventitious roots (ADV)															T29				

	Lp	Smp	Ps	Ai	Bp	Rm	Ca	Ac	Cv	Cpu	Gp	Fu	Vp	Cpa
R	0.71	0.60	0.56	0.48	0.32	0.36	0.40	0.40	0.36	0.36	0.33	0.20	0.25	0.20
P	0.17	0.24	0.24	0.32	0.40	0.28	0.20	0.16	0.16	0.12	0.13	0.32	0.17	0.24
V	0.13	0.16	0.20	0.20	0.28	0.36	0.40	0.44	0.48	0.52	0.54	0.48	0.58	0.56
HPPR	**1.58**	**1.44**	**1.36**	**1.28**	**1.04**	**1.00**	**1.00**	**0.96**	**0.88**	**0.84**	**0.79**	**0.72**	**0.67**	**0.64**

Fig. 7. Resistances and vulnerabilities of selected riverine plants to water stress, based on the expression of 32 functional traits. Percentages at the bottom correspond to the proportion of trait attributes that conferred resistance (R) (green scale), partial resistance (P) (yellow scale) or vulnerability (V) (red scale) to each species against water stress. Percentages on the right correspond to the resistance, partial-resistance and vulnerability conferred by each trait to the overall plant community (e.g., a resistance (R) equal to 0.7 means that 70% of the individuals expressed the trait in a fashion that conferred resistance against water stress).

g., flapping leaves, elastic deformation of stems; efficient control of stomatal aperture; well-developed aerenchyma structures) may potentially help these species to withstand flooding and water fluctuations triggered by HP.

Most species presenting intermediate HPPR values (i.e., *Alnus incana*, *Comarum palustre*, *Galium palustre*, *Salix myrsinifolia* × *phylicifolia* and *Viola palustris*; 1.20 < HPPR < 0.80) grow in soaked, poorly aerated soils, or at least can tolerate wet soils for a limited amount of time (Hultén and Fries, 1986; Chytrý et al., 2021). These species might resist soil riverbank waterlogging resulting from short-lasting HP events, but may not endure long-lasting inundations as grasses can potentially do.

Functional trait calculations also mirrored the potential higher capacity of plants occupying higher elevations on the riverbank (i.e., trees and shrubs) to cope with water flow restrictions. Trait attributes adapting plants to dry conditions include woody stems (present in the six riparian species evaluated), thick cuticles (present in *Pinus sylvestris*, *Alnus incana*, *Ledum palustre*, *Salix myrsinifolia* × *phylicifolia*), needle-shaped leaves (i.e., *Ledum palustre* and *Pinus sylvestris*), dense covering of trichomes (especially abundant in *Ledum palustre* and *Rosa majalis*), and thick lignified walls (present in all riparian species except *Betula pubescens*).

Our results agree with most previous (and still few) experimental results on plant performance under HP. Low morphological performance and/ or lack of germination detected in seedlings and seeds of *Filipendula ulmaria* and *Galium palustre* reported by Baladrón et al. (2022) exposed to HP water stress coincide with these species' low HPPR scores for this type of disturbance. Conversely, high HPPR scores obtained by *Pinus sylvestris* and *Salix myrsinifolia* × *phylicifolia* suggest resistance to water stress, which agree with the resistance that these taxa displayed under lab and power plant-induced HP drought scenarios (Baladrón et al., 2022). Samely, most HPPR scores corresponding to water fluctuations and flooding were lined up with the morphological and physiological performance of seedlings exposed to daily submergence and daily water fluctuations mimicking those occuring during HP (Baladrón et al., 2022). Although HPPR values scored outside the expected range for some species (e.g., *Comarum palustre* (HPPR = 1.07) and Gp (HPPR = 1.03) were expected to score higher under flooding, and Bp (HPPR = 1.04) was expected to do so under water stress), most deviations were not substantial since in most cases the classification of the species as resistant or vulnerable did not change with respect to what had been observed in previous HP experiments. The exception to this was *Alnus incana*, whose high HPPR scores for flooding, water stress, and water fluctuations classify it as very resistant to the three disturbances. These results are in contrast to Baladrón et al. (2022), who reported low morphological performance under similar environments. This discrepancy might derive from a limited number of traits used in our functional

FUNCTIONAL TRAIT	Ca	Cv	Ac	Cpu	Smp	Ai	Ps	Lp	Gp	Fu	Vp	Cpa	Bp	Rm
Plant growth-form (PGF)	R	R	R	R	P	R	R	P	R	R	R	R	R	P
Below-ground organs and mass allocation (BGO)	R	R	R	R	P	P	P	P	R	R	R	R	V	V
Leaf mass per leaf area (LMA)	R	R	R	R	P	P	V	V	R	R	R	R	P	P
Shoot growth-form (SGF)	R	R	P	P	P	P	P	P	P	P	P	R	P	P
Woodiness (WD)	R	R	R	R	V	V	V	V	R	R	R	R	V	V
Leaf venation network (LVN)	V	V	P	V	R	P	V	P	R	R	R	P	P	R
Shape reconfiguration (SHRE)	R	R	R	R	P	V	V	V	P	P	P	P	V	V
Rooting depth (RDE)	R	R	R	R	R	V	P	P	V	V	V	V	V	P
Leaf consistency (LCON)	P	P	V	V	R	R	R	R	V	P	V	V	V	P
Plant height (PHE)	V	V	V	V	P	R	R	P	V	V	V	V	R	P
Leaf cuticle thickness (LCT)	V	V	V	V	R	R	R	R	V	V	V	V	V	V
Root morphology (RMO)	R	V	V	V	V	V	P	R	V	V	V	V	P	R
Leaf area (LAR)	V									V	V		V	V
Leaf shape (LSH)														
Leaf anatomy (LAN)														
Suberin/lignin barriers (SLB)														
Presence of chloroplasts in epidermis (PCHE)														
Location of stomata (LSTO)														
Presence of trichomes (PTRI)														
Seed germination (SG)	R	R	R	R	R	R	R	R	R	R	R	R	R	R
Leaf persistence (LPER)	R	R	P	P	P	P	R	R	R	P	R	P	P	P
Resprouting ability (RA)	P	P	R	R	R	R	V	R	R	P	P	P	P	V
Stomatal control (STOC)	R	R	R	R	P	P	P	P	P	P	P	P	P	P
Corticular photosynthesis (COPH)	V	V	V	V	R	R	R	V	V	V	V	V	R	V
Presence of coleoptile (PCOL)	R	R	R	R	V	V	V	V	V	V	V	V	V	V
CO2 concentrating mechanisms (CO2-CM)														
Antioxidants generation (AG)														
Non-structural carbohydrates accumulation (NSC)														
Aerenchyma structures and root ventilation systems (AER)														
Adventitious roots (ADV)														
Chloroplasts movement under changing light intensities (CHMOV)														
Mycorrhizal symbioses (MYCSYM)														

	R	P	V	HPCR
T1	0.79	0.21	0.00	**1.79**
T14	0.57	0.29	0.14	**1.43**
T9	0.57	0.29	0.14	**1.43**
T2	0.21	0.79	0.00	**1.21**
T3	0.57	0.00	0.43	**1.14**
T16	0.36	0.36	0.29	**1.07**
T12	0.29	0.36	0.36	**0.93**
T10	0.36	0.21	0.43	**0.93**
T7	0.29	0.29	0.43	**0.86**
T15	0.21	0.21	0.57	**0.64**
T4	0.29	0.00	0.71	**0.57**
T11	0.21	0.14	0.64	**0.57**
T6	0.00	0.00	1.00	**0.00**
T5				
T8				
T13				
T17				
T18				
T19				
T25	1.00	0.00	0.00	**2.00**
T20	0.43	0.57	0.00	**1.43**
T21	0.43	0.43	0.14	**1.29**
T26	0.29	0.71	0.00	**1.29**
T31	0.29	0.00	0.71	**0.57**
T24	0.29	0.00	0.71	**0.57**
T22				
T23				
T27				
T28				
T29				
T30				
T32				

	Ca	Cv	Ac	Cpu	Smp	Ai	Ps	Lp	Gp	Fu	Vp	Cpa	Bp	Rm
R	0.63	0.61	0.56	0.56	0.39	0.39	0.39	0.33	0.44	0.32	0.37	0.33	0.21	0.16
P	0.11	0.11	0.17	0.11	0.44	0.33	0.28	0.39	0.17	0.32	0.21	0.28	0.37	0.42
V	0.26	0.28	0.28	0.33	0.17	0.28	0.33	0.28	0.39	0.37	0.42	0.39	0.42	0.42
HPPR	**1.37**	**1.33**	**1.28**	**1.22**	**1.22**	**1.11**	**1.06**	**1.06**	**1.06**	**0.95**	**0.95**	**0.94**	**0.79**	**0.74**

Fig. 8. Resistances and vulnerabilities of selected riverine plants to water fluctuations, based on the expression of 32 functional traits. Percentages at the bottom correspond to the proportion of trait attributes that conferred resistance (R) (green scale), partial resistance (P) (yellow scale) or vulnerability (V) (red scale) to each species against water fluctuations. Percentages on the right correspond to the resistance, partial-resistance and vulnerability conferred by each trait to the overall plant community (e.g., a resistance (R) equal to 0.7 means that 70% of the individuals expressed the trait in a fashion that conferred resistance against water fluctuations).

analysis and highlights the importance of including an exhaustive set of traits. Nonetheless, despite having obtained some unexpected results, species tolerance to HP may be accurately predicted by analyzing the resistance contributed by each of its morphological and physiological attributes, and then calculating the cumulative resistance granted by all the attributes as a whole.

Our results also reveal that species may achieve similar levels of resistance to HP even when they present a substantial number of differences in expressing trait attributes. This means that plants can adopt multiple morphological and physiological solutions and converge from a functional perspective in order to survive extreme conditions. For instance, tissue oxygenation in submerged plants can be achieved by true arenchyma structures, but ventilation systems such as lenticels can likewise provide sufficient oxygenation (Björn et al., 2022) to withstand HP. Several examples help illustrate the fact that plants can reach similar HPPR values but score as "resistant" or "vulnerable" for different functional traits. *Calamagrostis purpurea* and *Salix myrsinifolia* × *phylicifolia* differed in 66% of their trait atributes, yet they both presented a moderate-strong resistance to water fluctuations (HPPR = 1.22); *Rosa majalis* and *Carex acuta* scores were the same under water stress (HPPR = 1.00) in spite that 60% of their trait attributes did not match; likewise, *Alnus incana* and *Calamagrostis purpurea* displayed the exact same level of resistance to flooding (HPPR = 1.21) although they differed in the expression of 70% of their attributes. These results, again, evidence the importance of including as many traits as possible in the analysis since each new trait added incorporates additional information on the overall capacity of plants regarding their adaptability and phenotypic plasticity against HP. Future research may focus on understanding the relative weight of each trait in making plants resistant to HP, and how to incorporate it in the HPPR to increase its calculation accuracy.

Dam operating rules determine the duration and frequency of HP phases (i.e., low base discharge, rapid changes in discharge, and high peak discharge; Bruder et al., 2016), which in turn determines the magnitude, frequency, and duration of HP disturbances. Having a ranking of species resistance against each type of HP disturbance allows the detection of species that may acceptably tolerate all disturbances combined (i.e., minimum HPPR > 1 under inundation, water fluctuation, and water stress). This is key to select the most suitable set of native species to restore rivers subjected to any specific HP scheme. In our specific case, two riparian species (i.e., *Alnus incana* and *Salix myrsinifolia* × *phylicifolia*) and two herbs (i.e, *Carex acuta* and *Agrostis capillaris*) would be strong candidates for restoring HP rivers in northern Europe. Other species could also be selected if restrictions to dam operating rules were imposed. For instance, *Carex vesicaria* and *Calamagrostis purpurea* could be restoration candidates as long as the duration and frequency of drawdown periods were reduced to the maximum extent possible. The remaining species might be vulnerable to at least one source of HP disturbance, and dam reoperating efforts might be necessary to be implemented for these species to thrive in hydroelectric rivers.

The functional method here proposed is a double-entry model that provides complementary information (HPPR and HPCR (i.e., HP community resistance index). The HPPR index results from the sum of resistances conferred by each trait, and helps ranking species based on the resistance conferred by the accumulation of "hydropeaking-resistant" traits. The HPCR allows detecting the "hydropeaking-resistant" traits most commonly expressed within the plant community and ranking them based on their relevance for protecting the community as a whole. The joint interpretation of both indexes allows identifying what taxa from the local species pool might thrive under HP, and what functional traits may be capable of preserving riverine plant communities' composition by preventing HP species filtering.

HPCR results highlighted the prevalence of certain trait attributes within the community. Erosion under highly fluctuating waters may hamper seed germination, and fast submergence and drawdown can even inhibit it (Bejarano et al., 2018), hence, the fact that all selected species for the study were perennial plants reduces the risk of seeds not germinate under HP. The widespread presence of below-ground structures within the community might be of great importance for the survival of its taxa under any of the three forms of HP analyzed. Rhizomes, runners, tillers, and other storage organs constitute carbohydrates stockings that may sustain energy production via ethanolic fermentation during submergence (Sato et al., 2002), promote lateral spreading (Klimešová et al., 2018) to facilitate root water uptake during drawdown events, and enhance recolonization of patches eroded by turbulent flows and fast water-level fluctuations derived from HP (see Xiong et al., 2001). Plant growth forms with emergent leaves and flexible shoots, nutrient recovery from senescent leaves, a high capacity to resprout after disturbance (Paula and Pausas, 2006; Lawes and Clarke, 2011; Clarke et al., 2010, 2013c), and fast stomatal movements to favor efficient leaf gas exchange under environmental stress (Gerardin et al., 2018; Nunes et al., 2020) were trait attributes detected in most species within the community and may play a key role in protecting its integrity against flooding, water stress, and water fluctuations.

The ability of our method to predict plant resistance against HP is limited by a number of aspects. Habitats, processes and interactions in real river systems are usually much more complex than those predicted by indices and theoretical models. In this regard, our plant resistance predictions need to be tested with field and laboratory experiments to fully understand the range of applicability of the indices here proposed.

HP operations may vary significantly and so plant specieś resistance to a given HP scheme may depend on the intensity, duration and timing of fluvial disturbances. Unfortunately, our method does not account for disturbance variability resulting from differing HP schemes. Further improvements to the method may include this aspect for a better understanding of plant trait-fluvial disturbance interactions (i.e., to which extent functional traits can help plants to counterbalance the disturbance resulting from different HP operation modes).

Classifying riverine plant species under functional trait categories are constrained by the information and data available in the scientific literature. For some riverine species there is little data available for specific traits (e.g., data available on physiological traits of riverine plants is usually limited), while for others the published studies may be contradictory, making it necessary to categorize species based on reasoned assumptions and expert judgment. This will inevitably incorporate subjectivity in the functional characterization of species, therefore affecting our indices results. Quantitative research on how physiological and morpho-anatomical traits help riverine species to cope with HP would contribute to fill current gaps of knowledge, provide new data and reduce subjectivity on plant functional characterization. In this regard, future experiments should focus on "hard" traits (i.e., physiological traits), which are usually more closely related to a precise plant function (Cornelissen et al., 2003; Liu et al., 2021).

Some traits included in our method might be intercorrelated and, as a result, they may be functionally redundant. By including intercorrelated traits in our indication method, we might be "double-counting" plant resistance. Consequently, further method improvements should include a comprehensive analysis to detect traits strongly correlated (i.e, traits considered as a single spectrum; He et al., 2019) and avoid functional redundancies.

Finally, the methodology here presented can also be improved and scaled up by adding more plant traits and individual species from different bioclimatic regions.

Despite its limitations, the work here presented constitutes the first attempt in creating a systematic tool to assess the impact of HP operations on riverine vegetation. The improvements indicated above should increase our methodologýs capacity to detect suitable species to restore rivers subjected to hydropower production, to evaluate potential damages of HP operations on riparian areas, and to define riparian-friendly HP schemes worldwide.

5. Conclusions

Hydropeaking (HP) is a hydropower operation mode with outstanding capabilities for fast regulation with changing electrical demands, but its use also causes the degradation of fluvial ecosystems and resources, including the riverine vegetation. New methodological frameworks are required to identify plant species resistant to HP disturbances. We provide a new methodology (i.e., a "hydropeaking-resistant" functional trait filtering method) for this purpose, which includes novel trait-based indices (i.e., HPPR and HPCR) aimed at ranking plant species based on their resistance to HP. These indices provide complementary information, and their joint interpretation allows identifying taxa resistant to HP, as well as the "hydropeaking-resistant" traits most commonly expressed within the plant community.

Our results prove that the use of indices can help to identify the functional reasons why a riverine plant may perform better or worse in HP systems. Coincidences in functional trait expression, usually common between plant species with similar growth forms, anticipate a similar ability to withstand fluvial alterations derived from HP. In addition to ranking plant species from the most resistant to the most vulnerable, plant resistance predictions obtained with our indices sometimes differed from predictions solely based on general descriptions of species ecology and habitat requirements. The differences observed between the resistance expected and the obtained for several species illustrate the importance of using a systematic, structured approach (as the one presented here) to fine-tune the diagnostics on plant species vulnerability to HP.

The work here presented should be understood as a demonstrator, a first step to build a global assessment framework aimed at preserving, restoring and managing in a sustainable way the margins of hydropower rivers worldwide. Efforts to further improve the assessment capabilities of the method may include adding more plant traits and individual species from different bioclimatic regions; the method can also benefit from further research on how functional traits help riverine species to thrive under flow regulated environments, an in-depth understanding of "plant trait-fluvial disturbance" interactions, and comprehensive trait-based characterizations of riverine plants species across the globe.

Author contribution

Alejandro Baladrón and María Dolores Bejarano conceived the study. Alejandro Baladrón collected and analyzed the data, and wrote the paper with contributions from María Dolores Bejarano and Isabel Boavida. All authors contributed critically and gave final approval for publication

8. Data statement

Data supporting this research are sensitive and not available publicly. Data are available to qualified researchers upon request from Natural Resources Department, Universidad Politécnica de Madrid (UPM), Calle José Antonio Novais, 10, 28040 Madrid (Spain) by contacting María Dolores Bejarano at lolesbejarano@yahoo.es. Data supporting this research are available to peer-reviewers who require it in the review process.

CRediT authorship contribution statement

Alejandro Baladrón: Conceptualization, Methodology, Data curation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **María Dolores Bejarano:** Supervision, Conceptualization, Writing – review & editing. **Isabel Boavida:** Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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References

Baladrón, A., Bejarano, M.D., Sarneel, J.M., Boavida, I., 2022. Trapped between drowning and desiccation: Riverine plants under hydropeaking. Sci. Total Environ. 829, 154451 https://doi.org/10.1016/j.scitotenv.2022.154451.

Bejarano, M.D., Maroto, J., Nilsson, C., Aguiar, F.C., 2016. Traits of riparian woody plants responding to hydrological and hydraulic conditions: a northern Swedish database. Ecology 97, 2892. https://doi.org/10.1002/ecy.1533.

Bejarano, M.D., Jansson, R., Nilsson, C., 2018. The effects of hydropeaking on riverine plants: a review. Biol. Rev. 93, 658–673.

Bejarano, M.D., Sordo-Ward, Á., Alonso, C., Jansson, R., Nilsson, C., 2020. Hydropeaking affects germination and establishment of riverbank vegetation. Ecol. Appl. 30, e02076.

Bielak, K., Dudzinska, M., Pretzsch, H. 2014. Mixed stands of Scots pine (*Pinus sylvestris* L.) and Norway spruce [*Picea abies* (L.) Karst] can be more productive than monocultures. Evidence from over 100 years of observation of long-term experiments Forest Systems, 23, 573–589.

Björn, L.O., Middleton, B.A., Germ, M., Gaberšcik, A., 2022. Ventilation systems in wetland plant species. Diversity 2022 (14), 517. https://doi.org/10.3390/d14070517.

Bornette, G., Puijalon, S., 2011. Response of aquatic plants to abiotic factors: a review. Aquat. Sci. 73, 1–14.

Bruder, A., Tonolla, D., Schweizer, S.P., Vollenweider, S., Langhans, S.D., Wüest, A., 2016. A conceptual framework for hydropeaking mitigation. Sci. Total Environ. 568, 1204–1212.

Catford, J.A., Jansson, R., 2014. Drowned, buried, and carried away: effects of plant traits on the distribution of native and alien species in riparian ecosystems. New Phytol. 204 (1), 19–36.

Chaves, M.M., Pereira, J.S., Maroco, J., Rodrigues, M.L., Ricardo, C.P.P., Osorio, M.L., Carvalho, I., Faria, T., Pinheiro, C., 2002. How plants cope with water stress in the field? Photosynthesis and growth. Ann. Bot. 89, 907–916.

Chytrý, M., Danihelka, J., Kaplan, Z., Wild, J., Holubová, D., Novotný, P., Pyšek, P., 2021. Pladias Database of the Czech Flora and Vegetation. Preslia 93, 1–87.

Clarke, P.J., Lawes, M.J., Midgley, J.J., 2010. Resprouting as a key functional trait in woody plants – challenges to developing new organizing principles. New Phytol. 188 (3), 651–654.

Clarke, P.J., Lawes, M.J., Midgley, J.J., Lamont, B.B., Ojeda, F., Burrows, G.E., Enright, N.J., Knox, K.J.E., 2013. Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. New Phytol. 197, 19–35. https://doi.org/10.1111/nph.12001.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Steege, H.T., Morgan, H.D., Heijden, M.G.A.V.D., Pausas, J.G., Poorter, H., 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Aust. J. Bot. 51 (4), 335.

Díaz, S., Cabido, M., Casanoves, F., 1998. Plant functional traits and environmental filters at a regional scale. J. Veg. Sci. 9, 113–122. https://doi.org/10.2307/3237229.

Fitter, A.H., Hay, R.K.M., 2002. Environmental physiology of plants, 3rd Ed. Academic, London.

Forseth, T., Harby, A. 2014. Handbook for environmental design in regulated salmon rivers. NINA Special Report, 53. Trondheim, Norway.

Frye, J., Grosse, W., 1992. Growth responses to flooding and recovery of deciduous trees. Zeitschrift für Naturforschung C 47, 683–689. https://doi.org/10.1515/znc-1992-9-1008.

Gerardin, T., Douthe, C., Flexas, J., Brendel, O., 2018. Shade and drought growth conditions strongly impact dynamic responses of stomata to variations in irradiance in *Nicotiana tabacum*. Environ. Exp. Bot. 153, 188–197.

Gorla, L., Signarbieux, C., Turberg, P., Buttler, A., Perona, P., 2015. Effects of hydropeaking waves' offsets on growth performances of juvenile *Salix* species. Ecol. Eng. 77, 297–306. https://doi.org/10.1016/j.ecoleng.2015.01.019.

Greenway, H., Armstrong, H.W., Colmer, T.D. 2006. Conditions leading to high CO2 (>5 kPa) in waterlogged-flooded soils and possible effects on root growth and metabolism. Annals of Botany, 98, 9–32. doi:10.1093/aob/mcl076.Grime, J.P., Hodgson, J.G., Hunt, R. 1988. Comparative Plant Ecology. A Functional Approach to Common British Species, 1st Ed, Unwin Hyman Ltd. London.

Grime, J.P., 1988. The CSR model of primary plant strategies—origins, implications and tests. Plant evolutionary biology 371–393.

He, N., Liu, C., Piao, S., Sack, L., Xu, L.i., Luo, Y., He, J., Han, X., Zhou, G., Zhou, X., Lin, Y.i., Yu, Q., Liu, S., Sun, W., Niu, S., Li, S., Zhang, J., Yu, G., 2019. Ecosystem traits linking functional traits to macroecology. Trends Ecol. Evol. 34 (3), 200–210.

Hultén, E., Fries, M. 1986. Atlas of north European vascular plants north of the Tropic of Cancer. 3 vols. Koeltz Scientific Books, Königstein, Federal Republic of Germany.

Johansson, M., Nilsson, C., 2002. Responses of riparian plants to flooding in free-flowing and regulated boreal rivers: an experimental study. J. Appl. Ecol. 39, 971–986. https://doi.org/10.1046/j.1365-2664.2002.00770.x.

Klimešová, J., Klimeš, L., 2007. Bud banks and their role in vegetative regeneration – a literature review and proposal for simple classification and assessment. Perspect. Plant Ecol. Evol. Syst. 8, 115–129.

Klimešová, J., Martínková, J., Ottaviani, G., Field, K., 2018. Belowground plant functional ecology: Towards an integrated perspective. Funct. Ecol. 32 (9), 2115–2126.

Lawes, M.J., Clarke, P.J., 2011. Ecology of plant resprouting: populations to community responses in fire-prone ecosystems. Plant Ecol. 212, 1937–1943.

Liu, C., Li, Y., Yan, P., He, N., 2021. How to improve the predictions of plant functional traits on ecosystem functioning? Front. Plant Sci. 12, 622260 https://doi.org/10.3389/fpls.2021.622260. PMID: 33633766; PMCID: PMC7901955.

Maberly, S.C., Spence, D.H.N., 1989. Photosynthesis and photorespiration in freshwater organisms: amphibious plants. Aquat. Bot. 34, 267–286.

Maczey, N. 2016. CABI Compendium. *Agrostis capillaris* (common bent). doi: 10.1079/cabicompendium.383.

Madsen, J.D., Chambers, P.A., James, W.F., Koch, E.W., Westlake, D.F., 2001. Hydrobiologia 444, 71–84. https://doi.org/10.1023/a:1017520800568.

Manzur, M.E., Grimoldi, A.A., Insausti, P., Striker, G.G., 2015. Radial oxygen loss and physical barriers in relation to root tissue age in species with different types of aerenchyma. Funct. Plant Biol. 42, 9. https://doi.org/10.1071/fp14078.

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., Yepez, E.A., 2008. Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? New Phytol. 178 (4), 719–739.

Naiman, R.J., Decamps, H., 1997. The ecology of interfaces: riparian zones. Annu. Rev. Ecol. Syst. 28, 621–658.

Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought and waterlogging of temperate northern hemisphere trees and shrubs. Ecol. Monogr. 76, 521–547. https://doi.org/10.1890/0012-9615(2006)076[0521: TTSDAW]2.0.CO;2.

Nunes, T.D.G., Zhang, D., Raissig, M.T., 2020. Form, development, and function of grass stomata. Plant J. 101 (4), 780–799.

Onoda, Y., Westoby, M., Adler, P.B., Choong, A.M., Clissold, F.J., Cornelissen, J.H., Yamashita, N., 2011. Global patterns of leaf mechanical properties. Ecol. Lett. 14, 301–312.

Palmquist, E.C., Ralston, B.E., Sarr, D., Merritt, D.M., Shafroth, P.B., Scott, J.A., 2017. Functional traits and ecological affinities of riparian plants along the Colorado River

in Grand Canyon. Western North American Naturalist 77. https://doi.org/10.5066/F7QV3JN1.
Paula, S., Pausas, J.G., 2006. Leaf traits and resprouting ability in the Mediterranean basin. Funct. Ecol. 20, 941–947.
Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J., Villar, R., 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. New Phytol. 182, 565–588. https://doi.org/10.1111/j.1469-8137.2009.02830. x.
Puijalon, S., Bouma, T.J., Douady, C.J., van Groenendael, J., Anten, N.P.R., Martel, E., Bornette, G., 2011. Plant resistance to mechanical stress: evidence of an avoidance–tolerance trade-off. New Phytol. 191, 1141–1149. https://doi.org/10.1111/j.1469-8137.2011.03763.x.
Pukkala, T., Vettenranta, J., Kolström, T., Miina, J., 1994. Productivity of a mixed Scots pine-Norway spruce stand. Scandnavian Journal of Forest Research 9, 143–153.
Raunkiær, C., 1934. The life forms of plants and statistical plant geography. University Press, Oxford.
Riis, T., Olesen, B., Clayton, J.S., Lambertini, C., Brix, H., Sorrell, B.K., 2012. Growth and morphology in relation to temperature and light availability during the establishment of three invasive aquatic plant species. Aquat. Bot. 102, 56–64.
Sack, L., Scoffoni, C., 2013. Leaf venation: structure, function, development, evolution, ecology, and applications in the past, present and future. New Phytol. 198, 983–1000. https://doi.org/10.1111/nph.12253.
Sato, T., Harada, T., Ishizawa, K., 2002. Stimulation of glycolysis in anaerobic elongation of pondweed (Potamogeton distinctus) turions. J. Exp. Bot. 53, 1847–1856.
Schnitzler-Lenoble, A., 2007. Forêts alluviales d'Europe. Tec et Doc, Lavoisier, Paris.
Solomentseva, A.S., Kolmukidi, S.V., Lebed, N.I., Mezhevova, A.S., Berestneva, Y.V., Bikmetova, K.R., Isakov, A.S., 2020. IOP Conf. Series: Earth and Environmental. Science 579, 012056. https://doi.org/10.1088/1755-1315/579/1/012056.
Speck, O., 2003. Field measurements of wind speed and reconfiguration in *Arundo donax* (Poaceae) with estimates of drag forces. Am. J. Bot. 90, 1253–1256.
Stace, C., 1997. New flora of the British Isles, 2nd Ededitioned. Cambridge University Press, Cambridge.
Štech, M., Koutecký, P., Tribsch, A., Schratt-Ehrendorfer, L., Paszko, B., Pachschwöll, C., 2020. *Calamagrostis purpurea* (Poaceae) – A long neglected boreal element, new for the flora of Austria. Neilreichia 11, 133–152. https://doi.org/10.5281/zenodo.4016760.
Valladares, F., Gianoli, E., Gómez, J.M., 2007. Ecological limits to plant phenotypic plasticity. New Phytol. 176, 749–763.
Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! Oikos 116, 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559. x.
Visser, E.J.W., Bögemann, G.M., Van de Steeg, H.M., Pierik, R., Blom, C.W.P.M., 2000. Flooding tolerance of Carex species in relation to field distribution and aerenchyma formation. New Phytol. 148 (1), 93–103. https://doi.org/10.1046/j.1469-8137.2000. 00742.x.
Weitkamp, D.E., 2008. Total Dissolved Gas Supersaturation Biological Effects, Review of Literature 1980–2007. Parametrix, Bellevue.
Xiong, S., Nilsson, C., Johansson, M.E., Jansson, R., 2001. Responses of riparian plants to accumulation of silt and plant litter: the importance of plant traits. J. Veg. Sci. 12, 481–490.
Young, P.S., Cech, J.J., Thompson, L.C. 2011. Hydropower-related pulsed-flow impacts on stream fishes: a brief review, conceptual model, knowledge gaps, and research needs.Reviews in Fish Biology and Fisheries, 21, 713–731. doi: 10.1007/s11160-011- 9211-0.