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Functional diversity as indicator of ecosystem functioning in Mediterranean riparian forests

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THESIS PRESENTED TO OBTAIN THE DOCTOR DEGREE IN
FORESTRY ENGINEERING AND NATURAL RESOURCES

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To my family…

List of papers

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Functional diversity assessment in riparian forests – multiple approaches and trends: a review
Ecological Indicators, 95, 781–793.
https://doi.org/10.1016/j.ecolind.2018.08.039
Chapter II

2) Lozanovska, I., Ferreira, M.T., Segurado, P., & Aguiar, F.C. (2018)
Limited resilience in hotspots of functional richness: the Mediterranean riparian shrublands
Aquatic Sciences, 80, 1–12.
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Chapter III

3) Lozanovska, I., Bejarano, M.D., Martins, M.J., Nilsson, C., Ferreira, M.T., & Aguiar, F.C. (2020)
Functional diversity of riparian woody vegetation is less affected by river regulation in the Mediterranean than boreal region
Frontiers in Plant Science, 11:857.
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Chapter IV

4) Lozanovska, I., Rivaes, R., Vieira, C., Ferreira, M.T., & Aguiar, F.C.
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Chapter V

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Abstract

Riparian forests are ecosystems of high biodiversity and complexity driven by diverse environmental factors and increasingly threaten by anthropogenic pressures. Understanding and predicting vegetation responses to these factors have become one of the most challenging tasks in riparian ecology. This thesis aims to analyze the functional diversity responses of the Mediterranean riparian forests affected by multiple stressors to give insights into ecosystem functioning. The specific objectives were: (i) to assess the worldwide application of functional trait-based approaches in riparian forests; (ii) to determine the key habitat and regional environmental factors that influence the functional diversity of different forests; (iii) to assess the functional diversity patterns of aquatic plants and riparian woody vegetation to streamflow regulation. The results showed that the functional diversity concept has a long history of evolution. Its application to riparian forests has been increasing in the last two decades, with guild approaches becoming more popular than functional diversity indices. Functional richness is the most applied index in riparian plant studies. Amongst the environmental key-factors, precipitation plays a determinant role on the functional diversity of Mediterranean riparian forests, though especially pronounced for Mediterranean shrublands due to their low functional redundancy. Streamflow regulation can foster diverse stress-related functional strategies in contrasting biomes (boreal and Mediterranean), resulting in diverse functional diversity patterns. This result is likely related to a long legacy of adaptations to natural hydrological stress and to the magnitude of streamflow regulation. Further, diverse types of streamflow regulation (run-of-river dams and storage reservoirs) impair differently the cover and functional diversity of bryophytes, vascular macrophytes and riparian woody vegetation. The observed patterns of functional diversity can inform on the conservation status of the Mediterranean riparian forests and allow anticipating the vulnerability of the riparian ecosystems to future changes, which can guide mitigation, conservation or restoration plans.

Keywords: functional diversity, riparian forests, environmental factors, river regulation, Mediterranean biome

Resumo

As florestas ribeirinhas são ecossistemas de elevada biodiversidade e complexidade, influenciados por diversos fatores ambientais e sujeitos a crescentes pressões antropogénicas. Compreender e prever a resposta da vegetação face a estas alterações é uma das tarefas mais desafiantes atuais da ecologia ripária. Esta dissertação centra-se no estudo das respostas da diversidade funcional em florestas ripárias Mediterrânicas influenciadas por múltiplos fatores, com o objetivo de compreender o funcionamento destes ecossistemas. Os objetivos específicos são: (i) conhecer a aplicação das aproximações funcionais em florestas ripárias no mundo; (ii) a determinação dos principais fatores ambientais regionais e de habitat que influenciam a diversidade funcional de diferentes tipos de florestas ripárias; (iii) avaliar e prever as respostas e alterações na diversidade funcional da vegetação aquática ribeirinha devido à regularização de caudais. Os resultados permitiram reconhecer um longo historial de evolução do conceito de diversidade funcional, bem como a sua crescente utilização em estudos de vegetação ribeirinha nas últimas duas décadas. As metodologias baseadas em guildas são presentemente mais utilizadas que os índices de diversidade funcional, nos quais a riqueza funcional o índice mais utilizado. Entre os fatores ambientais-chave, a precipitação tem uma importância fundamental na diversidade funcional em todos os tipos de florestas mediterrânicas, embora com particular relevância nos matos ripários Mediterrâneos devido à sua baixa redundância funcional. A regularização pode mediar diversas estratégias adaptativas em diferentes biomas (boreais e Mediterrâneos), originando diversos padrões funcionais. Este resultado está provavelmente relacionado com um longo legado de adaptações desenvolvidas pelas florestas ribeirinhas para suportar o stress hidrológico natural, e com a magnitude das alterações hidrológicas. Diversos tipos de regularização por barragens (fio-de-água e armazenamento) têm diferentes impactos na abundância e na diversidade funcional de briófitos, macrófitos vasculares e vegetação lenhosa ripária. Os padrões de diversidade funcional permitem conhecer o estado de conservação das florestas ripárias mediterrânicas, e antecipar a vulnerabilidade destes ecossistemas a alterações futuras, contribuindo para planos de mitigação, conservação ou restauro.

Palavras-chave: diversidade funcional, floresta ripária, fatores ambientais, regularização, Mediterrâneo

Resumo alargado

As florestas ribeirinhas são ecossistemas de grande biodiversidade e complexidade dependentes da variabilidade hidrológica natural, e influenciados por diversos fatores ambientais e de perturbação. Consideradas como um pilar dos ecossistemas fluviais, as florestas ribeirinhas estão relacionadas tanto com o fornecimento de matéria orgânica, como a retenção de sedimentos, ou a provisão de alimentos e abrigo para a fauna e flora. No entanto, tem-se assistido a alterações composicionais e funcionais das florestas ribeirinhas causadas por perturbações humanas que podem modificar o funcionamento destes ecossistemas e, consequentemente comprometer os serviços que providenciam. Desta forma, compreender e prever os padrões de vegetação em função de múltiplos agentes de perturbação antrópica tornou-se, atualmente, uma das tarefas mais desafiantes em ecologia ripária.

A utilização de medidas de diversidade funcional é cada vez mais frequente em investigação ecológica, permitindo compreender e prever as respostas da vegetação face às alterações e tirar conclusões sobre o funcionamento dos ecossistemas. De facto, a diversidade funcional pode ser associada à estabilidade, resistência e resiliência da vegetação ribeirinha. No entanto, a relevância da utilização destas medidas de diversidade nas florestas ribeirinhas encontra-se ainda largamente inexplorada.

Esta tese centra-se nas respostas de diversidade funcional das florestas ribeirinhas mediterrânicas a agentes de perturbação regionais e de habitat, bem como à perturbação originada pela regularização fluvial na vegetação aquática e ribeirinha.

O primeiro estudo da tese apresenta uma visão geral dos conceitos fundamentais da diversidade funcional e analisa a sua evolução temporal desde o aparecimento da primeira classificação da vegetação com base em características funcionais. Apresenta

uma revisão da utilização das abordagens baseadas em atributos funcionais em florestas ribeirinhas de todo o mundo, bem como o número e tipo de atributos funcionais utilizados, objetivos dos trabalhos realizados, distribuição geográfica e as perspetivas de investigação futuras.

O segundo estudo centra-se na avaliação da diversidade funcional de quatro tipos de florestas ribeirinhas mediterrânicas (amiais, freixiais, urzais e matos mediterrânicos) com base em troços fluviais com bom estado de conservação localizados em Portugal Continental. Neste trabalho, caracterizam-se as florestas ribeirinhas segundo atributos morfológicos, fenológicos, fisiológicos e reprodutivos e relacionam-se os múltiplos filtros ambientais (variáveis regionais e de habitat) com a diversidade funcional. A diversidade funcional é representada pela riqueza e redundância funcionais – aspetos funcionais relacionados com a estabilidade, resistência e resiliência dos ecossistemas. Desta forma, é possível listar os principais filtros ambientais que, em última análise, poderão estar relacionados com a vulnerabilidade dos tipos de floresta a futuras perturbações.

No terceiro estudo, compara-se o efeito da regularização na vegetação ripária entre rios boreais (caso de estudo Suécia) e mediterrânicos (Portugal), usando a presença/ausência das espécies lenhosas ribeirinhas. Com este propósito é determinada a riqueza e a redundância funcional em locais regularizados e não regularizados, com base em nove atributos funcionais relacionados com o escoamento. Discute-se ainda se a regularização de caudais em dois biomas com legados de adaptações de plantas e constrangimentos ambientais distintos poderia levar a padrões ecológicos semelhantes de diversidade funcional na vegetação ribeirinha lenhosa.

No quarto e último estudo, avaliam-se os padrões de diversidade funcional da vegetação aquática e ribeirinha lenhosa em dois rios mediterrânicos perturbados por diferentes formas de regularização (barragem fio-de-água e de albufeira). Pretende-se compreender como os diferentes grupos de plantas (macrófitas, briófitas e ribeirinhas lenhosas) respondem à perturbação a jusante das barragens ao longo do rio e transversalmente à zona ribeirinha. Outro objetivo é a determinação do grau de regularização (DOR) e a distância à barragem (DFD), onde a regularização fluvial deixa de afetar significativamente as comunidades estudadas. Para estas finalidades recorreu-se a uma abordagem de guildas (grupos de espécies com atributos funcionais semelhantes) e a modelos lineares para antever as alterações dessas guildas, comparativamente com os locais não regularizados, ao longo do gradiente de DOR e DFD.

Os resultados da revisão sobre a diversidade funcional mostram que o conceito tem uma existência longa, e com um aumento da aplicação em florestas ribeirinhas nas últimas duas décadas. Estes trabalhos procuraram principalmente avaliar a hidrologia como um elemento-chave condutor da vegetação ribeirinha. Os estudos mostram a existência de similaridades no tipo de atributos usados nos vários trabalhos, sendo os morfológicos e anatómicos facilmente mensuráveis (tais como área foliar específica, altura da planta e massa da semente) mais utilizados que os fisiológicos. Ainda assim, foi visível uma grande variação no número de atributos em cada estudo (variando entre 1 a 36 atributos), com média compreendida entre oito e nove atributos. A riqueza funcional é o índice de diversidade mais frequentemente utilizado em estudos de diversidade de florestas ripárias. Contudo, este índice tem sido associado a outros índices tal como a uniformidade funcional, a divergência funcional, a dispersão funcional, ou a redundância funcional, que se focam noutros atributos funcionais ao invés do espaço funcional ocupado pelas espécies. Novas abordagens estão a emergir, procurando melhorar as ligações entre as redes ecológicas existentes com as interações bióticas e abióticas, embora algumas orientações sobre o tipo e número de atributos funcionais, ou a seleção de métricas funcionais, ainda estejam em debate.

O estudo comparativo de diversidade funcional de florestas mediterrânicas revelou uma maior riqueza funcional e uma mais baixa redundância funcional dos matos mediterrânicos em comparação com os outros tipos de florestas ribeirinhas. Ambos os filtros regionais e de habitat foram preditores importantes de diversidade funcional nos tipos de floresta estudados, embora a precipitação tenha sido o fator mais frequentemente selecionado nos vários modelos. Assim, face às previsões das alterações climáticas com diminuição e alteração na frequência e sazonalidade da precipitação na área estudada, todas as florestas ribeirinhas serão afetadas. No entanto, os matos mediterrânicos são os mais vulneráveis, devido à reduzida proporção de atributos compensatórios (baixa redundância funcional) que atenuem estas perturbações.

No estudo sobre efeitos da regularização fluvial na diversidade funcional da vegetação ribeirinha lenhosa em dois biomas distintos, concluiu-se que tanto os fatores ambientais como a regularização influenciam a vegetação lenhosa ribeirinha. Não obstante, a extensão das alterações funcionais diferiram entre o bioma mediterrânico e o boreal, sendo apenas significativo na Suécia. Aí, a regularização reduziu efetivamente a riqueza e redundância funcionais, favorecendo espécies ribeirinhas de pequeno porte com folhas de pequena dimensão, caules pouco lenhificados, e sistemas radiculares pouco profundos, como adaptações para lidar com as alterações do escoamento do rio. Por oposição, no bioma Mediterrânico, os valores de diversidade funcional não foram significativamente diferentes entre rios regularizados e não regularizados. As diferenças nos resultados podem estar relacionadas com a contribuição mútua da adaptação dos atributos à perturbação hidrológica natural em rios não regularizados da região mediterrânica, e à menor grandeza das variações de caudal em Portugal. Para além disso, o estudo não incluiu medidas de abundância de espécies, o que é relevante no caso dos ecossistemas ribeirinhos mediterrânicos.

No estudo de regularização fluvial em dois casos de estudo (fio-de-água, Rio Lima e albufeira, Rio Alva), observou-se uma modificação da cobertura de plantas mas não uma perda de guildas a jusante das barragens. Similarmente ao estudo anterior, as adaptações dos atributos mediaram a resposta da diversidade funcional das comunidades macrófitas e ribeirinhas lenhosas estudadas. O aumento da abundância destas comunidades relaciona-se com a adaptação ao escoamento, isto é à presença de atributos funcionais adaptados a perturbação hidrológica. À exceção da guilda composta pela espécie *Fontinalis*, a abundância de briófitos não foi alterada significativamente com a regularização. Os tipos de regularização influenciaram a abundância de plantas aquáticas e ribeirinhas, com mais alterações na barragem de armazenamento (albufeira) comparativamente com o caso de estudo de barragem a fio-de-água. Foi notória a invasão do canal ativo do rio pela vegetação, motivada pela barragem de albufeira, e uma expansão para o exterior da zona ribeirinha a jusante da

barragem a fio-de-água. As alterações estarão provavelmente relacionadas com as condições ecológicas espoletadas pelo tipo de regularização, nomeadamente, cheias repentinas e disponibilidade de água suficiente nos rios originadas pela barragem fio-de-água em comparação com os caudais de cheia reduzidos e menores escoamentos a jusante da barragem de albufeira.

A avaliação da diversidade funcional proporcionou uma visão geral sobre os padrões funcionais da vegetação ribeirinha em todo o mundo (Capítulo II) e particularmente em Portugal (Capítulo III, IV, V). Demonstrou-se que o legado das adaptações relacionadas com o escoamento pode mitigar até certo ponto os efeitos da regularização (Capítulo IV, V) embora acompanhados por diversas grandezas de mudança relacionadas com as modificações de caudal (Capítulo IV), assim como com as alterações hidrológicas e fluviais induzidas pelos diferentes tipos de regularização (Capítulo V). Todavia, em circunstâncias de diversidade funcional reduzida, a vegetação ribeirinha pode ser mais vulnerável a perturbações complementares (Capítulo III).

De um modo geral, as conclusões desta tese permitem uma melhor perceção do funcionamento dos ecossistemas ribeirinhos, permitindo-nos prever as trajetórias potenciais deste em resultado de impactos antropogénicos adicionais. Os resultados obtidos podem dar apoio na orientação de práticas de conservação e gestão com vista à manutenção da diversidade da vegetação ribeirinha. Contribuem na priorização de ações de restauro de comunidades aquáticas e ribeirinhas ou troços de rio sob maior impacte, com o objetivo global de melhorar o funcionamento dos ecossistemas ribeirinhos e a distribuição de serviços dos ecossistemas.

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List of Abbreviations

AIC	Akaike's information Criterion
ANOVA	Analysis of variance
CPOM	Coarse Particulate Organic Matter
CWM	Community Weighted Mean
DFD	Distance from Dam
DOR	Degree of Regulation
FAD	Functional Diversity Attribute
FD	Functional Diversity index
FDc	Community-based Functional Diversity
FDis	Functional Dispersion
FDiv	Functional Divergence
FEve	Functional Evenness
FR; FRed	Functional Redundancy index
FRic	Functional Richness
FRO	Functional Regularity index
HSD	Honestly Significant Difference
LDMC	Leaf Dry Matter Content
MFAD	Modified Functional Attribute Diversity index
MST	Minimum Spanning Tree
PFT	Plant Functional Types
PCA	Principal Component Analyses
Q	Rao index
SES	Standardized Effect Size
SLA	Specific Leaf Area
wFDc	Extended Functional Diversity

Chapter I.

Introduction

Background

The world's ecosystems are experiencing natural and anthropogenic impacts that affect biological communities causing unprecedented biodiversity loss (Dornales, 2010). These changes may alter the functioning of ecosystems and jeopardize the goods and services provided to humanity (Mouillot et al., 2013). Consequently, predicting ecosystem responses to multiple natural stressors and human disturbances has become one of the most challenging tasks for scientists to guide conservation proposals and management of natural resources.

Riparian ecosystems and riparian vegetation

Riparian ecosystems are transitional semiterrestrial areas, extending from the edges of water bodies to the edges of upland communities. Because of their spatial position, they integrate interactions between the aquatic and terrestrial components of the landscape (Naiman et al., 2005). Despite that riparian ecosystems only cover small proportions of the landscapes, they are unusually rich in species, making them in terms of species diversity one of the richest ecosystems (Naiman and Decamps, 1997).

Riparian vegetation consists of diverse plant communities growing on stream banks along the river channels, variously adapted to benefit the dynamic nature of rivers and to deliver multiple ecosystem services. The delivered ecosystem services are discussed in the global overview of riparian vegetation linked to the provision of genetic material by seeds, spores and wildflowers; flow regulation by physically slowing the water, absorbing it or increasing the rates of evapotranspiration; erosion control by protecting soils against surface erosion and strengthen their resistance to destabilization; nutrient cycling by providing annual litterfall; water filtration by nutrients retention from agricultural runoff waters, thus counteracting the enrichment of rivers by phosphorus or nitrogen; refugia and habitats for many species (Riis et al., 2020).

Concerning the aquatic environment, riparian canopies affect microclimates by controlling wind speed and reducing light penetration by shading, hereby limiting increases in water temperature during the summer and reduce algal and macrophyte growth. Further, riparian woody debris within the active channel can act as a substrate for colonization, protecting young macrophytes from flood scour, and providing nutrients and moisture at critical times (Gurnell et al., 2001).

Unfortunately, due to the anthropogenic influence on riparian vegetation (Dufour et al., 2019), it is not an exception to the general trend of biodiversity loss (Tockner and Stanford, 2002).

The zonation of riparian vegetation within riparian ecosystems reflects species' differences along the hydrologic gradient, with trade-offs between adaptations to drought tolerance and aeration during submergence. Along Mediterranean rivers and streams, the zonation goes laterally, from agricultural and forest areas or Mediterranean shrublands to the riparian zone. Examples of willow and alder forests in Portugal are shown in Figure 1. According to the hydrological conditions of the water bodies, described zonation by Costa *et al.* (2011), Amigo *et al.* (2017), Espírito-Santo *et al.* (2017) is the following:

- on relatively permanently waterlogged soils with some degree of peat formation, woodlands are dominated by alder (*Alnus glutinosa*) or by grey willow (*Salix atrocinerea)* with the presence of macrophytes - Portuguese tussock sedge (*Carex paniculata* subsp. *lusitanica*), *Iris pseudacorus*, *Sparganium* sp., *Phragmites australis, Schoenoplectus tabernaemontani* and *Thelypteris palustris*;
- on perennial rivers with moderately irregular flow, riparian forests are dominated by narrow-leaved ash (*Fraxinus angustifolia*);
- on a temporary water-table with almost no waterlogging *Fraxinus angustifolia* might be co-dominated by *Quercus pyrenaica*;
- in torrential rivers, a shrubby willow *Salix salviifolia,* endemic for Iberian Peninsula, is found;
- on slow-moving waters at the mouth of large rivers, riparian forests are dominated by *Salix neotricha*, *Populus nigra* and *Populus alba* instead of alder forests;
- Mediterranean rivers with very irregular flow or brackish waters: (i) tall-scrub formations of *Nerium oleander* and *Tamarix africana* in riverbeds with irregularly flowing freshwater; (ii) *Flueggea tinctoria* on the rocky margins of large Mediterranean rivers that are temporarily inundated in winter and dry throughout the rest of the year; (iii) *Tamarix africana* dominated communities on mesotrophic slow-moving brackish waters in estuaries;
- upstream of rivers of mountainous areas of central Portugal over rocky substrates tall shrub communities dominated by white heather (*Erica arborea*) and alder buckthorn (*Frangula alnus*) are found.

Figure 1. Riparian forests in northern Portugal: willow forests (top), and alder forests (bottom). (Photo credits: Ivana Lozanovska and Rui Rivaes).

Riparian vegetation response to multiple stressors and disturbances

Riparian vegetation responds to environmental factors such as climate (precipitation, temperature), flow, geomorphology (Stella et al., 2013; Gurnell et al., 2015; Janssen et al., 2018). Therefore, environmental changes (global warming), and direct anthropogenic disturbances related with flow regulation and land use (Dufour et al., 2019) may modify streamflow and fluvial hydromorphology, and thus trigger compositional, diversity and functional alterations in riparian plant communities (Aguiar et al., 2009; Rivaes et al., 2013).

Main environmental factors for riparian vegetation

Flow is recognized as the main abiotic factor which governs riparian vegetation composition, structure, and abundance and the overall quality of the riparian zone (Poff et al., 2007; Belmar et al., 2013). The flow attributes – magnitude, frequency, duration, timing and rate of change, control flow fluctuations (i.e. inter-annual/intra-annual variability - low flow and floods) and fluvial disturbances consequently, having an impact on riparian vegetation establishment, growth, mortality and succession (Merritt et al., 2010; Corenblit et al., 2010; Martínez-Fernández et al., 2016). For instance, low flow periods in summer represent the major growth time for riparian plants provided that there is sufficient precipitation to avoid water stress (Stella and Battles, 2010; González et al., 2012), whereas, seasonal flooding promotes channel dynamics, sediment, and organic debris deposition, promoting seeds delivery and regeneration (Cooper et al., 2003; Camporeale et al., 2013). However, prolonged flooding can cause waterlogging of the root zone and/or complete submergence of aboveground plants, obstructing gas exchange (Catford and Jansson, 2014).

In European Mediterranean regions, besides the flow importance for riparian vegetation dynamics, attention should be also paid to land-use, since in some cases this disturbance may even outcompete hydrology (Fernandes et al., 2011; Aguiar et al., 2016, 2018).

Local geomorphic characteristics such as geology, channel confinement and channel slope (Higgins et al., 2005; Magdaleno and Fernández-Yuste, 2011b) are also important factors determining riparian vegetation diversity (Aguiar et al., 2013a; Hough-Snee et al., 2015; Janssen et al., 2018). In that sense, the physical setting of a river will influence how the flow regime is translated into the hydraulic habitats experienced by, and available to, the riverine biota (Poff et al., 2010). For instance, a wide river channel with slow flows is often developed on deposits of fine material (fine sand, silt, and clay). In contrast to a narrow channel, with a steep slope and rapid flow, which usually consists of a coarse riverbed with the bank material composed by cobbles and boulders. Coarse substrates potentially contain less stagnant water because of a high turnover of oxygenated water relative to that of finer-textured soils. Accordingly, habitats with the coarser substrate are more resistant to anoxia during flooding, which might be important for plants during prolonged floods and associated waterlogging of the soil (Renofalt et al., 2007; González del Tánago et al., 2015). However, coarse-textured riverbeds have low moisture availability as a result of limited capillary action on coarse materials (McBride and Strahan, 1984) and coupled with confined channel results in high shear stresses and potential scouring thus constraining seedling rooting and survival (Bejarano et al., 2012b).

To which extent riparian plant species can be promoted or disfavoured under the prevailing environmental constraints depends on their morphological, physiological, and phenological functional attributes so-called functional traits (Violle et al., 2007). Those functional attributes reflect the outcome of evolutionary and community assembly processes responding to abiotic and biotic environmental constraints (Valladares et al., 2007) and enable plants to survive, exploit and even depend on those constrains (Lytle et al., 2017). In riparian vegetation context, a surplus of water requires plant adaptations to cope with inundation and waterlogging such as gas exchange facilitation with dissected leaves or/and thin cuticle (Mommer et al., 2007); or to avoid anoxia with shoot elongation or/and adventitious roots (Blom et al., 1999; Voesenek et al., 2004). Adaptations subjected to drought are related to optimizing water use efficiency and can be divided into facilitating water uptake such as deeper root depth (Schenk and Jackson, 2002); minimizing evapotranspiration through thick cuticles and small leaf areas (Maroco et al., 2000), reduced water use by decreased canopy height (Stromberg and Merritt, 2016), or/and high wood density (Lawson et al., 2015a). To ensure recolonization, vegetative reproduction (Barrat–Segretain, 1996), persistent seed banks (Thompson and Grime, 1979), increased seed buoyancy (Boedeltje et al., 2004), ability for hydrochory (Nilsson et al., 2010) which enable long-distance dispersal are beneficial.

Not all organisms can successfully establish and persist in all abiotic conditions, however, species that possess traits suitable for a given environment will continue to persist regardless of the drifting from optimal conditions (Kraft et al., 2015). If environmental conditions change, specific life-history strategies and traits will be selected for at a given location, leading to the new assembly of communities with morphological and physiological tolerances suited to a given environment (Keddy, 1992a). These changes contribute to riparian vegetation dynamics and the overall riverine ecosystem functioning.

River regulation effect on riparian vegetation

Rivers have been dramatically modified by humans and with the current operation of numerous large dams along with uncountable small hydropower plants, dams impair more than one-half of the large river systems in the world, regulating 83% of their total flow (Zarfl et al., 2015; Grill et al., 2019) (Figure 2). Dams affect the longitudinal, lateral and vertical dimensions of rivers through the creation of physical barriers that interfere with the river's hydrology and connectivity both upstream and downstream of the infrastructure (Nilsson et al., 2005). Consequently, negatively affecting an array of freshwater communities from plankton, benthos, to fish, birds, and aquatic and riparian flora (Wu et al., 2019), and ultimately compromising many functions and ecosystem services of rivers (Arthington et al., 2010).

Dams induce river morphological alterations such as a reduction in channel widening, which affects the regeneration of riparian species (González et al., 2018). Further, it homogenizes the flow which is fostering succession. Namely, in circumstances of reduced flooding disturbance, the bare riparian areas are colonized by pioneer vegetation, which is then progressively replaced by early successional species and finally by late-successional species (Garófano-Gómez et al. 2017). Moreover, river regulation reduces sediment load and alters sediment type, thus affecting the geomorphic dynamics (Lobera et al., 2015). The coarser sediments downstream of the dam have a decreased soil water-holding capacity consequently, hampering the survival of young seedlings (González et al. 2010). The dam's altered flows and fluvial disturbances are linked to reduced and simplified riparian functional diversity (Bejarano et al., 2017), and abundance shifts from obligate riparian trees to drought-tolerant species (Aguiar et al., 2018).

The magnitude of riparian vegetation alterations may vary depending on modified hydrological features (the regulation types, i.e. run-of-river and reservoir dam) (Schmutz and Moog, 2018), as well as on the species intrinsic adaptations to hydrological disturbances acquired during the evolutionary history (Balmford, 1996; Dynesius et al., 2004). Run-of-river dams used for hydropower production are subjected to hydropeaking, which involves rapid high within-day and day-to-day flow variation (Moog, 1993). Hydropeaking usually operates over a narrower portion of the river margin than does natural flow regime, exposing riparian habitats to frequent inundation. While natural flow regimes foster an unusually species-rich riparian vegetation, the repeated wetting and drying under hydropeaking exclude riparian plants that can only tolerate infrequent or short such events (Bejarano et al., 2018). Storage reservoir dams suppress, homogenize and alter the occurrence of the annual floods (Kondolf and Batalla, 2005; Aguiar et al., 2016; Tonkin et al., 2018). The lack of floods and fluvial disturbance lead to *terrestrialization* of the riverbanks (Rivaes et al., 2013; García de Jalón et al., 2019). Stored water during winter and spring and rising river flows during summer months disrupt plant establishment and growth since most plant species have lower flood tolerance during the growing season (Siebel and Blom, 1998).

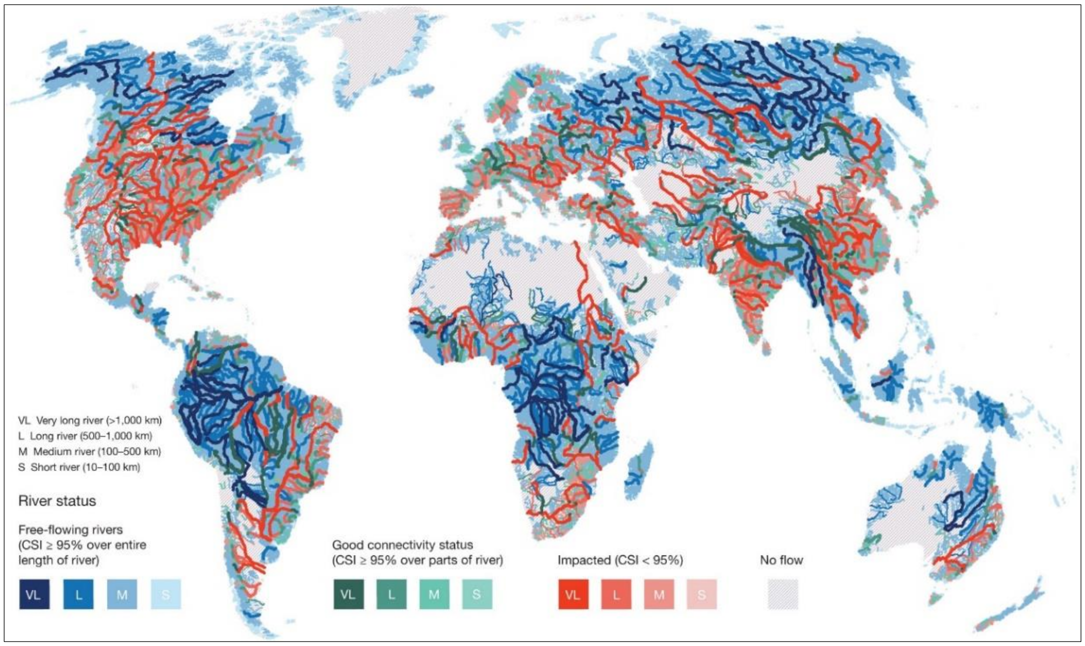

Figure 2. Map of the world’s free-flowing rivers. This map shows the global distribution of free-flowing rivers (blue color), contiguous river stretches with good connectivity status (green color) and impacted rivers with reduced connectivity (red color). Published Grill et al., 2019.

Challenges of riparian vegetation in the Mediterranean region

Rivers in the Mediterranean region reflect the principal attributes of the Mediterranean climate - seasonality, and variability of precipitation, therefore they are characterized with sequences of floods in autumn-winter and droughts over the summer (Gasith and Resh, 1999). In the semi-arid regions, small changes in precipitation can bring about large changes in generated surface runoff (Dahm and Molles, 1992; Belmar et al., 2019b), making differences in seasonal flow distribution and/or amount of precipitation to have important negative implications for riparian vegetation (Rivaes et al., 2013). Besides riparian vegetation, the projected water deficits in the Mediterranean region, is expected to affect the aquatic flora (Lefebre et al., 2019) and the associated functional traits (Manolaki et al., 2020).

River damming in the Mediterranean region has long been used to cope with the natural seasonality of precipitation (Hooke, 2006), placing the region among the most dammed in the world (Lehner et al., 2011). Differences between free-flowing and regulated river reaches are shown in Figure 3. Besides the intensive dam construction, the land-use change is found relevant in Mediterranean context. In the Mediterranean areas, both human-induced changes can interact or even exacerbate the natural stressors of the river ecosystems imposing the riparian vegetation to multiple pressures (Bruno et al., 2014; Fernandes et al., 2020). Although Mediterranean riparian vegetation to some level is naturally adapted to hydrological stress by suitable morphological and reproduction attributes (Santos, 2010), the riparian plant spatial composition, succession and functional distribution is compromised (Aguiar et al., 2001; 2016; 2018; González et al., 2010; 2012; Bejarano et al., 2012a; Martínez-Fernández et al., 2018).

Figure 3. Free-flowing river reach (left) at river Vez, regulated river reach while turbinating (right) at river Lima. (Photo credits: Ivana Lozanovska and Rui Rivaes).

Functional diversity – a link to ecosystem functioning

Functional traits determine how plants will respond to environmental stressors and anthropogenic disturbances (Carmona et al., 2017). The responses will further affect other trophic levels and overall biodiversity (Lavorel et al., 2013), resulting in cascade reactions that ultimately affect ecosystem functioning and derived benefits (Lavorel and Garnier, 2002; Díaz et al., 2004). Therefore, a focus on functional traits approaches can provide a basis for predictive ecology (McGill et al., 2006; Díaz et al., 2016). Recent advances in trait-based approaches showed that due to the ability for generalization across multiple species, communities, and entire ecosystems, it can answer a variety of ecological questions (Funk et al., 2017; Roos et al., 2019; Thonicke et al., 2020).

Functional diversity defined as ‘‘the value and range of the functional traits of the organisms in a given ecosystem’’ has emerged as a facet of biodiversity (Tilman, 2001) (Figure 4). Stress associated with environmental or anthropogenic impacts may trigger irreversible processes leading to rapid functional diversity shifts/declining, resulting in erosion of resilience of the ecosystems (Folke et al., 2004). However, high functional diversity appears to help prevent shifts to ecosystem states that are unable to sustain the desired level of ecosystem services (Elmqvist et al., 2003). The functional richness and functional redundancy represent two components of functional diversity that may be important for maintaining ecosystem functioning when facing disturbances (Mouillot et al., 2013). For instance, a combination of multiple, diverse traits (high functional richness) enables the ecosystem to cope better with various pressures (Tilman et al., 1997). In contrast, the decline of functional richness reduces ecosystem multifunctionality and may eventually lead to ecosystem degradation (Mori et al., 2013). Functional redundancy describes the situation when more than one species present similar species traits, and thus can compensate for species loss following disturbance (Walker, 1992; Angeler and Allen, 2016). The larger the number of functionally similar species in a community, the greater the probability that at least some of these species will survive changes in the environment hereby, sustaining the functionality of ecosystems (Naeem, 1998; Diaz and Cabido, 2001).

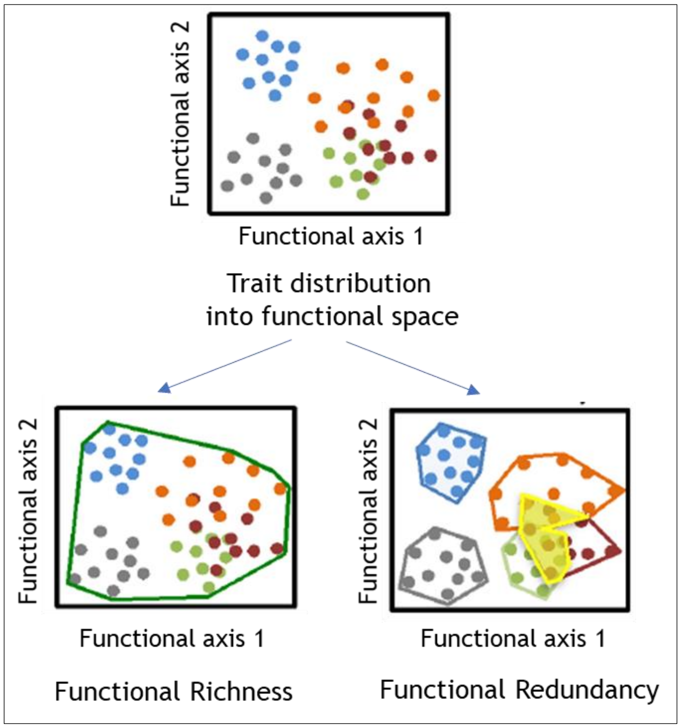

Figure 4. Traits distribution in functional traits space. Modified from Gutiérrez-Cánovas et al., 2015.

Aim and outline of the thesis

Global environmental effects are complex and entangled, and the increasing trend of river dams and human developments is a fact, therefore understanding and predicting the patterns of riparian vegetation is crucial. The present research is devoted to assessing the functional diversity of riparian forests in Portugal and the underlying factors which induce functional changes. We aimed to extend our knowledge of the relationship between riparian vegetation and the dominant environmental and flow-regulation factors. From the current functional diversity responses, the magnitude that factors affect functional diversity can be assessed and this outcome can help to predict future functional diversity trajectories. Overall the results can serve as an indicator of changes in riparian ecosystems' functioning.

To meet the general aim of the thesis we asked the following questions:

i) What are the key functional diversity concepts, their evolution, relevance and application in riparian forests?

ii) What is the pattern of functional diversity in riparian forests in Portugal and how does it change along with environmental factors?

iii) Are functional diversity responses of riparian woody vegetation from contrasting biomes (boreal and the Mediterranean) similar?

iv) How do multiple vegetation groups - vascular macrophytes, bryophytes and riparian woody vegetation - respond to disturbance along the river and across the riparian zone downstream of dams?

This doctoral thesis is divided into seven chapters and four appendices. Four of these chapters (**Chapters II**, **III**, **IV**, and **V**) are self-contained manuscripts that comprise the research work originally elaborated regarding the development of a specific topic. These chapters were written as independent articles so they may contain similar information in terms of theoretical background, site description and methodological approach. The text, figures, and tables of each of these articles are reproduced entirely identical to the published version, but the formatting was necessary to adapt them to the rest of the thesis. General discussion for the observed results and trends was given in **Chapter VI**. Finally, main conclusions described in the previous chapters, as well as perspectives for further research, were presented in **Chapter VII.** All references have been compiled in just one chapter to avoid repetition.

Essential background for understanding the issues tackled in this thesis, the main aim, and specific research objectives are provided in **Chapter I**

Functional diversity frameworks as assessment tools in riparian forests were described in **Chapter II.** An overview of the utilized functional diversity measures worldwide was presented. The specific topics were: timeline of the functional diversity concepts, methods and their application in riparian forests; the justification and use of plant functional traits; the main drivers of change in functional diversity and provides future research directions.

Functional diversity of the main riparian forest types in Portugal - Alder woodlands, Ash woodlands, Tree-heath shrublands and Mediterranean shrublands were investigated in **Chapter III**. Regional and habitat environmental variables were used for predicting potential functional change (functional richness and redundancy) in those riparian forest' types.

River regulation as one of the biggest anthropogenic disturbance for riparian woody communities was assessed in **Chapter IV** and **V**.

In **Chapter IV**, the functional diversity changes (functional richness and redundancy, and flow-related traits) in riparian forests as affected by streamflow regulation in boreal and Mediterranean biomes were assessed.

The effect of Degree-of-regulation (DOR) and distance from the dam (DFD) where river regulation no longer significantly affects plant communities in two different regulation types – a run-of-river dam and a reservoir dam were analyzed in **Chapter V**.

References from all chapters are brought together in a single chapter.

Appendices comprise information that was included as supplementary material in each article.

Chapter II.

Functional diversity assessment in riparian forests – multiple approaches and trends: a review

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Abstract

Measures of functional diversity are increasingly being used in ecological research to understand and predict vegetation ecosystem changes. However, there is currently no summary of how, why and where these indicators have been used in riparian forest studies around the world. The present article addresses the key concepts and their evolution across time and reviews the relevance of the use and application of functional trait-based approaches in riparian forests in the last two decades (1997–2017; 70 SCI articles). Our overview contains five sections: I. Evolution of concepts, applications, and methods; II. Functional diversity measures: application in riparian forests; III. Plant functional traits: which traits, how many and why; IV. Functional diversity responses and drivers of change; and V. Future research directions. It would appear that the advances in functional diversity frameworks in the last 20 years have led to an increase in the number of studies using riparian plant guilds and functional diversity indices, with a widespread distribution across Europe and the USA. The use of easily measurable ('soft') traits is more prevalent than that of 'hard traits' consisting of direct measurements of individual processes. Specific Leaf Area (SLA), plant height, and seed mass were the most common traits used in riparian studies. The number of traits per case study varied greatly, ranging from 1 to 36 traits (median=6), most of which were selected with the goal of describing ecosystem processes. Among the functional diversity indices, Functional Richness was the most common metric, usually coupled with indices that incorporate trait abundances such as Functional Evenness, Functional Divergence, Functional Dispersion, Rao, and Functional Redundancy. Future research should seek to integrate ecological networks and connectivity in such a way as to produce guidance with regard to trait selection, applications to large spatial scales, and comparable frameworks (guilds, index values) across regions. Novel approaches are emerging in this field of science, seeking to improve both the connection to both prevailing ecological networks and biotic and abiotic interactions.

Keywords: Concepts, evolution, functional diversity indices, guilds, traits, riparian forests

Introduction

The use of functional traits and measures of functional diversity to quantify and/or represent the diversity of species niches or functions is increasingly serving to link species to ecosystem functioning and its dynamics (Díaz et al., 1999). The frequency of distribution of functional traits that are important to community assembly processes means that functional diversity can also account for biotic interactions (McGill et al., 2006). In addition, it has been suggested that prediction of the relationship between biodiversity and ecosystem functioning can be improved by focusing on the diversity of functional attributes rather than on taxonomic diversity (Hooper et al., 2005; Mokany et al., 2008; Gagic et al., 2015).

The functional attributes of plants are determined by the latter's distinctive strategies manifested as functional traits (Violle et al., 2007), which vary according to abiotic factors in the environment, thereby providing insights into the prevailing local environmental filters. This can help anticipate which species from a regional pool might colonize and survive in a given area (Keddy, 1992a). For instance, it is predicted that in the tropics, the warmer temperatures and less precipitation in future climate-change scenarios will support shorter trees with smaller leaves (Madani et al., 2018). Besides trait variation due to abiotic factors, biotic factors such as facilitation or competition should be taken into account as well (Kraft et al., 2015). Otherwise, it is difficult to assess whether trait variation it is a result of abiotic tolerance of species or it is a result of biotic interaction. In the case of ecosystem functions, the use of functional diversity relies on the extent to which organisms extract resources from the environment (McGill et al., 2006) and on the species coexistence (Kraft et al., 2015). As the diversity of functional traits increases, the ecosystem increases both its portion of the total available resources and thus the efficiency with which those resources are used (Díaz and Cabido, 2001). This in turn determines the stability of the ecosystem, enabling it to serve as a buffer against abiotic variation (Walker et al., 1999) and resist invasions (Mason et al., 2005). By assessing the functional diversity in natural communities, researchers improve their understanding of the spatial and temporal distribution of biodiversity, and this can ultimately facilitate conservation prioritization (Petchey and Gaston 2002; Devictor et al., 2010). At the same time as recognition of the concept of functional diversity is growing (Petchey et al., 2004; Flynn et al., 2011), various new indicators have appeared, such as functional diversity indices and the distribution of 'plant guilds' (hereinafter referred to as 'functional diversity measures'). Functional diversity measures have been applied worldwide in diverse plant community types ranging from mountain vegetation, grasslands and arable fields to wetlands and riparian forests. They have been used to provide ecological understanding at the habitat level (Kumordzi et al., 2015), serve as a predictable link for environmental changes (e.g. Aguiar et al., 2013a; de la Riva et al., 2016a), assess the effects of human disturbance (e.g. Janeček et al., 2013; Brice et al., 2017), prioritize management and conservation practices (e.g. Brym et al., 2011; Bejarano et al., 2017), and evaluate restoration projects (e.g. D'Astous et al., 2013; Hedberg et al., 2013; Laughlin et al., 2017). Functional diversity measures were initially based on a few common traits within a community (e.g. Root, 1967) and on linkages to resources (Grime, 1977), and then later on the trait range of both rare and dominant species (Villéger et al., 2008) or on the average trait range of the most dominant species (Garnier et al., 2004). However, it is still not clear which of these functional diversity measures perform best and how redundant they are among each other (Mouchet et al., 2010; Clark et al., 2012). Mason et al. (2005) and Villéger et al. (2008) emphasized that there may not be a single "best" metric for measuring functional diversity and advocated that the decision should be based on the objectives of each individual study.

There are several reviews on the applicability of functional diversity in plant communities (e.g. Merritt et al., 2010; Cadotte et al., 2011; Kominoski et al., 2013). However, there is no summary of the knowledge on how, why and where these functional diversity indicators have been used in riparian forest studies around the world. The present study aims to respond to these questions and discuss the relevance of these indicators to the description and prediction of ecosystem responses to changing environments. Our overview is divided into five sections:

I. Evolution of concepts, applications, and methods
II. Functional diversity measures: applications in riparian forests
III. Plant functional traits: which traits, how many and why
IV. Functional diversity responses and drivers of change
V. Future research.

Methods

We collected data from the Scopus database. The search was performed using several combinations of keywords: "riparian forests" OR "riparian plant communities" OR "riparian vegetation" AND "functional diversity" OR "functional indices" OR "functional richness" OR "functional evenness" OR "functional divergence" OR "functional redundancy". The search returned 376 SCI articles starting in 1997, from which we removed both reviews and viewpoint articles and standard research studies targeting other communities (fish, invertebrates, birds, mammals, grasslands, wetland and herbaceous vegetation). The final dataset for the quantitive analyses included 70 original research articles for a 20-year period (1997-August 2017) (Table A1). All proportions shown in this review were calculated using the routine Multiple Response Frequencies procedure available in the SPSS software. The procedure was applied to the overall dataset (n=70 case studies) and quantifies the relative importance of frequency counts for a given issue when references for multiple responses are collected. Reviews and viewpoint papers (n=58) were used for Sections I and V.

Evolution of concepts, applications, and methods

From traits to concepts

There is a long history to the development of the concept of 'functional diversity'. It originated in ancient times (c. 300 BCE) with Aristotle and Theophrastus' use of the term 'trait' and the subsequent development of the first known plant classifications, based on plant height and stem density (Weiher et al., 1999). Efforts have also long been made to describe and classify vegetation from combinations of traits, in the so-called 'functional groups' (Grisebach, 1872; Raunkiaer, 1907). Vegetation assemblages have been classified according to life forms (Raunkiaer, 1934), and based on climatic data (Holdrige, 1947). Later, the concept of ‘guild’ as co-occurring species with similar traits gained recognition in community ecology. It was first used to describe groups of functionally similar species in a community (Root, 1967), and then for a mechanistic understanding of ecosystems and in predictive science. Another concept dealing with a functional grouping of plant species which incorporates plant responses to environmental conditions is ‘plant functional types’ (PFT). The term was coined by Walker (1992) and Skarpe (1996), although the same concept had already been published with different terminology by Grime (1977). By providing a morphological classification of plant life forms, Hutchinson (1975) represented a milestone in the functional ecology of wetland and riparian vegetation, and was followed by Menges and Waller (1983), who applied functional groups in order to describe wetland plants growing along an elevational gradient on a floodplain. In addition, the pioneering study by Boutin and Keddy (1993) used guilds for the functional classification and ecological understanding of wetland plants. However, the terminology for the various emergent functional diversity approaches remains challenging, especially following the introduction of functional ecology as a discipline (Calow, 1987; Keddy, 1992a). For instance, ‘plant functional types’ (Walker, 1992; Díaz and Cabido, 1997) has been used as a synonym for ‘functional groups’ (Hooper et al., 2005). Further confusion was generated by the use of the ‘guild’ approach, which often refers to ‘plant functional types’ and ‘functional groups’ (Leonard and Orth, 1988; Poff and Allan, 1995). What is more, Wilson (1999) introduced the term ‘ecological groups’ and Lavorel et al. (1997) used ‘emergent groups’, ‘strategies’ and ‘functional groups’ for plant classification purposes. However, the fact is that despite the varying terminology used by the different approaches, the objective is the same – to describe functional groups of plant species along environmental gradients (Figure 5a).

Quantification of functional diversity relies on trait assessment, which can be obtained in different ways: as a community-weighted mean (CWM), using trait values weighted by the relative numerical abundance and biomass of species in order to calculate a community aggregated trait value (Violle et al., 2007); and as functional diversity indices, based on the use of trait-range assessment to calculate distinct functional diversity attributes (Mason et al., 2005).

One of the first proposed methods for simplifying species assemblages into quantifiable units relied on using an a priori classification to divide species into various functional groups (Hooper and Vitousek, 1997; Tilman et al., 1997).

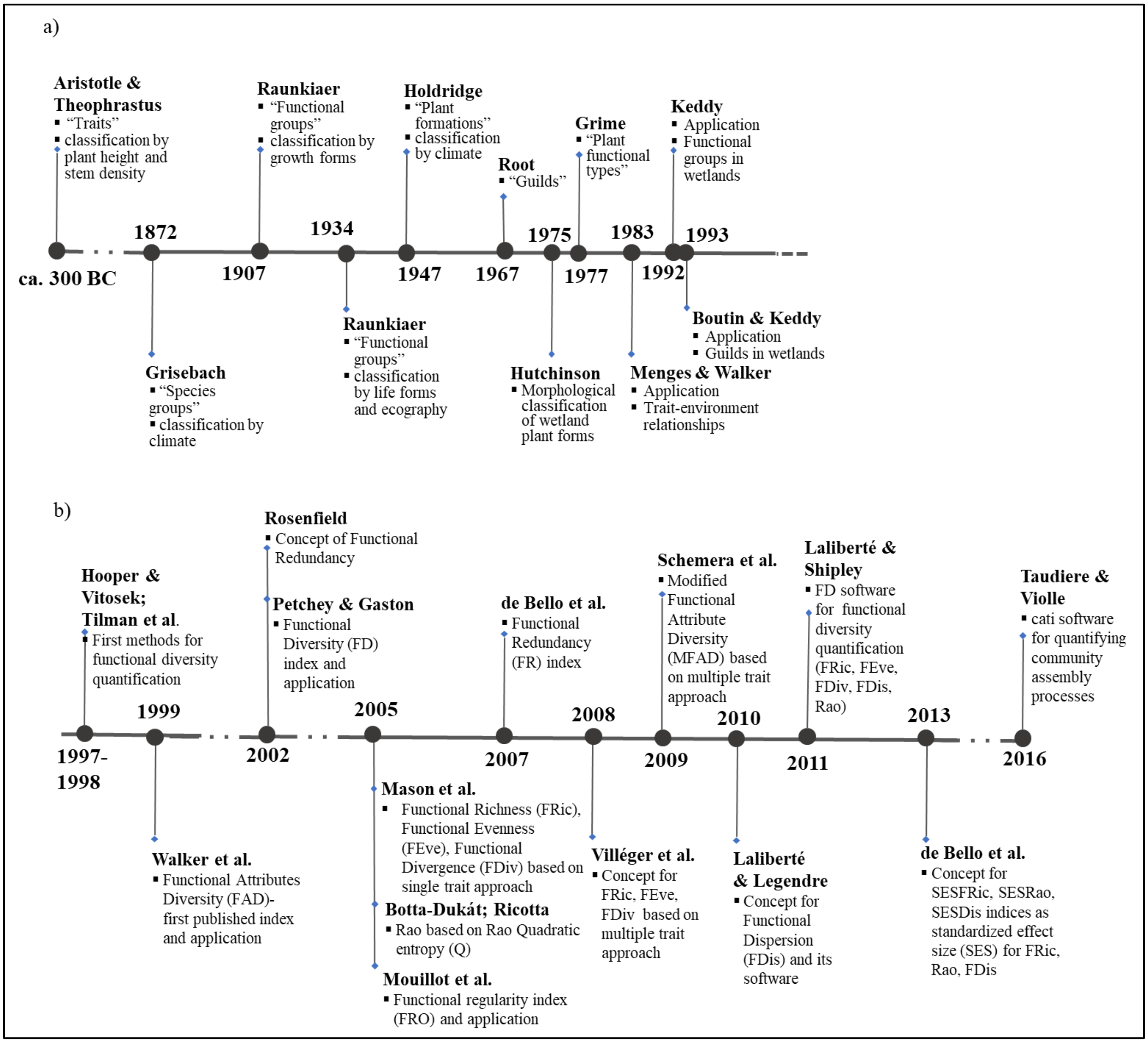

Figure 5. Timeline showing: a) key concepts and applications for functional plant ecology; b) quantifications of functional diversity, software, and applications. Source for Aristotle and Theophrastus: Weiher et al., 1999.

However, the choice of functional groups was not based on objective (mathematical or statistical) methods, but on an arbitrary decision taken by the experimenter (Wright et al., 2006), and this arbitrariness underlined the need to work with objective measurements of functional diversity (Petchey et al., 2004). The first published index measuring functional diversity in an objective way was the Functional Diversity Attribute (FAD) (Walker et al., 1999). This index evaluates the average functional contribution of each species to the total diversity of a community and is extremely sensitive to species richness (Ricotta, 2005). Subsequent modifications of FAD led to the creation of a new index – the Modified Functional Attribute Diversity index (MFAD) (Schmera et al., 2009), which is not sensitive to species richness. In a step forward, inspired by evolutionary biology, Petchey and Gaston (2002) proposed the Functional Diversity (FD) index. This index relies on functional dendrograms and measures the extent of the complementarity among species trait values by estimating the dispersion of species in trait space. Two modifications of the FD index then emerged: Community-based Functional Diversity (FDc) (Petchey and Gaston, 2006), and Extended Functional Diversity (wFDc) (Pla et al., 2008). The former is the total branch length of the functional dendrogram and does not account for species weights, while the latter considers a relative measure of abundance before creating the dendrogram, thereby accounting for species weights. Botta-Dukát (2005) recommended using the Rao (Q) index (following Rao, 1982) as a functional diversity measure, because in addition to species abundance, it incorporated the functional distance between species. The Rao was then used in conjunction with the Gini-Simpson index to calculate the Functional Redundancy (FR) index (de Bello et al., 2007). Another method for calculating FR is to divide species richness, abundance or biomass by functional groups based on clustering a dendrogram for each experimental unit (Laliberté et al., 2010), whereupon FR becomes the average number of species per functional group. The concept of functional redundancy relies on the saturation of functionally similar species in a community (Rosenfeld, 2002). Based on the concept of functional trait variation among the species in a community, Mason et al. (2005) divided functional diversity into three components: functional richness – amount of trait space occupied by the species, functional evenness – regularity of the distribution of species abundance in the functional space and functional divergence – degree to which species abundance differ from the center of the functional space. In parallel, Mouillot et al. (2005) proposed an univariate index for quantifying functional evenness – the Functional Regularity Index (FRO). As a measure for functional divergence, an univariate index FDvar was used (Mason et al., 2003). The emergence of multivariate measurements – Functional Richness (FRic), Functional Evenness (FEve), and Functional Divergence (FDiv) for the functional diversity components – therefore represented a significant improvement in relation to the univariate indices (Villéger et al., 2008). Laliberté and Legendre (2010) introduced Functional Dispersion (FDis) as a multivariate analog of the weighted mean absolute deviation (MAD), thus rendering the new index unaffected by species richness. Recently, Mason et al. (2012) proposed modified versions of FRic, FDis, FDiv, Rao, and FD. The new SESFRic, SESFDis, SESFDiv, SESRao, SESFD indices incorporate the standardized effect size (SES) in order to ensure correct conclusions about assembly processes excluding stochasticity effects (Figure 5b; Table 1).

With the proliferation of functional diversity indices, different software applications have been created in order to quantify functional diversity. They include: the FD-R package that measures multiple traits for functional ecology (Laliberté and Shipley, 2011) and is used to calculate FRic, FEve, FDiv, FDis, and Rao; the SYNSCA-R package, which not only incorporates functional patterns, but also the phylogenic patterns in metacommunities, and is used to calculate FR (Debastiani and Pillar, 2012); and the recent cati-R package, which introduces the influence of individual differences and intraspecific variation in the assembly of ecological communities (Taudiere and Violle,2016). The implementation of the R packages has greatly facilitated the measurement of functional diversity for a wide range of ecological applications (Figure 5b).

Table 1. List of the functional diversity indices with the given description.

Functional diversity index	Description	References
Community-Weighted Means (CWM)	A community aggregated trait value based on trait values weighted by species relative numerical abundance and biomass	Violle et al., 2007
Functional Diversity Attribute (FAD)	Sum of pairwise distances between species	Walker et al., 1999
Modified Functional Diversity Attribute (MFAD)	Sum of pairwise distances between functional units	Schmera et al., 2009
Functional Diversity (FD)	Sum of branch length of a functional dendrogram	Petchey and Gaston 2002
Community-based Functional Diversity (FDc)	Sum of branch length	Patchey and Gaston, 2006
Extended Functional Diversity (FDw)	Sum of branch length weighted by abundance before dendrogram constriction	Pla et al., 2008
Rao (Q)	Sum of distances between pairs of randomly chosen species in trait space weighted by relative abundance	Botta-Dukát, 2005; Ricotta, 2005
Functional Regularity Index (FRO)	Species evenness in functional space weighted by species abundances	Mouliot et al., 2005
Functional Richness (FRic)	Minimum convex hull which includes all species of interest	Mason et al., 2005; Villéger et al., 2008
Functional Evenness (FEve)	Sum of the minimum spanning tree branch length weighted by relative abundance of the two species	Mason et al., 2005; Villéger et al., 2008
Functional Divergence (FDiv)	Species deviance from the mean distance to the center of gravity weighted by relative abundance	Mason et al., 2005; Villéger et al., 2008
Functional Dispersion (FDis)	Mean distance in functional space of individual species to the centroid of all species	Laliberté and Legendre 2010
Functional Redundancy (FR)	Difference between species diversity (Gini-Simpson diversity index) and Rao; average number of species per functional group	de Bello et al., 2007 Laliberté et al., 2010
Standardized effect size of FRic, FDis, FDiv, Rao, FD (SESFRic, SESFDis, SESFDiv, SESRao, SESFD)	Comparing values for FRic, FDis, FDiv, Rao and FD against a null model using standardized effect size (SES)	de Bello et al., 2013

Functional diversity measures: applications

The initial applications of functional diversity indices were conducted in savannah communities (Walker et al., 1999), and then in animal communities (Petchey and Gaston, 2002; Mouillot et al., 2005). Recent applications have taken place in grasslands (Pakeman, 2011; de Bello et al., 2013; Catorci et al., 2014; Vandewalle et al., 2014; Rota et al., 2017), Mediterranean shrublands (de Frutos et al., 2015), arable fields and serpentine communities (Plaza et al., 2015; Carmona et al., 2017; Flinn et al., 2017), tundra (Spasojevic and Suding, 2012), and coastal plant communities (Castro-Díez et al., 2016). In the case of riparian woodlands, FR has been used as a tool for bioassessment (Bruno et al., 2016b), FRic, FEve and FDiv for environmental stress (Kotowski et al., 2010; Giehl and Jarenkow, 2015; de la Riva et al., 2016a), FDis for land use change (Brice et al., 2017), and FD for plant invasions (Dechoum et al., 2015). According to our search, the earliest published ISI paper on functional diversity of riparian forest assemblages dates from 1997 (Higgins et al., 1997). Since then, and especially after 2001, the number of case studies has greatly increased, with the 'riparian guild' approach outnumbering the use of functional diversity indices (Figure 6). This pattern might be a result of the fact that the concept of guilds was developed earlier than that of functional diversity indices. However, most recently, and especially since 2011, there has been an increasing trend in the use of functional diversity indices that has paralleled the development of software for computing them (Figure 5b).

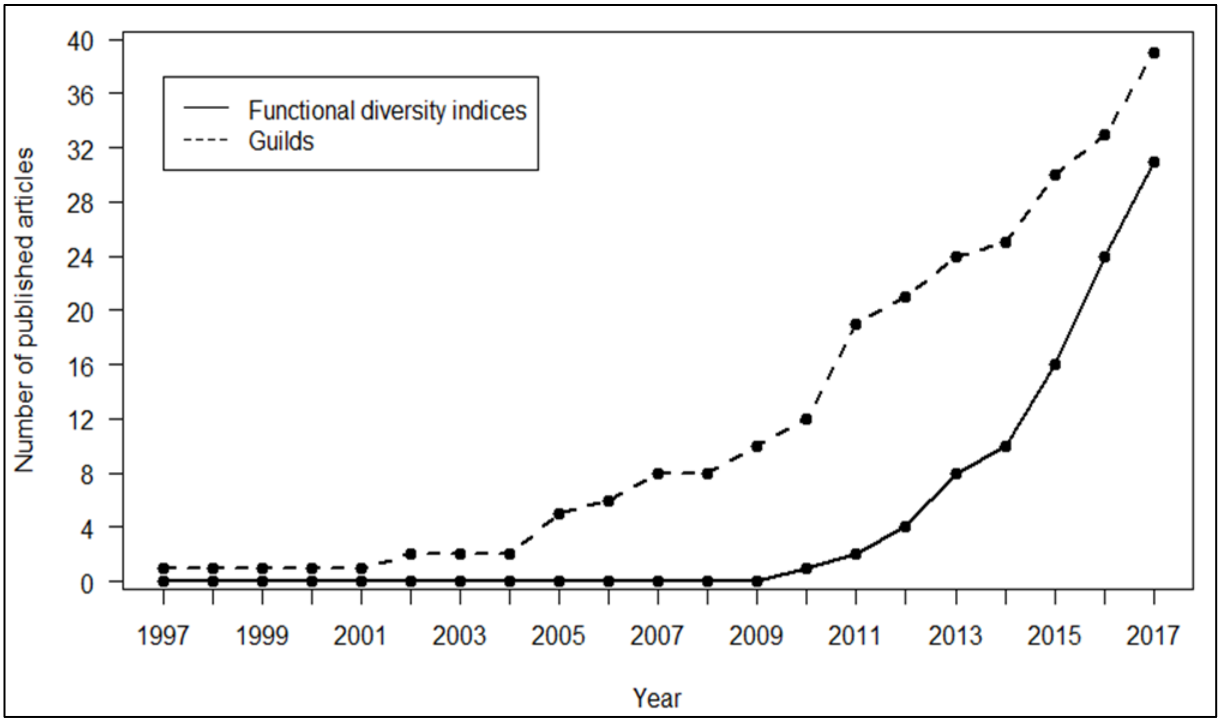

Figure 6. Number of scientific publications collected from the Scopus database (1997-2017) using the keywords 'functional diversity' and 'riparian vegetation' applied to the title or the abstract and classified into papers using the concept of 'functional diversity.

Functional diversity measures: application in riparian forests

Geographical distribution of case studies

Studies on the functional diversity of riparian forests were not evenly distributed worldwide (Figure 7). Most of the research was conducted in Europe, followed by North America (United States and Canada). South America, Asia, Africa and Australia were poorly represented. Patterns in terms of the distribution of case studies by continents using guilds (mostly in America) and functional diversity indices (mostly in Europe) were slightly different.

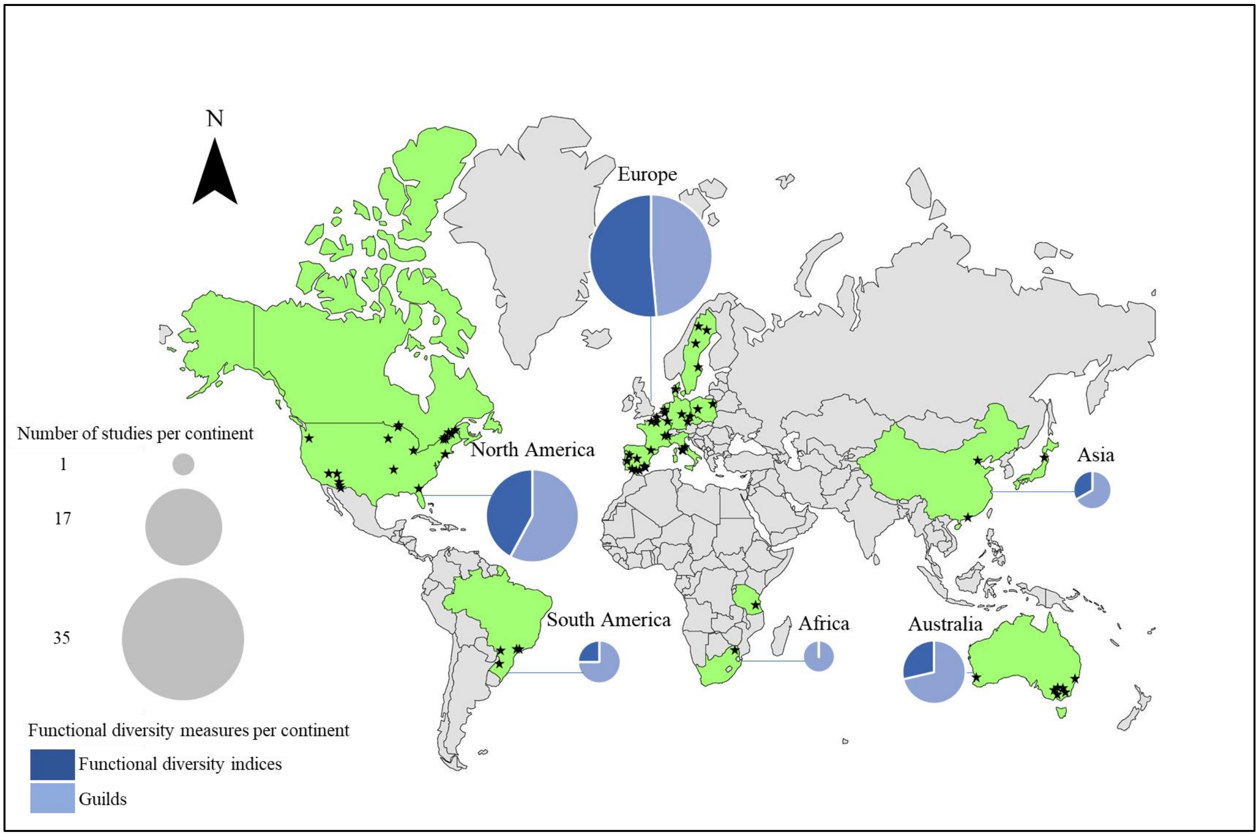

Figure 7. World map showing the geographical distribution of functional diversity studies in riparian forests. The size of the gray circles is proportional to the number of studies on functional diversity in riparian forests on each continent (1997-August 2017).

Functional diversity indices

Each functional diversity index reflects different aspects of the functional characteristics of the community (Table 1). The choice of functional diversity indices should therefore be based on the a priori expectation that one of the chosen aspects would be related to a certain ecological variable of interest, ecosystem processes, and community assembly (Mouchet et al., 2010).

In riparian forests, numerous functional diversity indices have been applied in order to describe functional diversity and derive conclusions about community assembly and ecosystem functioning (Table 2). Functional Richness (FRic) appears to be the most widely used functional diversity index, mainly coupled with Functional Evenness (FEve) and Functional Divergence (FDiv) (Kotowski et al., 2010; Savage and Cavender-Bares, 2012; de la Riva et al., 2016a). A enhanced group of functional diversity indices (FRic, FEve, FDiv and Functional Dispersion (FDis) has been also used (Kotowski et al., 2013; Hedberg et al., 2016), as have single functional diversity indices, such as FDis (Lawson et al., 2015b; Craven et al., 2016; Göthe et al., 2016; Brice et al., 2017), Functional Redundancy (FR) (Bruno et al., 2016b); and Rao (Q) (Sasaki et al., 2014).

Table 2. Frequency and number of functional diversity indices in the reviewed case studies. Frequencies were calculated using a Multiple Response Frequencies procedure.

Functional diversity index	Frequency of studies that used the index (%)	Number of studies that used the index	Number of studies that used the index as a single index
Functional Richness (FRic)	25.7	19	1
Functional Evenness (FEve)	20.3	15	0
Functional Divergence (FDiv)	17.6	13	0
Functional Dispersion (FDis)	13.5	10	4
Rao (Q)	4.1	3	1
Functional Redundancy (FR)	2.7	2	1
Extended functional diversity (wFDc)	2.7	2	0
Functional Diversity (FD)	1.4	1	0
Modified Functional Attributes Diversity (MFAD)	1.4	1	0
Community based functional diversity (FDc)	1.4	1	0
Community Weighted Means (CWM)	9.5	7	5
Total	100	74	12 (38%)

Environmental and anthropogenic impacts on functional diversity in riparian forests have been assessed with distinct functional diversity indices. FRic, FEve, and FDiv seem to be those most commonly used for environmental analysis (e.g. climate, geomorphology, hydrology), whereas FRic and FDis were the most frequently applied in cases of anthropogenic disturbances, such as stream flow regulations, land use, and species invasions. However, we found that the predictive capacity of the different functional diversity indices varied among the case studies. For instance, notwithstanding their frequent application in environmental studies, neither FEve nor FDiv presented significant changes in the values for different communities (Savage and Cavender-Bares, 2012; de la Riva et al., 2016a; Abgrall et al., 2017), whereas Q did appear to be a significantly responsive index instead (Sasaki et al., 2014; Pérez-Ramos et al., 2017). FRic was the most successful at explaining land use changes (Janeček et al., 2013) and plant invasions (Hejda and de Bello, 2013; Lawson et al., 2015b; Kuebbing et al., 2017), whereas FDis demonstrated capacity to predict functional changes caused by altered hydrology and flooding (Lawson et al., 2015b; Brice et al., 2017). It was reported that some functional diversity indices proved better than others at drawing conclusions about ecosystem functioning. De la Riva et al. (2017) and Fu et al. (2015) reported an advantage to using FRic rather than FEve and FDiv when identifying functional diversity change affected by climatic gradient, whereas Bruno et al. (2016a) reached a different conclusion, finding that FRic's predictive capacity was exceeded by that of FR when assessing environmental stress on riparian woodlands.

There is an ongoing debate as to which of the many functional diversity indices can best predict ecosystem functioning: is the mechanism based on single trait level weighted by abundance (Community-weighted means (CWM), or alternatively that based on the complementarity of multiple trait levels non-weighted (FRic) or weighted by abundance (FEve, FDiv, FDis, Q). Recent testing on the predictive power of different functional diversity indices using animal communities stressed that indices which account for abundance and single trait measures possess a greater capacity to predict ecosystem functioning (Gagic et al., 2015). The dimensionality of functional diversity indices when it comes to representing distances between objects has also been shown to be important (Legendre and Legendre, 1998). For instance, one-dimensional diagrams – functional dendrogram indices – have been less efficient than multidimensional functional diversity indices and have led to a bias in functional diversity and an overestimation of functional dissimilarity (Maire et al., 2015). Where single functional diversity index performance is concerned, FRic has statistically been the best predictor of ecosystem functioning in grasslands, although Q and FDiv have also proven adequate (Clark et al., 2012). On the contrary testing along land use gradients in grasslands by Pakeman (2011), revealed no pattern in FDiv, but produced a significantly reduced value in FRic. Such patterns can be due to the inherited characteristics of the functional diversity index, the dataset and the study objective. For instance, FDiv can be highly predictive for abundant species that are functionally distinct, because trait abundance contributes to the index in a meaningful way. For a dataset consisting of rare species with low abundance, FRic can be a suitable measure since it does not account for taxon abundance. Q, which simultaneously represents functional richness and functional divergence, can be considered a suitable metric if the objective of the study is to develop a summary variable, or a weak one if the goal is to decompose different functionality components.

If the aim is to produce unbiased functional diversity, it is crucial to consider whether the functional diversity index accurately measures what it is intended to describe and the functional diversity indices are mutually independent (Schleuter et al., 2010). The existing recommendations as to which functional diversity indices should and can be combined are limited. Mouillot et al. (2011) supported the combination of FRic, FEve and FDiv as a predictor of decomposition, productivity and nutrient cycling in grasslands, but functional diversity assessments still mainly rely on considering independent facets of functional diversity (Villéger et al., 2008). Despite these limitations, their potential for revealing the processes which structure plant communities (Mouchet et al., 2010) means that functional diversity indices can be suitable measures for linking community and ecosystem processes to ecosystem functioning (Flynn et al., 2011; Mouillot et al., 2011; Pakeman, 2011).

Riparian plant guilds

The concept of guilds as co-occurring species sharing similar traits responsive to natural environmental changes or human disturbances has been applied in riparian forests in diverse climatic regions, ranging from boreal regions of Sweden (Bejarano et al., 2017) to semi-arid streams in Arizona and Colorado (Stromberg and Merritt, 2016), and Mediterranean climates (e.g. Aguiar et al., 2018; Bejarano et al., 2012a). To date, the distribution, occurrence, and abundance of guilds (and functional groups) have been used to assess, model and predict the effects of hydrological alterations caused by regulation and the impacts of land use and land cover changes and climate change, and to address environmental gradients and plant invasions.

There is no consensual riparian-guild terminology for different regions, although the linkage to hydrologic conditions (flood, drought, baseflow) or hydrologic species preferences (obligate riparian, facultative riparian, non-riparian) plays a prominent role in relation to species assembly in guilds. For instance, Lytle et al. (2017) used five flow-response guilds for western US forests – hydroriparian tree, xeroriparian shrub, hydroriparian shrub, mesoriparian meadow, and desert shrub; whereas for Sweden, Bejarano et al. (2017a) used a compromise combination of hydrological linkages, morphological and phenological traits (e.g. deciduous wetland plants, evergreen dwarf shrubs). Aguiar et al. (2018) used a quantitative analysis to assign species to a certain guild, and the main indicator 'functional traits' to name the guilds (e.g. non-riparian evergreen, deciduous competitive, water-stress tolerant). A comparison of guilds among diverse regions of the globe using a common trait-based dataset would probably make it possible to create a shared systematic terminology for guilds. Starting with a given trait – water requirements, for example – the prefixes Xero-, Hydro-, Meso-, Desert-, and 'Other-' could define the first step of a 'multi-entry key'. Other relevant traits, such as life-form (tree, shrub) or phenology (deciduous, evergreen), could then complete a short and meaningful guild identification system. Given that guilds can become specific to a certain region, additional key branches would permit a sole designation for this type of uncommon guild.

Plant functional traits: which traits, how many and why

Collection, justification, and number of traits

It has been suggested that incorporating community changes into models for ecosystem functioning through effect and response traits can greatly improve predictive capacity (Laliberté and Legendre, 2010). The effect-response approach relies on how species respond to disturbances (response traits) and how traits impact ecosystem function (effect traits) and can help provide resistance and resilience to ecosystem functions, taxa and communities (Suding et al., 2008). However, there are still a number of doubts regarding the use of trait-based approaches – for example, Paul Keddy's questions as to the type and number of traits needed to predict community assembly (Keddy, 1992b). Many authors have contributed to the discussion about the critical steps needed to use trait-based approaches in practice. For instance, in his theoretical review and empirical study, Laughlin (2014) showed that although the optimal number of traits relies on the type of ecosystem, "there appears to be a tractable upper limit to the dimensionality of plant traits", suggesting that a threshold of eight independent traits would optimize research efficiency and reflect the functional diversity of most plant communities. This contrasts with Petchey and Gaston's (2006) view that no threshold should be set for the appropriate number of traits, while other studies (e.g. Pillar, 1999) have proposed a fuzzy-set approach in order to optimize trait selection, and Maire et al. (2015) proposed a framework for assessing the quality of a functional space by computing all the possible functional trait spaces and selecting the most parsimonious one. With regard to the process of trait selection, some authors have also employed a prior hypothesis and rationale in terms of expected differences between traits and how traits relate to plant functions that are relevant to the study goals (Bonada et al., 2007; Castro-Díez et al., 2016). Fonseca and Ganade (2001) highlighted the question of trait redundancy, which in turn determines the level of functional diversity (Petchey and Gaston, 2002). Selecting a large number of functional traits increases the ability to detect functional differences between species, thereby decreasing the probability that species will be functionally redundant. At the other end of the scale is the practice of only considering a few traits (Petchey and Gaston, 2002). In the light of all this, in his review Laughlin (2014) proposes that a core set of independent traits should be measured from multiple organs, especially leaves (e.g. Specific Leaf Area), stems (e.g. bark thickness), roots (e.g. specific root length), and flowers (emphasis on flowering time). He says that in order to achieve a more accurate functional diversity assessment, trait number should be minimized and trait independency increased (Laughlin, 2014), because incorporating an excessive number of traits that are positively correlated causes an artificial convergence of functional diversity (Naeem and Wright, 2003).

In our review, we found that the average number of traits per study was 8.4, although it was highly variable among studies. For instance, Aguiar et al. (2013a), Bruno et al. (2016a), Biswas and Mallik (2010) included 28, 30 and 36 traits respectively, while others considered just 3 or 4 (e.g. Hejda and de Bello, 2013; Hedberg et al., 2013).

The trait selection rationale in the reviewed case studies was mainly associated with traits' potential to address ecological processes at different scales, such as ecosystem processes (productivity, nutrient cycling, hydrological gradient), community processes (competition, succession, community invasibility) and organismal processes (growth rate, nutrient uptake, drought tolerance), following the classification established by Funk et al. (2016) (Figure 8b). However, data availability can constrain trait selection (Biswas and Mallik, 2010; Giehl and Jarenkow, 2015). In the reviewed studies, traits were mostly collected from databases, while only a few combined field data and databases (Figure 8a; Table A2). Trait values retrieved from databases have been criticized for not accounting for site-specific differences, but plant databases do enable researchers to derive functional groups, aggregate species into guilds, calculate functional diversity, and map trait distributions (Cordlandwehr et al., 2013).

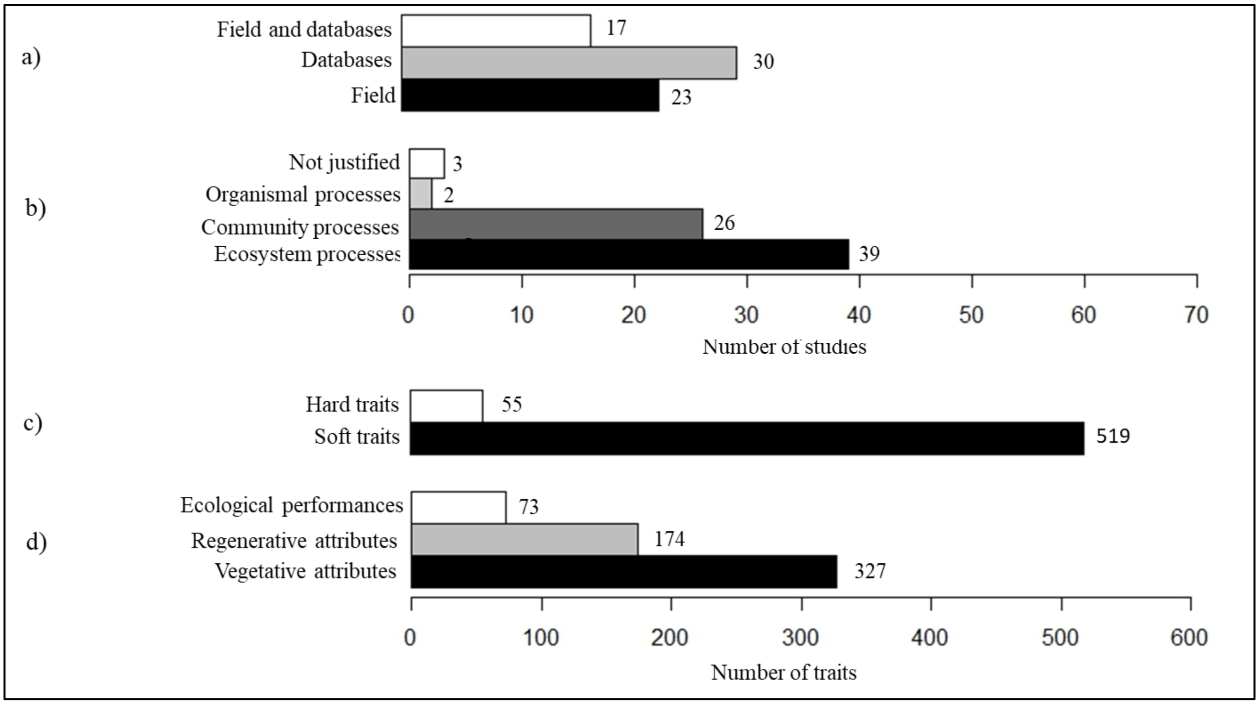

Figure 8. Proportions using multiple response frequencies between studies for: a) trait collection; b) justification for trait selection; c) hard and soft traits; d) trait attributes. Graphs 4a and 4b were based on a total number of studies (n=70); graphs 4c and 4d were based on the total number of traits (n=574).

Hard traits versus soft traits

Many traits which are considered relevant to a particular ecosystem function are difficult or expensive to measure (Hodgson et al., 1999; Weiher et al., 1999; Lavorel and Garnier, 2002). These so-called ‘hard’ traits are assumed to be more accurate indicators of plant functions that are responsible for ecosystem dynamics. For instance, dispersal distance and propagule longevity are related with the species response to ecosystem disturbance, plasticity is a measure of ecosystem change and species adaptations (Weiher et al., 1999), and relative growth rate is an indicator of ecosystem primary productivity (Lavorel and Garnier, 2002). The problem is that they can’t be quantified for a large number of species in many regions of the world. In comparison, their counterpart ‘soft’ traits are easily or cheaply measured and can be used as proxies for other ‘hard’ traits (Hodgson et al.,1999). Different researchers have favored different traits due to their familiarity, the available research facilities, or the occurrence of certain traits in particular regions (Cornelissen et al., 2003). There is no consensus as to which traits should be used to calculate functional diversity, but researchers have been encouraged to combine ‘soft’ and ‘hard’ traits in order to increase the predictive power of their studies (e.g. Cornelissen et al., 2003).

From our dataset of 70 studies, we collected the traits that were used to represent functional diversity in riparian forests (Table A3). Of these, the predominant traits were ‘soft’ ones, whereas ‘hard’ traits were rarely applied (Figure 8c). The most widely used trait was plant height, which is characterized as a ‘soft’ trait. It has been recognized as responsive to both environmental parameters and anthropogenic disturbance and to have an effect on ecosystems (Díaz et al., 1999; Weiher et al., 1999; Lavorel and Garnier, 2002). Moreover, the global relevance of plant height has been confirmed by cross-continental analysis (Díaz et al., 2004). Plant height has been used to address responses to hydrology (Lawson et al., 2015a), extreme climatic events (Craven et al., 2016; de la Riva et al., 2016b) and land use change (Janeček et al., 2013), and also as a proxy for plant invasions (Hejda and de Bello, 2013). Along with growth rate ('hard trait'), plant height integrates the trade-off between benefits derived from access to light and costs of stem construction and maintenance (Falster and Westoby, 2003). Slower growth rates promote greater mechanical strength and increased ability to tolerate water stress (Suding et al., 2003), shade tolerance (Goldberg and Landa, 1991) and disturbance (Preston et al., 2006), thereby stressing the importance of growth rate to the determination of ecological strategies within communities (Grime, 1977; Reich, 2014). In riparian forests, growth rate was the most commonly used hard trait, and was applied as an indicator of hydrological performance (Savage and Cavender-Bares, 2012; Abgrall et al., 2017) and as a proxy for shade tolerance (Brice et al., 2016). The applicability of the growth rate is dependent on the potential of soft traits to explain the wide variation in growth rates across herbaceous and woody plant species (Hunt and Cornelissen, 1997; Nguyen et al., 2014).

Vegetative and regenerative traits and ecological performance

Identifying the key traits for calculating functional diversity indices or aggregate species within guilds is a crucial step in empirical research and must be based on the traits' implications for ecosystem functioning or community responses of interest (Gross et al., 2009). Traits are commonly divided into two main categories: vegetative (whole-plant traits, leaf traits, stem traits, belowground traits) and regenerative (dispersal mode, dispersule shape and size, seed mass, resprouting capacity after major disturbance) (Cornelissen et al., 2003). In addition to these trait categories, another one has emerged as a response to environmental factors. Violle et al. (2007) argued that this category should be called 'ecological performance' rather than 'ecological traits', as in Hough-Snee et al. (2015) and Bejarano et al. (2017a), since it embraces external factors in order to determine species tolerances, habitat or ecological preferences, and depends on the coordinated response of multiple traits to environmental factors. The reviewed studies revealed that vegetative traits were the most frequently used category, followed by regenerative traits (Figure 8d). Within the former, leaf traits were used in more than 50% of the studies (Table A3), due to the widespread application of SLA (Wright et al., 2004; Kotowski et al., 2010). SLA, plant height and seed mass are some of the traits that have been most widely used in ecological studies to explain plant distributions (Verheijen et al., 2016). The relationship between them can help explaining species co-existence strategies: while plant height and seed mass reflect capacity to cope with environmental stress, SLA distinguishes between competitors and stress-tolerators (Westoby, 1998). Fast-growing species with high SLA have greater access to light, reflecting the trade-off in favor of tree investment in height at the expense of woody density and longevity (Westoby et al., 2002). While the relationship between leaf traits and water availability in structuring riparian plant communities was confirmed in the studies by Lawson et al.

(2015b) and Oddershede et al. (2015), Padilla and Pugnaire (2007) suggested that Mediterranean woodland assemblages in arid and semi-arid regions are better assessed using root traits as opposed to leaf traits. However, root traits have been largely neglected in functional diversity assessments of riparian forests (de la Riva et al., 2017), despite the fact that plant assemblages are not “homogenous” entities and their above and belowground compartments respond differently to environmental stressors (Kumordzi et al., 2015).

The regenerative category includes traits related to regeneration processes, post-disturbance colonization, competitive response, and tolerance to abiotic stress (Venable and Brown, 1988; Westoby et al., 2002). In riparian forests, the most commonly used traits in the regenerative category were seed traits – seed mass, and seed weight, to be exact. High seed production was a preferred strategy in response to drought, due to seeds’ abilities to establish themselves in different soil moisture conditions, thereby ensuring plant survival (Arthaud et al., 2012; Brice et al., 2017). Further significance of seed traits was found in the evaluation of habitat disturbances (Göthe et al., 2016) and plant community resistance and resilience (Janeček et al., 2013; Abgrall et al., 2017), emphasizing the role of high seed mass as an adaption that helps tolerate stress in the environment (Santini et al., 2017).

Functional diversity responses and drivers of change

Since traits reflect abiotic and biotic factors, changes in the environment can be seen as filters that select specific species (Keddy, 1992a), thereby causing trait variation. Such filters influence the stability, resistance and resilience of riparian vegetation and consequently affect functional diversity (Hooper et al., 2005). Understanding the effect of the filters that exert selective pressures on riparian vegetation is hugely important when it comes to establishing expectations with regard to functional diversity responses to multiple environmental and anthropogenic factors.

The dataset of case studies in riparian forests showed that research has addressed multiple factors, both natural (e.g. substrate, geology, hydrology) and anthropogenic (e.g. flow regulation, and land use and land cover change). However, the most common use of functional diversity measures has been to assess the effects of hydrology in riparian ecosystems, followed by land use and land cover change (Figure 9). The pattern for functional diversity indices and for guilds is similar. The effect of management (restoration, forest management) on functional diversity was assessed in only c. 20% of the case studies.

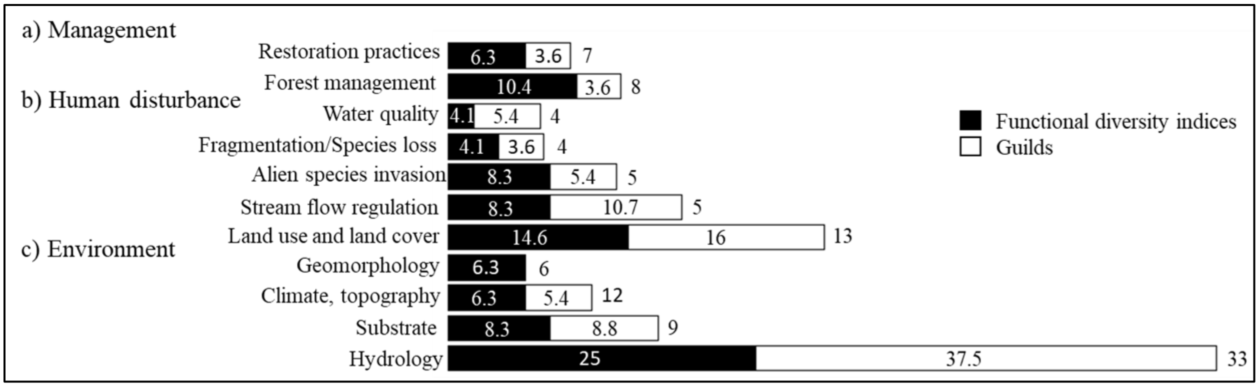

Figure 9. Frequency of the main factors addressed in the case studies: a) management; b) human disturbance; c) environment. Number of cases as a percentage of the respective approach (functional diversity indices; guilds) inside bars, calculated using multiple frequency tables. Total number of cases for both approaches outside bars.

It is widely recognized that hydrology is among the most important determinants of riparian vegetation (Poff et al., 1997b). There is a growing interest in how these water-dependent communities will respond to climate change (Parmesan and Yohe, 2003). We found that most recent studies using functional diversity indices and guilds have focused on modeling riparian vegetation responses to hydrology (e.g. Hough-Snee et al., 2015; Lawson et al., 2015a,b; de la Riva et al., 2017), corroborating the perception of the relevance of plant-flow responses in changing hydrological regimes (Figure 9). Species' ability to tolerate flooding and acquire soil moisture and nutrients differentiates riparian plants from terrestrial ones. Response of riparian assemblages caused by waterlogging resulted in increased SLA among the communities (Wright et al., 2017), although the response was variable according to the tree species (Lawson et al., 2017). However, species with greater SLA have a higher capacity for underwater gas exchange that positively affects plant survival and recovery after flood occurrences (Mommer and Visser, 2005; Winkel et al., 2016). Other flood-tolerant strategies include leaf dry matter content (LDMC), helping plants resist leaf losses and thus promoting their survival (Oddershede et al., 2015), and plant height, enabling plants to emerge above the water surface and thereby facilitating gas diffusion (Luo et al., 2016). Trait changes according to selective stressors was confirmed by Stromberg and Merritt (2016), who found that water availability and fluvial disturbances governed vegetation structure in riparian ecosystems. Water table decline caused shifts towards small woody mesic trees with great root length that allow plants to survive fluctuating water tables and shallow seasonal moisture sources (Merritt et al., 2010). Dry environments select plants with better water-conservation strategies, such as high seed mass and small leaf size, thereby ensuring a greater volume of stored resources for seed establishment. Oddershede et al. (2015) found low SLA in riparian assemblages that experience drought. Besides SLA and seed mass, seed dispersal has been shown to be affected by fluctuating water tables, which ultimately impact plant distribution (Jansson et al., 2005; Nilsson et al., 2010). Vegetation zonation in freshwater habitats can be further influenced by seed buoyancy and seed banks. Seed buoyancy influences the dispersal and colonization of new sections in shoreline areas (van Leeuwen et al., 2014), and species with great seed banks can opportunistically establish themselves when suitable germination sites occur (Bagstad et al., 2005). It is interesting to note that in regulated rivers vegetation shifts were based from tolerance to water stress (Douma et al., 2012) to abilities to cope with waterlogging (Bejarano et al., 2017). In this sense, assemblages with drought adaptations, such as shrubby forms with small evergreen leaves, have been found to be more sensitive to regulation, compared to other species that were more resilient despite poorer drought adaptations (Lite and Stromberg, 2005; Aguiar et al., 2013a).

Land use and land cover change was listed as the second most important driver of riparian forest communities (Figure 9). The change from unmanaged forests to open areas has promoted shade-intolerant species capable of long-distance seed dispersal, thereby decreasing the presence of wind-dispersed and animal or bird-dispersed species with various light requirements (Aubin et al., 2007). The indirect effect of land use in nearby floodplain areas has also been found to influence the composition of riparian plant assemblages, triggering colonization of riverbanks by terrestrial plants (Angiolini et al., 2016). The consequences of land cover change in riparian areas and the presence of species with fast growth rates and moderate life spans have had similar effects (Burton et al., 2009). Plant delineation according to past land use and land cover has been primarily driven by life-forms (Hérault and Honnay, 2005). Plants with generalist characteristics, such as small seeds, anemochory seed dispersal and/or long-lived seed banks, have been shown to survive land use and land cover change, perhaps because these traits enabled them to colonize soils of newly emerging forest fragments, thereby establishing themselves as pioneers in riverine areas.

Future research

The literature stresses multiple research gaps and pressing directions for future research methodologies in functional ecology and riparian ecosystems. The challenges include:

- Ecological connectivity and ecological networks: how should ecological networks be tackled in order to understand functional linkages along riparian corridors, across fluvial landscapes and over time? How does the functional diversity of primary producers affect the structure of co-occurring communities, such as fish, invertebrates or diatoms? Recent research points to the need to use local experiments to test conceptual models. Examples include Ebeling et al. (2018) and Feio et al. (2017) on the cascade effects of functional diversity and deterministic interactions in other trophic levels of ecosystems, while other authors address the linkage of functional diversity and the overall abiotic and biotic interactions in floodplains (Auffret et al., 2017; Tonkin et al., 2018). Other examples are emerging from knowledge about landscape genetics and molecular ecology (Epps and Keyghobadi, 2015).

- Guidance for assessing functional diversity: how can methodological decisions (e.g. type and number of traits, disregarding rare species) affect the responses given by functional diversity measures? How do inter-specific variability, trade-offs and synergies between traits affect our understanding of ecological systems? Over a decade ago, McGill et al. (2006) argued that variability must be taken into account. Since then, empirical and theoretical research has provided clues to a better use of trait-based frameworks (e.g. Villéger et al., 2008). Recently, Carmona et al. (2016) introduced a new functional diversity framework which unifies existing functional diversity approaches, effectively incorporating intraspecific variability and thereby making it possible to quantify functional diversity components from the organismal to the macroecological levels. Solving the ongoing discussions on the relevance of trade-offs among traits, intra- and interspecific variability and trait overlapping, and how the type and number of traits addressed influence the assessment of ecosystem properties, will permit an accurate assessment of ecosystem resilience and functional redundancy in riparian ecosystems (Mouchet et al., 2010; Mason et al., 2012; Funk et al., 2016).

- The question of spatial scales: How can we transpose local-based knowledge to large/global scales? Predicting time and spatial scales that are relevant to large-scale conservation and management planning on the basis of limited empirical datasets is a difficult task. One alternative is to include field assessments and remote sensing. For instance, Schmidtlein et al. (2012) propose mapping Grime’s three-strategy (CSR) scheme at a large scale in order to express disturbance and threats to conservation. Fernandes et al. (2014) also used geometric, spectral and textural traits to detect alien plant invasions in target riparian ecosystems. Similarly, laser-guided imaging spectroscopy has made it possible to use canopy traits to map different forest types and thus reveal functional variations derived from land use (Asner et al., 2017). Mapping trait distribution and trait variability can provide more accurate large-scale variation and may offer a good option in terms of the ability to quantify functional diversity.

- The use of novel methodological approaches to enlarge contributions from traditional techniques: “How can understanding be improved using the limited available data?” We have seen an increasing emergence of novel and multidisciplinary perspectives on functional diversity, such as species originality instead of traditional phylogenetic approaches (Pavoine et al., 2017). Similarly, new methodological approaches are being developed in order to connect the distribution and occurrence of riparian plant guilds to multiple stressors and support the prediction of threats to riparian ecosystem conservation (Bejarano et al., 2017a; Aguiar et al., 2018). We can expect the next few years to bring further advances in analytical techniques, software and modelling approaches.

- Anticipating the effects of global change in order to provide guidance for managers: How do climatic and land use changes as species-limiting factors affect the dynamics of functional diversity? Can shifts in functional diversity be predicted to an extent that can serve to guide management, conservation and restoration? Although major advances have been made in both predictive approaches and understanding the effects of global changes, there is still a long way to go before functional diversity can be used to effectively inform management decisions.

Conclusions

It seems that the advances in functional diversity frameworks in the last 20 years have led to an increase in the number of studies using riparian plant guilds and functional diversity indices, with a widespread distribution across Europe and USA. The key theoretical concepts were mostly developed between the 19th century and the 1990s, while applications, indicators, and associated software mostly emerged after that. There is still need for guidance on the use of functional plant traits and functional diversity indices. In summary, our main outcomes include:

- Functional diversity measures in riparian studies have numerous applications, from ecological studies to the management and assessment of restoration success.
- There is no consensus on the number of traits that should be used, although there is some evidence that a shortlist of independent and relevant traits (6–8) can offer advantages compared to a large trait dataset.
- The literature has frequently supported the use of soft traits as proxies of ecosystem processes, although drawbacks are also often reported and hard traits are recognized as more accurate indicators of plant functions.
- Specific Leaf Area (SLA), plant height, and seed mass were the most common traits used in riparian studies, however there is some evidence that the use of traits from multiple plant organs (leaves, stem, roots, flowers) would increase our understanding of ecosystem functions.
- Trade-offs and overlapping and intra- and interspecific variability of traits are some of the issues that still need to be solved for there to be a more consensual framework.
- The sensitivity of functional richness to species richness and the difficulty of comparing functional measure values (both for guilds and indices) across regions are relevant issues, not only for riparian forests but also across other plant ecosystems.
- Recommendations as to how functional diversity indices should be coupled are limited, and to date no index is capable of accounting for multiple functional facets occurring in an ecosystem.
- Multiple stressors were often addressed in the studies, but the hydrological regime (natural and regulated stream flows) was by far the most frequently assessed driving factor, followed by land use and land cover change.
- There is a need for future research on quantitative and qualitative trait selection, functional diversity indices, application at large spatial scales, and claims regarding comparable worldwide frameworks (guilds, index values).
- Novel approaches are emerging in this field of science, with a view to achieving a better connection between the prevailing ecological networks and the biotic and abiotic interactions and thereby improving the ability to assess the functional diversity of ecosystems.

Chapter III.

Limited resilience in hotspots of functional richness: the Mediterranean riparian shrublands

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Abstract

Functional diversity indices are increasingly being used to describe plant community assembly processes and ecosystem functioning. However, their relevance for predicting alterations in ecosystem functioning of riparian plant communities is still largely unknown. We investigated the functional patterns of riparian forests along environmental gradients, using biological and environmental data from 189 well-preserved riverine locations in mainland Portugal. We calculated functional diversity indices (e.g. Richness, Redundancy, Divergence) for four riparian forest types, namely the Alder woodlands, Ash woodlands, Tree-heath shrublands and Mediterranean shrublands, using their plant species composition and 25 plant functional traits.

We used multiple linear regression to predict the effect of the environment in the functional structure of riparian forests and ultimately evaluate the resilience of the riparian forests to environmental fluctuations. We found that Mediterranean shrublands have a significantly higher Functional Richness and a lower Functional Redundancy in comparison to the other riparian forest types. Both regional and habitat variables were important for predicting the functional diversity of riparian forests, with varying patterns according to forest types. In particular, we found that the redundancy of Mediterranean shrublands is mostly affected by precipitation, suggesting their potential vulnerability to climate change in the study area. Our results suggest the usefulness of functional diversity measures for conservation and monitoring the ecological functioning of riparian forests.

Keywords: Functional diversity indices, functional richness, functional redundancy, riparian forests, resilience, Portugal

Introduction

Non-disturbed riparian zones are some of the most diverse, dynamic and complex habitats worldwide (Naiman and Décamps, 1997). Riparian plant communities are vital components of these semiterrestrial habitats and are shaped by multidimensional environmental gradients (Naiman and Décamps, 2005; Stella et al., 2013a). Stream flow magnitude and variation play a major role in plant dispersal, establishment and abundance of riparian species (Naiman et al., 2002; Biggs et al., 2005). Nevertheless, besides the influence of hydrology and the geomorphic processes (Florsheim et al., 2008; Gurnell et al., 2012), climate, river hierarchy, and habitat features contribute to the spatial variation in species and trait composition (Bendix, 1994; Renöfält et al., 2005; Aguiar et al., 2013a). These environmental factors can be seen as filters determining the spatial variation of vegetation communities (Johansson and Keddy, 1991; Poff ,1997a). Recent climatic changes of frequent and prolonged drought events, especially in arid and semi-arid areas (Dai, 2011) will decrease the resilience of riparian vegetation (Camporeale and Ridolfi, 2006; Flanagan et al., 2015) and ultimately affect riparian ecosystem functioning (Balvanera et al., 2006). Therefore, understanding and predicting the response of riparian plant communities to environmental changes has become one of the major challenges in riparian ecology, since it can assist conservation planning, provide management and restoration guidelines of riparian ecosystems.

Traditionally, environmental-vegetation relationships have been accessed via species-centered approaches (Díaz and Cabido, 2001; Vandewalle et al., 2010). However, understanding ecological function at the community level is required to link vegetation assembly processes to environmental variability (Mason et al., 2012). Therefore, the concept of functional diversity is gaining more recognition due to its potential to reveal responses of plant communities to environmental gradients (McGill et al., 2006; Cadotte et al., 2011), hence to detect changes in ecosystem processes (Mason et al., 2005; Poff et al., 2006; Mouillot et al., 2013). In that sense, functional diversity measures could close the gap between ecosystem functioning and community ecology (Mouchet et al., 2010). Functional diversity relies on biological attributes of species, so called plant functional traits (Violle et al., 2007) and derive from the composition of plant assemblages. A variety of indices have been introduced to measure diverse aspects of functional diversity (Schleuter et al., 2010; Pavoine et al., 2013) and to relate functionality matrices to ecosystem stability (Hooper et al., 2005). For instance, Functional Richness, reveals the system's ability to face environmental fluctuations (Tilman et al., 1997) and alien plant invasions (Mason et al., 2005); Functional Divergence gives insights about niche differentiation and resource competition (Mason et al., 2005; Roscher et al., 2014), whereas Functional Evenness is related with system productivity and robustness (Mason et al., 2005). As a measure of ecosystem resilience, Functional Dispersion (Laliberté and Legendre, 2010) can be used as it enables to perceive how disturbances affect the functional trait range. Functional Redundancy can also assess ecosystem resilience to species loss and it is hence related with the ability of the system to buffer against environmental fluctuations (Walker, 1995; Naeem and Wright, 2003; Hooper et al., 2005). Rao index (Rao, 1982; Villéger and Mouillot, 2008) allows assessing the amount of species turnover among assemblages due to its decomposition into alpha-, beta- and gamma-diversities.

There is no consensus on the best functional diversity indices to assess functional structure of vegetation. Instead, distinct functional indices are being used to examine different functionality attributes of plant communities to single or multiple environmental factors and/or anthropogenic stressors. For instance, Functional Divergence, Evenness, and Richness were conjointly applied to investigate the effects of land use in arable lands, grasslands, moorlands and woodland communities (Pakeman, 2011), Functional Richness and Dispersion were applied to scrubland communities to assess the impacts of fragmentation (de Frutos et al., 2015), while single functional measures as the Functional Redundancy (Pillar et al., 2013) or the Rao index (Sasaki et al., 2014) were used in subtropical grasslands affected by grazing, and in moorland plant communities, respectively.

Some attention has been paid to the resilience and resistance of Mediterranean vegetation to disturbance events, using functional measures (e.g. de Frutos et al., 2015; de la Riva et al., 2016a, b). However, there are few studies on the use of functional diversity indices to forecast responses of riparian vegetation to environmental change. Examples are the work of Kominoski et al. (2013) that discussed how shifts in riparian plant composition can alter biodiversity patterns and decrease functional redundancy, and the field experiment of Bruno et al. (2016a) on the selection of the best functional diversity index for predicting responses of riparian woodlands to disturbance, and assessing the stability, resistance and resilience of these ecosystems. In this study, we aim to (1) characterize the patterns of functional diversity of riparian forests in Portugal and (2) predict the variation of functional diversity along environmental gradients. The ultimate goal is to assess the resilience of the riparian forests to environmental change and to understand the trajectories of the functional structure of riparian vegetation within an environmental change context.

For this purpose, we used trait data from the most frequent and abundant species in riparian forests from near-natural locations across mainland Portugal. We then calculated functional diversity indices for each location and compared the diverse riparian forest types occurring in Portugal, namely Alder woodlands, Ash woodlands, Mediterranean shrublands and Tree-heath shrublands. Finally, we explored and predicted the effect of the environmental change at habitat and regional scale in the functional diversity.

Materials and methods

Study area and sampling sites

Our study was conducted throughout the mainland of Portugal (Figure 10). The country is located at the western edge of the Iberian Peninsula, Western Europe, with an area of approximately 89,000 km^2 and around 800 km of Atlantic Ocean coastline.

The country is characterized by a highly diverse topography (from coastal lowlands to central plateaus and mountains), landscapes and human occupation. The western coastal area is densely populated and impacted by agriculture and industry, while the southern inland area is characterized by scattered settlements, and extensive agro-forests of olm-oaks (*Quercus ilex* L.) and cork-oaks (*Quercus suber* L.). The climate is mostly Mediterranean temperate, with mild winters and hot dry summers, except for the northwestern tip of Portugal with an Atlantic temperate climate (temperature < 7.5 °C, precipitation > 2800 mm year^{-1}). The Mediterranean influence increases from north to south, reaching in the south continental regions average annual temperature values above 16.5 °C, and precipitation below 500 mm year^{-1}.

The Portuguese river network is complex, with most of the rivers flowing from east to west, including four main transnational rivers (Minho, Douro, Tagus, Guadiana), large tributaries, a complex of small streams and large estuarine areas along the occidental and meridional coastal regions.

We used 189 sites, covering most of the river types occurring in Portugal, including both perennial and temporary rivers. Large rivers with catchment areas above 10,000 km^2 and the calcareous rivers of the south meridional coast were not included.

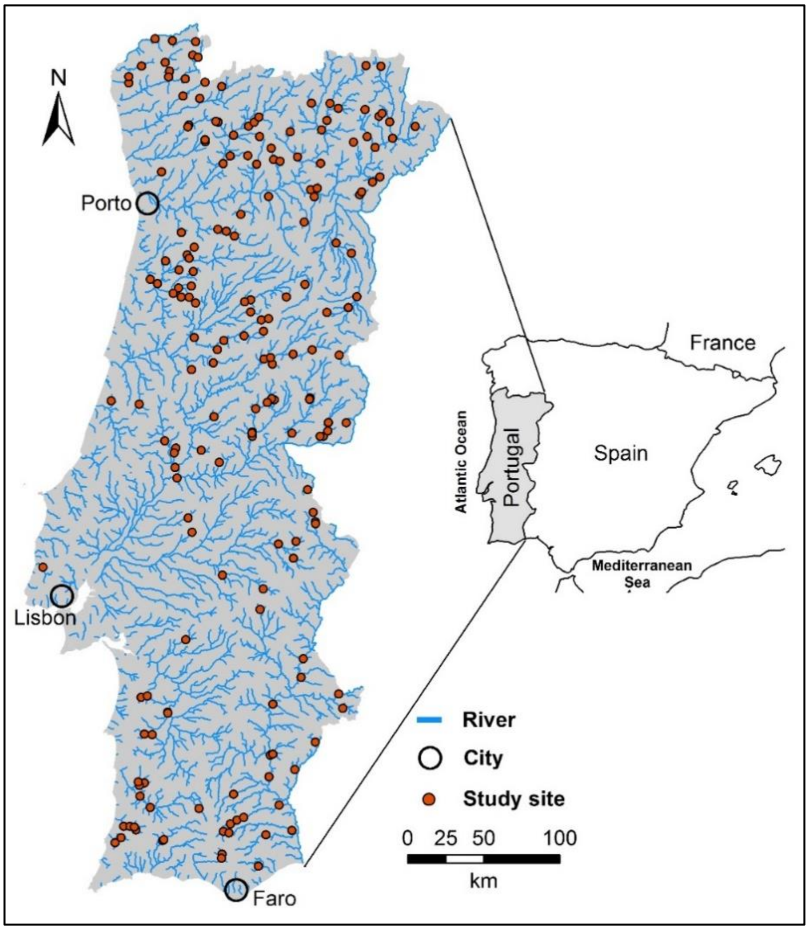


Figure 10. Location of Portugal in Europe. Map on the left shows the river network and the studied sites.

Floristic and environmental data

We used the field data collected by the Environmental Portuguese Agency, APA I.P. in Spring of 2004 and 2005 for the implementation of the EU-Water Framework Directive (2000/60/EC) in Portugal. The floristic surveys were carried out in 100 m-long riparian forests and the sampled area varied with the riparian zone width. The foliage projected cover of each riparian woody species (trees, shrubs, and lianas) in the sampled area was used as an estimate of relative species abundance. The EU standardized sampling methods and trained teams of plant experts were used for this particular campaign (details can be found in Aguiar et al., 2009). The surveyed river stretches were screened for anthropogenic disturbances and selected those with nearly undisturbed conditions for this study. The abiotic criteria used was: (1) good chemical quality (nitrate, nitrite, phosphates, ammonia, pH, BOD5, COD); (2) minimal changes in the riparian zone; (3) no signs of recent changes in channel morphology; (4) low levels of urbanization and industrial activity in the catchment area; (5) minimum impacts on the natural hydrological regime; and (6) low levels of fine sediment load. In addition, a further screening of these sites was made by expert judgement on the general conservation status of the riparian forests.

For the present study, we used the classifications of riparian forest types of Aguiar et al. (2013a, pp 633–635) shrublands were reported in Aguiar et al. (2013a) and supported by Amigo et al. (2017). Four riparian forest types were considered in this study (Table 3), namely:

- Alder woodlands (Alnetea glutinosae vegetation class): located in lentic waters, and siliceous substrates with various degrees of peat formation; dominated either by the black alder (*Alnus glutinosa* (L.) Gaertn.) or by grey willow (*Salix atrocinerea* Brot.). Portuguese tussock sedge (*Carex paniculata* L. subsp. *lusitanica* (Schkuhr ex Willd.) Maire) is common in swampy soils of these formations;

- Ash woodlands (Salici purpureae-Populetea nigrae vegetation class): located in perennial rivers with seasonally irregular flows; mostly composed by narrow-leaved ash (*Fraxinus angustifolia* Vahl) under the influence of a temporary water table with almost no waterlogging; in torrential rivers, it is common the occurrence of hedges of *Salix salviifolia* Brot., an endemic willow from the Iberian Peninsula;

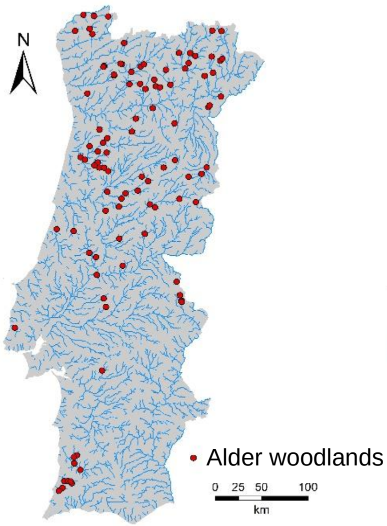
- Mediterranean shrublands (Nerio-Tamaricetea vegetation class): located in Mediterranean rivers with very irregular flow; it includes: (1) tall-scrub formations of *Nerium oleander* L. (oleander) and *Tamarix Africana* Poiret (African tamarisk); (2) Communities of *Flueggea tinctoria* (L.) G.L. Webster (tamujo; an endemic Iberian species) on the rocky riverbanks of Mediterranean rivers; (3) communities of slow-moving (lentic and brackish) waters dominated by *T. africana;*

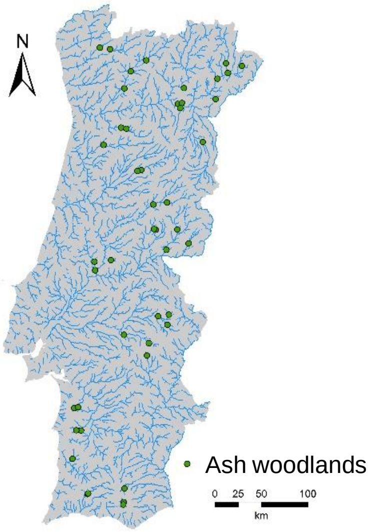
- Tree-heath shrublands (Erica arborea-Frangula alnus communities): located upstream of rivers of mountainous areas of central Portugal over rocky (cobbles and boulders) substrates; tall shrub communities dominated by white heather (*Erica arborea* L.) and alder buckthorn (*Frangula alnus* Miller).

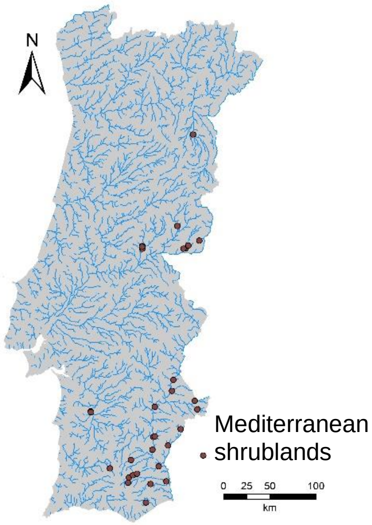
Table 3. Characterization of the riparian forest types (sources: Aguiar et al. 2013a; 2013b; Espírito-Santo et al. 2017; Amigo et al. 2017). Photo credits: FC Aguiar.

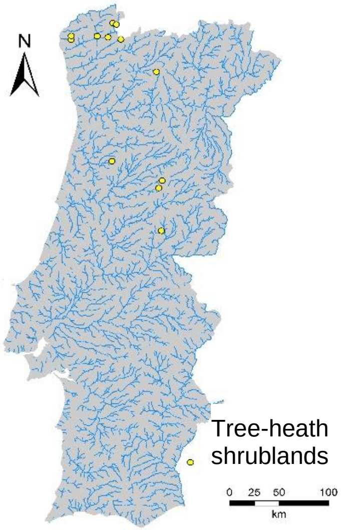
	Alder woodlands	Ash woodlands	Mediterranean shrublands	Tree-heath shrublands
Sampling sites (Nº.)	100	46	31	12
Species richness ±SD	6.5±1.9	5.4±1.6	3.8±2.1	4.7±1.7
Dominant species	*Alnus glutinosa* (L.) Gaertn. *Salix atrocinerea* Brot. *Hedera hibernica* Hort. *Sambucus nigra* L.	*Fraxinus angustifolia* Vahl *Crataegus monogyna* Jacq *Salix salviifolia* Brot *Rubus ulmifolius* Schott.	*Flueggea tinctoria* (L.) G.L. Webster *Nerium oleander* L. *Tamarix africana* Poiret	*Erica arborea* L. *Frangula alnus* Mill.
Strata complexity	Highly complex; trees, shrubs (diverse heights), herbs; transversal zonation	Highly complex; trees, shrubs (diverse heights), herbs; transversal zonation	Low complexity; mostly shrubs (same height) and herbs	Low-medium complexity; shrub and herbaceous strata
Riparian width	Potentially large woods	Potentially medium-large woods	Low-medium riparian widths	Low riparian widths
Leaf characteristics	Mostly deciduous, hygromorphic or mesomorphic large leaves	Mostly deciduous, mesomorphic, hydromorphic and scleromorphic leaves	Evergreen, scleromorphic or coreaceous leaves with thickened epidermis and cuticular wax coating	Deciduous, mesomorphic leaves
Reproductive strategies	Vegetative and mostly sexual	Vegetative and mostly sexual	Mostly sexual	Mostly sexual

Geographic location









Landscape view

For the present study, we used the most frequent riparian woody species (trees, shrubs, and lianas) on these forest vegetation types, i.e. species occurring in more than 5% of the sites (Table B1). We considered two subsets of non-correlated environmental variables: regional [altitude (m asl), distance to river source (m), average annual precipitation (mm)] and habitat [length of the river with no flow (%), channel width, channel depth, and riverbank substrate (bedrock, boulders, cobbles, gravel, sand, fine elements-silt, clay and Coarse Particulate Organic Matter, CPOM)].

Trait data and functional diversity indices

Twenty-five soft functional plant traits were selected to express the key vegetation processes and population dynamics in riparian plant communities (Table B2). Traits were formerly collected from FLOWBASE-a riparian trait database of riparian woody species from the Iberian Peninsula (Aguiar et al., 2013b).

Aiming to investigate the underlying patterns of functional diversity in riparian forests of Portugal, we used a set of recognized indicators that quantify components of functional diversity (Mouchet et al., 2010). Here, we explored the Functional Richness (FRic), Functional Divergence (FDiv), Functional Evenness (FEve), Functional Dispersion (FDis), Functional Redundancy (FR) and Rao index (Q). FRic is defined as the amount of niche space filled by species in the community (Villéger et al., 2008). It was measured as the volume inside the minimum convex hull which includes all species traits of interest (Cornwell et al., 2006). FDiv is defined as the degree to which abundance distribution in niche space maximizes functional divergence characteristics within the community (Villéger et al., 2008). It was calculated as species deviance from the mean distance to the center of gravity weighted by relative abundance. If all taxa are equally distant from the centroid and have equal abundances, then FDiv equals 1. FEve combines both the evenness of species distribution and the evenness of species abundances and is defined as the evenness of abundance distribution in occupied niche space (Villéger et al., 2008). FEve was calculated as the sum of the minimum spanning tree (MST) (Ricklefs and Travis, 1980) branch length weighted by the relative abundance of the two species. The index is 1 if all species have equal abundance and if all the branch lengths have equal length and decline towards zero with increasing unevenness in either aspect. Both, FDiv and FEve are based on trait values. FDis is defined as the mean distance in multidimensional trait space of individual species to the centroid of all species (Laliberté and Legendre, 2010). FDis is unaffected by species richness and can take into account the species relative abundances. When all species have equal abundances, FDis is simply the average distance to the centroid (i.e. multivariate dispersion) as originally described by Anderson (2006). FDis has no upper limit. Since some species perform similar roles in communities and ecosystems, FR is defined as the capacity of one species to functionally compensate for the loss of another (Steneck and Dethier, 1994; Rosenfeld, 2002). FR is based on trait values and was measured as the difference between species diversity (using the Gini-Simpson diversity index) and the Rao index (de Bello et al., 2007). Rao index (Q) (Rao, 1982), is the only functional diversity measure that is not clearly related to one of the functional diversity components, however, embraces functional richness and divergence. Q was measured as the sum of distances between pairs of randomly chosen species (Botta-Dukat, 2005) in trait space, weighted by their relative abundance (Villéger and Mouillot, 2008) and will increase as the most abundant species have increasingly extreme traits.

The SYNCSA package was used for computing these functional indices (available at http://ecoqu a.ecolo gia.ufrgs.br/ecoqu a/SYNCS A.html).

Data analysis

We performed regression analyses to assess the coefficient of determination between the functional diversity indices. Analysis of variance (one-way ANOVA) was used to test for the significant difference ($p < 0.05$) between the riparian forest types and post-hoc Tukey Honestly Significant Difference (HSD) tests were conducted to determine the statistically significant distinct groups in relation to FRic and FR. We used multiple linear regression to model the relationship between the aforementioned regional and habitat environmental variables as explanatory variables and different functional diversity indices for each riparian forest type as response variables. Tree-heath shrublands were represented only at 12 sampling sites which were insufficient for the regression analysis. By mixing regional and habitat variables we obtained models that incorporated processes occurring at different spatial scales, allowing to assess and compare the relative influence of each kind of variables.

Model selection was based on a multimodel inference procedure. Several models were fitted and were ranked according to a weight measure based on the Akaike's information criterion (AIC). The Akaike weight of a given model can be defined as the probability that the same model would be selected as the best-fitting model if data were collected again under identical circumstances (Burnham and Anderson, 2002). However, frequently more than one model is needed so that the sum of their weights is close to 1. Therefore, we used an average modelling in which the resulting regression coefficients were given by the weighted means of the coefficients of individual models. This method also allowed to compute variable importance given by the sum of the weights of models where each variable is present. We computed all possible models using all possible explanatory variable combinations but limiting the number of variables to a maximum number of 5 to avoid too complex models to be fitted. In the model averaging summary two alternatives are available: full averaging (average values include zero when the variable is not present) and conditional averaging (average values only use models where the variables are present). The second alternative was used for the data interpretation.

We ran a single model for all sites using the environmental variables and also including riparian forest types as an explanatory variable to test its relative influence. Then we performed a second round of multiple linear regression models separately for each riparian forest type. All variables were log-transformed and standardized before fitting multiple linear regressions.

The statistical analyses were performed in the R statistical software (R Development Core Team 2017). Multimodel inference was performed using the "dredge" function of the MuMIN library for R (Barton, 2016).

Results

Functional characteristics of the riparian forest types

Regression analyses between functional indices revealed a high coefficient of determination ($R^2 = 0.95$) between Functional Dispersion (FDis) and Rao index (Q), whereas coefficient of determination between Functional Richness (FRic), Functional Divergence (FDiv), and Functional Redundancy (FR) showed weak correlation ($R^2 < 0.10$) (Table B3). FRic and FR were retained for further analyses due to their complementarity to describe how much of the functional space is occupied (FRic) and how much of the functions in the functional space are overlapping between each other (FR).

We found significant differences (ANOVA, $p < 0.001$) for FRic in the studied riparian forest types, however, the ANOVA results for FR ($p = 0.07$) were not conclusive about the existence of significant differences among riparian forest types (Table B4).

Post-hoc pairwise comparisons using HSD tests showed that Mediterranean shrublands were significantly different from the other riparian forest types (Figure 11). Mediterranean shrublands have the highest FRic and the lowest FR in comparison to Alder woodlands, Ash woodlands, and Tree-heath shrublands. Moreover, in the best fitting model for FRic and FR, Mediterranean shrublands as a dummy variable describing the “Riparian forest type” showed significant regression coefficients ($p < 0.001$ and $p < 0.002$, respectively) (Table 4).

The “Riparian forest type” was ranked as the first explanatory variable for FRic and fourth for FR in the best-fitting model with average modeling (Table B5).

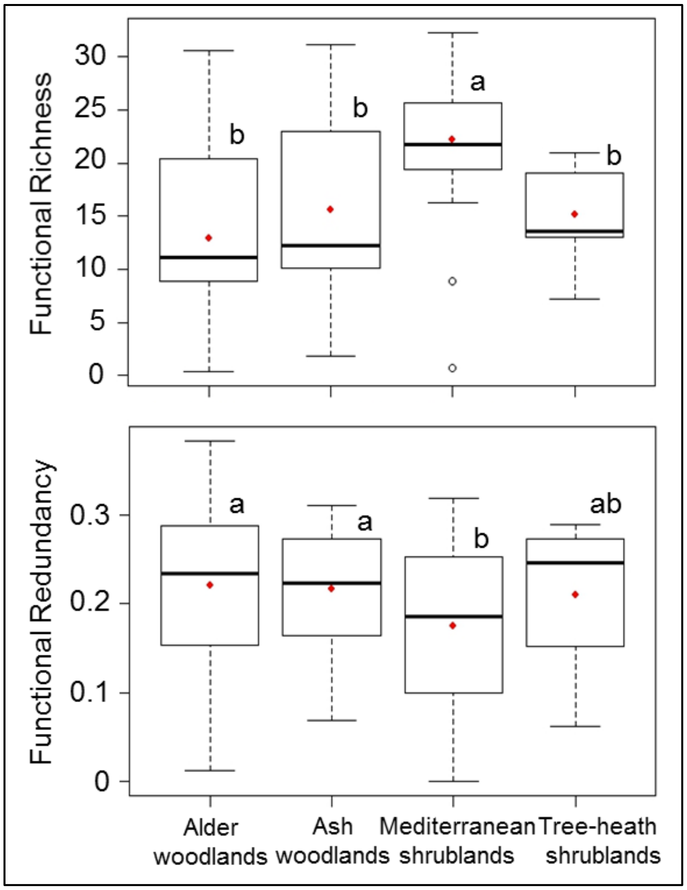


Figure 11. Boxplots indicating the proportion of Functional Richness and Functional Redundancy for Alder woodlands, Ash woodlands, Mediterranean shrublands and Tree-heath shrublands. Diamonds represent the average values for each riparian forest. Average values with the same letter are not significantly different ($p < 0.05$).

Table 4. Results showing the best-fitting model chosen through average modeling (including separate riparian forest types as explanatory variables) for Functional Richness and Functional Redundancy.

Index	Variable	Estimate	SE	Adjusted SE	Z value	R^2	P value
Functional	Altitude	-1.141	0.600	0.604	1.890	0.21	0.059
Richness	Bedrock_boulders	0.948	0.629	0.633	1.498		0.134
	Riparian vegetation type:	1.624	1.383	1.392	1.167		0.243
	-Ash woodlands						
	-Mediterranean shrublands	8.000	2.024	2.036	3.927		0.000***
	-Alder woodlands	0.613	2.538	2.556	0.240		0.811
	Sand	-1.983	0.600	0.604	3.285		0.001**
	Channel depth	1.021	0.624	0.628	1.626		0.104
	Fine elements_soil	0.918	0.689	0.694	1.323		0.186

	Length no flow	0.832	0.642	0.647	1.286		0.199
	Cobbles_gravel	-0.649	0.589	0.593	1.093		0.274
	Distance to source	-0.891	0.854	0.860	1.036		0.300
	Precipitation	0.618	0.749	0.754	0.820		0.412
Functional Redundancy	Channel width	0.010	0.006	0.007	1.506	0.05	0.132
	Length no flow	-0.017	0.006	0.007	2.533		0.011*
	Sand	0.007	0.006	0.006	1.235		0.217
	Distance to source	0.007	0.006	0.006	1.075		0.283
	Riparian vegetation type:	-0.002	0.016	0.016	0.105		0.917
	-Ash woodlands						
	-Mediterranean shrublands	-0.048	0.021	0.021	2.320		0.020*
	-Alder woodlands	-0.010	0.026	0.026	0.384		0.701
	Bedrock_boulders	0.005	0.006	0.006	0.808		0.419
	Channel depth	0.004	0.006	0.006	0.616		0.538
	Altitude	0.004	0.007	0.007	0.556		0.578
	Fine elements_soil	-0.003	0.006	0.006	0.498		0.618
	Precipitation	-0.003	0.007	0.007	0.450		0.653

Relationship between functional diversity indices and environment

Regional and habitat variables had a distinct predictive capacity for the functional diversity of the studied riparian forests (Figure 12). Broad-scale gradients of climate, elevation and river hierarchy were frequently selected as predictive variables. The precipitation was the variable that was more frequently selected across riparian forest types for both indices, except for the FRic of Ash woodlands. Local variables, such as sand and channel width and channel depth contribute also to the prediction of changes in FRic and FR (Figure 12b). In Mediterranean shrublands, FRic was mainly predicted by regional variables, whereas FR relied on both regional and habitat variables (Figure 12c).

The most parsimonious model of FRic of Mediterranean shrublands explained 37% of the total variance (Table B6). FRic of Mediterranean shrublands increase with precipitation and decrease with altitude and distance to the source. FR in Mediterranean shrublands was mostly affected by precipitation (positive contribution). Besides precipitation, FR of Mediterranean shrublands increased with channel depth and decreased with the river length with no flow and the amount of gravel and cobbles on the riverbanks. The same pattern of increased FR with precipitation was observed in Ash woodlands (Table B6). The best fitting model explained 35% of the deviance and precipitation showed a positive effect on FR ($p = 0.001$). An increase of FR downstream was revealed for Ash woodlands and Alder woodlands, where the distance to the source had a significant effect on the model ($p = 0.001$ and $p = 0.025$, respectively).

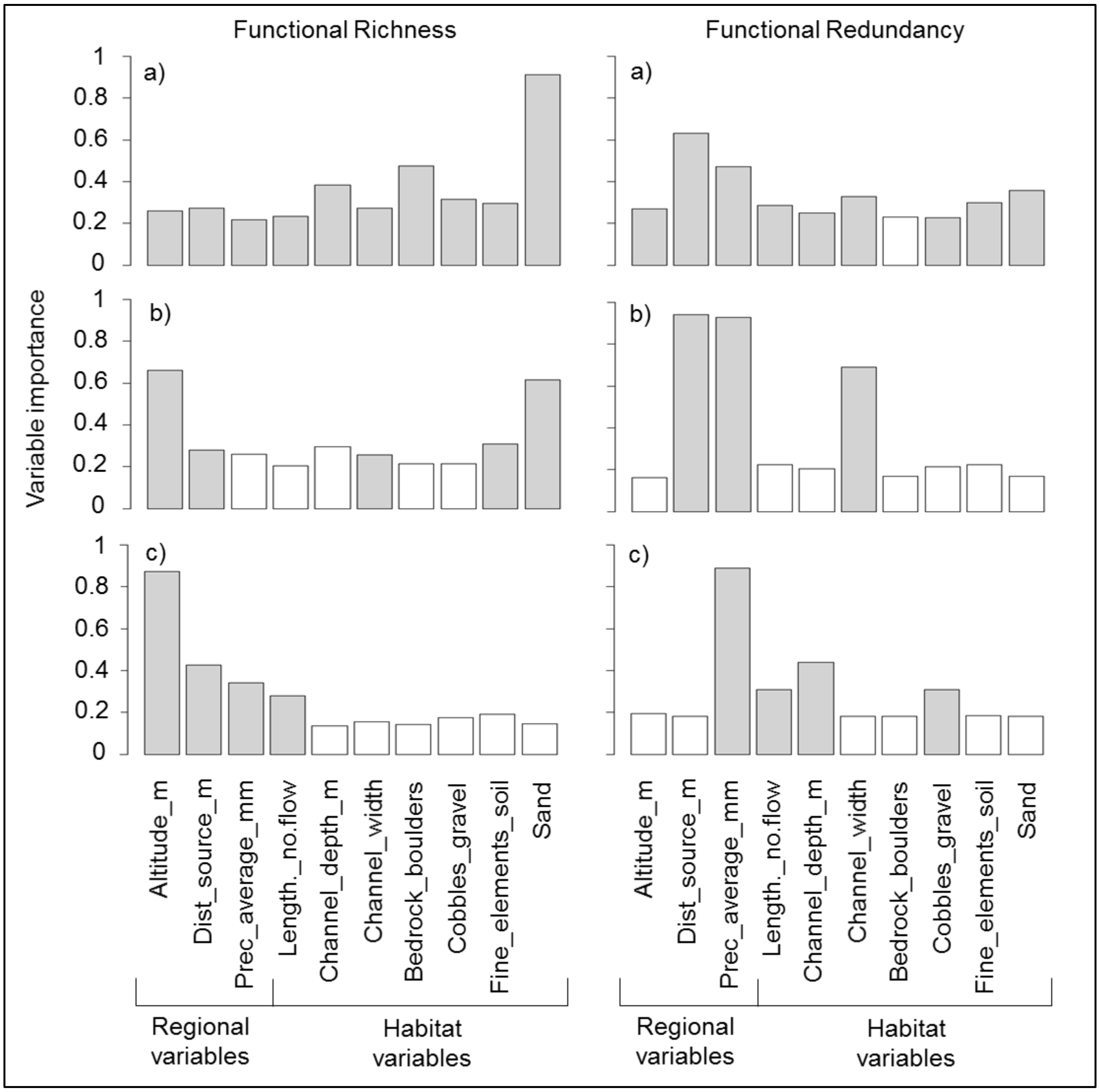


Figure 12. Importance of each environmental variable as measured by the sum of models Akaike's weights for the riparian forest types. a) Alder woodlands; b) Ash woodlands; c) Mediterranean shrublands. Grey bars represent variables selected in the best approximating model.

Discussion

Functional diversity indices are considered measures of ecosystem functioning and can be used to characterize the relationship between ecosystem processes, functional traits and environmental conditions (Díaz and Cabido, 1997; Mouchet et al., 2010). In the present study, one of the most remarkable results were the contrasting functional diversity patterns of Mediterranean shrublands in relation to other studied riparian forests. In addition, these riparian communities displayed the highest functional richness of all groups and the lowest functional redundancy. Below, we discuss these results and their implications on the resilience of the riparian forests.

Functional richness of riparian forests

FRic increases when niche complementarity facilitates probability of species occurrence (Mason et al., 2012). FRic values revealed that in the study area Mediterranean shrublands were characterized with a high occupation of niche space and high resource utilization (alpha niches), hereby increasing the resilience to species invasions. Contrasting explanations are reported in literature when high FRic is observed. Mason et al. (2008) relate high FRic to species rich communities, whereas Díaz and Cabido (2001) suggest that FRic does not always correspond to species richness. In fact, functional diversity may increase rapidly even at low species diversity levels if trait diversification is present in the community as a strategy to adapt to the environmental conditions (Micheli and Halpern, 2005). Therefore, if the traits are widely dispersed in the trait space, FRic can be high since its calculation takes into account the distance of the traits from the centroid (Elmqvist et al., 2003; Laliberté et al., 2010). In the Mediterranean shrublands, high FRic was observed at low floristic richness. This can be a consequence of high species specialization in harsh environmental conditions (Alados et al., 2004; Navarro et al., 2009) which may lead to traits divergence within the community viable traits range (de la Riva et al. 2016b). Trait diversification, which consequently increases FRic, have been reported under strong abiotic constrains (Cornwell and Ackerly, 2009; Spasojevic and Suding, 2012), including Mediterranean rangelands (Bernard-Verdier et al., 2012). In particular, Mediterranean shrublands occurred at well-defined environmental conditions, mostly to lowland continental rivers with high annual thermal ranges (9.8–13.5 °C) and low annual precipitation (average < 595 mm year^{-1}) (Aguiar et al., 2013a). Due to the natural environmental stress, riparian adaptations consist of deep roots, late seeds dispersion, and long flowering duration. These functional characteristics enable Mediterranean shrublands to be more competitive than other species at harsh environmental conditions (Futuyma and Moreno, 1998; Jasmin and Kassen, 2007). In contrast, Alder woodlands and Ash woodlands displayed lower and similar FRic, but are composed of a larger number of species than Mediterranean shrublands (and Tree-heath shrublands). These more diverse communities have a smaller amount of the niche space filled by the species, and thus in comparison are more prone to introspection of other species. In fact, it is common that these communities under disturbed conditions increase their floristic diversity, either by alien species or non-hygrophylous species from the adjacent ecosystems (Aguiar et al., 2007).

Limited functional redundancy of Mediterranean shrublands in relation to Alder woodlands and Ash woodlands

The strength and the shape of the relationship between taxonomic and functional diversity depend on the extent of redundancy within the assemblage, i.e. the number of taxonomically distinct species that exhibit similar ecological functions (Walker, 1992, 1995; Naeem, 1998).

Functional redundancy involves diverse niche dimensions that are difficult to be assessed and properly interpreted (Rosenfeld, 2002). Several authors agreed (e.g. Laliberté et al., 2010; Bruno et al., 2016a) that stress can decrease the values of FR. However, low FR has been reported in absence of stress (Petchey et al., 2007; Mason et al., 2011). Lack of redundancy occurs when changes in functional diversity are proportional to changes in species richness (Walker, 1992; Petchey et al., 2007) but also in the functionally diverse communities where high niche differentiation leads to divergence in trait values (Laughlin et al., 2015). In our case, indeed, Mediterranean shrublands displayed high niche occupation (high FRic) at the expense of low FR. Limited FR in Mediterranean shrublands corresponds to their constrained occurrence to dry and warm locations (Aguiar et al., 2013a), hence narrower trait ranges. This is in line with the studies which reported small trait range in Mediterranean ecosystems with prevailing environmental extremes (Cornwell et al., 2006; Bernard-Verdier et al., 2012). In contrast, a broad species pool occurring in wide environmental context could facilitate FR in riparian communities (Lawson et al., 2015b) as it was observed in Alder and Ash woodlands. Tree-heath shrublands showed similar redundancy from the other forests, but this can be an effect of the small number of surveys. Redundant species are considered necessary to ensure ecosystem resilience to perturbation (Walker, 1992, 1995). In non-redundant communities as Mediterranean shrublands, the loss or replacement of one species would lead to loss of unique traits or functions in the system (Hooper et al., 2005) thus increasing ecosystem vulnerability to environmental changes (Elmqvist et al., 2003).

Environmental predictors of functional change

Translating the relationships between species traits and environmental variables into functional diversity and forecasting functionality patterns is crucial to understand ecosystem processes in a time of global change (Lavorel and Garnier, 2002; Kominoski et al., 2013). Since environmental variability is a strong force in shaping plant communities (Poff, 1997a; Freschet et al., 2011; Maire et al., 2012), and the direction of environmental change is unknown, it is critical that the plant communities are modeled in a trait-based species distribution (Laughlin et al., 2015). Trait–environment relationships could be related to different spatial scales which strongly influences the relationships among variables. Therefore, the scale of observation is essential to be interpreted in the results of a study (Cooper et al., 2003; Borcard et al., 2004). It has been suggested that habitat variables influence riparian forests at the local level and generally do not affect riparian forests at large scale, whereas regional variables ultimately influence local riparian communities (Naiman and Décamps, 2005). Precipitation, one of the most recognized factors affecting plant traits at a global scale (Donoghue, 2008; Moles et al., 2014), was the most common environmental predictor of functional diversity across riparian forest types in our study. Rainfall patterns are especially important for riparian vegetation in Mediterranean Europe, and in particular on the Iberian Peninsula (Kilsby et al., 2007), where the future climate predictions point to the increase of hot waves, drought events, as well as uncertainty in rainfall patterns (IPCC, 2014). In fact, despite the inherited ability of Mediterranean shrublands to tolerate periods of drought (Salinas et al., 2000), it was reported that its functional richness tends to diminish after an extreme climatic episode of drought (de la Riva et al. 2016a, b). Thus, it can be assumed that climate change will ultimately decrease the functional diversity of Mediterranean shrublands, hereby, decreasing their resilience to mitigate the climate change effects. The same decreasing pattern of functional diversity with reduced precipitation was observed in Alder woodlands and Ash woodlands. As floristic heterogeneous groups with wide trait range, these riparian forests have high FR, but FRic remains low, which also suggests susceptibility to environmental shifts and to alien plant invasions.

Besides precipitation, distinct riparian forest types responded differently to habitat and regional variables. We expected that functional diversity of spatially dispersed groups such as Ash woodlands would be determined by a high number of environmental factors. Instead, we found that FR in Ash woodlands is strictly confined by river hierarchy, namely by the distance to the source and channel width. However, for Mediterranean shrublands, FR was constrained by few environmental variables and mainly related to habitat characteristics.

The study highlights the potential of functional measures for monitoring purposes by detecting ecosystem changes in riparian forests. We expect that using the same functional traits we can distinguish non-disturbed from disturbed communities by comparing the values for FRic and FR. We expect that disturbance will lower FRic and FR in Mediterranean shrublands by filtering out the species that will not be adapted to the newly created environmental conditions, whereas in Alder woodlands and Ash woodlands might be noticed the presence of new traits from “outlier” species (e.g. alien species, terrestrial species) which outcompete native species in disturbed environment. Extreme anthropogenic disturbance can also lead to homogenization of traits as was observed by Stromberg et al. (2007) in riparian zones of Arizona, USA. Further research in disturbed sites should be conducted to enlarge our understanding of the functional diversity of disturbed ecosystems.

Conclusions

In this study, we aimed to characterize the functional diversity of four riparian forest types of Portugal and to assess the predictive capacity of functional measures to environmental change. We found that the more distinct, but also more vulnerable riparian woody communities were the Mediterranean shrublands located in the hotter and drier areas of the country and dominated by sclerophyllous evergreen and water-stress tolerant species, namely the oleander (*Nerium oleander*), the African tamarisk (*Tamarix africana*), or the tamujo (*Flueggea tinctoria*), an endemic Iberian shrub. These formations showed lower Functional Redundancy, but higher Functional Richness, when compared with the more floristically heterogeneous communities, namely those dominated by ashes, alders, and willows. However, given that both Alder woodlands and Ash woodlands displayed a high Functional Richness it is expected that they are more susceptible to invasions and *terrestrialization* (i.e., introspection of terrestrial plants from uplands). In general, precipitation was a common driver of functional redundancy for all riparian communities, which increased with increasing precipitation values. Thus, potentially, the on-going climate change in the study area, with uncertain rainfall patterns and increasing drought events may lead to less stable and less resilient riparian ecosystems. Our results strongly encourage further research in other well-preserved riparian ecosystems in similar climatic regions, such as southern and eastern Spain and in disturbed riparian ecosystems. Such knowledge is required to define threshold values of functional diversity for awareness of degradation and for conservation and monitoring purposes.

Chapter IV.

Functional diversity of riparian woody vegetation is less affected by river regulation in the Mediterranean than boreal region

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Abstract

River regulation may filter out riparian plants often resulting in reduced functional diversity, i.e., in the range of functions that organisms have in communities and ecosystems. There is, however, little empirical evidence about the magnitude of such reductions in different regions. We investigated the functional diversity patterns of riparian woody vegetation to streamflow regulation in boreal Sweden and Mediterranean Portugal using nine plant functional traits and field data from 109 sampling sites. We evaluated changes in mean plant functional traits as well as in indices of multidimensional functional traits, i.e., Functional Richness (FRic) and Functional Redundancy (FRed) within regions and between free-flowing and regulated river reaches. We found that regulation significantly reduced functional diversity in Sweden but not in Portugal. In Sweden, the increased magnitude of variations in water flow and water level in summer, the prolonged duration of extreme hydrological events, the increased frequency of high-water pulses, and the rate of change in water conditions were the likely main drivers of functional diversity change. Small riparian plant species with tiny leaves, poorly lignified stems, and shallow root systems were consistently associated with regulated sites in the boreal region. In Portugal, the smaller streamflow alterations by regulation combined with the species legacy adaptations to the Mediterranean natural hydrological regimes likely result in similar functional diversity values for free-flowing and regulated rivers. We conclude that streamflow regulation may reduce the functional diversity of riparian woody vegetation, but the magnitude of these effects will vary depending on the adaptations of the local flora and the patterns of streamflow disturbances. Our study provides insights into functional diversity patterns of riparian woody vegetation affected by regulation in contrasting biomes and encourages further studies of the functional diversity thresholds for maintaining ecosystems.

Keywords: functional diversity, functional traits, functional richness, functional redundancy, riparian woody vegetation, streamflow regulation, boreal biome, Mediterranean biome

Introduction

The alteration of streamflow regime is recognized as a key threat to many riverine plant species and compromises many functions and ecosystem services of rivers (Arthington et al., 2010; Tonkin et al., 2018). Dams, reservoirs and other infrastructures for river regulation are changing the natural streamflow regimes resulting in homogenization of river dynamics, reconstruction of riparian habitats and ultimately a reshaping of riparian vegetation (Lytle et al., 2017).

Riparian vegetation is particularly sensitive to fluctuations in flow and water-level and must cope with variations in inundation, water-stress and water currents (Bornette et al., 2008; Merritt et al., 2010). The adaptations of riparian species resulting from specific combinations of functional traits determine the fate of species under different flow conditions (Stromberg and Merritt, 2016). Since combinations of functional traits vary with environmental conditions, streamflow variations, among others, can filter out sensitive riparian plant species, leading to a reduction in the range of trait values and, ultimately, changes in functional diversity (Keddy, 1992a, Hooper et al., 2005).

Functional diversity reflects the range of functions that organisms have in communities and ecosystems (Mouchet et al., 2010) and has been shown to respond to environmental filters (Bruno et al., 2016a; Lozanovska et al., 2018a). Functional richness and functional redundancy represent two components of functional diversity that may be important for maintaining ecosystem functioning in response to stressors (Mori et al., 2013; Angeler and Allen, 2016). A combination of differences in the range of functional traits enables an ecosystem community to cope better with various environmental and/or anthropogenic disturbances by having at least one trait out of multiple which can mitigate the disturbance, thus maintaining ecosystem functioning (Tilman et al., 1997; Mouillot et al., 2013). Functional redundancy describes the situation when more than one species present similar species traits, and thus can compensate for species loss following stress (Walker, 1992). On the contrary, species loss in non-redundant communities leads to loss of traits or functions, further increasing ecosystem vulnerability to disturbances (Rosenfeld, 2002).

The critical attributes of the streamflow regime – magnitude, frequency, duration, timing and rate of change (Poff et al., 2007) – which govern riparian vegetation dynamics, vary with biogeographic, geomorphic, and climatic settings (Nilsson and Svedmark, 2002). In Mediterranean regions, rivers are influenced by the seasonality and variability of precipitation with dry summers and mild winters, and large interannual variability. Such rivers are naturally subjected to extremes, ranging between no or low flows to flash floods (Gasith and Resh, 1999). Temporary reductions in water availability play an important evolutionary role in adapting riparian vegetation to such conditions (Stromberg and Boudell, 2013). In the boreal region, however, most rivers and streams have permanent streamflow. The flow regime is driven by snow accumulation during winter when flows and water levels are at their lowest, and by melting of snow and ice during spring and early summer when floods reach their annual maximum levels (Woo et al., 2008). In the far northern latitudes, recurrent ice formation and ice jams can cause physical damage and physiological alterations in riparian plants (Nilsson et al., 2015).

Despite the diverse constraints of Mediterranean and boreal biomes in the physiology and physiognomy of riparian vegetation, altered seasonal and daily streamflow variations by dams are known to impair riparian ecosystems in general (Webb et al., 2013). In Portugal, damming has long been used to cope with the natural seasonality of precipitation and since the middle of the 20th century also to favor hydropower generation. In Sweden, due to the rapidly changing energy markets, rivers have been exploited for large-scale hydropower production since the early 20th century, with increased hydropeaking over recent decades (Ashraf et al., 2018).

Our main goal was to investigate if streamflow regulation in two biomes with a diverse legacy of plant adaptations and environmental constraints would lead to similar ecological patterns for functional diversity in riparian woody vegetation. We did this through an analysis of nine flow-related functional traits and two indices, i.e., Functional Richness and Functional Redundancy, in free-flowing and regulated rivers from both regions. We hypothesized that streamflow regulation would be reflected in the functional diversity patterns of riparian woody vegetation, affecting functional traits that are not tolerant to streamflow regulation and reducing functional diversity in both regions. However, we expected that changes in functional diversity patterns would differ based on the streamflow regime and species' natural adaptations to flow-related disturbances i.e., that biome can mediate the effect of streamflow regulation on functional diversity. Specifically, we asked the following questions: (i) how do functional diversity in the Mediterranean and boreal rivers change with regulation? (ii) which hydrological attributes affect functional diversity in Mediterranean and boreal ecosystems?

Materials and methods

Study area and sampling design

Our study was undertaken in the north and central mainland of Portugal and in the boreal coniferous zone in northern Sweden (Figure 13). European Mediterranean and boreal biomes differ in climate, vegetation and fluvial dynamics (Table 5). Seasonality is the main factor controlling streamflow regimes in Mediterranean rivers, whereas rivers in the boreal biome are strongly influenced by frost formation, ice regimes and snowmelt. Hydromorphic disturbances are common in both biomes.

The Portuguese study sites represent a Mediterranean climate with hot, dry summers and mild, wet winters. Riparian woodlands comprise heterogeneous assemblages dominated by winter deciduous species. Alder woodlands composed of the black alder (*Alnus glutinosa*) and grey willow (*Salix atrocinerea*), with *Rubus* spp. on the edge of the riparian zone and the Portuguese tussock sedge (*Carex paniculata* subsp. *lusitanica*) on and along the river channel. In perennial rivers with seasonally irregular flows, Ash woodlands occur and are dominated by narrow-leaved ash (*Fraxinus angustifolia*) and an Iberian willow (*Salix salviifolia*). Along the perennial rivers, the riparian shrub strata frequently include *Crataegus monogyna* and *Rubus* spp. In torrential rivers, *Salix salviifolia* commonly border rivers and streams. Riparian forests in Portugal are usually constrained by the agricultural and forestry land-uses adjacent to rivers. In regulated reaches, occurrence of alien invasive species, such as *Acacia* spp. and *Arundo donax* is common.

While the species richness between the free-flowing and regulated river reaches is similar, the regulated river reaches are more fragmented and narrower, and are lacking the natural spatial zonation of the riparian communities (Aguiar et al., 2016). For instance, willow species can invade rivers downstream of dams in almost monospecific stands. The Swedish study sites have a cold-temperate climate. The riparian vegetation along the free-flowing rivers is distinctly vertically zoned, from forest communities at the top with *Pinus sylvestris* and *Alnus incana* among the dominant tree species, to shrub vegetation of predominantly *Salix* spp., to herbaceous communities with *Carex* spp. and amphibious species such as *Ranunculus reptans* at the bottom. The riparian vegetation along the regulated rivers generally lacks the distinctive zonation. Instead, it can be separated into a narrow strip without clear ripairian plants dominants close to the high-water level, and below this is a sparse occurrence of amphibious species such as *Ranunculus reptans* and *Subularia aquatica*.

Portuguese sampling sites include small and medium-sized rivers with an average of the mean monthly flow of 7 m^3/s. The dataset included 30 slightly impaired river reaches (hereafter ‘free-flowing’), from the national reference database of the Portuguese Environment Agency (Agência Portuguesa de Ambiente, APA), and 22 reaches downstream from dams (hereafter ‘regulated’). Swedish sampling sites include large rivers with an average of the mean monthly flow of 135 m^3/s. We selected 32 and 25 reaches in free-flowing and regulated rivers, respectively. The selection was conditioned by the existence of vegetation surveys and nearby gauging stations or, in their absence, of modeled flow data. We also ensured that reaches were well distributed along the rivers and throughout the whole study area. The combined dataset consisted of 62 free-flowing and 47 regulated sites. For Portugal, the site selection was validated to ensure that the free-flowing sites were not significantly different from the regulated in terms of geomorphology, climate and land-use (Aguiar et al., 2018). For Sweden, historic documentation indicates that prior to regulation vegetation was similar between the rivers – this has been assumed by previous studies on the same area (Bejarano et al., 2017a, Nilsson and Jansson, 1995, Nilsson et al. 1991).

In Portugal, free-flowing sites are located upstream of a dam or in a river with similar geomorphic and climatic features in relation to the respective regulated sites. Regulated reaches are mostly impaired by storage reservoirs with high productivity and smaller hydropower schemes that divert flows further downstream or directly to another reservoir. We included some run-of-river impoundments having fewer constraints in the magnitude of flows, but higher in number and duration of rise and fall rates. Rivers are mainly regulated for hydropower generation and additionally for flood defense and irrigation. The main hydrological alterations are related to a decrease of the magnitude of flows, but also to the artificial daily wetting and drying cycles (hydropeaking) and alteration of the numbers, timing and durations of seasonal floods. Regulation in Sweden included large storage reservoirs as well as run-of-river impoundments used for hydropower production through peaking operations. Therefore, regulation involved both seasonal flow stabilization resulting from the capacity of large reservoirs to store water and manage releases, and weekly and daily flow fluctuation resulting from the operation of the dams to produce hydroelectricity according to prices and demands.

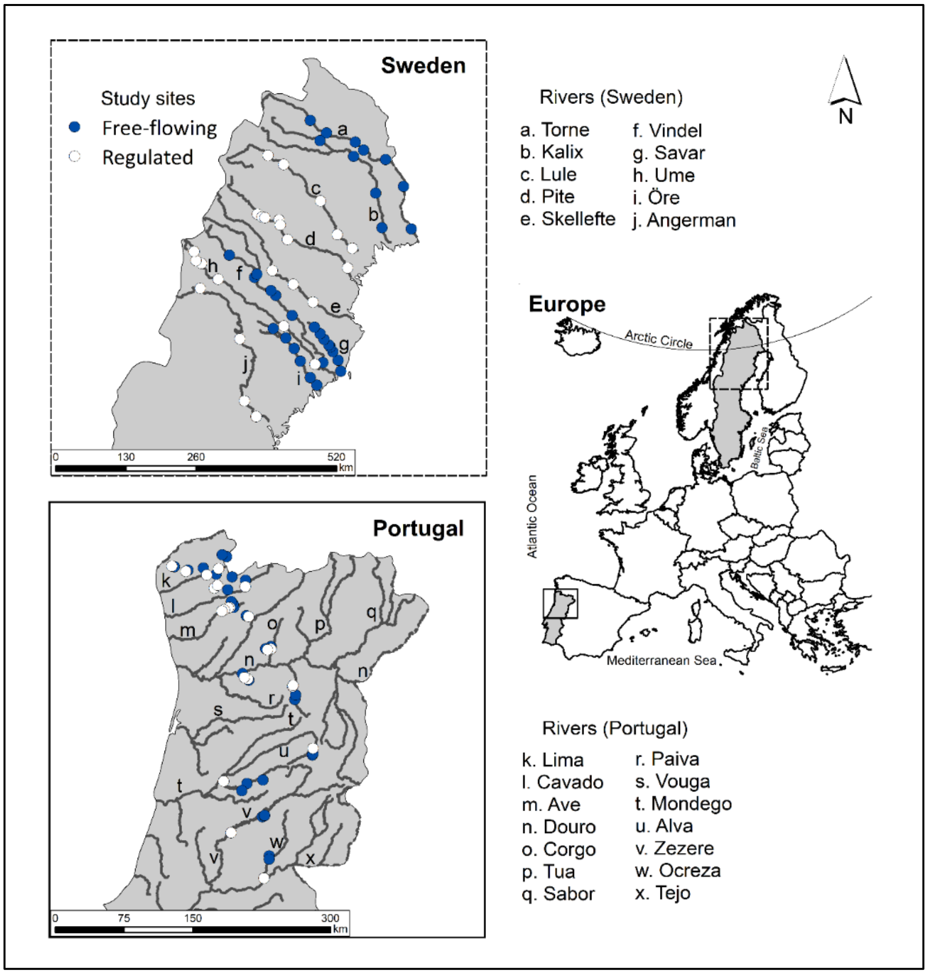

Figure 13. Location of the study sites in Sweden and Portugal. Filled circles represent sites at free-flowing rivers and unfilled circles represent sites at regulated rivers. Tributaries in Sweden are not shown.

Table 5. Legacy effects that influence riparian woody vegetation in Mediterranean and boreal biomes. References are given in Table C4.

EU Mediterranean biome	EU Boreal Biome
Location	
Between the latitudes of 30° and 45°N	The arctic and subarctic (or boreal) latitudes between the North Pole to about 55°N
Surrounding the Mediterranean Sea, extends across 4,300,000 km^2	Extends across 10 million km^2 of the northern circumpolar region including Fennoscandia and large parts of North America and Russia
Climate	
Mediterranean climate (rainy winters; hot and dry summers)	Subarctic climate and humid continental climate

Average annual temperature 7.5- 16.5 °C	Average annual temperature 14-17°C in July, +1 to -14°C in January-February
Precipitation below 500 mm to 2800 mm	Precipitation average 300 mm to 1500 mm Snow as half of the annual precipitation Snowpack formations persistent for several months
Geology and geomorphology	
Composed by a pre-Mesozoic complex geologic unit – the Hesperic Massif (granite, schist and quartzite) in the inland area. Tertiary layers under Quaternary deposits at the western coastal fringe	Erosional and depositional landforms heavily formed by past periods of glaciation and present glacierisation Depositional glaciated and glacierised landscapes-moraines, eskers and drumlins
Low relief and extensive tributary networks	High relief cirques and U-shaped valley
Soil formation and characteristics	
Dissolution and leaching of calcium carbonate during winter and development of red dehydrated oxidized iron compounds-hematite, magnetite during summer	Soil transition from mineral soils (generally podzols) in upslope areas to organic soils (generally histosols) in the near-stream zone
Streamflow patterns	
Rivers are characterized by sequences of floods in autumn–winter and droughts in summer	Extensive permafrost thaw, ice regimes and snowmelt events determine the hydrological regimes
Vegetation	
Sclerophyllous and evergreens due to soil infertility and as an additional defense against herbivory; wetter range with deciduous species highly responsive to flooding and hydrological dynamics	Evergreens due to a longer photosynthetic season and nutrient poor substrata
Biomass production and decomposition	
Leaf litter decomposition slower than in temperate areas Prolonged riparian inputs to the streams (rather than concentrated in autumn)	Biomass production variable with flood frequency and duration (increasing towards lower riparian elevations)
Low accumulation of organic matter	Accumulation of high levels of organic matter
Riparian species adaptations	
Adapted to natural water variability (shorter canopy height, higher colonization rates)	Elevated biological activities during growing season and depressed/dormant during the frozen period
Ecosystem invasibility	
High susceptibility to invasion	Few occurrences of exotic species; absence of invasive species
Main threats in fluvial systems	

Damming Water abstraction for irrigation Land-use and land-cover change Plant invasions Fire	Damming Ditching

Data collection

Floristic and trait data

The floristic dataset consisted of presence/absence of woody plants (trees, shrubs, dwarf shrubs, and lianas) from Portuguese and Swedish rivers. In Portugal, surveys were carried out according to the Protocol for assessment of macrophytes and riparian woody plants in Portugal (INAG IP, 2008). Data were collected along 100-m long riparian reaches at both river margins (i.e., a total of 200 m) during late spring and early summer in 2012, 2013 and 2014 for regulated sites. The reference floristic data on free-flowing reaches were collected in 2004 and 2005 using the same protocol. The sampling area varies according to the width of the riparian zone, and averages from 1500 to 2000 m^2. In Sweden, all woody plants between summer water level and upland forest edges were identified and noted along 200-m long riparian reaches for both free-flowing and regulated sites at one river margin during the late 1980s and early 1990s. This design was necessary to capture species at all hydrologic levels. The average sampling area was 4648 m^2 (Jansson et al., 2000). Variation between sites can be wide, for instance, the Vindel and Ume rivers, which are known to have been very similar prior to hydroelectric development, the area of the free-flowing study sites (Vindel) varied between 1320 and 30.000 m^2 because of geomorphic variation whereas in the regulated river (Ume) the corresponding numbers were 300 and 75.200 m^2 (Nilsson et al., 1991). The high variation in width of the study sites in the regulated river is due to the regulation schemes. In run-of-river impoundments the riverbank is narrow because of a decrease in annual water-level fluctuations whereas in storage reservoirs with annual fluctuations of several tens of meters vertically it can be very large. In both cases, however, most of the vegetation was confined to a narrow strip close to the high-water level. The Swedish study was designed to inventory all vascular plant species. For both types of river, however, the area of the study sites would be less variable if only the area occupied by woody plants would have been measured. The combined dataset consisted of 109 species (65 in Portugal and 44 in Sweden) (Table C1). Riparian woody communities in the Mediterranean biome overall can be discriminated with canopy height, leaf area, rooting depth, diaspore type (Stella et al., 2013a; Aguiar et al., 2018), and in boreal biome, with stem flexibility, canopy height and leaf area, diaspore type, dispersal vector and reproduction type (Bejarano et al., 2017a). Trait values for each species are given in Table C5.

Functional diversity data

We used nine functional traits (from multiple organs – leaf, stem, root and reproduction characteristics) responsive to streamflow to describe the riparian vegetation (Table 6).

The ecological relevance of the selected traits was obtained from Nilsson et al. (2010), Merritt et al. (2010), and Stromberg and Merritt (2016). Further information on traits' quantitative values is given in Table C6

Trait data were gathered primarily from local databases and literature (Aguiar et al., 2013a,b; Bejarano et al., 2016), whenever this option was limited, other trait databases were used (Klotz et al., 2002; Kleyer et al., 2008).

We computed Functional Richness and Functional Redundancy indices i.e. two metrics well adapted to presence/absence data sets as ours, to compute multidimensional trait indices (Laliberté et al., 2014). The indices were used to compute previously selected multidimensional traits. Functional Richness (FRic) reflects the range of trait diversity, i.e., how much of the functional space is occupied by different functional traits (Villéger et al., 2008). This index does not have an upper limit. Functional Redundancy (FRed) reflects the amount of saturation in multidimensional space with species with similar traits. Species are functionally redundant if they occupy the same portion of the functional space. If FRed is zero, all species are functionally different, conversely, if FRed reaches its maximum (i.e., 1) then all species are functionally identical.

Table 6. Description of the selected functional traits used to assess functional diversity in riparian woody vegetation affected by regulation. Their definition and units, ecological relevance and potential indicators for ecosystem functioning are given.

Trait	Definition (units)	Ecological relevance	Potential indicator
Canopy height	Shortest distance between the upper boundary of the main photosynthetic tissues on a plant and the ground level (m)	Associated with competitive vigor, whole plant fecundity and time intervals for plant growth between disturbances	Flow permanence, ground water depth
Leaf area	One-sided projected surface area of a single or an average leaf or leaf lamina (mm^2)	Relevant for light interception, leaf energy and water balance	Water availability
Seed weight	Air dried weight of germinules or dispersules (mg)	Indicates maternal investment in individual offspring	Seedlings ability to tolerate environmental stress and inundation
Seed buoyancy	Floating capacity of diaspores on water (h)	An important role in structuring riparian communities	Plant survival and dispersal during floods
Stem flexibility	Tissue density of each species (woody and semi-woody)	Surrogate of the stem tissue density and flexibility	Hydrological variability
Rooting depth	Vertical length of the main root (deep, moderate and shallow)	Potential of an individual to acquire moisture and nutrients	Hydrological variability

Reproduction type	Type of generating new individuals (vegetatively, seeds, seeds and/or vegetatively)	One of the plant reproductive strategies	Environmental stability in riparian habitats
Diaspore type	Plant´s most common dispersal units (seeds and fruits)	Individual strategy for dispersal and establishment	Reproduction type
Dispersal vector	Transporting means of plant's dispersal units (anemochory, hydrochory, anemochory and hydrochory; zoochory)	Facilitate continuity between spatially separated populations and determine species richness	Species’ abilities to colonize river margins

Environmental data

We used daily streamflow from Portuguese and Swedish stations (https://snirh.apambiente.pt/; http://vattenwebb.smhi.se/) to compute 30 ecologically relevant hydrological attributes, which encompassed the inherent characteristics of the streamflow regime (data from Aguiar et al., 2018; Bejarano et al., 2017a). We selected 10 important hydrological predictors of functional diversity (see the next section for details). The hydrological attributes characterize the intra-annual variation in water conditions and the inter-annual changes in streamflow components before and after the alteration of the streamflow regime. It can be classified into four categories of indicators: (i) magnitude of monthly water variations, (ii) duration of annual extreme water events; (iii) frequency of high/low water pulses; (iv) rate of change in water conditions (Richter et al., 1996). Further information on the hydrological attributes is given in Table C9.

Data analyses

We calculated the mean values of the selected traits. The statistical significance of the difference between the means of each functional trait, in each biome, between free-flowing and regulated sites was assessed using the Welch test or the Wilcoxon test depending on the validity of the normality assumption, which was initially checked with the Shapiro-Wilk test. Welch tests were used for the functional traits where normality is plausible, whereas the non-parametric Wilcoxon test was used for the functional traits where the normality was rejected.

We used a trait matrix (species vs. traits) and a sampling matrix (sites vs. species) to compute functional diversity indices. We calculated all indices in R software (R Core Team 2014) using the R packages “FD” (Laliberté et al., 2014) and “SYNCSA” (Debastiani and Pillar, 2012). The difference in indices between countries and regulation regimes were evaluated using a two-way ANOVA with interaction (Table C2) and the post-hoc Tukey Honestly Significant Difference (HSD) test. The homogeneity of variances was tested with the Levene test (R package “car”, Fox and Weisberg, 2011). A 5% confidence level was considered in all tests (the null hypothesis was rejected whenever $p<0.05$).

Two-way ANOVA was used to test the main effects and interaction of the hydrological variables with the factors ‘biome’ (both Portugal, Sweden) and ‘hydrological regime’ (free-flowing, regulated).

Linear models were used to analyze the relationship between the two functional diversity indices (FRic and FRed) and the hydrological attributes. Sub-model selection was carried out with an exhaustive search for the best subsets of predictors, implemented in R package “leaps” (Lumley and Miller, 2017). Since the algorithm returns the best model of each size, the results do not depend on the choice of a cost-complexity tradeoff. Thus, it does not make any difference whether to use R^2, adjR^2 or AIC as the optimization criterion. The number of predictors in each sub-model was selected as follows: we accepted as plausible models those that contained less hydrological attributes but could explain over 50% of the observed variability. To ensure that the obtained sub-models were not significantly worse than the complete models (indicating the need to increase the number of predictors), we compared the best sub-models with the respective complete model using partial F-tests. As usual in multiple linear regression, given the lack of independence of residuals, the estimators of the model random errors, the adequacy of each linear model was assessed through visual inspection (Figure C3). All analyses were performed using the R Statistical Software version 3.2.3 (www.r-project.org).

Results

Mean functional traits

We observed significant differences in average characteristics of plant species between free-flowing and regulated sites in Sweden for canopy height, leaf area, seed weight, rooting depth, stem flexibility, diaspore type and dispersal vector. There were no differences in seed buoyancy and reproduction from seeds. We also found that regulation enabled riparian woody species with small size, tiny leaves, poorly lignified stems, and shallow roots to persist at regulated sites in Sweden (Figure 14). In Portugal, the average trait values of plant species were not significantly different between free-flowing and regulated sites (Figure 14; Figure C1).

Functional diversity indices

We observed a significant decrease in FRic and FRed with regulation in Sweden and a non-significant variation in Portugal (Figure 14; Figure C2). This result is supported by the previous functional trait analyses, showing that filtering out of certain traits leads to constrained functional richness and redundancy in Sweden. On the contrary, in Portugal, due to the persistence of the same functional traits in regulated sites, functional diversity indices did not differ significantly between free-flowing and regulated sites (Table C3).

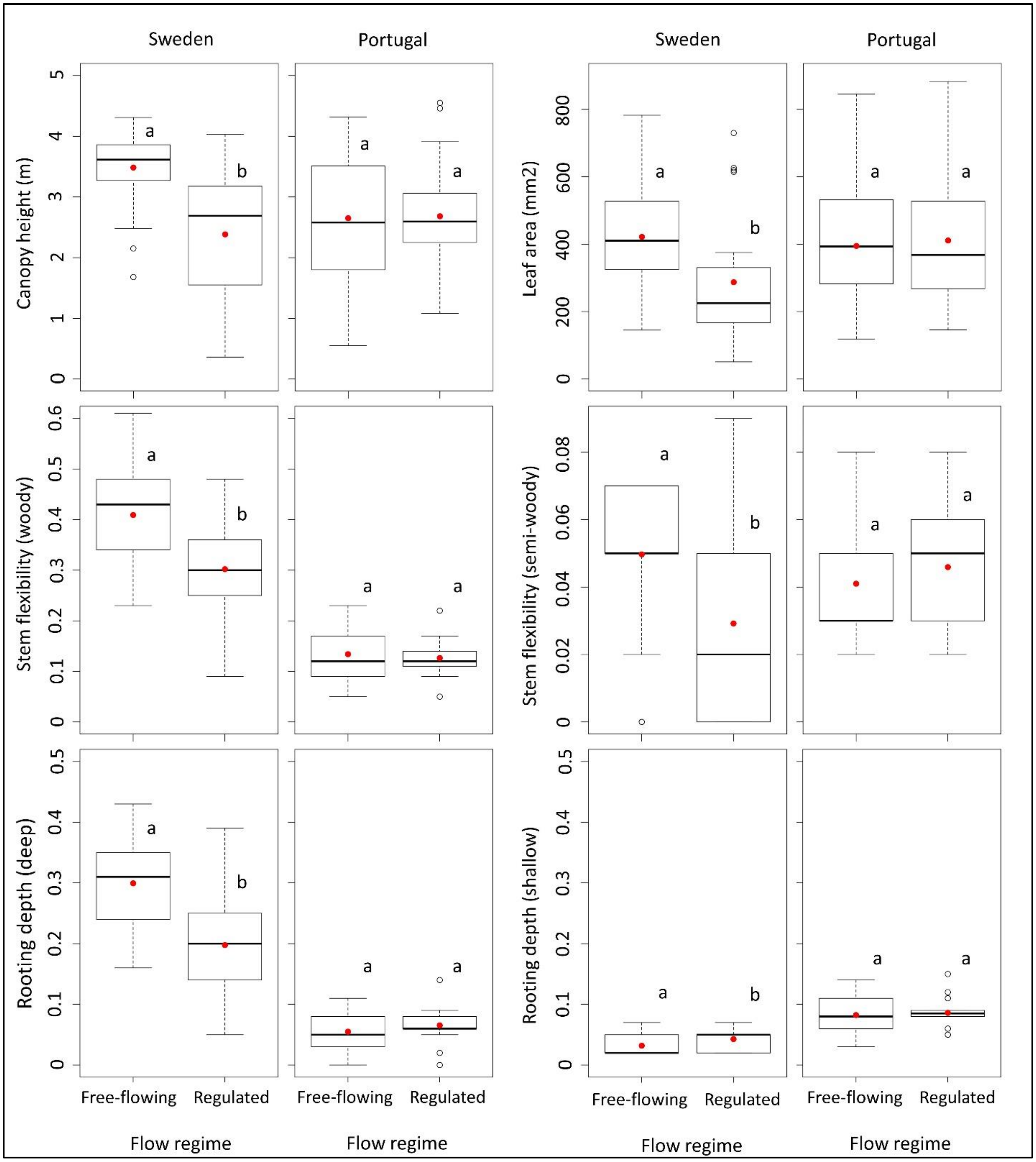

Figure 14. Box-and-whisker plots for canopy height, leaf area, stem flexibility and rooting depth from free-flowing and regulated sites in Sweden and Portugal. Letters identify the significantly different trait values ($p < 0.05$). Red circles represent trait averages. Canopy height and leaf area represent continuous traits, stem flexibility and rooting depth represent categorical traits. For assessment of all traits (n=9), please consult Figure C1.

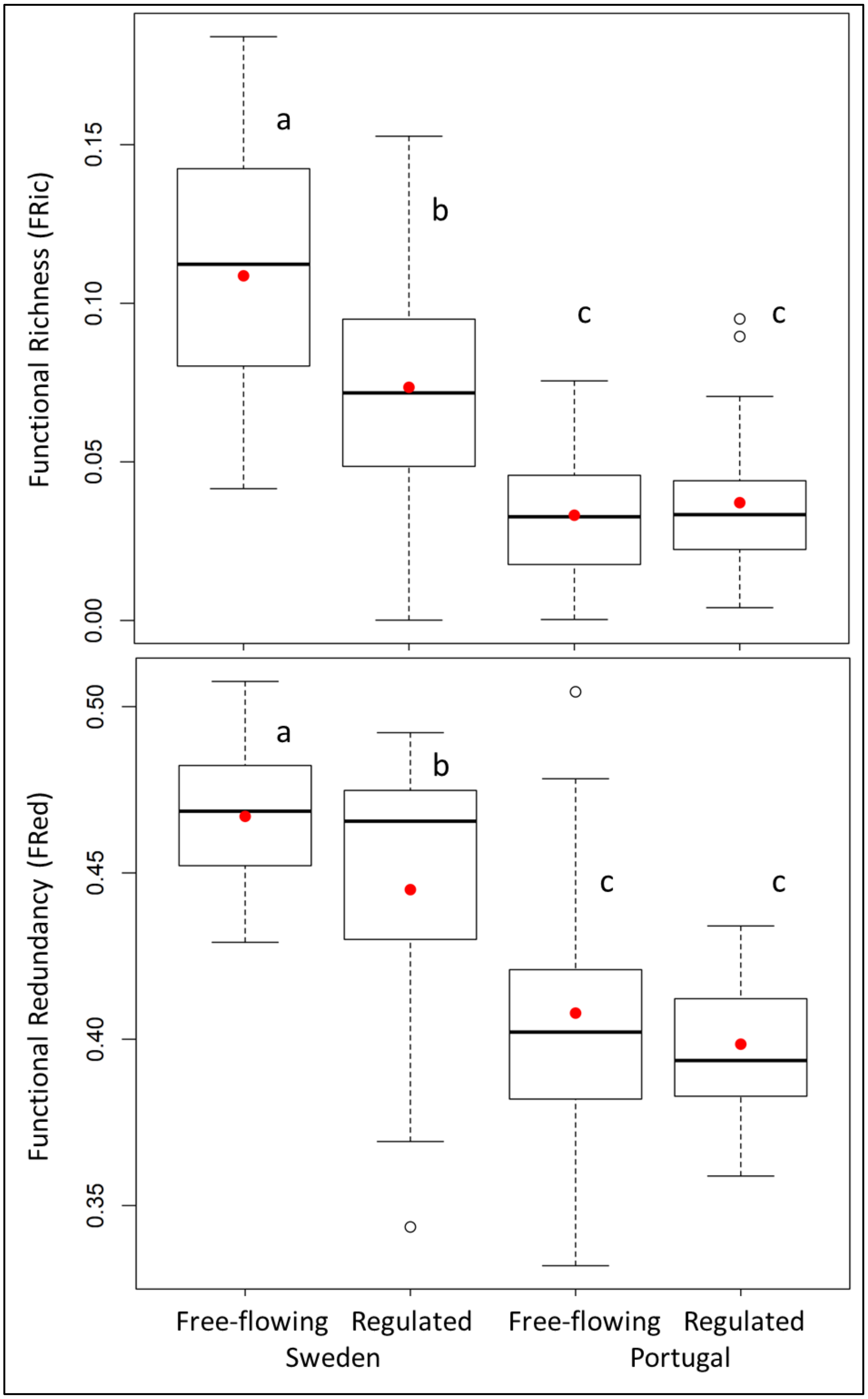

Figure 15. Functional diversity indices (Functional Richness and Functional Redundancy) from free-flowing and regulated sites in Sweden and Portugal. Letters identify significantly different means (red circles) ($p < 0.05$).

Hydrological attributes

The streamflow regulation had distinct impacts on the hydrological attributes between the biomes. Some similarities in regulation between biomes were observed (such as maximum flows in Summer months and high pulse count). However, the magnitude of the hydrological alterations and the number of hydrological variables affected was smaller in Portugal than in Sweden (Table C7, Table C8).

Two-way ANOVA revealed that the regulation caused significantly decreased FRic and FRed in Sweden but not in Portugal (Figure 15). We observed that the hydrological attributes did not contribute to the understanding of observed variability in functional diversity patterns in Portugal. Accordingly, analyses of hydrological attributes that could better explain the functional diversity were only made for Sweden.

In general, the hydrological attributes in the categories ‘Duration of annual extreme water events’ and ‘Rate of changes’ were key for both FRic and FRed in Swedish rivers (Table 7). ‘Magnitude of monthly water variations’ was an additional descriptor for FRic and ‘Frequent pulses of high water’ for FRed. The best model for FRic explained 65% of the total variability and consisted of five streamflow attributes. Mean June streamflow, 90-day moving average of maximum streamflow and number of daily reversals had negative effects, whereas mean streamflow in August and 1-day moving average maximum had positive effects on FRic values. The best model for FRed explained 51% of the total variability: seven-day moving averages of minimum and maximum flows and frequencies of high pulses and daily streamflow reversals had negative effects on FRed, whereas the 1-day moving average of minimum streamflow and rise rates affected FRed positively.

Table 7. Coefficients of the hydrological attributes used in the linear submodels for FRic and FRed for Swedish rivers, considering FRic (FRed) = $\beta_0 + \sum_i \beta_i x_i + \varepsilon$ where x_i represents an hydrological attribute (predictor) and ε is the random error, supposed normally distributed with zero mean. FRic (FRed) uses 5 (6) predictors. R2, AdjR2 and P-value of global F-test of the selected models are given. Global F-test tests the hypothesis H0: all β_i = 0 (null model) vs. H1: at least one $\beta_i \neq 0$.

Category	Hydrological attribute	Functional Richness	P-value	Functional Redundancy	P-value
Magnitude of monthly water variations	June mean flow	-0.003	0.04		
	August mean flow	0.001	<0.001		
Duration of annual extreme water events	1-day minimum			0.003	<0.001
	7-day minimum			-0.004	<0.001
	1-day maximum	0.005	<0.001		
	7-day maximum			-0.001	0.0001
	90-day maximum	-0.001	0.0002		
Frequencies of high/low water pulses	High pulse count			-0.03	<0.001
Rate of change	Rise rate			0.008	<0.001

	No. of hydrologic reversals	-0.001	<0.001	-0.001	0.0002
R^2		0.50		0.65	
$AdjR^2$		0.45		0.60	
P-value		<0.001		<0.001	

Discussion

In line with the assumptions, our results showed that the effect of regulation can differ among biomes, likely related to species' natural adaptations to flow-related disturbances and to the magnitude of the hydrological alterations. In the boreal region, the changed streamflow regime disfavored certain traits that shaped the riparian woody vegetation in free-flowing sites, leading to a reduced range of traits in regulated sites.

Regulation effect on functional traits

In regulated rivers of the boreal region, we observed species with lower canopies, smaller leaves, and more flexible stems, all being disturbance-tolerant traits typically linked to high-flow-velocity environments. More compact plants are more resistant to mechanical disturbance from flowing water and flexible stems reduce the risk of biomass loss because of fast flows (Madsen et al., 2001). Rooting depth, which is considered as a stress indicator of water availability and which may be extensive in dry soils, was lower in regulated rivers. This may be a result of the almost constantly moist riverbanks following flow releases from upstream reservoirs under which conditions riparian vegetation does not need to invest in root elongation for water uptake (West et al., 2012). Therefore, given the climate in Sweden, even during water recession, the risk of water stress is limited, suggesting that traits resistant to water stress may be irrelevant. Although vegetative propagation has been reported in rivers subjected to high or low fluvial disturbances (Bellingham and Sparrow, 2000; Riis and Sand-Jensen, 2006) and in relatively stable riparian conditions (Douhovnikoff et al., 2005), in our case, species with seed regeneration persisted. It was noticeable, however, that heavy seeds were disfavored by regulation, most probably because the repeated flood events may facilitate the transport of light seeds downstream of dams, where plant establishment will be more likely (Johansson et al., 1996). The concentration of transported seeds remains unknown, because even if floods can assist in seed transport, their concentration may be drastically reduced due to the difficulties for plants to pass dams (Merritt and Wohl, 2006).

In Mediterranean regions, riparian communities of woody species in regulated rivers may be affected by suppressed stream flows and largely variable flood patterns (Magdaleno and Fernández, 2011a) which are comparable to natural hydrological regimes, and may result in some common functionality patterns (Belmar et al., 2019a). In fact, the observed small streamflow changes with regulation in Portugal, did not change the already existing pool of traits, with trait values remaining similar between free-flowing and regulated sites. Further, there is evidence that traits in free-flowing rivers of Mediterranean-climate regions may occur also in regulated ones as an adaptation to natural hydrological stress (Stella et al., 2013b). In accordance, the observed short plants can be a result of water shortage, i.e., less time to grow to maturity (Pakeman and Eastwood, 2013); semi-woody characteristics and large leaves are adaptations to rapid growth during periods of water supply (Lawson et al., 2015b; Grady et al., 2013); and persistence of deep roots an adaptation to fluctuating water levels (Schenk and Jackson, 2002).

Regulation effect on functional diversity indices

It is showed that dams alter streamflow across biogeographic regions (Poff et al., 2010), but the alterations depend not only on dam operation but also on the regional hydrological context (McManamay et al., 2012). In that sense, regulation on large rivers as in those of boreal region may have severe consequences for riparian vegetation (Nilsson et al., 2005). Several reasons make regulation stand out as a strong factor impacting riparian woody vegetation in the boreal region. First, upstream impoundments and canals downstream of dams used for hydropower production are subjected to hydropeaking, which involves high within-day and day-to-day variations in flow and water-level. Second, storage reservoirs have large water-level magnitudes and a reversed flow regime. In both these cases of regulation, the environment may be harsher than plants can tolerate and consequently result in species loss since only a few species share traits adequate for such novel hydrology (Catford and Jansson, 2014). The strong filtering effect decreases trait space occupied by communities and limits functional overlap (Bruno et al., 2016a; de la Riva et al., 2017). The absence of compensatory dynamics in communities with limited functional richness and redundancy decreases the capacity of species to buffer disturbances (Elmqvist et al., 2003; Pillar et al., 2013).

Regulation of rivers in the Mediterranean region does not seem to impose further stress to similar extents as regulated rivers in the boreal region. Indeed, there was no significant change in FRic and FRed and only constrained variability in functional diversity. This is likely due to two reasons. First, hydrological stress is typical for Mediterranean regions under natural, free-flowing conditions, and over evolutionary scales it has shaped communities by exposing them to rapid shifts between droughts and floods (Bonada and Resh, 2013). Second, the streamflow alteration induced by regulation was not markedly distinct from the natural streamflow. Those combined exposures could explain why regulation in the Mediterranean region did not cause any significant trait loss in the resident plant communities and consequently, did not result in a reduction of functional richness and redundancy. A similar observation was made by Aguiar et al. (2018) who found that, for rivers in Mediterranean Europe, riparian woody communities did not change their trait composition following river regulation, but several trait values became less abundant. According to Sandel et al. (2010), such reductions of trait abundances may precede functional diversity loss.

Effect of regulated streamflow attributes on functional diversity

We found that the rate of change, frequency of high pulses, duration of extreme water events and monthly mean streamflow all had a significant impact on the functional diversity of boreal rivers. The reduced functional diversity due to the increased daily streamflow changes can be related to scouring capacity of moving water, resulting in mechanical damage or riparian plants removal (Bejarano et al., 2018). Further negative effect on functional diversity was imposed by the frequent high pulses and prolonged duration of extreme high-water events (90-day moving average maximum and 7-day moving average maximum). Under an extended duration of inundation in riparian areas, physiological processes are hampered, consequently reducing the survival and growth of riparian vegetation (Johansson and Nilsson, 2002). Similarly, an extended duration of extreme low-water conditions (7-day moving minimum) can reduce functional diversity due to soil moisture deficits. While the prolonged duration of both, inundation and low-water conditions cause negative effect on riparian vegetation, 1-day hydrological events are too short to cause severe disturbance. In fact, they may even support the transport of propagules and nutrients and remove or create new habitats for plant establishment (Corenblit et al., 2007) resulting in increased functional diversity. However, the positive effect of rise rates on riparian vegetation was surprising nevertheless, in natural streamflow regimes, rapid rise rates have also been linked to functional heterogeneity (Lawson et al., 2015a). We also observed that timing of the monthly streamflow can have consequences on riparian vegetation. For instance, the June mean streamflow overlaps with the boreal growing season, which typically occurs between May and October. Thus, the combined effect of the natural early summer flood and higher June mean streamflow may reduce germination due to the long period of waterlogged soils (Sarneel et al., 2019). Such a condition may disrupt plant establishment and reduce functional diversity, since most plant species have lower flood tolerance during the growing season (Siebel and Blom, 1998).

Limitations

We showed that the functional diversity approach can be used to evaluate the impacts of streamflow regulation on riparian woody communities. However, some methodological aspects deserve further explanation. First, the chosen functional diversity indices. The available dataset of species presence/absence permits the use of indices computed with binary data, namely Functional Richness and Functional Redundancy. Articles on functional diversity consisting of binary data sets have been published on riparian vegetation (Brice et al., 2017; Sonnier et al., 2014) and those datasets have been considered as reliable for predicting plant trait distributions globally (Boonman et al., 2020). In a conceptual study with an illustrated ecological hypothesis, Boersma et al. (2016) stated that presence/absence data can serve to make the most straightforward interpretation of the results when disturbance acts as an environmental filter. Nevertheless, possible bias may rise when the filtering factor does not have a significant effect on communities, for instance, due to intrinsic adaptations. Therefore, the effect might not be projected in species loss but rather in abundance change. Under that assumption, species abundance likely can be important for the Mediterranean riparian woody communities, as species are resilient to disturbance, and still occur in the riparian zone (Aguiar et al., 2018). Second, selection and collection of traits (Lozanovska et al., 2018b). In this regard, the selection of many functional traits increases the ability to detect functional differences between species, thereby increasing the estimate of functional diversity (Fonseca and Ganade, 2011). On the other hand, considering few traits may undervalue functional diversity (Petchey and Gaston, 2002). Therefore, to allow for deeper insights in functional diversity–ecosystem functioning relationships, the number of traits should be balanced and measured from multiple organs such as leaves, stems and roots (Laughlin, 2014). In the present study, we selected nine functional traits that summarize adaptations of riparian woody vegetation to deal with anoxia, drought and fluvial disturbances. However, using a “performance trait” which contributes directly to fitness (i.e., ability of a species to grow, reproduce or survive) instead of “functional trait” which has an impact on performance traits and thus indirectly on fitness may provide more accurate indications of functional diversity and ecosystem functioning (Violle et al., 2007). Third, are the temporal and spatial aspect of the study. Due to the differences in the timing of the data collection in Portugal and Sweden, a time lag might affect the results. Although the effect potentially may decrease the observation of functional differences between biomes, we have assumed that the influence would be smaller compared to the effect of regulation on riparian woody communities. The difference in sampling areas reflect the smaller riparian zones in Portugal compared to the larger ones in Sweden. Extending the sampling area in Portugal to be equal to Sweden, would mean inclusion of species from the terrestrial zone. Nevertheless, the fact that the species number in Portugal is higher despite the smaller sampling area strongly suggests that differences in species richness are not a sampling area effect.

Conclusions

Previous studies have recognized that altered streamflow regimes can lead to shifts, and loss of traits and species (Kominoski et al., 2013), and ultimately loss of ecosystem functions, thus jeopardizing ecosystem services provided by riparian ecosystems (Cadotte et al., 2011). We showed that the differences induced by regulation between the Mediterranean and boreal riparian woody vegetation are related to species legacy adaptations, and differences in the magnitude of streamflow alteration. Also, streamflow regulation can foster stress-related functional strategies to deal with regulation, resulting in functional diversity reduction.

Our study highlights the potential of functional measures for monitoring riparian vegetation changes caused by dam-induced hydrological alterations. By specifically targeting and managing the streamflow attributes, functional diversity may potentially be maintained or even improved. To facilitate such actions, future research should focus on the tolerance limits of species or certain functional traits to specific hydrological variables that are altered as a result of river regulation.

Chapter V.

Streamflow regulation effects in the Mediterranean rivers: how far and to which extent aquatic and riparian communities are affected?

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Abstract

Dam-induced disruption of the natural continuum of rivers has manifold consequences on the fluvial ecosystems, and on the structure and functioning of plant communities. In this work, we focused on understanding how different plant groups - vascular macrophytes, bryophytes and riparian woody vegetation - respond to disturbance along the river and across the riparian zone downstream of dams. We specifically aimed to determine the degree-of-regulation (DOR) and distance from the dam (DFD), where river regulation no longer significantly affects plant communities, by addressing two case studies – a run-of-river dam and a reservoir dam in Portugal, SW Europe.

We collected data on abiotic variables and the cover of plant species in 31 free-flowing and regulated sites in June-July 2019. We performed a cluster and ordination analysis to derive plant guilds for each plant group using flow-responsive traits, and used linear models to predict guild alterations from the free-flowing sites along the gradient of DOR and DFD.

We obtained 3 macrophyte guilds, 6 bryophyte guilds, and 5 riparian guilds. Our results show that the vegetation response to regulation was plant group-reliant and guild-specific. Overall, plant community's differences with regulation were expressed, by change in plant abundance cover, and not by guilds loss. We verified an increase in the abundance cover of macrophytes under river regulation and a decrease in bryophytes' cover, which do not seem to be favored by regulation conditions, especially in reservoir settings. Riparian guilds presented diverse responses depending on the type of river regulation. We also observed riparian vegetation encroachment of all riparian guilds in "reservoir rivers" and an expansion outwards the riparian zone downstream of the run- of-river dam.

Understanding this biological adaptation patterns can be vital to predicting and understanding communities' responses to regulation, which can guide river restoration projects as well as environmental flow designs to address rivers sustainability goals.

Keywords: functional traits; guilds; run-of-river dam; reservoir dam; longitudinal change; lateral change

Introduction

Rivers are dynamic habitats where plant communities thrive under seasonal and even sub-daily variation of streamflow. Aquatic and riparian plants respond to prevailing environmental settings and internal mechanisms of succession across the transversal, longitudinal, vertical and temporal river dimensions. The artificial disruption of the natural continuum of rivers by dams has manifold consequences in fluvial ecosystems and on the structure and function of the plant communities (Abati et al., 2016; Rivaes et al., 2017a; Aguiar et al., 2018). The alteration of river hydraulics, hydrology, and water quality concur with shifted sediment, nutrients, and organic matter dynamics to hinder plant propagules and seed dispersal, change succession patterning and community assembly (Bejarano, et al., 2018; Janssen et al., 2020). To explain such disruptive changes, Ward and Stanford (1983) proposed the Serial Discontinuity concept, and state that for reservoirs, the recovery of natural conditions mostly depends on dam size, position along the river, and tributary inputs. The Flood Pulse theory (Junk et al., 1989) for river-floodplain interactions and its extension for temperate rivers (Tockner et al., 2000) allowed a better understanding of internal processes of river dynamics under episodic flows and flood pulses. More recently, attention has been driven to the theory of Pulse Dynamics and Disturbance of Jentsch and White (2019), as disturbance events (e.g. fire, floods, hydropeaking, droughts) are being increasingly important on ecosystems.

The applications of these theoretical bases enlarged our knowledge on the resilience and resistance of biota and on the ability to predict biota recovery time from pulse events. However, diverse dam types can display different impacts on plant communities. For instance, in rivers impaired by run-of-river dams that are subjected to hydropeaking, drag forces cause physical plant injury, uprooting and sediment burial (Madsen et al., 2001). This artificial variation in the water regime can lead to riparian vegetation exclusion close to the active channel (Webb et al., 2012; Aguiar et al., 2016). In rivers impaired by storage reservoirs, the lack of seasonal floods and fluvial disturbance may lead to riparian vegetation encroachment and induce a diverse spatial rearrangement of aquatic communities (Yi et al., 2020). Shifts in species composition tend to occur towards communities richer in water-stress tolerant species and/or with alternative dispersal strategies to hydrochoric dispersal (Rivaes et al. 2015, 2017b; Aguiar et al., 2018).

Whether aquatic and riparian vegetation can sustain their survival in a hydrological disturbed environment depends on a combination of morphological, physiological, phenological and reproductive attributes, summarized as plant functional traits (Violle et al., 2007). It is known that these functional elements display abilities to cope with some level of hydrological disturbances (Vieira et al., 2012; Gurnell, 2014; Bejarano et al., 2018). For instance, as an adaptation to inundation *Myriophyllum spicatum* (Strand and Weisner, 2001) tends to increase biomass allocation to shoot, grow taller and thus form dense canopies for enhancing light interception. Increased leaf area to improve light absorption efficiency and cope with anoxia are beneficial adaptations to prolonged flood events (Enriquez and Sand-Jensen, 2003). Small individuals, flexible stems, reduced leaf size, and streamlined leaf form proved efficient protection to mechanical injuries under high flow velocities (Bornette et al., 2008, 2011; Lang and Murphy, 2012, Stromberg and Merritt, 2016). Also, dissected leaves as in *Ranunculus penicillatus* ensure resistance to drag forces (Usherwood et al., 1997; Nikora, 2010; Albayrak et al., 2012). Plants with large and long-lived seeds are also common traits as a response to water stress, ensuring survival until suitable germination conditions occur (Brock et al., 2003; Stromberg and Boudell, 2013). Perennial life-strategies of aquatic bryophytes tend to dominate in substrate subjected to permanent flows and, in contrast, colonists emerge in reduced water flow conditions (Vieira et al., 2012).

While most studies are designed for upstream versus downstream or pre- versus post-dam comparisons, how communities respond to disturbance along the fluvial longitudinal dimension is largely unknown (Braatne et al., 2008; Ellis and Jones, 2013). Most of the recovery research downstream of dams addressed invertebrates, (e.g. Growns et al., 2009; Ellis and Jones, 2013), anuran species richness (Guzzy et al., 2018) or fish (e.g. Kinsolving and Bane, 1993) while few authors addressed the effect of the distance from the dam or the decay of regulation effects on biota (but see Mor et al., 2018; Mellado-Diaz et al., 2019). Moreover, seldom research has addressed distinct plant functional groups and, particularly, the contribution of non-vascular plants, such as mosses and liverworts (Martin and Mallik, 2017).

The primary objective of this study was to assess how far downstream dam flow regulation has a significant effect on aquatic and riparian plant groups (vascular macrophytes, bryophytes and riparian woody vegetation). We also aimed to address the shifts in plant communities across the river and the riparian zone.

We expected diverse responses within and between the studied plant groups due to the adaptive strategies to streamflow alterations, and to distinct plant-environment interactions occurring in disturbed ecosystems. Using a functional trait-based approach, we asked the following questions:

i) are all plant groups (macrophytes, bryophytes and riparian woody vegetation) responsive to flow regulation?

ii) is it possible to determine a minimum distance from the dam from which the regulation does not have a significant impact on the studied communities?

iii) are there location shifts of plant communities across the channel and the riparian zone induced by regulation?

iv) do different regulation types (i.e. induced by run-of-river or storage reservoirs) impair differently the plant communities?

Given the large number of extant dams and ongoing dam construction worldwide, understanding the longitudinal and lateral effects of river regulation can help water managers to optimize decision-making procedures and prioritize the most affected river stretches. We hoped to answer these questions to compile crucial knowledge on river management that increasingly seeks to restore lost river functions and ecosystem services.

Materials and methods

Study area and sampling design

The research was undertaken in north and central mainland of Portugal, on the western edge of the Iberian Peninsula (Figure 16). The study area has a temperate Mediterranean climate with hot, dry summers and, yet, mild and wet winters. Average annual precipitation in the study sites ranges from ca. 1380 to 2090 mm year^{-1} and temperature from ca. 11 to 12°C (APA, 2020).

We selected as case studies river Lima impaired by the run-of-river (Touvedo) dam and river Alva impaired by a storage reservoir (Fronhas), representing hydropower dams with different regulation types (Table D1). We surveyed 13 river sites downstream of the dam, in river Lima. Upstream of the Touvedo dam, river Lima is also regulated, thus free-flowing sites, four in total, were located in close-by tributaries. In river Alva, we surveyed 14 river sites, from which three were upstream of the reservoir in free-flowing conditions. River sites comprised an area of approx. 1000 m^2 of the channel and the riparian zone.

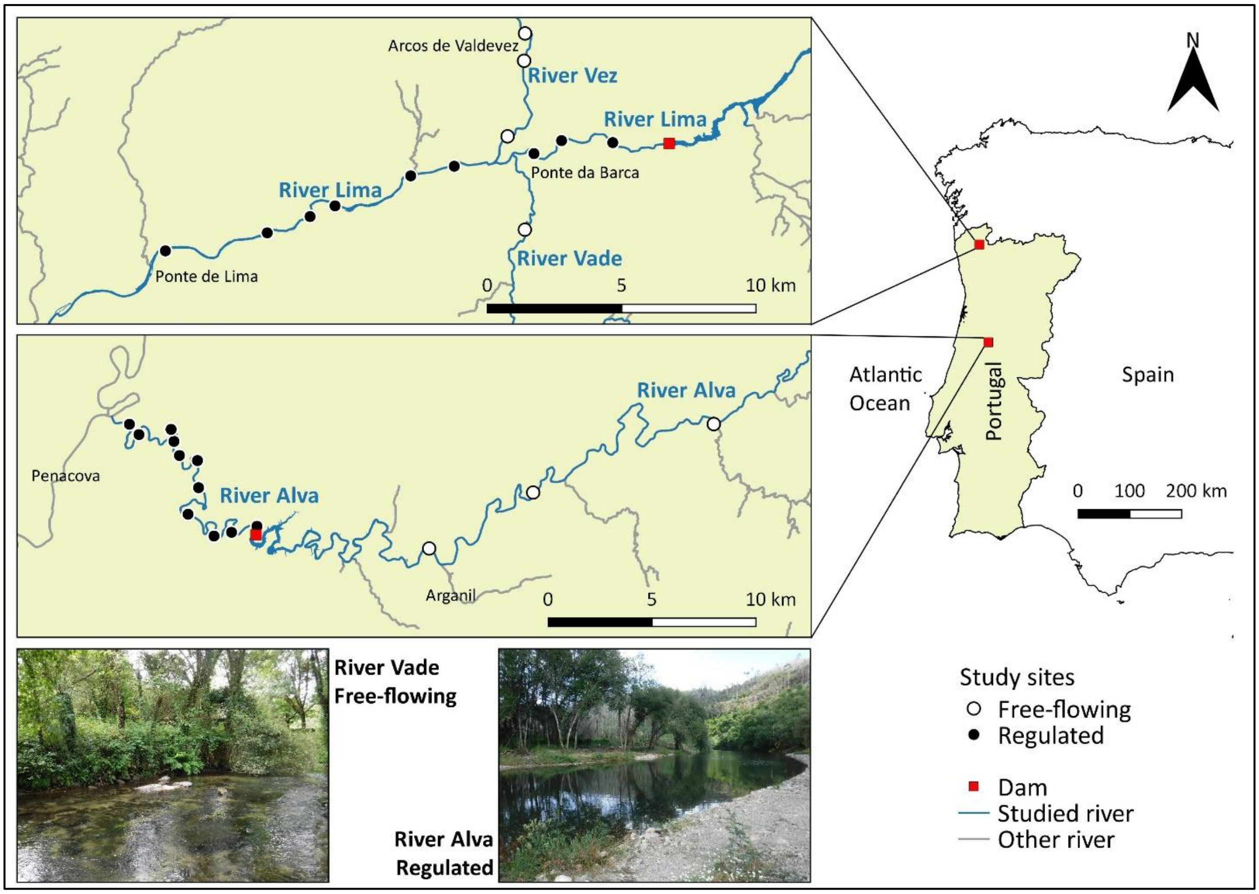

Figure 16. Location of the case studies in Portugal (right map). Maps on the upper left show the rivers' networks and the sampling sites' location (white circle = free-flowing sites; black circle = regulated sites).

Species data

The field campaigns were undertaken during June-July 2019. We surveyed macrophytes, bryophytes and riparian woody vegetation. Macrophytes refer to a diverse group of aquatic photosynthetic organisms, all large enough to see with the naked eye (Chambers et al., 2008). This group includes (among others) divisions Pteridophyta (ferns) and Spermatophyta (seed-bearing plants). In this study, we used the term “macrophytes” only for ferns and herbaceous Spermatophyta. For Bryophyta Division, we chose to use the term “bryophytes” - mosses and liverworts either seasonally submerged, hygrophilous or terrestrial growing on the margins of the active channel. Riparian woody vegetation referred for trees, shrubs, and lianas occurring on the margins of the active channel.

The percentage superficial or canopy cover of each species was taken as an estimate of relative species abundance. We also recorded the distance (m) of each riparian woody species to the channel, and the location of macrophytes and bryophytes (either on the margin or channel). Most species were identified in the field. In case of doubtful identification, material was collected for later identification in the João Carvalho e Vasconcellos Herbarium (LISI) or, in the case of bryophytes, collected specimens were identified and deposited as vouchers in PO Herbarium. Macrophytes identification was mostly supported by Franco and Rocha-Afonso (1994; 1998; 2003) while nomenclature of bryophytes followed the criteria of Ros et al. (2007, 2013). The full species list is given at Table D2.

Trait data

Species were characterized by morphological and reproductive functional traits reflecting plant functions and strategies as a response to the hydrological regime. To enhance the predictive ability of functional diversity-environment relationships, the number of traits should be minimized to 6-8 traits, and when possible, measured from multiple organs such as leaves, stems, and roots (Laughlin, 2014; Lozanovska et al., 2018b). In the present study, we selected seven traits (growth form, life span, clonal spread, leaf shape, leaf anatomy, reproduction type, and dispersal vector) for macrophytes; eight traits (canopy height, stem flexibility, rooting depth, leaf area, seed buoyancy, seed weight, reproduction type, diaspore type, and dispersal vector) for riparian woody vegetation, and three traits (life form, life strategy, and leaf length) for bryophytes (Table D3). Trait data were primarily gathered from literature and published trait databases (Willby et al., 2000; Klotz et al., 2002; Hill et al., 2004, 2006; Aguiar et al., 2013b). The ecological relevance of the selected traits is given in Table 8.

Table 8. Traits relevance for altered hydrological regimes according to previous studies.

Trait	Ecological relevance	Reference
Whole plant traits		
Canopy height, growth form, life span, life form, life strategy	Indicators for high flow velocities tolerance; related to flow velocity and sediment disturbances	Willby, 2000; Bornette et al., 2008; Viera et al., 2012; O'Hare et al., 2016; Stromberg and Merritt, 2016; Baattrup-Pedersen 2018
Leaf traits		
Leaf area, leaf anatomy, leaf shape, leaf length	Indicators for the light interception, leaf energy, and water balance; related to high flow velocities disturbances	Albayrak et al., 2012; Stromberg and Merritt, 2016; Baattrup-Pedersen 2018
Stem traits		
Stem flexibility	Indicator for hydrological disturbances; related to hydrological stability	Stromberg and Merritt, 2016
Belowground traits		
Rooting depth	Indicator for moisture and nutrient acquisition; related to hydrological variability	Stromberg and Merritt, 2016
Seed traits		
Seed weight, seed buoyancy	Indicators for inundation tolerance; related to plant survival and dispersal during floods	Nilsson et al., 2010; Stromberg and Merritt, 2016; Baattrup-Pedersen 2018
Regeneration traits		
Reproduction type, clonal growth	Indicators for environmental stability; related to plant survival	Bornette et al., 2011; O'Hare et al., 2016; Stromberg and Merritt, 2016; Baattrup-Pedersen 2018
Dispersal traits		
Dispersal type, dispersal vector	Indicators for environmental stability; related to plant establishment and colonization	Bornette et al., 2011; Nilsson et al., 2010

Regulation variables

The sampling sites were characterized in terms of "degree of regulation" (DOR, Dynesius and Nilsson, 1994), and "distance from dam" (DFD) as quantification measures for assessing the downstream effects of dams. DOR is an index measuring the regulation level of a dam, defined as the ratio of the total storage volume of the reservoir with the total annual flow of the river section watershed. The index has been suggested for river regulation assessment (e.g. Vörösmarty et al., 1997; Nilsson et al., 2005; Grill et al., 2015). DFD is a direct measure of the disturbance source remoteness and it was measured along the river course - from the location of each regulated sampling site to the upstream dam. Unregulated sampling sites do not present distance to an upstream dam and therefore were not included in the guilds modeling according to this measure. Notwithstanding, these were used as guild threshold determined by unregulated conditions.

Data treatment

Biotic and abiotic matrices were produced and treated in the R environment. Principal Component Analyses (PCA) were used to ensure that free-flowing and regulated sites shared similar environmental settings. Two PCA were performed: a “physically-based PCA” using only abiotic variables unrelated to regulation, namely geomorphological variables, and an “environmental PCA” considering both geomorphological and environmental variables. The former was used to look for possible geomorphologic difference effects between regulated and unregulated sampling sites while the latter served to understand the relative importance of geomorphology and environmental conditions in general on the sampling sites' distinction.

In our study, the functional trait matrix (species and traits) was used to create dissimilarity matrices considering the Gower’s dissimilarity measure. We used a hierarchical method of average agglomerative clustering to derive guilds for macrophytes, riparian woody vegetation and bryophytes. Elbow point and average silhouette width methods were applied to determine the optimal number of clusters in each community (Thorndike, 1953; Rousseeuw, 1987).

We validated the obtained clusters by comparing the variances within and between clusters. We implemented a Principal Coordinates Analysis (PCoA) to trait data to ascertain the effect of the traits on the variability of species data. In this case, PCoA was better suited due to the binary character of trait data and the possibility of using non-Euclidean distance matrices. Based on the PCoA results, the values of functional traits for each species belonging to a guild were averaged and the most distinctive traits in relation to the remaining guilds were interpreted in their connection to streamflow disturbance and used to name the guilds. Correlation of traits with guilds (Spearman correlation >0.5; p>0.01) was also used to validate the former approach. Lastly, we used the species cover data to derive guild abundances at each site, which was calculated as the sum of the abundance of the species belonging to a particular guild recorded at the sampling site. Differences of guild cover between regulated and free-flowing sampling sites were assessed through Wilcoxon-Mann-Whitney tests, due to the small sample size and non-assurance of data normality.

We used linear models to determine the relationship between guild coverage and both DOR and DFD. The framework to determine the levels of DOR or DFD at which guilds cover at regulated sites become similar to the expected reference guild cover at free-flowing sites was based on the confidence intervals settlement for the expected covers in regulated and free-flowing circumstances, and the assessment of the hinge regulation levels from which confidence intervals do not overlap. The statistical assumptions of linear modeling, namely, linearity and independence between variables and, normality and homoscedasticity of the residuals, were assured. Particularly, linearity was assessed using Harvey-Collier collinearity test in which all tests were non significant. Independence between variables was tested by calculating Spearman correlation between variables which were in every case lower than 0.7. Normality and homoscedasticity of the residuals were visually assessed by the regression diagnostics plots, without any noteworthy problems in general.

Results

Plant guilds as responsive plant functional groups to regulation

The traits of the surveyed macrophytes (42 species), bryophytes (18 species) and riparian woody vegetation (17 species) were used to derive the species clusters (i.e. guilds). The optimum number of guilds was three for macrophytes, six for bryophytes and five for riparian woody vegetation (Figure 17). This decision was corroborated by the analyses of variance between clusters, showing significantly (p = 0.001) lower variance within clusters compared to the variance between clusters, for all plant groups. R-values for the paired tests among guilds for each community were higher than 0.775, revealing good segregation between clusters (R-value = 1 indicates total dissimilarity).

Averaged functional trait values for each guild and correlations of guilds vs. traits are given in Figure D2 and Table D4. For macrophytes, guilds were named as: *Disturbance-resilient macrophyte guild* (e.g. *Juncus effusus*, *Carex pendula*, *Cyperus eragrostis*), which is composed by emergent perennials with clonal spread (rhizomes); *Disturbance-favored macrophyte guild* (e.g. *Lythrum salicaria*, *Bidens frondosa, Osmunda regalis*), consisting by emergent species with sexual reproduction (seeds) and *Disturbance-adapted macrophyte guild* (e.g. *Ranunculus penicillatus, Myriophyllum spicatum, Lemna minor*), represented by hydrophytes with clonal spread (fragmentation) and hydrochoric dispersal. All these three guilds existed in both rivers.

For bryophytes, the six identified guilds were named as Hygrophilous lotic bryophyte guild (e.g. Brachythecium rivulare, Scapania undulata); Heliophilous lentic bryophyte guild (e.g. Bryum capillare, Dicranella heteromalla); Hydrophilous lotic bryophyte guild (e.g. Leptodictyum riparium, Hygrohypnum ochraceum); Hydrophilous lentic bryophyte guild (e.g. Fissidens crispus, Fontinalis hypnoides var. duriaei); Sciophilous lentic bryophyte guild (e.g. Bryum pseudotriquetrum, Plagiomnium affine, Trichostomum brachydontium) and Rheophilous bryophyte guild (e.g. Thamnobryum alopecurum). For bryophytes, there are guilds that only existed in one river, such as Hygrophilous lotic and Rheophilous - exclusive for the run-of-river case study, and Heliophilous lentic and Sciophilous lentic - exclusive for the reservoir case study.

For riparian woody vegetation, the five identified guilds were named as: *Highly disturbance-adapted riparian guild* (e.g. *Rubus spp., Acacia dealbata*) composed by shallow-rooted species with diverse reproduction strategies and hydrochoric dispersal (diaspore=fruits), *Disturbance-adapted riparian guild* (e.g. *Fraxinus angustifolia*, *Frangula alnus*), species with sexual reproduction and hydrochoric dispersal (diaspore=fruits);

Poorly-disturbance adapted riparian guild (e.g. *Alnus glutinosa*, *Quercus robur*), deep-rooted species, mostly with non-hydrochoric dispersal (diaspore=seeds); *Disturbance-resilient riparian guild* (e.g. *Crategus monogyna, Sambucus nigra*), deep-rooted with diverse reproduction strategies and non-hydrochoric dispersal (diaspore=fruits) and *Disturbance-favored riparian guild* (e.g. *Salix salviifolia*, *Salix atrocinerea*), shallow rooted, diverse reproduction strategies and hydrochoric dispersal (diaspore=seeds). All these five guilds were present in both studied rivers.

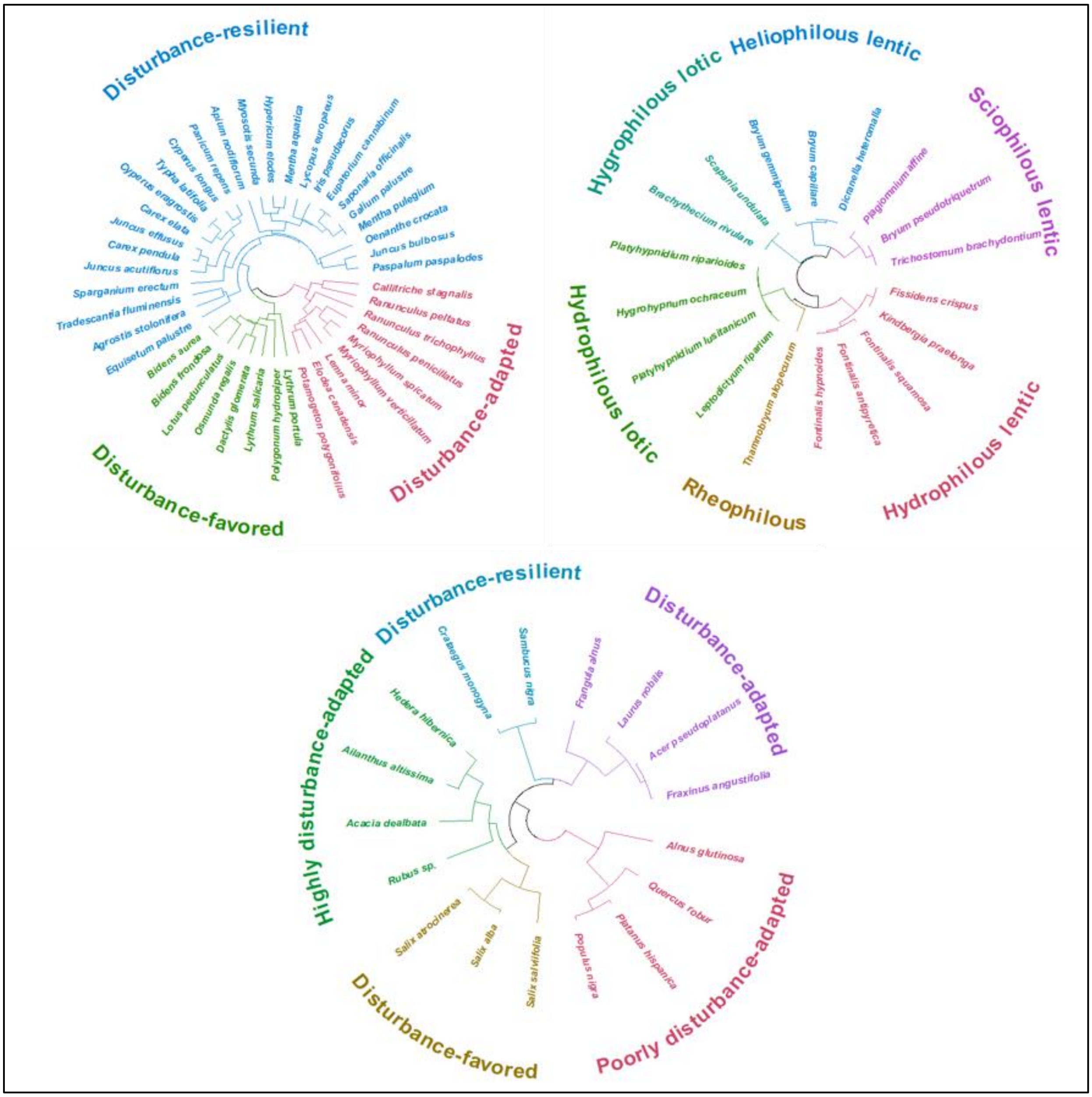

Figure 17. Guilds obtained by hierarchical clustering of plant species based on traits for macrophytes (upper left panel), bryophytes (upper right panel), and riparian woody vegetation (lower panel). Guild names are given for each plant group. See Table D2 for details on species.

Regulation effects on guilds cover and location

Differences between sampling sites of this study were not attributed to the different river typologies but to the regulation variables (Figure D1). The physically-based PCAs were able to explain 58% and 56% of the data variability in the first two axes, in run-of-river and reservoir case studies, respectively (73% and 67% in the first three) and did not reveal any difference between regulated and unregulated sampling sites. Furthermore, in both rivers, the environmental PCAs were able to explain, respectively, 55% and 57% of data variability in the first two axes, revealing a dominance of the regulation variables over geomorphologic. More precisely, for the run-of-river case study, the most correlated variables with axis 1 were watershed regulation variables, namely, total area of the sampling site watershed, sampling site regulated watershed area and ratio of the sampling site watershed regulated area, while most correlated variables with axis 2 were geomorphology and habitat variables, e.g., cobble percentage in substrate, cobbles as main substrate and macrophytes presence as main substrate. In the reservoir case study, most correlated variables with main axis were sampling site regulated watershed area, mean regulated watershed flow and the ratio between total watershed flow and regulated watershed flow, whereas most correlated variables with second dimension were fine elements percentage in substrate, mean water depth and land use in the margins.

In general, regulation promotes changes in the guilds' cover of the studied plant groups and shifts in the spatial location of riparian woody vegetation guilds on the riparian zone (Figure 18; Table D5).

River regulation determines a cover increase of all macrophyte guilds, both in reservoir and run-of-river case studies. Notably, the cover significantly differs from free-flowing and regulated sites for the *Disturbance-resilient macrophyte guild*. Furthermore, when comparing regulation types, it is evident that cover increases in regulated circumstances are greater in the run-of-river than in the reservoir case study for *Disturbance-favored macrophyte guild* (riverine ferns and emergent macrophytes) and *Disturbance-adapted macrophyte guild* (i.e. aquatic macrophytes).

For bryophytes, river regulation promotes the decrease of cover of most bryophyte guilds, but not significantly. *Hydrophilous lotic bryophyte guild* in the run-of-river case study increased the cover, however not significantly, whereas *Hydrophilous lentic bryophyte guild* in the reservoir case study significantly increased the cover (Figure 18; Table D5).

Riparian woody vegetation present distinct trajectories facing regulation, depending on the guild, or even different responses according to the occurrence in the reservoir or in run-of-river case studies. In the reservoir case study, regulation promotes a cover increase of *Disturbance-favored riparian guild* (e.g. willows, *Salix* spp.; diverse reproduction strategies)*, Disturbance-adapted riparian guild* (e.g. ash, *Fraxinus angustifolia*; species with sexual reproduction and hydrochoric dispersal), and *Highly disturbance-adapted riparian guild* (e.g. *Acacia*), while the *Disturbance-resilient riparian guild* (e.g. *Sambucus nigra*; non-hydrochoric dispersal) and the *Poorly disturbance-adapted riparian guild* (e.g. alder, *Alnus glutinosa*) present larger covers in free-flowing river sites. Similarly, in the run-of-river case study, *Disturbance-favored riparian guild, Disturbance-adapted riparian guild* also increased the cover, whereas *Poorly disturbance-adapted riparian guild* also decreased. The occurrence of the *Disturbance-*

resilient riparian guild was only visible in regulated sites, however with small abundance cover.

Furthermore, in the reservoir case study, river regulation determines the encroachment of the riparian woody vegetation into the river channel, whereas in the run-of-river case study expands outwards the riparian zone. Exception from this pattern has the *Disturbance-favored riparian guild* (willows) which in both regulation case studies is located in a similar distance as in the free-flowing sites.

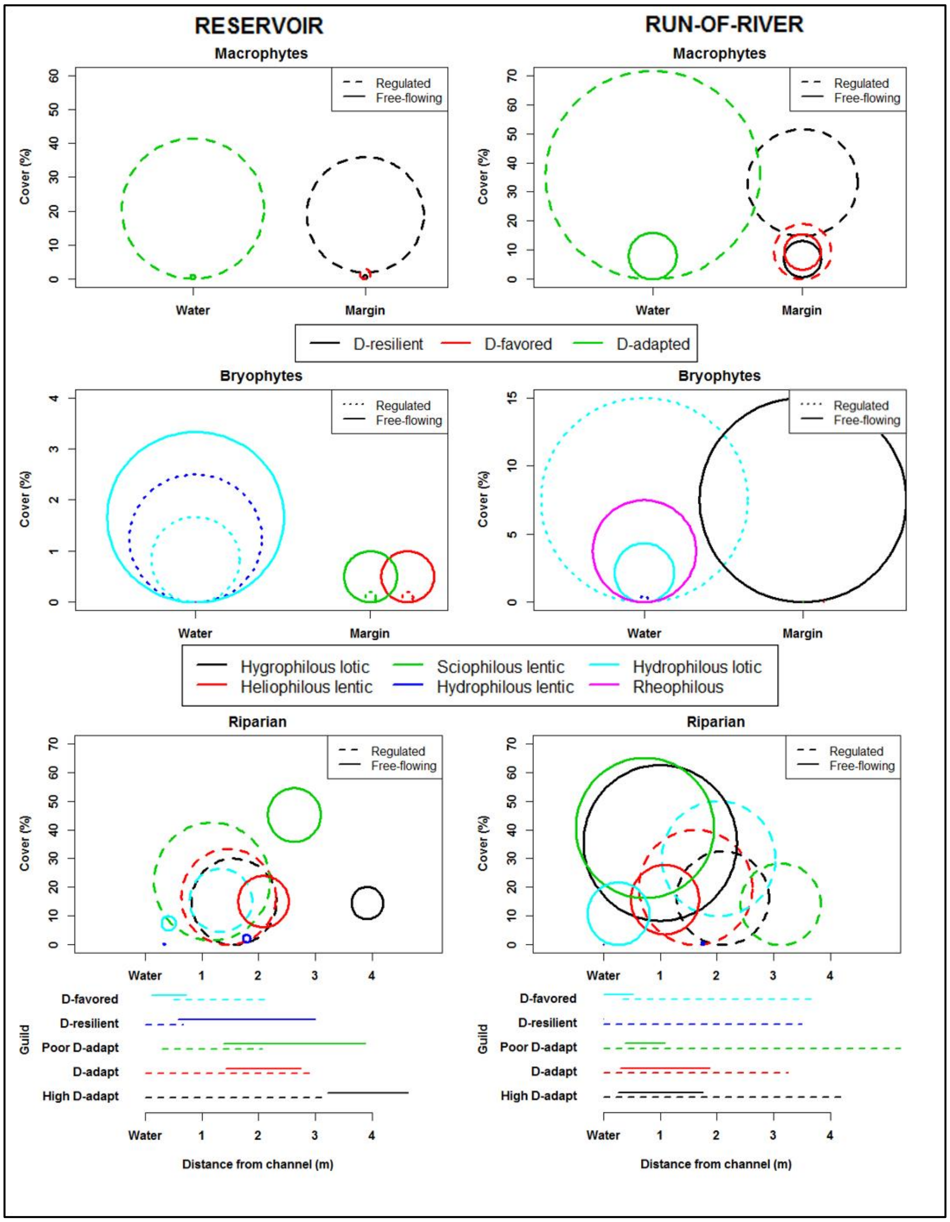

Figure 18. Fluvial vegetation changes in cover and location along the river’s lateral gradient of reservoir (left panel) and run-of-river (right panel) case studies in regulated and free-flowing conditions. Circles diameter correspond to the average guild cover range (minimum-maximum). Observed riparian woody vegetation shifts across the riparian zone are shown at the respective bottom panel.

Differences in recovery patterns of plant guilds downstream of dams

The *Disturbance-adapted macrophyte guild* (aquatic macrophytes with vegetative reproduction by stem fragments) presented a significant response to regulation variables in both case studies. Guilds located in riverbanks, *Disturbance-favored macrophyte guild* (perennial emergent species with clonal spread) and *Disturbance-resilient macrophyte guild* (emergent species dispersed by seeds) only respond significantly in the reservoir case study (Table D5).

For a degree of regulation (DOR) lower than 0.10 in the reservoir case study, there is no significant differences in the *Disturbance-adapted macrophyte guild* cover between free-flowing sites and the regulated sites. The projected distance from dam (DFD), for the guild recovery (i.e. the distance from dam where the guild cover of free-flowing and regulated sites is not significantly different), was 12.24 km (Table D5).

In the run-of-river case study, modelling revealed higher DOR values (0.15) and higher DFD (17.8 km) in comparison to the reservoir case study (Figure 19).

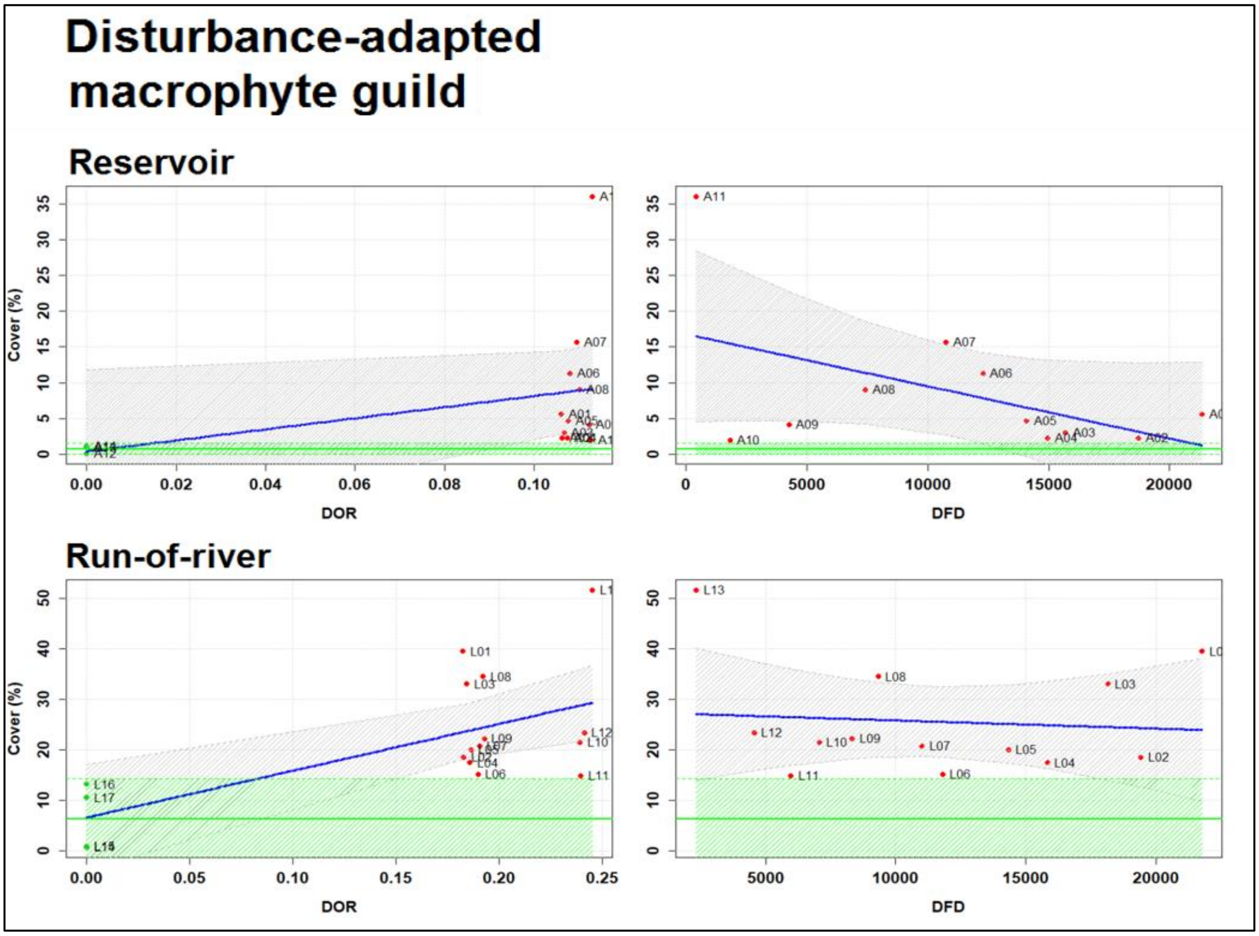

Figure 19. Expected cover of the Disturbance-adapted macrophyte guild (blue) according to the degree of regulation (DOR) and distance from the dam (DFD, in meters) in the reservoir (top) and the run-of-river (down) case studies. Blue shaded areas stand for 95% confidence intervals of the blue regression line, green shaded areas stand for the 95% confidence interval of the mean guild cover in free-flowing circumstances depicted by the green line.

Bryophytes did not show significant changes in their guild cover between free-flowing and regulated sites, in both regulation types, with an exception for the Hydrophilous lentic bryophyte guild (e.g. Fontinalis spp.) in the reservoir case study (Table D5). This guild significantly decreases in cover downstream and it was predicted a recover at a DOR of 0.09 and at a DFD of 12.28 km (Figure 20).

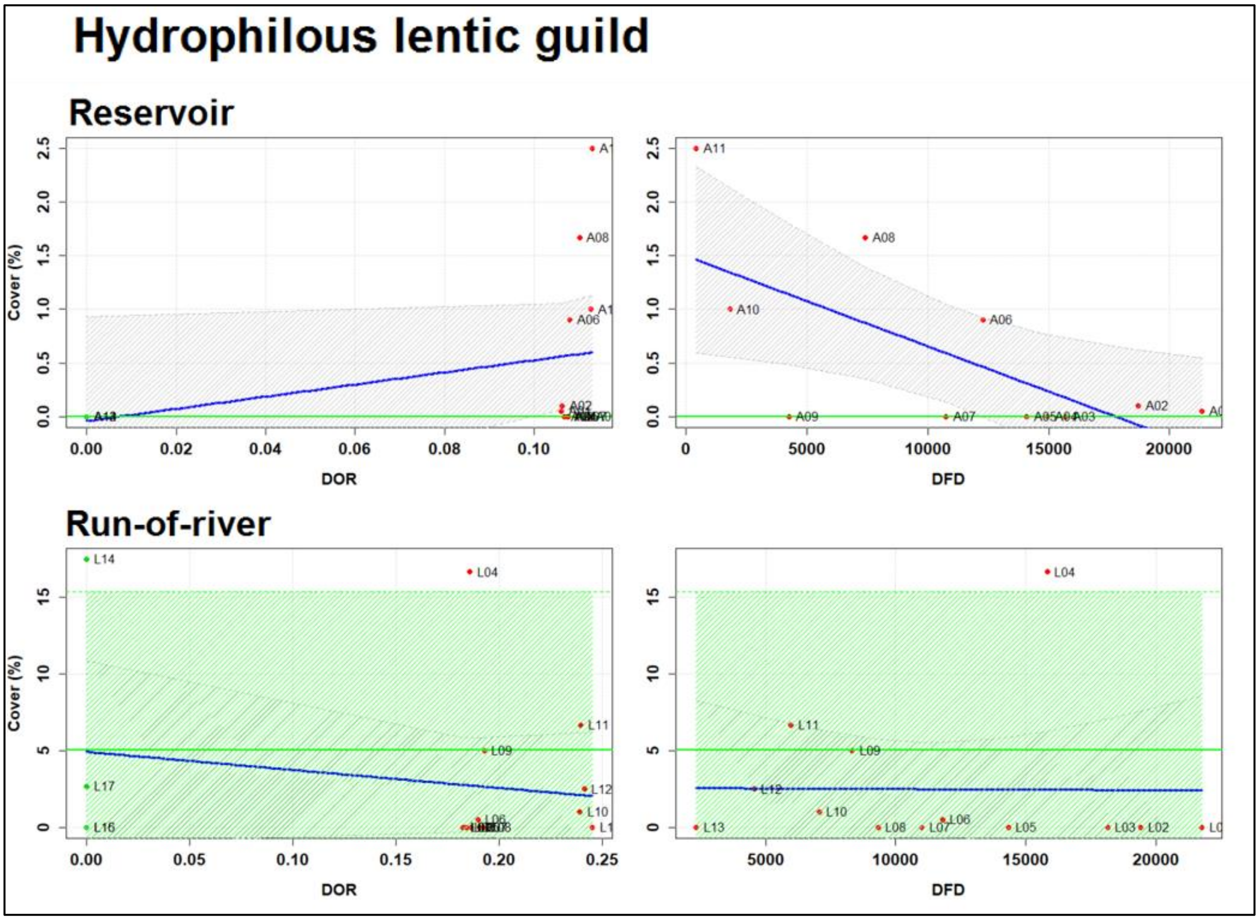

Figure 20. Expected cover of Hydrophilous lentic guild (blue) according to the degree of regulation (DOR) and distance from dam (DFD, in meters) in the reservoir (top) and in the run-off-river (down) case studies. Grey areas stand for 95% confidence intervals of the blue regression line, green areas stand for the 95% confidence interval of the mean guild cover in free-flowing circumstances depicted by the green line.

The *Disturbance-favored*, *Poorly disturbance-adapted*, and *Disturbance-resilient* riparian guilds have significant responses to regulation variables. DOR values for guild recovery are 0.10, 0.09 and 0.11, respectively for the in the reservoir case study (Table D5). The *Disturbance-favored riparian guild* (willows), was the only guild for which a DOR and DFD threshold levels could be determined in both regulation types. Modelling showed that this guild recovers from the effect of the reservoir at a lower value (DOR= 0.10) than at the run-of-river (DOR= 0.22). In the reservoir case study, the regulation effect was expected to “disappear” after 12.4 km, whereas a peculiar pattern with further increase in the guild cover after 10.2 km from the dam was displayed in the run-of-river. In this case, the guild cover near the dam was more similar to the reference cover and became more different as the sampling sites progresses away from the dam (Figure 21).

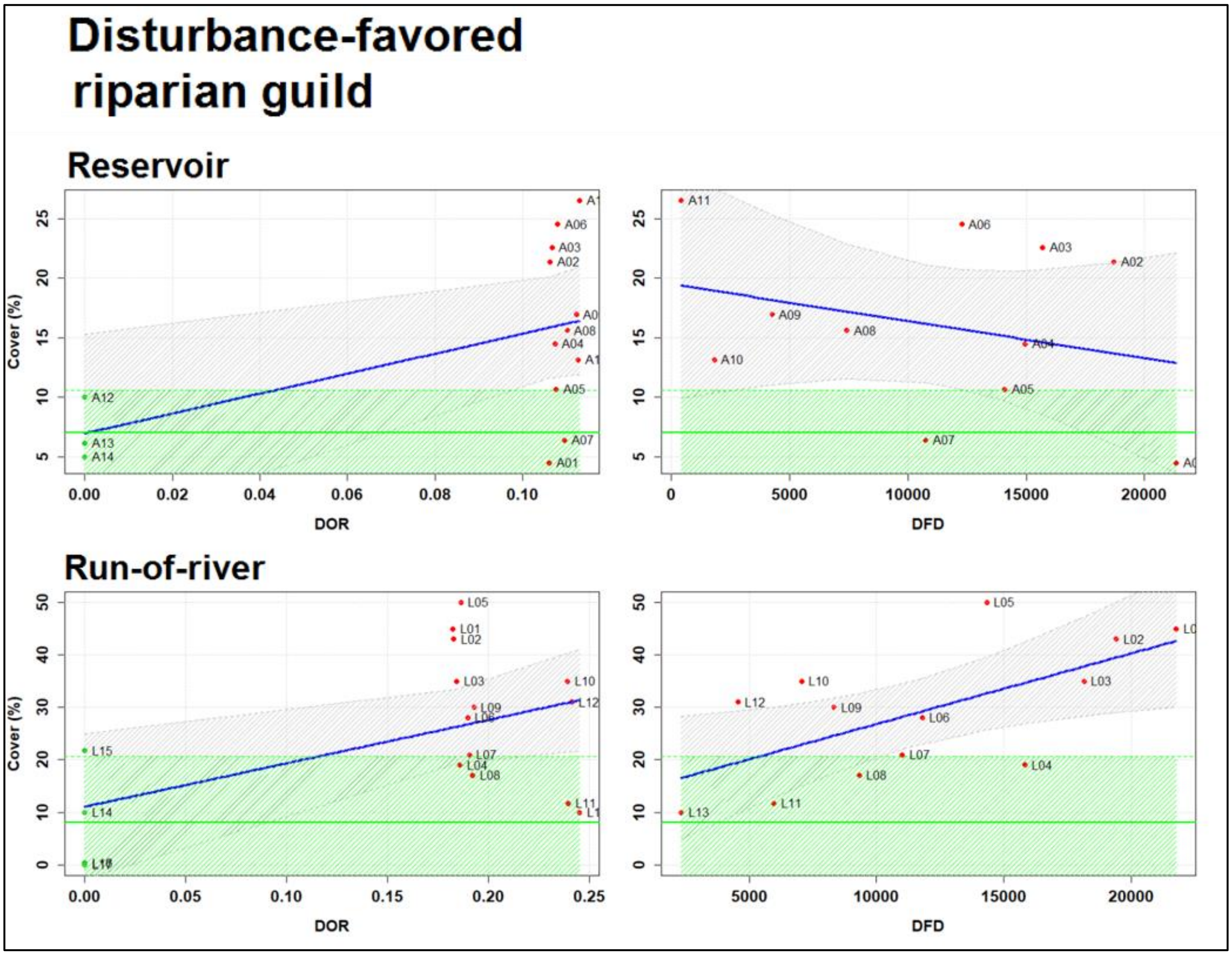

Figure 21. Expected cover of the Disturbance-favored riparian guild (blue) according to the degree of regulation (DOR) and distance from dam (DFD, in meters) in the reservoir (top) and in the run-of-river (down) case studies. Grey areas stand for 95% confidence intervals of the blue regression line, green areas stand for the 95% confidence interval of the mean guild cover in free-flowing circumstances depicted by the green line.

The cover of *Poorly disturbance-adapted riparian guild* (e.g. alder) decreased proportionally with regulation in both case studies. (Figure 22). The guild cover threshold for the reservoir case study occurred at a DOR of 0.09 and at a DFD of 6 km. Changes in the cover are also noticeable for the run-of-river study site but did not reach significant differences between regulated and free-flowing sites for the comprised ranges of DOR or DFD.

The *Disturbance-resilient riparian guild* (e.g. *Sambucus nigra*) showed a decreased cover on the reservoir case study. A high DOR threshold level of 0.11 was predicted for this riparian guild to attain a significantly similar cover in relation to the free-flowing conditions (Table D5).

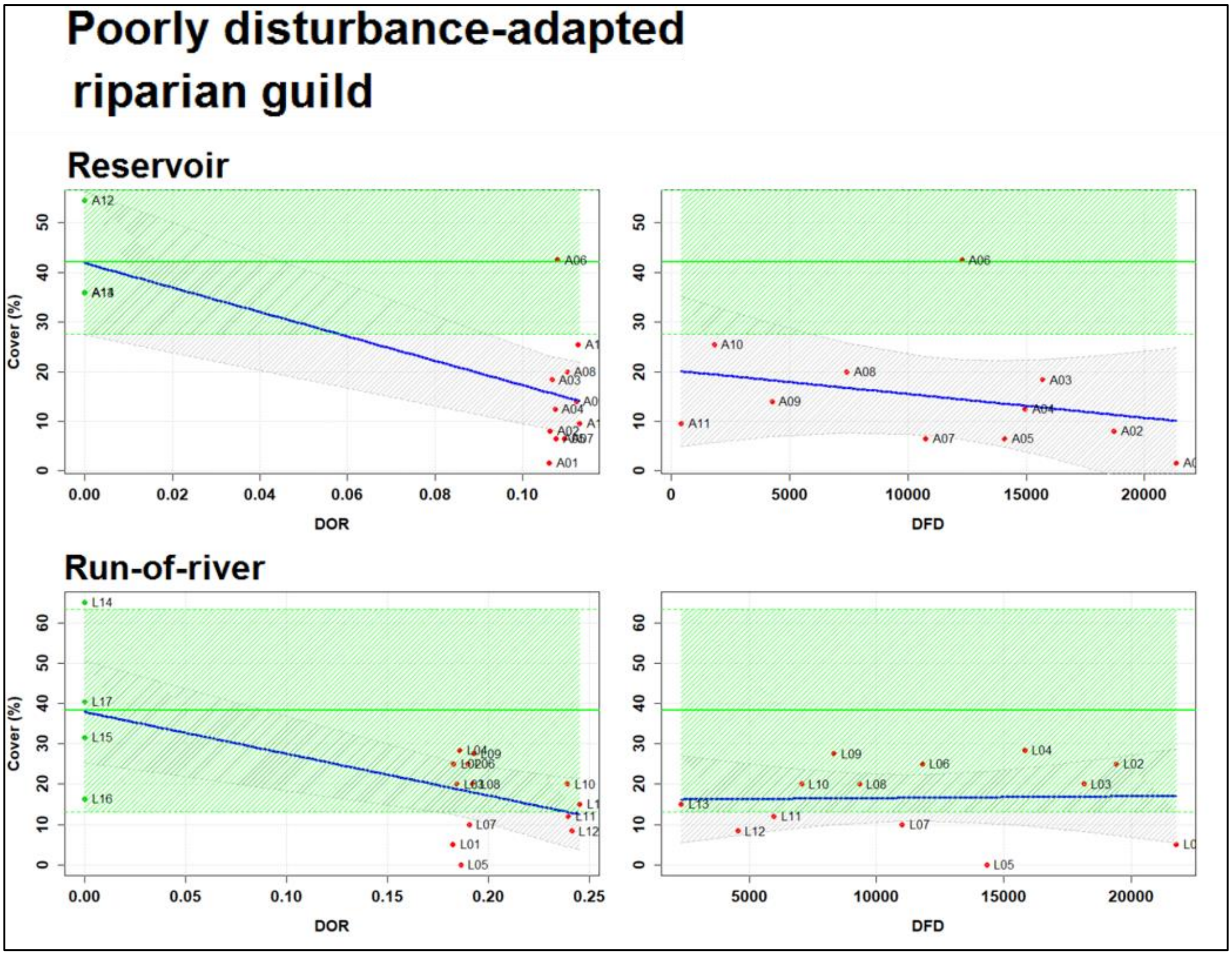

Figure 22. Expected cover of Poorly disturbance-adapted riparian guild (blue) according to the degree of regulation (DOR) and distance from dam (DFD, in meters) in the reservoir (top) and in the run-of-river (down) case studies. Grey areas stand for 95% confidence intervals of the blue regression line, green areas stand for the 95% confidence interval of the mean guild cover in free-flowing circumstances depicted by the green line.

Discussion

The main objective of this study was to assess the effects of river regulation on aquatic and riparian plant communities along the longitudinal and lateral fluvial dimensions. We further assessed how far and to which extent river regulation affects these communities. In this section, we discussed how the observed changes from free-flowing to regulated setting could be explained by plant functional traits alterations and trade-offs and by influence of the different regulation types.

Regulation effects vary among and within plant groups

Our results show that the response of aquatic and riparian vegetation to regulation was plant group-reliant and guild-specific, resulting in plant abundance changes and not by guilds loss in the regulated rivers.

Overall, we observed that there was an increase in the abundance cover of macrophytes under river regulation circumstances, while bryophytes respond to river regulation with a decrease in cover. Riparian guilds, on the other hand, present diverse responses depending on the guild and on the type of river regulation. This differing pattern among the plant groups is likely a result of the specific adaptation traits blend of each guild, reflecting species distinct abilities to avoid or tolerate hydrological disturbances (Gurnell et al., 2012; Belmar et al., 2013; Yi et al., 2020). However, for bryophytes, the indirect effects of regulation on the habitat, such as water quality and/or thermal regime modifications, changes in low-depth substrate stability of their habitats can be as important as the magnitude and timing of flows for performing community's lifecycle (Manolaki et al., 2019).

Within each plant group, responses are guild-specific. All macrophyte guilds increased in abundance cover, but only the *Disturbance-adapted macrophyte guild* (aquatic plants) was significantly affected by regulation. For this guild, the water availability is essential for growth, reproduction, and establishment. Hydromorphic leaves (large air spaces in mesophyll), no cuticle, stomata on the upper leaf surface and regeneration by vegetative fragments and hydrochoric dispersal determine these species with traits associated with constantly flooded habitats (O'Hare et al., 2016). The two other macrophyte guilds comprise emergent waterlogging tolerant species that mostly differ within each other in regeneration type (sexual reproduction or vegetative propagation). Nevertheless, they are both good anemochoric and zoochoric dispersers, less affected by drought-like flows in riverbanks and active channels.

But water availability or magnitude of flows is not the sole factor that promotes plant cover increases in regulated rivers. The *Disturbance-favored riparian guild* (riparian pioneers such as *Salix* spp.) have linear leaves, small seeds dispersed by water or wind, flexible stems and can reproduce by fragmentation of stems. The uprooting resistance is also higher compared to other riparian pioneers such as *Alnus* and *Populus* (Karrenberg et al., 2003). Those characteristics ensure successful establishment at flooded and drought susceptible habitats, and in wet habitats frequently disturbed by erosion or sediment deposition (Merritt et al., 2010a; Stromberg and Merritt, 2016). On the other hand, these pioneer species have also great colonization promptness in newly available areas originated by the water storage and diversion, such as riverbanks in downstream reaches.

Other guilds such as *Poorly disturbance-adapted riparian guild* (deep-rooted species, mostly with non-hydrochoric dispersal such as *Alnus glutinosa* and *Populus nigra*) cover decreased with regulation. Lack of major floods downstream of dams and irregular water flow intervals hampered regeneration and persistence of this guild (Fraaije et al., 2016). For instance, Merritt and Poff (2010b) found decreased recruitment probability and abundance for *Populus* under even slight decrease in flow. In the Mediterranean setting, where water is naturally a limiting factor, to prevent further loss of the taxa with regulation - hydrologic thresholds for water table depth, flood duration, and flood frequency have been proposed (González et al., 2013). Access to water restricts the occurrence of *Alnus glutinosa*, as this species requires soil moisture for growing and completing its life cycle (Rodríguez-González et al., 2014), which is hampered downstream of the reservoir. The presence of upland species (*Platanus spp.* and *Quercus spp.*) in the riparian zone, points to limited water availability and successive encroachment of the upland species towards the active channel. This pattern was already been foreseen and observed in Mediterranean rivers (e.g. Rivaes et al., 2013; Aguiar et al., 2018; García de Jalón et al., 2019). The natural water limitation is amplified with flood reduction from the reservoirs leading to poor recruitment of the woody vegetation (Stella et al., 2011). Establishment of riparian woody species, is also limited under run-of-river regulation (Bejarano et al., 2020), where the rapid and frequent flow variation over a short period of time pose a strong negative effect on the germination stage on species with almost exclusively seeds propagation (Grime et al., 1989). Likely hampered recruitment to be a reason for the decreased cover also in the *Disturbed-resilient riparian guild*, besides their morphological ability to tolerate water limitations.

Diverse regulation types promote varying responses along and across the river

The magnitude, timing, duration, and frequency of peak flows are especially critical for aquatic and riparian species, and over evolutionary time they provide strong selective forces for the fluvial biota (Lytle and Poff, 2004). Deviation from the natural flow regime and sediment dynamics induced by different dam types lead to a variety of plant feedbacks (Gurnell, 2014; Politti et al., 2018).

Importantly, we found that there are significant differences in the response of plant groups and guilds with hydrological alterations induced by the reservoir and the run-of-river dams.

In the reservoir case study, the significantly responsive guilds (eight in total) presented a very similar degree of regulation (DOR) hinge level ranging from 0.09 to 0.11 (DOR is comprehended between 0 and 1). Therefore, it suggests that there is a narrow range of river regulation levels, transversal to plant groups and guilds, from which river regulation does not affect plant communities. For the run-of-river case study, higher threshold levels (0.15 and 0.22) were observed and there were only two significantly responsive guilds. Hydrological alterations and fluvial disturbances induced by reservoirs promote changes in the cover of more plant communities than the run-of-river settings. A similar pattern was observed for the riparian vegetation cover (herbaceous and woody vegetation) on a remote sensing study in these regulated rivers, with major changes in reservoir rivers (Aguiar et al., 2016). Run-of-rivers maintain high flow variability and flashiness in closer dependence of inflows upstream, while reservoirs in Mediterranean areas frequently imprint water scarcity downstream of dams, and mostly rely on electricity demands and seasonal rainfall patterns. The former having greater consequences on fluvial biota.

However, hinge threshold levels between ca. 6 and 12 km of distance from the reservoir were enough to dissipate the regulation effects on the communities. These results are comparable to those in Mediterranean rivers for which the invertebrate's recovery from regulation occurred at 10 km from the dam, and food-web chain was improved to the preregulated condition at 14 km (Mor et al., 2018; Mellado-Díaz et al., 2019). However, we observed that for the downstream of the run-of-river dam, the recovery distance for aquatic macrophytes is longer (ca. 17 km). Alterations of flow regime are less pronounced in rivers impaired by run-of-river dams than by the reservoirs. For the former case, river margins are frequently inundated providing likely enough available water and sediment transport for macrophytes and riparian woody communities' survival, though shifts in plant communities still occur (Nilsson et al., 1991; Aguiar et al., 2016).

Another difference induced by the different regulation types was the feedback trajectory of riparian woody vegetation. The expansion inwards the active channel, i.e. vegetation encroachment, in the reservoir observed for all riparian guilds is likely related to the reduction in magnitude and frequency of floods (Räpple et al., 2017; García de Jalón et al., 2019). In contrast, there was an outwards expansion in the run-of-river setting possibly linked to the daily high discharges, inundation of riverbanks and increased scour which were formerly unsuitable to the riparian establishment (Aguiar et al., 2016; Bejarano et al., 2018).

Run-of-river regulation supported more lotic bryophytes than reservoir rivers. Likely *Hydrophilous lotic bryophyte guilds* composed by *Leptodictyum riparium* and *Hygrohypnum ochraceum* are dependent on the low-depth high-energy flow river zone, can find more suitable living conditions to the natural habitats in the run-of-river. The *Hydrophilous lentic bryophyte guild* in the reservoir case study benefited from a certain level of DOR, and further, disappeared at some distance of the dam with the increased river depth, which corresponds to the functional characteristics and environmental conditions needed for *Fontinalis* genus. Those taxa react to the water column permanence, being only capable of surviving in shallow, permanent waters and having an optimal growth attached to stable substrates immersed up to 1 meter of running or standing water. It is typical that at decreased or deepen water column for longer periods these taxa (and almost every other bryophyte) disappear given their limitation for photosynthetic uptake of bicarbonate and CO_2 extraction from the water (Vieira et al., 2018). Bryophyte higher cover in free-flowing circumstances can be related to the larger daily flow variability that allows for greater variety of hydrological habitats and margins' ranges subjected to river flooding and, therefore, more suitable microhabitat with the necessary levels of submersion for these communities.

Macrophyte changes are similar in diverse regulation settings

Disturbance-adapted macrophyte guild significantly increases the cover independently of regulation type. In hydropeaking circumstances such as those of the run-of-river case study, the high discharges imposed by dams during hydropower production can facilitate vegetative reproduction along the river where plant establishment will be more likely (Johansson et al., 1996). In that sense, the stem fragments of the *Disturbance-adapted macrophyte guild* can be detached from the mother plant during disturbance caused by water velocity or sediment mobility (Riis and Sand-Jensen, 2006). Because many species of this macrophyte guild (e.g. *Ranunculus* spp., *Myriophyllum* spp. and *Elodea canadensis*) have meristems closely distributed along their stems, only small-sized stem fragments are needed to regrow into viable individuals and establish new populations (Riis et al., 2008). Despite some adaptations to high discharges, yet, high flow velocities also increase the probability of plants to be washed away rather than only transported (Friedman and Auble, 1999).

Then, we may ask why reservoirs promote a similar effect on this water-dependent macrophyte guild? Looking inside the guild, we find a homogeneous set of truly aquatic macrophyte species, with similar morphology, dispersal mode, and reproduction types. However, the regulated river impaired by the reservoir increases its cover mostly by the pond water-crowfoot (*Ranunculus peltatus*), and also *R. tricophyllus* while in the run-of-river case, this species was not observed. The more abundant species in the latter was the Eurasian watermilfoil (*Myriophyllum spicatum*), from the same guild. *M. spicatum* grows well in shallow, moderately turbid waters and nutrient-rich sediments (Smith and Barko, 1990), conditions that can be found in our case study, while *Ranunculus peltatus* and *R. tricophyllus* thrive in still waters and stressful environments that alternate flooding and drying (Lumbreras et al., 2009).

Conclusions

Overall, our findings point to varying effects of regulation on the spatial distribution and cover of plant communities. The drivers of the distinct vegetation groups and guilds' responses to regulation were likely based on the functional adaptations to hydrological alterations, and to the different dam operational types. The results allowed us to understand how regulation effects dissipate downstream of dams and what are the minimum distances from dams or regulation intensities that can cope with hydropower demands. Accordingly, the gradient of regulation and the distance for plant species recovery can guide river restoration projects, as well as environmental flow designs to address sustainability goals. This knowledge is especially important with the unprecedented magnitude of river flow alterations and the associated biota changes or losses, hence putting into question the long-term sustainability of freshwater ecosystems and their ecosystem services.

Chapter VI.

Discussion

This chapter aims to discuss the results obtained during the thesis work and how these can potentiate future knowledge about functional diversity in Mediterranean riparian forests governed by natural and anthropogenic factors. By doing so, it shows the obtained functional diversity responses (the functional diversity losses, gains, or shifts), and explains the underlying mechanisms of the observed patterns. This understanding can help to anticipate future trajectories of riparian vegetation. Ultimately, the results will provide insights into the riparian ecosystem functioning.

In the beginning, the thesis identified the applicability of the functional diversity measures in riparian forests and revealed the main current issues in the functional diversity research area. It was a crucial step for the further use of a functional diversity framework throughout the thesis (Chapter II). Further, we found that functional diversity of the Mediterranean riparian forests was susceptible to precipitation (Chapter III); differences in functional diversity to regulation were revealed between the Mediterranean and boreal riparian forests (Chapter IV); longitudinal and lateral functional diversity patterns were regulation types and plant communities dependent (Chapter V). Different factors underline those findings. The influence of precipitation as a revealed key filter for the functional diversity in riparian forest communities is expected to be the most severe in those communities with the already low level of functional redundancy. Since the reduced functional redundancy implies the lower capacity of the community to mitigate disturbances, the decreased rainfall in the Mediterranean biome likely will impose consequences on riparian vegetation stability, resistance and resilience. This can be an important outcome within the environmental change context, taking into account the climatic conditions in the Mediterranean biome. Therefore, future conservation activities should be targeted toward the most vulnerable communities, i.e. those with reduced functional redundancy. The impact of river regulation as one of the most important factors for riparian forests was analyzed in settings of hydrologically different biomes. When species presence/absence is used, the persistence of similar functional diversity levels between free-flowing and regulated sites in the Mediterranean biome highlighted the effect of vegetation' exposure to natural hydrological stressors similar to regulation. In a broader context, legacy hydrological adaptations may mitigate to some extent regulation induced changes, but, not solely. In the Mediterranean biome, if the future extreme drought events increase the need for drinking water and agricultural purposes, and consequently further alter the streamflow, the functional diversity of riparian forests can be compromised. Differently regulated Mediterranean rivers by run-of-river dams and storage reservoirs allowed closer observation on the functional diversity patterns in aquatic and riparian vegetation. Namely, regulation induced longitudinal and lateral abundance shifts but not in guilds' loss. The result likely reflects groups and trait' adaptations to cope with hydrological disturbances and expresses the streamflow and fluvial "severity" triggered by different regulation types. The acquired knowledge can guide river restoration projects and environmental flow designs which are especially important with the current unprecedented magnitude of river flow alterations and the associated biota changes or losses.

This chapter is divided in four parts:

i) Functional diversity development and application in riparian forests;

ii) Environmental filters in Mediterranean riparian forests;

iii) Streamflow regulation effects on riparian woody communities in two contrasting biomes;

iv) Regulation effect on aquatic and riparian communities along the longitudinal gradient and across the riparian zone.

Functional diversity development and application in riparian forests: an overview

By moving beyond species identity, functional diversity approaches enabled comparisons of communities across systems and thus better-generalized research results. With the recognition of the functional diversity approach in unraveling patterns linked to environmental and anthropogenic impacts various functional diversity frameworks, such as functional diversity indices and the occurrence and distribution of ‘plant guilds’, have appeared. Studies on the applicability of functional diversity in riparian plant communities (e.g. Merritt et al., 2010; Stromberg and Merritt, 2016) or in riparian restoration (Capon and Pettit, 2018) exists, but comprehensive overview of the functional indicators in riparian forests worldwide was limited.

Lozanovska et al. (2018b) used a set of 70 works on riparian forests from the last two decades and showed that the development of the ‘functional diversity’ concept has a long history. It originated in ancient times (c. 300 BCE) when Aristotle and Theophrastus’ developed the first known plant classification, based on plant height and stem density, but more advances have been reached in the 20th and 21st centuries. Multiple terminologies have been used in functional diversity studies related to diverse objectives. Namely, related to attempts to describe ‘vegetation clusters’ based on a few common traits within a community (e.g. Root, 1967), or on linkages to resources (Grime, 1977), or on the trait range (Garnier et al., 2004; Villéger et al., 2008), various terms (plant functional types, plant functional groups, ecological groups) for describing the same concept of vegetation clusters emerged. Then, multiple measures of functional diversity have been used. At first, the functional diversity quantification was based on *a priori* classification to divide species into various functional groups (Hooper and Vitousek,1997; Tilman et al., 1997), which further was enhanced with the statistical ground to classify species into functional groups. In that light emerged the functional diversity index - Functional Diversity Attribute, FAD (Walker et al., 1999). Since then many indices were developed assessing distinct functional diversity aspects - such as functional richness (how much of the functional space is occupied by traits), functional redundancy (how much of the traits are overlapping), functional evenness (how traits are distributed), functional divergence (how much traits differ between them) (Mason et al., 2005; de Bello et al., 2007; Villéger et al., 2008). Nevertheless, functional richness appeared to be the most widely used in riparian forests, likely due to the index range which is indicative of environmental or anthropogenic intensities (Funk et al., 2017). Some advances in the most appropriate index selection were achieved (Schleuter et al., 2010; Mouillot et al., 2011), but no index yet combines multiple aspects simultaneously. As a result, among the majority of the studies, several indices were implemented simultaneously (functional richness mainly coupled with functional evenness and divergence). In addition, indices selection has been also discussed. On the one hand, there are non-weighted by abundance indices that produce a more straightforward interpretation of results, on the other hand, there are weighted ones that put higher “weight” on the dominant species. Therefore, to be able to select the most suitable index, the flowing criteria should be followed: i) data type (rare; dominate species) – rare species may increase functional richness whereas dominant species give higher weight to the most common ones; ii) the research question of interest (which functional aspect can be related to certain ecosystem function or process). Further highlighted challenge was the number and type of traits used in riparian forest studies. If a large number of functional traits are selected, then the ability to detect functional differences between species increases, resulting in “artificially” high functional richness (Petchey and Gaston, 2002). From the analyzed studies, the average trait number was eight, the result which in line with Laughlin (2014) who also proposed a threshold of eight independent traits assessed from multiple plant organs (leaves, stems, roots) to produce a more accurate functional diversity evaluation. The riparian vegetation assessment showed the use of “soft traits”- plant height, specific leaf area, and seed mass to be prevalent. Those three traits have high ecological relevance concerning the hydrological regime (Hough-Snee et al., 2015, Lawson et al., 2015a,b; de la Riva et al., 2017), which was listed in our study as the most determinant factor in riparian forests. Since riparian vegetation evolved within the context of flooded and fluvially disturbed habitats, species composition, distribution and abundance are reflective of the prevailing hydrological conditions. In that sense, plants with better water-conservation strategies such as short canopy height and small leaf area, high seed mass are favored, ensuring a greater volume of stored resources for seed establishment to be fostered in a hydrologically limited environment (Stromberg and Merritt, 2016).

Overall, the functional diversity framework can benefit from improved current knowledge gaps on the traits and indices selection. However, despite the existing challenges, functional diversity which relies on species traits i.e. capture different aspects of species’ resource use and habitat requirements was responsive to disturbance. The functional diversity level can derive conclusions about riparian forest's capacity to recover or mitigate environmental or anthropogenic impacts.

Environmental filters in Mediterranean riparian forests

Environmental constrains contribute to the functional distribution and diversity of riparian species (Aguiar et al., 2013a; Bruno et al., 2016a), underlying local, regional and across-scales factors as crucial for understanding species richness of Mediterranean riparian forests (Leo et al., 2019). Consequently, those factors can be also seen as a filter determining which traits can persist in a given environment (Johansson and Keddy, 1991; Díaz et al., 2016), thus shaping the level of functional diversity. If environmental filtering excludes traits not suitable for the given environmental conditions and hence, changes functional diversity, it may alter riparian ecosystem stability, resistance, and resilience (Hooper et al., 2005).

Lozanovska et al. (2018a), assessed the functional richness and redundancy of different riparian forest types and analyzed the relationship between those functionality aspects and environmental filters. Identifying the environmental variables that exert selective pressures on the functional diversity in riparian forest communities is a critical step in setting baseline expectations on how riparian vegetation may respond with the anticipated global change scenarios.

The results showed that the Mediterranean shrublands were functionally the most distinctive riparian forest type significantly different from the rest groups. Further, varying importance of habitat and regional environmental factors according to the forest types, and importance of precipitation for the functional diversity of all riparian woody communities (exception for functional richness in Ash woodlands). This outcome of precipitation importance has functional implications for the riparian forests in Mediterranean Europe where the future climate predictions of increased hot waves, drought events, and uncertain rainfall patterns (IPCC, 2014) may compromise their functioning (Madrigal-González et al., 2018). Mediterranean shrublands will be especially threatened by decreased precipitation due to their displayed low functional redundancy. Lack of functionally redundant traits can be attributed to community high trait specialization to survive under strong environmental filtering (de la Riva et al., 2017). Indeed, Mediterranean shrublands have constrained occurrence at the driest and hotter locations of Portugal. The strong filtering is promoting only specific plant adaptations to survive under harsh environments hereby constraining the trait pool and reducing functional redundancy (Jacobsen et al., 2008; de la Riva et al., 2016b). In non-redundant communities as Mediterranean riparian shrublands, the loss or replacement of one species would lead to loss of unique traits or functions increasing the community's vulnerability to environmental changes (Elmqvist et al., 2003). Despite the inherited ability of Mediterranean shrublands to tolerate periods of drought (Salinas et al., 2000), increased environmental filtering is diminishing functional redundancy (Bruno et al., 2016a), making them thrive in global environmental change context challenging.

The obtained findings have twofold importance. First, it allows detecting the most vulnerable communities which are lacking a broad pool of traits to mitigate disturbances, accordingly, the management goals should be focused on these. Second, identifies the key driver for functional diversity in Mediterranean riparian forests thus can help to anticipate riparian ecosystem alterations if the current environmental conditions change. Alterations to the established functional diversity-environment relationship will affect the structure, diversity and functioning of riparian forest communities.

Streamflow regulation effects on riparian woody communities in two contrasting biomes

Alterations of streamflow regime are widely recognized as a key anthropogenic threat to the riverine plant species (Lytle et al., 2017), compromising many functions and ecosystem services provided by rivers (Tonkin et al., 2018). However, the critical attributes of the streamflow regime which govern riparian vegetation, geographically vary in response to climate (Poff and Zimmermann, 2010), having an important evolutionary role in adapting species to the prevailing hydrological circumstances (Dynesius et al., 2004). An emerging question then is, whether the altered streamflow regime would lead to similarities or differences in the functional diversity patterns of riparian forests between contrasting biomes.

Lozanovska et al. (2020) study was conducted between riparian woody communities in Mediterranean and boreal streams. The assessment of the hydrology related legacy effects and the magnitude of streamflow alterations from each biome were discussed as potential reasons for the differences in the functional diversity responses. On one hand, is the Mediterranean biome with no significant changes in the functional diversity values and on the other is the boreal biome with the significant functional diversity losses. In that sense, largely variable flood patterns induced by regulation, to a certain extent are comparable to natural hydrological regimes prevailing in the Mediterranean region resulting in some common functionality patterns (Gasith and Resh, 1999; Magdaleno and Fernández, 2011a; Stromberg and Boudell, 2013) and consequently the absence of functional diversity reduction. The previous exposure of riparian vegetation to hydrological alterations could be linked the persistence of the existing pool of traits between free-flowing and regulated sites such as short canopy, semi-woody flexibility, and deep roots reflected the already developed species' adaptation to hydrological stress (Stella et al., 2013a; Pakeman and Eastwood, 2013; Lawson et al., 2015b). However, the legacy adaptations were not exclusively contributors to the absence of significant functional changes in the Mediterranean biome. In comparison to boreal, the magnitude of streamflow alteration was also lower in the Mediterranean, underlying the importance of both factors for the functional diversity responses. In the boreal region, where the streamflow alterations were higher and riparian woody communities have not been evolutionally exposed to hydrological stress, a new pool of traits favoring stress-tolerant characteristics (lower canopies, smaller leaves, and more flexible stems) and reduced functional diversity were found at regulated sites.

The identified functional differences between the biomes are emphasizing two factors. First, the vegetation legacy adaptations play a role when assessing the effect of streamflow regulation. Namely, the presence of flow-related traits in the system (as it was in the Mediterranean) or lack of it (as it was in boreal), mediates the strength and direction of the interactions between riparian woody communities and the hydrological disturbances. Second, the magnitude of streamflow alterations. In a situation when fewer flow attributes change, the effect on the riparian woody communities may not be projected in species but only in abundance loss (Sandel et al., 2010; Aguiar et al., 2018). Therefore, the 'initial trait buffer' in the Mediterranean riparian vegetation should be taken with caution because it does not guarantee survival in a circumstance of intensified flow regulation, which can trigger species loss.

Regulation effect on aquatic and riparian communities along the longitudinal gradient and across the riparian zone

The artificial disruption of the natural continuum of rivers by dams has manifold consequences in fluvial ecosystems and on the structure and function of the plant communities (Abati et al., 2016; Rivaes et al., 2017; Aguiar et al., 2018). The extent of regulation-induced changes may reflect the differences in the hydrological disturbances between different dam types (Webb et al., 2012; Aguiar et al., 2016) and on the species plant functional traits to cope or avoid hydrological disturbances (O'Hare et al., 2016; Stromberg and Merritt, 2016).

To understand those plant-environment interactions in a hydrologically disturbed ecosystem, Lozanovska et al. 2020 (submitted in Science of The Total Environment), assessed how far downstream flow regulation has a significant effect on aquatic and riparian plant groups - macrophytes, bryophytes, and riparian woody vegetation.

The results showed alterations in plant cover from free-flowing to regulated settings but not guilds loss. The observed changes highlighted the plant functional traits trade-offs in a disturbed environment. In that sense, guilds distinct strategies towards affinity to flooding and fluvial disturbance facilitated the increase in the abundance of *Disturbance-adapted macrophyte guild* (consisting of aquatic plants), and *Disturbance-favored riparian guild* (riparian pioneers such as *Salix* spp.) but the absence of those strategies limited the abundance in *Poorly disturbance-adapted riparian guild* (deep-rooted species, mostly with non-hydrochoric dispersal). Differences in the regulation type triggered distinct longitudinal and lateral responses. In the storage reservoir case study, the threshold for significant abundance change from free-flowing sites was at a lower degree of regulation and with a higher number of responsive guilds compared to the run-of-river case study. A pattern that reflects the magnitude of hydrological and fluvial differences between the diverse dam impacts. Namely, run-of-river dams maintain high flow variability and flashiness in closer dependence of inflows upstream, while storage reservoirs in Mediterranean areas frequently imprint water scarcity and peak flow reduction downstream of dams (Aguiar et al., 2016), likely having different consequences on fluvial biota. While the threshold levels between ca. 6 and 12 km distance from the reservoir were enough to dissipate the regulation effects on the communities, the recovery distance for aquatic macrophytes downstream of the run-of-river dam, was longer (ca. 17 km). For the former case, river margins are frequently inundated providing likely enough available water and sediment transport for macrophytes and riparian woody communities' survival (Nilsson et al., 1991), though shifts in plant communities still occur. Further, riparian woody vegetation encroachment inwards the active channel in the reservoir in contrast to the outwards in the run-of-river setting again likely indicates the differences in hydrological and fluvial disturbances between the regulation types. Reduction in magnitude and frequency of floods in the storage reservoir triggered expansion towards the available water (Räpple et al., 2017; García del Jálon et al., 2019), while flushing flows, inundation of riverbanks and increased scour initiated riparian woody establishment further from the active channel in the run-of-river dam (Bejarano et al., 2018).

The results allowed us to assess how regulation effects dissipate downstream of dams and what are the minimum distances from dams or regulation intensities that can cope with hydropower demands. The findings can be applied in river restoration plans to assist flow design. The plans should be tailored according to the regulation type and to the targeted communities' specific characteristics/adaptations, as noted in the study to be also a driver of change, to maintain the “natural” vegetation dynamics and to maximize the benefits and ecosystem services provided from rivers.

Chapter VII.

Concluding remarks and future perspectives

In this thesis, results allowed us to assess the functional diversity development and its application in riparian forests worldwide, which application in our case yielded increased, decreased, or no significant alterations in the functional diversity considering the interplay of environmental and anthropogenic factors. Based on the work performed, the following conclusions can be proposed:

- The key theoretical concepts for functional diversity were mostly developed between the 19th century and the 1990s, but the application of functional diversity measures in riparian forests exponentially increased in the last 20 years, especially in Europe and the USA;
- Still, no consensus has been reached over the functional diversity terminology, number and type of traits, and combination of functional diversity indices;
- Some progress has been made suggesting 8 independent relevant traits to offer advantages compared to a large trait dataset, which was in line with our finding of 8 traits per study used;
- Soft traits frequently supported by Specific Leaf Area (SLA), plant height, and seed mass were the most commonly used in riparian studies;
- Multiple ecological and anthropogenic drivers were often addressed, but the hydrological regime (natural and regulated streamflow) was, by far, the most frequently assessed;
- Further development should seek to integrate ecological networks and connectivity in such a way as to produce guidance to trait selection, applications to large spatial scales, and comparable frameworks (guilds, index values) across regions;
- Mediterranean shrublands were functionally the most distinct riparian forest type compared with the other floristically heterogeneous forests dominated by ashes, alders, and willows;
- Precipitation was the common driver of functional redundancy for all riparian communities, but especially important for the Mediterranean shrublands (due to the low functional redundancy);
- The uncertain rainfall patterns and an increase in drought events in the study area may potentially lead to less stable and resilient riparian ecosystems;
- Functional diversity changes between biomes induced by streamflow regulation were mediated by the legacy adaptations and the magnitude of streamflow alternations;
- In the Mediterranean biome, plant adaptations to the natural hydrological stress combined with the smaller magnitude of streamflow alterations resulted in a similar trait pool in free-flowing and regulated sites and no significant change in the functional diversity indices based on species presence/absence data;
- In the boreal biome, the absence of flow-related adaptations and higher streamflow alteration favored new pool of traits - small riparian plant species with tiny leaves, poorly lignified stems, and shallow root systems and resulted in a significant change in the functional diversity indices;
- Regulation triggered longitudinal and lateral functional shifts based on trait adaptations and regulation type;
- Presence of flow-related traits in macrophytes and riparian woody communities fostered species abundance (and another way around), but regulation did not significantly change bryophytes abundance;

- Differences in hydrological alternation between the regulation types indicated - a higher number of responsive guilds, and a lower degree of regulation to differentiate communities at free-flowing and regulated sites in the storage reservoir case study compared to the run-of-river one; macrophytes “recovery” at a longer distance from the dam in the stream impaired by the run-of-river dam; riparian vegetation encroached inwards the active channel in the storage reservoir case study and expanded outwards in the run-of-river case study.

Based on the presented research work on functional diversity of the Mediterranean riparian forests, some prospects for future perspectives can be summarized:

Monitoring. Future work could be a replication of the same methodology in other riparian forests in a similar climatic context. By using the same functional traits, non-disturbed from disturbed communities can be distinguished by comparing the values of functional diversity indices, generating a firm base for conservation or monitoring purposes. Additionally, providing functional thresholds for riparian vegetation would increase the awareness of ecosystem degradation. At the moment, value of the indices related to such ecosystem aspects is either limited between 0 and 1 or does not have an upper border, making the value ‘per se’ difficult for interpretation. Therefore, by combining indices’ values from multiple studies - functional diversity thresholds for ‘level of community disturbance’ can be established, leading to improved interpretation of the obtained results. This will facilitate to observe functional diversity levels worldwide.

Holistic understanding. Another aspect could be complementing functional diversity indices that incorporate ‘species abundance’ to provide a further understanding of functional diversity responses if significant functional diversity loss is not observed. Loss in species abundance may precede species loss, so in that regard, it will complement the studies. Further, despite flow as a primary driver of riparian vegetation, the trajectories of vegetation responses to river regulation would benefit from the inclusion of geomorphological and sedimentary aspects, for a more holistic understanding of the regulation effect. This can be relevant for the Mediterranean climatic setting where hydrological disturbances naturally occur therefore the observed changes maybe not solely hydrologically explainable.

Flow design. Since we observed that the flow regulation alterations are community’ and trait’ dependent, yet freshwater ecosystems comprise multiple aquatic floral and faunal components, future flow management studies should be designed to benefit not only one river component but multiple ones and simultaneously. Further, as noted importance of different regulation types to the communities, adjusting altered streamflow components towards the natural flow regime should be a high priority for river managers. Considering both aspects can maximize the river ecosystem benefits.

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Appendices

Appendix A

Table A1. List of the used case studies and functional diversity measures applied.

Name of the case studies	Authors	Functional diversity measures
Riparian plant guilds become simpler and most likely fewer following flow regulation	Bejarano et al., 2017	Guilds
Riparian forests of Southwest Europe: are functional trait and species composition assemblages constrained by environment?	Aguiar et al., 2013	Guilds
Multi-scale environmental filters and niche partitioning govern the distributions of riparian vegetation guilds	Hough-Snee et al., 2015	Guilds
Indicators of restoration success in riparian tropical forests using multiple reference ecosystems	Suganuma et al., 2015	Guilds
Riparian plant guilds of ephemeral, intermittent and perennial rivers	Stromberg et al., 2016	Guilds
How resilient are northern hardwood forests to human disturbance? An evaluation using a plant functional group approach	Aubin et al., 2007	Guilds
Flow variability maintains the structure and composition of in-channel riparian vegetation	Greet et al., 2011	Guilds
Response of herbaceous riparian plants to rain and flooding on the San Pedro River, Arizona, USA	Bagstad et al., 2005	Guilds
Stream salinization is associated with reduced taxonomic, but not functional diversity in a riparian plant community	Doupé et al., 2006	Guilds
Using multivariate analyses to assess effects of fluvial type on plant species distribution in a Mediterranean river	Angiolini et al., 2011	Guilds
Riparian woodland encroachment following flow regulation: a comparative study of Mediterranean and Boreal streams	Bejarano and Sordo-Ward, 2011	Guilds
Regional and local patterns of riparian flora: comparison between insular and continental Mediterranean rivers	Nucci et al., 2012	Guilds
A description of the functional vegetation pattern of a semi-arid floodplain, South Africa	Higgins et al., 1997	Guilds
On the beautiful diverse Danube? Danubian floodplain forest vegetation and flora under influence of river eutrophication	Molder et al., 2011	Guilds
Effects of stream flow patterns on riparian vegetation of a semiarid river: implications for a changing climate	Stromberg et al., 2010	Guilds
What drives riparian plant taxa and assemblages in Mediterranean rivers?	Angiolini et al., 2016	Guilds
Converting simple vegetation surveys in functional dynamics	Fernandes et al., 2013	Guilds
Riparian vegetation of two semiarid Mediterranean rivers: basin scale responses of woody and herbaceous plants to environmental gradients	Salinas and Casas, 2007	Guilds
Interactive effects of waterlogging and atmospheric CO_2 concentration on gas exchange, growth and functional traits of Australian riparian tree seedlings	Lawson et al., 2017	Guilds

Disturbance effects on species diversity and functional diversity in riparian and upland plant communities	Biswas and Mallik, 2010	Guilds
Riparian woody plant traits across an urban–rural land use gradient and implications for watershed function with urbanization	Burton et al., 2009	Guilds
Plant functional trait variation in relation to riparian geomorphology: the importance of disturbance	Kyle et al., 2009	Guilds
Predicting restored communities based on reference ecosystems using a trait-based approach	Rosenfield and Müller, 2017	Guilds
Plant functional traits suggest novel ecological strategy for an invasive shrub in an understory woody plant community	Brym et al., 2011	Guilds
Phylogenetic patterns of Atlantic forest restoration communities are mainly driven by stochastic, dispersal related factors	Schweizer et al., 2015	Guilds
Correspondence analysis of functional groups in a riparian landscape	Lyon et al., 2002	Guilds
Species composition and functional structure of herbaceous vegetation in a tropical wetland system	Andrew et al., 2012	Guilds
Effects of stream flow intermittency on riparian vegetation of a semiarid region river (San Pedro River, Arizona)	Stromberg et al., 2005	Guilds
Flow regulation reduces native plant cover and facilitates exotic invasion in riparian wetlands	Catford et al., 2011	Guilds
Plants are less negatively affected by flooding when growing in species-rich plant communities	Wright et al., 2017	Guilds
Plant dispersal traits determine hydrochorous species tolerance to connectivity loss at the landscape scale	Favre-Bac et al., 2017	Guilds
The relative importance of local, regional and historical factors determining the distribution of plants in fragmented riverine forests: an emergent group approach	Hérault and Honnay, 2005	Guilds
Responsiveness of performance and morphological traits to experimental submergence predicts field distribution pattern of wetland plants	Luo et al., 2016	Guilds
Using functional diversity as an indicator of restoration success of a cut-over bog	D’Astous et al., 2013	Guilds
Effects of mowing cessation and hydrology on plant trait distribution in natural fen meadows	Opdekamp et al., 2012	Guilds
Variations in CSR strategies along stress gradients in the herb layer of submediteranean forests (central Italy)	Catorci et al., 2011	Guilds
Topographically determined water availability shapes functional patterns of plant communities within and across habitat types	Oddershede et al., 2015	Guilds
Hydrology, shore morphology and species traits affect seed dispersal, germination and community assembly in shoreline plant communities	van Leeuwen et al., 2014	Guilds
Directed dispersal by an abiotic vector: wetland plants disperse their seeds selectively to suitable sites along the hydrological gradient via water	Soons et al., 2017	Guilds
Impacts of environmental filters on functional redundancy in riparian vegetation	Bruno et al., 2016a	Functional diversity indices
A multidimensional functional trait approach reveals the imprint of environmental stress in Mediterranean woody communities	de la Riva et al., 2017	Functional diversity indices

Does urbanization lead to taxonomic and functional homogenization in riparian forests?	Brice et al., 2017	Functional diversity indices
Disturbance and stress gradients result in distinct taxonomic, functional and phylogenetic diversity patterns in a subtropical riparian tree community	Giehl et al., 2015	Functional diversity indices
Functional redundancy as a tool for bioassessment: a test using riparian vegetation	Bruno et al., 2016b	Functional diversity indices
Functional and taxonomic plant diversity for riverbank protection works: bioengineering techniques close to natural banks and beyond hard engineering	Cavaillé et al., 2015	Functional diversity indices
Hydrological conditions explain variation in wood density in riparian plants of south-eastern Australia	Lawson et al., 2015a	Functional diversity indices
Structural and functional responses of floodplain vegetation to stream ecosystem restoration	Göthe et al., 2016	Functional diversity indices
Habitat specialization and the role of trait lability in structuring diverse willow (genus Salix) communities	Savage and Cavender-Bares, 2012	Functional diversity indices
Shifts and linkages of functional diversity between above- and below-ground compartments along a flooding gradient	Abgrall et al., 2017	Functional diversity indices
Evaluating resilience of tree communities in fragmented landscapes: linking functional response diversity with landscape connectivity	Craven et al., 2016	Functional diversity indices
Linking functional diversity and ecosystem processes: a framework for using functional diversity metrics to predict the ecosystem impact of functionally unique species	Kuebbing et al., 2017	Functional diversity indices
The importance of functional diversity in the stability of Mediterranean shrubland communities after the impact of extreme climatic events	de la Riva et al., 2016	Functional diversity indices
Climate variability and community stability in Mediterranean shrublands: the role of functional diversity and soil environment	Pérez-Ramos et al., 2017	Functional diversity indices
The hierarchy of predictability in ecological restoration: are vegetation structure and functional diversity more predictable than community composition?	Laughlin et al., 2017	Functional diversity indices

Evidence for a direct negative effect of habitat fragmentation on forest herb functional diversity	Sonnier et al., 2014	Functional diversity indices
Species diversity and functional diversity relationship varies with disturbance intensity	Biswas and Mallik, 2011	Functional diversity indices
A functional-trait approach reveals community diversity and assembly processes responses to flood disturbance in a subtropical wetland	Fu et al., 2015	Functional diversity indices
Effects of land-use changes on plant functional and taxonomic diversity along a productivity gradient in wet meadows	Janeček et al., 2013	Functional diversity indices
Waterlogging and canopy interact to control species recruitment in floodplains	Kotowski et al., 2010	Functional diversity indices
A functional trait approach to fen restoration analysis	Hedberg et al., 2013	Functional diversity indices
Conservation management in fens: do large tracked mowers impact functional plant diversity?	Kotowski et al., 2013	Functional diversity indices
Functional diversity, succession, and human-mediated disturbances in raised bog vegetation	Dyderski et al., 2016	Functional diversity indices
Vulnerability of moorland plant communities to environmental change: consequences of realistic species loss on functional diversity	Sasaki et al., 2014	Functional diversity indices
Eutrophication and drought disturbance shape functional diversity and life-history traits of aquatic plants in shallow lakes	Arthaud et al., 2012	Functional diversity indices
Impact of plant invasions on functional diversity in the vegetation of Central Europe	Hejda and de Bello, 2013	Functional diversity indices
Spatial processes structuring riparian plant communities in agroecosystems: implications for restoration	Bourgeois et al., 2016	Functional diversity indices
Environmental filtering and spatial processes in urban riparian forests	Brice et al., 2016	Functional diversity indices

Heterogeneous flows foster heterogeneous assemblages: relationships between functional diversity and hydrological heterogeneity in riparian plant communities	Lawson et al., 2015b	Functional diversity indices
Plant assemblages do not respond homogenously to local variation in environmental conditions: functional responses differ with species identity and abundance	Kumordzi et al., 2015	Functional diversity indices
Identifying alien plants linkages between irrigated orchards and adjacent riparian habitats from a trait-based approach	Juárez-Escario et al., 2016	Functional diversity indices

Table A2. Databases used in the reviewed case studies.

Databases	References	Site (accessed 3 March 2018)
Baseflor	Julve, 1998	http://philippe.julve.pagesperso-orange.fr/catminat.htm
BioBase	van Duuren, L., 1987	http://repository.naturalis.nl/record/527051
BiolFlor	Klotz et al., 2002	http://www2.ufz.de/biolflor/index.jsp
BROT	Paula et al., 2009	https://www.uv.es/jgpausas/brot.htm
CLO-PLA	Klimešová and de Bello, 2009	http://clopla.butbn.cas.cz/
Global Wood Density Database	Chave et al., 2009	https://datadryad.org//handle/10255/dryad.235
Ecological Flora Database	Fitter and Peat, 1994	http://www.bath.ac.uk/research/data/
LEDA Traitbase	Kleyer et al., 2008	https://www.uni-oldenburg.de/en/landeco/research/leda/
PLANTS Database	United States Department of Agriculture	http://plants.usda.gov
PLANTATT	Hill et al., 2004	http://nora.nerc.ac.uk/id/eprint/9535/
Seed Information Database	Royal Botanic Gardens Kew, 2008	http://data.kew.org/sid/
TOPIC base	Aubin et al., 2012	http://www.nrcan.gc.ca/forests/research-centres/glfc/topic/20303
TRY Plant Trait Database	Kattge et al., 2011	https://www.try-db.org/TryWeb/Home.php

Table A3. Trait categories based on “hard”/“soft” traits and biological attributes used to describe riparian forests in the reviewed case studies.

Trait categories	Traits	Number of cases
1.Vegetative attributes		
1.1 Whole plant traits		
Soft trait	Growth form	10
Soft trait	Life form	20
Soft trait	Plant lifespan	29
Soft trait	Plant height	32
Soft trait	Clonality	12
Soft trait	Spinescence	2
1.2 Leaf traits		
Soft trait	Specific leaf area (SLA)	28
Soft trait	Leaf size	17
Soft trait	Leaf dry matter content (LDMC)	21
Soft trait	Leaf nitrogen (N) content; leaf phosphorus (P) content	12
Soft trait	Physical strength of leaves	3
Soft trait	Photosynthetic pathway; photosynthesis rate	12
Soft trait	Leaf form	5
Soft trait	Leaf anatomy; leaf texture; leaf type; leaf thickness	9
Soft trait	Leaf persistence; leaf phenology; leaf longevity; leaf retention	10
Hard trait	C:N ratio	8
Hard trait	Leaf litter chemical composition	4
Hard trait	Transpiration rate; stomata conductance; turgor loss point	6
1.3 Stem traits		
Soft trait	Stem specific density; stem dry matter	9
Soft trait	Woodiness	12
Hard trait	Growth rate	14
Soft trait	Shoot growth form; shoot elongation capacity	7
Soft trait	Shoot dry biomass	2
Soft trait	Leaf distribution along the stem	1
Soft trait	Stem porosity	1
1.4 Belowground traits		
Soft trait	Specific root length; specific root area	5
Soft trait	Root depth	11
Soft trait	Root dry matter content	8
Soft trait	Nutrient uptake strategy	11
Soft trait	Moisture use	6
2. Regenerative attributes		
Soft trait	Reproduction type	18
Hard trait	Fecundity	3
Soft trait	Resprouting capacity after major disturbance	5
Hard trait	Seedlings characteristics (leaf area and growth)	5
2.1 Dispersability traits		
Soft trait	Dispersal mode	24
Soft trait	Dispersal vector/pollen vector	6
Hard trait	Terminal velocity of dispersion	2
Soft trait	Dicliny	3

2.2 Seed traits		
Soft trait	Diaspore type	3
Soft trait	Diaspore morphology	2
Soft trait	Diaspore size; diaspore mass	2
Soft trait	Seed buoyancy	4
Soft trait	Origin of seeds	1
Soft trait	Seed number	10
Soft trait	Seed mass; seed weight	29
Soft trait	Seed shape; seed length; seed diameter	5
Hard trait	Seed longevity; seed bank	13
Soft trait	Seed shedding	4
Soft trait	Seed crop frequency	2
Soft trait	Germination phenology	5
Soft trait	Fruit type; fruit dimensions	3
Soft trait	Length of fruiting period	2
2.3 Flowering phenology		
Soft trait	Flower color	5
Soft trait	Duration of flowering	18
3. Ecological performances		
Soft trait	Grime strategies	8
Soft trait	Ellenberg values	8
Soft trait	Anaerobic tolerance	11
Soft trait	Drought tolerance	17
Soft trait	Fire tolerance	5
Soft trait	Shade tolerance	13
Soft trait	Acidity tolerance	1
Soft trait	Substrate preference	5
Soft trait	Dominance	1
Soft trait	Location in the riparian zone	1
Soft trait	Geographical distributions	1
Soft trait	Status in Québec	2

Appendix B

Table B1. Information on riparian woody species used in the study: scientific name, family, plant growth form, indicator species of the forest vegetation types (more dominant and abundant in the group and less on the others) found on the four forest vegetation types studied is give. *Iberian Peninsula endemism.

Species	Family	Plant growth form	Indicator species
Alnus glutinosa (L.) Gaertner	BETULACEAE	Tree	Alder woodlands
Crataegus monogyna Jacq.	ROSACEAE	Shrub	Ash woodlands
Erica arborea L.	ERICACEAE	Shrub	Tree heath shrublands
Flueggea tinctoria (L.) G.L. Webster *	PHYLLANTHACEAE	Shrub, but can occur as a small multi stemmed tree	Mediterranean shrublands
Frangula alnus Miller	RHAMNACEAE	Shrub, but can occur as a small multi stemmed tree	Tree heath shrublands
Fraxinus angustifolia Vahl	OLEACEAE	Tree	Ash woodlands
Hedera hibernica (G. Kirchn.) Bean	ARALIACEAE	Liana	Alder woodlands
Sambucus nigra L.	CAPRIFOLIACEAE	Shrub or small tree	Alder woodlands
Laurus nobilis L.	LAURACEAE	Shrub or small tree	
Nerium oleander L.	APOCYNACEAE	Shrub	Mediterranean shrublands
Populus nigra L.	SALICACEAE	Tree	
Rubus umifolius Schott	ROSACEAE	Liana	Ash woodlands
Salix alba L.	SALICACEAE	Tree	
Salix atrocinerea Brot.	SALICACEAE	Arborescent shrub or tree	Alder woodlands
Salix neotricha Goerz	SALICACEAE	Tree	
Salix salviifolia Brot. *	SALICACEAE	Shrub, but can occur as a small tree	Ash woodlands
Tamarix africana Poiret.	TAMARICACEAE	Shrub	Mediterranean shrublands

Table B2. Functional traits used in the present study (adapted from Aguiar et al. 2013a).

Functional traits	Categories
Life form	1, macrophanerophyte; 2, mesophanerophyte; 3, microphaneophyte; 4, nanophanerophyte; 5, lianas

Propagation	1, fragmentation; 2, shoot thorn; 3, root shoot; 4, adhesive root; 5, root+ fragmentation; 6, no vegetative propagation
Leaf anatomy	1, scleromorphic; 2, mesomorphic; 3, hygromorphic; 4, coriaceous
Leaf form	1, linear; 2, scale-like; 3, lanceolate; 4, oval or elliptic; 5, full; 6, lobate; 7, pinnate
Leaf pubescence	1, glabre; 2, moderately hairy; 3, hair in nerves; 4, heavily hairy; 5, tomentous
Leaf dimensions	maximum length, cm: 1, <0.5; 2, 0.5-3; 3, 3-12; 4, >12
Fruit type	1, dry indehiscent; 2, dry dehiscent; 3, fleshy indehiscent
Fruit dimension	maximum length, cm: 1, <0.5; 2, 0.5-2; 3, 2-5; 4, >5
Diaspore features	1, with simple, silky or plumose hairs or with wings; 2, esferic; 3, fleshy or with a fleshy structure
Diaspore type	1, fruit; 2, seed
Reproduction type	1, by seed; 2, mostly by seed, 3, rarely vegetatively; 4, by seed and vegetatively
Pollen vector	1, wind; 2, insects; 3, selfing; 3, wind+insects
Dicliny	1, hermaphroditic; 2, dioecious; 3, monoecious
Dispersal type	1, anemochory; 2, hydrochory; 3, zoochory; 4, anemochory+ hydrochory; 5, hydrochory+ zoochory
Number of seeds/kg	1, <1500; 2, 1500-20 000; 3, 20 000-500 000; 4, 500 000-1000 000; 5, >1000 000
Leaf phenology	1, spring green; 2, evergreen
Flowering season	1, pre-spring; 2, early-spring; 3, mid spring; 4, early summer; 5, autumn-winter
Flowering duration	Number of months: 1, <3; 2,3-4; 3, >4
Fructification season	1, spring; 2, spring-summer; 3, summer; 4, autumn-winter
Strategy type	1, competitor; 2, competitor/stress-tolerant; 3, stress-tolerant
Dominance	1, frequently dominant; 2, rarely dominant; 3, under-storey or edges of riparian woods; 4, isolated individuals
Drought tolerance	1: low; 2: medium; 3: high
Waterlogging tolerance	1: low; 2: medium; 3: high
Light requirements	1: light demanding; 2: half-shade tolerant; 3: shade-tolerant
Substrate	1, acidic; 2, no preferences

Table B3. Coefficient of determination (R^2) between functional diversity indices.

	Acronym	Functional Richness	Functional Divergence	Functional Dispersion	Rao index	Functional Redundancy
Functional Richness	FRic	-				
Functional Divergence	FDiv	0.020	-			
Functional Dispersion	FDis	0.093	0.002	-		
Rao index	Q	0.118	0.010	0.947	-	
Functional Redundancy	FR	0.025	0.005	0.588	0.427	-

Table B4. Analysis of Variance (One-way ANOVA) among riparian forest types (Alder woodlands, Ash woodlands, Mediterranean shrublands, Tree-heath shrublands) for Functional Richness and Functional Redundancy.

	Df	Sum Sq	Mean Sq	F value	P value
Functional Richness	3	1314.6	438.21	7.62	<0.001
Functional Redundancy	3	0.05	0.02	2.33	0.07

Table B5. Results showing the best-fitting model chosen through average modeling (including riparian forest type as explanatory variable) for Functional Richness and Functional Redundancy.

Index	Variable importance	
Functional Richness	Riparian forest type	0.963
	Sand	0.955
	Altitude	0.525
	Channel depth	0.430
	Bedrock_boulders	0.360
	Length no flow	0.279
	Cobbles_gravel	0.240
	Distance to source	0.193
	Fine elements_soil	0.189

	Precipitation	0.155
	Channel width	0.147
Functional Redundancy	Length no flow	0.756
	Channel width	0.461
	Sand	0.358
	Riparian forest type	0.354
	Distance to source	0.307
	Bedrock_boulders	0.276
	Chanel depth	0.239
	Precipitation	0.231
	Fine elements_soil	0.230
	Altitude	0.224
	Cobbles_gravel	0.218

Table B6. Results showing the best-fitting model chosen through average modeling in each riparian forest type for Functional Richness and Functional Redundancy.

	Variable	Estimate	SE	Adjusted SE	Z value	R^2	P value
Functional Richness							
Alder woodlands	Bedrock_boulders	1.093	0.688	0.697	1.568	0.11	0.117
	Channel depth	1.178	0.789	0.799	1.474		0.141
	Sand	-1.799	0.684	0.693	2.599		0.001**
	Channel width	0.928	0.705	0.714	1.299		0.194
	Altitude	-0.606	0.644	0.652	0.931		0.352
	Distance to source	1.199	1.186	1.200	0.999		0.318
	Cobbles_gravel	-0.775	0.721	0.730	1.062		0.288
	Fine elements_soil	-1.031	0.856	0.866	1.191		0.234
	Precipitation	-0.542	0.845	0.856	0.633		0.527
	Length no flow	0.420	0.801	0.812	0.517		0.605
Ash woodlands	Altitude	0.124	1.842	1.897	1.888	0.19	0.059
	Sand	-2.875	1.450	1.491	1.928		0.054
	Distance to source	-1.758	2.003	2.064	0.852		0.395
	Fine elements_soil	0.847	1.001	1.032	0.820		0.412
	Channel width	-1.095	1.439	1.483	0.738		0.460
Mediterranean shrublands	Altitude	-6.584	2.324	2.483	2.652	0.37	0.008**
	Distance to source	-2.190	1.242	1.334	1.641		0.101
	Precipitation	6.064	3.984	4.278	1.418		0.156
	Length no flow	3.299	2.589	2.781	1.186		0.235
Functional Redundancy							
Alder woodlands	Distance to source	0.034	0.015	0.015	2.248	0.07	0.025*
	Sand	0.010	0.008	0.008	1.119		0.263
	Precipitation	-0.014	0.011	0.011	1.210		0.226
	Fine elements_soil	-0.010	0.010	0.010	0.986		0.324

	Altitude	0.007	0.008	0.008	0.801		0.423
	Channel width	0.016	0.009	0.009	1.759		0.079
	Channel depth	-0.007	0.010	0.010	0.629		0.530
	Length no flow	-0.005	0.010	0.010	0.457		0.647
	Cobbles_gravel	0.004	0.009	0.009	0.444		0.657
Ash woodlands	Distance to source	0.086	0.024	-	3.581	0.35	0.001***
	Precipitation	0.039	0.011	-	3.657		0.001***
	Channel width	-0.041	0.018	-	-2.315		0.026*
Mediterranean shrublands	Precipitation	0.108	0.041	0.042	2.552	0.24	0.011*
	Channel depth	0.018	0.011	0.012	1.501		0.133
	Cobbles_gravel	-0.021	0.017	0.018	1.166		0.244
	Length no flow	-0.035	0.029	0.031	1.144		0.253

Appendix C

Table C1. Species list, family, origin and respective country.

Species	Family	Origin	Country
Acacia dealbata Link	FABACEAE	Exotic	Portugal
Acacia melanoxylon R. Br.	FABACEAE	Exotic	Portugal
Acer pseudoplatanus L.	ACERACEAE	Native	Portugal
Ailanthus altissima (Miller) Swingle	SIMAROUBACEAE	Exotic	Portugal
Alnus glutinosa (L.) Gaertner	BETULACEAE	Native	Portugal
Alnus incana (L.) Moench	BETULACEAE	Native	Sweden
Andromeda polifolia L.	ERICACEAE	Native	Sweden
Arbutus unedo L.	ERICACEAE	Native	Portugal
Arctostaphylos alpinus (L.) Sprengel	ERICACEAE	Native	Sweden
Arctostaphylos uva-ursi (L.) Sprengel	ERICACEAE	Native	Sweden
Betula nana L.	BETULACEAE	Native	Sweden
Betula pendula Roth	BETULACEAE	Native	Sweden
Betula pubescens Ehrh.	BETULACEAE	Native	Sweden
Betula pubescens Ehrh. subsp. *celtiberica* (Rothm. & Vasc) Rivas Martin.	BETULACEAE	Native	Portugal
Calluna vulgaris (L.) Hull	ERICACEAE	Native	Portugal; Sweden
Castanea sativa Miller	FAGACEAE	Exotic	Portugal
Cistus psilosepalus Sweet	CISTACEAE	Native	Portugal
Corylus avellana L.	BETULACEAE	Native	Portugal
Crategus monogyna Jacq.	ROSACEAE	Native	Portugal
Cytisus scoparius (L.) Link	FABACEAE	Native	Portugal
Cytisus striatus (Hill.) Rothm	FABACEAE	Native	Portugal
Daphne gnidium L.	THYMELAEACEAE	Native	Portugal
Daphne mezereum L.	THYMELAEACEAE	Native	Sweden
Dittrichia viscosa (L.) W. Greuter	ASTERACEAE	Native	Portugal
Empetrum nigrum L. subsp*. hermaphroditum* (Lange ex Hagerup) Böcher	ERICACEAE	Native	Sweden
Erica arborea L.	ERICACEAE	Native	Portugal
Erica australis L.	ERICACEAE	Native	Portugal
Erica ciliaris L.	ERICACEAE	Native	Portugal
Erica cinerea L.	ERICACEAE	Native	Portugal
Erica tetralix L.	ERICACEAE	Native	Portugal
Ficus carica L.	MORACEAE	Exotic	Portugal
Flueggea tinctoria (L.) G.L. Webster	PHYLLANTHACEAE	Native	Portugal

Frangula alnus Mill.	RHAMNACEAE	Native	Portugal; Sweden
Fraxinus angustifolia Vahl	OLEACEAE	Native	Portugal
Genista florida L.	FABACEAE	Native	Portugal
Hedera hibernica (G. Kirchn.) Bean	ARALIACEAE	Native	Portugal
Hypericum androsaemum L.	CLUSIACEAE	Native	Portugal
Hypericum humifusum L.	CLUSIACEAE	Native	Portugal
Ilex aquifolium L.	AQUIFOLIACEAE	Native	Portugal
Juglans regia L.	JUGLANDACEAE	Exotic	Portugal
Juniperus communis L.	CUPRESSACEAE	Native	Sweden
Laurus nobilis L.	LAURACEAE	Native	Portugal
Lavandula stoechas L.	LAMIACEAE	Native	Portugal
Ledum palustre L.	ERICACEAE	Native	Sweden
Linnaea borealis L.	CAPRIFOLIACEAE	Native	Sweden
Lithodora prostrata (Loisel.) Griseb	BORAGINACEAE	Native	Portugal
Lycopodium annotinum L.	LYCOPODIACEAE	Native	Sweden
Lycopodium clavatum L.	LYCOPODIACEAE	Native	Sweden
Lycopodium selago L. (*Huperzia selago* (L.) Bernh. Ex Schrank & Mart.)	LYCOPODIACEAE	Native	Sweden
Myrica gale L.	MYRICACEAE	Native	Sweden
Myrtus communis L.	MYRTACEAE	Native	Portugal
Phyllirea angustifolia L.	OLEACEAE	Native	Portugal
Phyllirea latifolia L.	OLEACEAE	Native	Portugal
Picea abies (L.) H.Karst.	PINACEAE	Native	Sweden
Pinus pinaster Aiton	PINACEAE	Native	Portugal
Pinus sylvestris L.	PINACEAE	Native	Sweden
Platanus hispanica Miller	PLANTAGINACEAE	Exotic	Portugal
Populus x canadensis Moench	SALICACEAE	Exotic	Portugal
Populus tremula L.	SALICACEAE	Native	Sweden
Prunus avium L.	ROSACEAE	Native	Portugal
Prunus padus L.	ROSACEAE	Native	Sweden
Pyrus cordata Desv.	ROSACEAE	Native	Portugal
Quercus faginea Lam. subsp. *broteroi* (Coutinho) A. Camus	FAGACEAE	Native	Portugal
Quercus pyrenaica Willd.	FAGACEAE	Native	Portugal
Quercus robur L.	FAGACEAE	Native	Portugal
Quercus suber L.	FAGACEAE	Native	Portugal
Ribes nigrum L.	GROSSULARIACEAE	Native	Sweden
Ribes rubrum L.	GROSSULARIACEAE	Native	Sweden

Rosa canina L.	ROSACEAE	Native	Portugal
Rosa majalis J. Herrmann	ROSACEAE	Native	Sweden
Rosa pouzinii Tratt.	ROSACEAE	Native	Portugal
Rubus brigantinus Samp.	ROSACEAE	Native	Portugal
Rubus genevieri Boreau	ROSACEAE	Native	Portugal
Rubus idaeus L.	ROSACEAE	Native	Sweden
Rubus lainzii H. E. Weber	ROSACEAE	Native	Portugal
Rubus radula Weihe	ROSACEAE	Native	Portugal
Rubus ulmifolius Schott	ROSACEAE	Native	Portugal
Rubus vagabundus Samp.	ROSACEAE	Native	Portugal
Salix alba L.	SALICACEAE	Native	Portugal
Salix atrocinerea Brot.	SALICACEAE	Native	Portugal
Salix aurita L.	SALICACEAE	Native	Sweden
Salix caprea L.	SALICACEAE	Native	Sweden
Salix cinerea L.	SALICACEAE	Native	Sweden
Salix glauca L.	SALICACEAE	Native	Sweden
Salix hastata L.	SALICACEAE	Native	Sweden
Salix herbacea L.	SALICACEAE	Native	Sweden
Salix lanata L.	SALICACEAE	Native	Sweden
Salix lapponum L.	SALICACEAE	Native	Sweden
Salix myrsinites L.	SALICACEAE	Native	Sweden
Salix myrtilloides L.	SALICACEAE	Native	Sweden
Salix neotricha Goerz	SALICACEAE	Native	Portugal
Salix pentandra L.	SALICACEAE	Native	Sweden
Salix salviifolia Brot.	SALICACEAE	Native	Portugal
Salix triandra L.	SALICACEAE	Native	Sweden
Sambucus nigra L.	CAPRIFOLIACEAE	Native	Portugal
Sesamoides suffruticosa (Lange) Kuntze	RESEDACEAE	Native	Portugal
Sorbus aucuparia L.	ROSACEAE	Native	Portugal; Sweden
Thymus mastichina (L.) L.	LAMIACEAE	Native	Portugal
Ulex minor Roth	FABACEAE	Native	Portugal
Vaccinium microcarpum (Turcz. ex Rupr.) Schmalh.	ERICACEAE	Native	Sweden
Vaccinium myrtillus L.	ERICACEAE	Native	Portugal; Sweden
Vaccinium oxycoccos L.	ERICACEAE	Native	Sweden
Vaccinium uliginosum L.	ERICACEAE	Native	Sweden
Vaccinium vitis-idaea L.	ERICACEAE	Native	Sweden
Vitis vinifera L. subsp. *vinifera*	VITACEAE	Native	Portugal

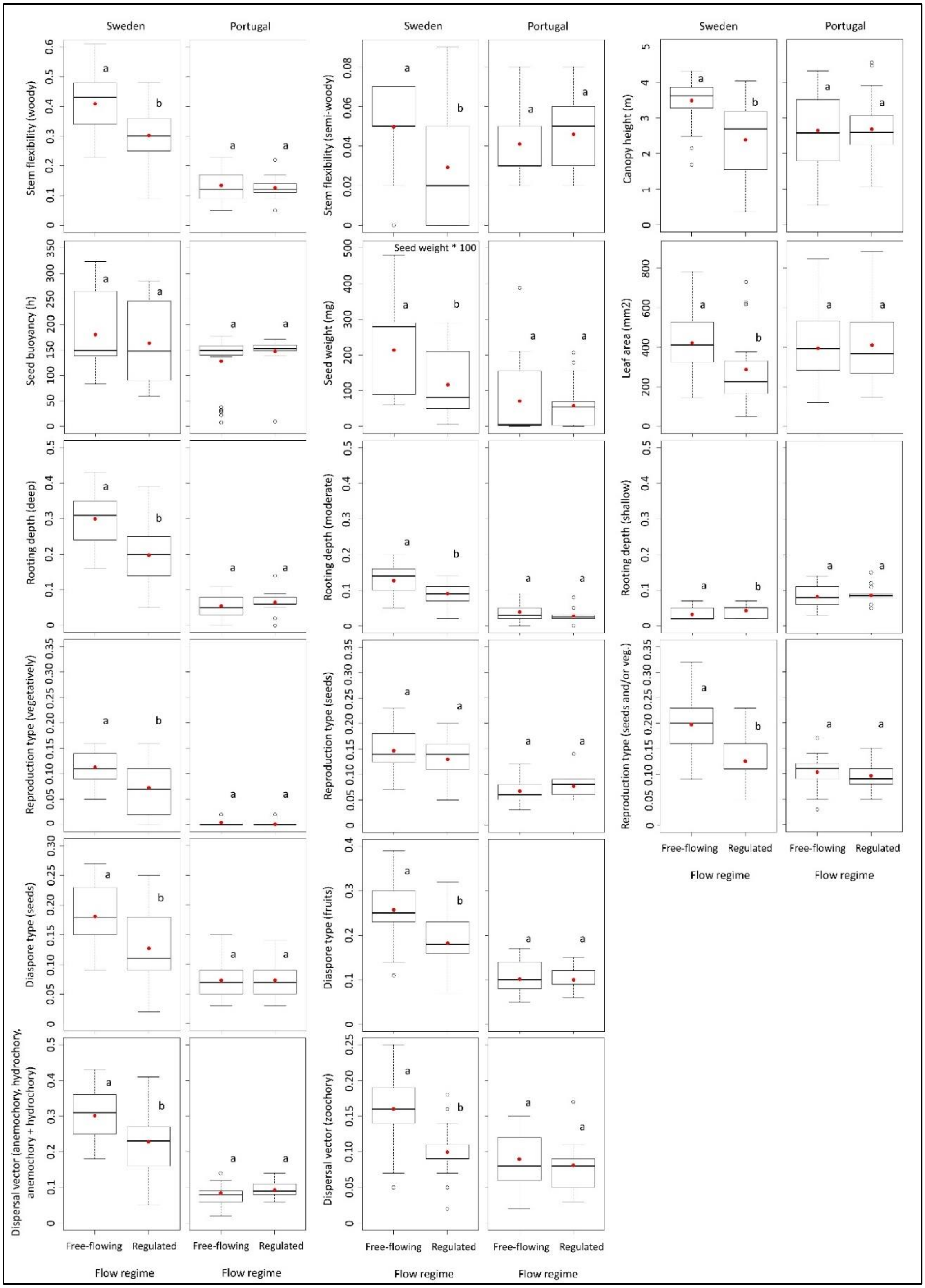

Figure C1. Box-and-whisker plots for the selected traits (n=9) for the free-flowing and regulated sites in Sweden and Portugal. Letters identify the significantly different changes in trait values ($p < 0.05$). Traits with multiple categories (stem flexibility, rooting depth, reproduction type, diaspore type and dispersal vector) were counted as single trait.

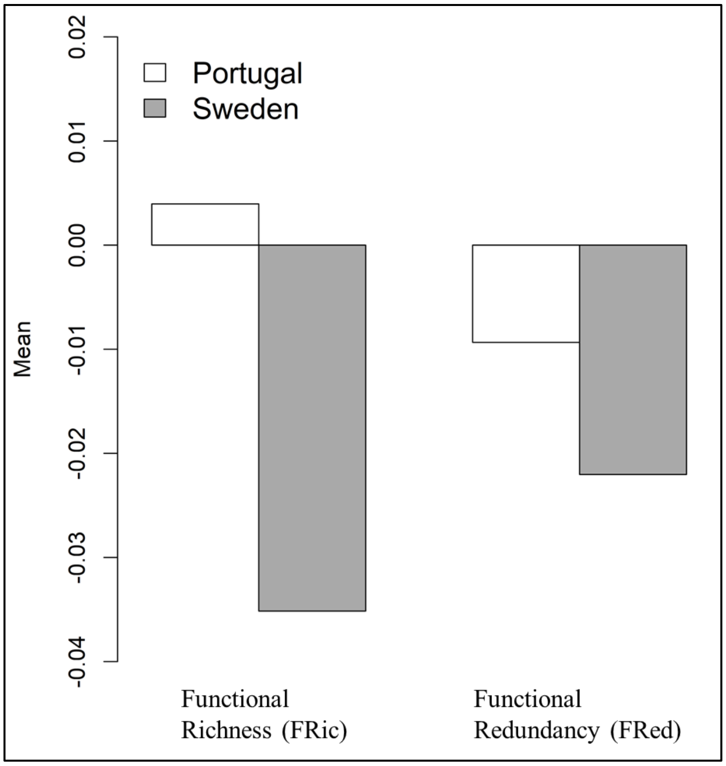

Figure C2. Functional diversity losses for Functional Richness and Functional Redundancy in Portugal and Sweden. Values at the y-axes represent mean differences in indices values between regulated and free-flowing sites.

Table C2. Analysis of variance (Two-way ANOVA) of Functional Richness and Functional Redundancy in countries (Portugal and Sweden) and in flow regimes (free-flowing and regulated).

	Df	SS	F	P-value
Functional Richness				
Country	1	0.377	80.861	<0.001
Regulation	1	0.023	4.914	0.029
Country:Regulation	1	0.043	9.155	0.003
Functional Redundancy				
Country	1	0.078	81.601	<0.001
Regulation	1	0.007	7.194	0.009
Country:Regulation	1	0.001	1.126	0.291

Table C3. Mean, standard deviation, minimum, maximum and range for regulation regimes (free-flowing, regulated) for Functional Richness and Functional Redundancy in Portugal and Sweden.

		n	Mean	SD	Range
Portugal	Functional Richness				
	Free-flowing	30	0.033	0.020	0.075
	Regulated	22	0.037	0.023	0.067
	Functional Redundancy				
	Free-flowing	30	0.408	0.035	0.173
	Regulated	22	0.399	0.021	0.075

Sweden	Functional Richness				
	Free-flowing	32	0.109	0.040	0.142
	Regulated	25	0.074	0.038	0.153
	Functional Redundancy				
	Free-flowing	32	0.467	0.021	0.078
	Regulated	25	0.445	0.041	0.149

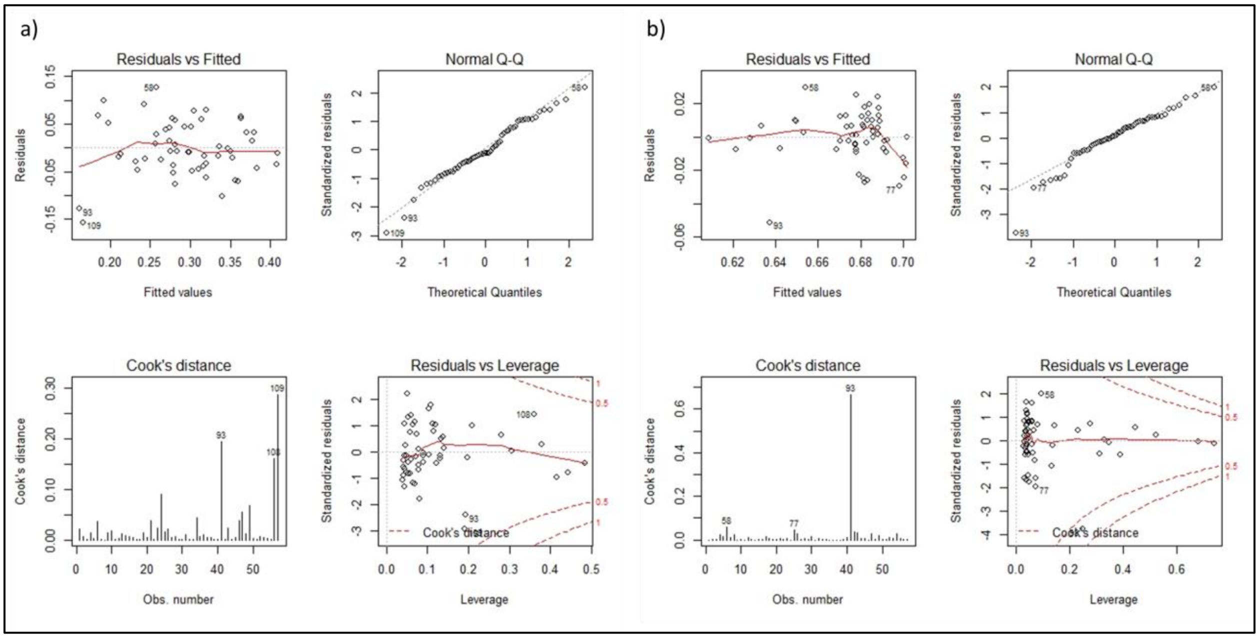

Figure C3. Residual analysis for the chosen models in Sweden: a) Functional Richness b) Functional Redundancy.

Table C4. References used in the Table 5 (Legacy effects which influence riparian woody vegetation in Mediterranean and boreal biomes).

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Table C5. Trait values for each species in Portugal and Sweden.

Species	Canopy height (m)	Leaf area (mm^2)	Seed buoyancy (h)	Seed weight (g)	Stem flexibility	Rooting depth	Reproduction type	Diaspore type	Dispersal vector
Acacia dealbata	30	3300	400	12.7	Woody	Moderate	Seeds and/or vegetatively	Fruits	Anemochory, hydrochory, anemochory+hydrochory
Acacia melanoxylon	30	2100	400	14	Woody	Moderate	Seeds and/or vegetatively	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Acer pseudoplatanus	25	8332	168	94.4	Woody	Deep	Seeds	Fruits	Anemochory, hydrochory, anemochory+hydrochory
Ailanthus altissima	30	1155	480	29.4	Woody	Shallow	Seeds and/or vegetatively	Fruits	Anemochory, hydrochory, anemochory+hydrochory
Alnus glutinosa	25	2735	8760	4	Woody	Deep	Seeds	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Alnus incana	14	2734.08	2544	1.4	Woody	Shallow	Seeds and/or vegetatively	Fruits	Anemochory, hydrochory, anemochory+hydrochory
Andromeda polifolia	0.2	80.75	72	0.2	Woody	Shallow	Vegetativley	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Arbutus unedo	7	1038	0.02	5.7	Woody	Shallow	Seeds and/or vegetatively	Fruits	Zoochory
Arctostaphylos alpinus	0.2	137.93	240	2.6	Woody	Shallow	Seeds and/or vegetatively	Fruits	Zoochory
Arctostaphylos uva-ursi	0.1	113	240	18.5	Woody	Shallow	Seeds and/or vegetatively	Fruits	Zoochory
Betula nana	0.5	48.24	0	0.38	Woody	Moderate	Vegetativley	Fruits	Anemochory, hydrochory, anemochory+hydrochory
Betula pendula	16.5	1000	5640	0.5	Woody	Deep	Seeds	Fruits	Anemochory, hydrochory, anemochory+hydrochory

Betula pubescens	14	1000	2184	0.76	Woody	Deep	Seeds	Fruits	Anemochory, hydrochory, anemochory+hydrochory
Betula pubescens subsp. *celtiberica*	20	1000	168	0.12	Woody	Moderate	Seeds	Fruits	Zoochory
Calluna vulgaris	2	1	96	0.03	Woody	Shallow	Vegetativley	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Calluna vulgaris	0.3	8	96	0.03	Woody	Shallow	Vegetativley	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Castanea sativa	30	7898	24	9944	Woody	Deep	Seeds	Fruits	Zoochory
Cistus psilosepalus	1.2	339	48	0.92	Semi-woody	Shallow	Seeds	Seeds	Zoochory
Corylus avellana	8	4024	420	1097.3	Woody	Deep	Seeds and/or vegetatively	Fruits	Zoochory
Crataegus monogyna	10	610	168	98	Woody	Deep	Seeds and/or vegetatively	Fruits	Zoochory
Cytisus scoparius	2	22.4	336	9	Woody	Deep	Seeds	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Cytisus striatus	3	25	336	7.8	Woody	Deep	Seeds	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Daphne gnidium	2	125	336	7.61	Woody	Deep	Seeds and/or vegetatively	Fruits	Zoochory
Daphne mezereum	0.75	930	336	85.9	Woody	Moderate	Seeds	Fruits	Zoochory
Dittrichia viscosa	1.3	157.5	60	0.3638	Semi-woody	Shallow	Seeds	Fruits	Zoochory
Empetrum nigrum subsp. *hermaphroditum*	0.2	3.14	408	1.03	Woody	Shallow	Seeds and/or vegetatively	Fruits	Zoochory
Erica arborea	7	3.6	480	0.2	Woody	Moderate	Seeds and/or vegetatively	Seeds	Zoochory

Erica australis	2.5	3	168	0.2172	Woody	Moderate	Seeds and/or vegetatively	Seeds	Zoochory
Erica ciliaris	1.8	3.3	168	0.04	Woody	Moderate	Seeds and/or vegetatively	Seeds	Zoochory
Erica cinerea	0.75	2.2	168	0.13	Woody	Moderate	Seeds and/or vegetatively	Seeds	Zoochory
Erica tetralix	0.7	3.7	168	0.02	Woody	Moderate	Seeds and/or vegetatively	Seeds	Zoochory
Ficus carica	10	18787	0.01	0.1	Woody	Moderate	Seeds and/or vegetatively	Fruits	Zoochory
Flueggea tinctoria	2	0.84	168	0.004	Woody	Moderate	Seeds and/or vegetatively	Seeds	Zoochory
Frangula alnus	4	1410	360	20.6	Woody	Shallow	Seeds and/or vegetatively	Fruits	Zoochory
Frangula alnus	5	961	360	20.6	Woody	Shallow	Seeds and/or vegetatively	Fruits	Zoochory
Fraxinus angustifolia	25	382	6	49.4	Woody	Deep	Seeds	Fruits	Anemochory, hydrochory, anemochory+hydrochory
Genista florida	2	364	168	6.63	Woody	Shallow	Seeds	Seeds	Zoochory
Hedera hibernica	30	4852	168	16.85	Woody	Shallow	Seeds and/or vegetatively	Fruits	Anemochory, hydrochory, anemochory+hydrochory
Hypericum androsaemum	2	404	168	0.07	Semi-woody	Shallow	Seeds	Seeds	Zoochory
Hypericum humifussum	0.3	35	168	0.0368	Semi-woody	Shallow	Seeds	Seeds	Zoochory
Ilex aquifolium	12	1608	240	36.1	Woody	Moderate	Seeds and/or vegetatively	Fruits	Zoochory
Juglans regia	25	3909	6	11490	Woody	Deep	Seeds	Fruits	Zoochory

Juniperus communis	3.2	20.4	528	12.5	Woody	Moderate	Seeds and/or vegetatively	Fruits	Anemochory, hydrochory, anemochory+hydrochory
Laurus nobilis	10	3675	168	0.19	Woody	Deep	Seeds	Fruits	Anemochory, hydrochory, anemochory+hydrochory
Lavandula stoechas	0.87	27	168	0.9	Semi-woody	Shallow	Seeds	Seeds	Zoochory
Ledum palustre	1.5	206.5	168	0.006	Woody	Moderate	Seeds and/or vegetatively	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Linnaea borealis	0.1	76	12	2	Semi-woody	Shallow	Vegetativley	Fruits	Zoochory
Lithodora prostrata	60	900	60	8.6	Semi-woody	Shallow	Seeds	Seeds	Zoochory
Lycopodium annotinum	0.3	5.8	0	0	Semi-woody	Shallow	Seeds	Seeds	Zoochory
Lycopodium clavatum	0.16	2.3	0	0	Semi-woody	Shallow	Seeds	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Lycopodium selago	0.15	3.9	0	0	Semi-woody	Shallow	Seeds	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Myrica gale	1.05	188	8760	1.57	Woody	Shallow	Seeds and/or vegetatively	Fruits	Anemochory, hydrochory, anemochory+hydrochory
Myrtus communis	5	325	14	8.76	Woody	Deep	Seeds and/or vegetatively	Fruits	Zoochory
Phillyrea angustifolia	4	278	14	36	Woody	Shallow	Seeds and/or vegetatively	Fruits	Zoochory
Phillyrea latifolia	8	419	14	19	Woody	Shallow	Seeds and/or vegetatively	Fruits	Zoochory
Picea abies	40	39.8	360	7	Woody	Shallow	Seeds and/or vegetatively	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Pinus pinaster	40	250	6	47	Woody	Deep	Seeds	Seeds	Anemochory, hydrochory, anemochory+hydrochory

Pinus sylvestris	30	87.3	360	6	Woody	Shallow	Seeds	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Platanus hispanica	35	3570	168	3	Woody	Deep	Seeds	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Populus tremula	20	2556.3	168	0.12	Woody	Shallow	Seeds and/or vegetatively	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Populus x canadensis	40	6250	168	0.9	Woody	Deep	Seeds	Seeds	Zoochory
Prunus avium	30	5775	24	186	Woody	Moderate	Seeds	Fruits	Zoochory
Prunus padus	7	2978	12	84	Woody	Moderate	Seeds and/or vegetatively	Fruits	Zoochory
Pyrus cordata	15	1408	24	9.98	Woody	Moderate	Seeds	Fruits	Zoochory
Quercus faginea subsp. *broteroi*	20	1018	168	2510	Woody	Deep	Seeds and/or vegetatively	Fruits	Zoochory
Quercus pyrenaica	25	9600	168	155.4	Woody	Moderate	Seeds	Fruits	Zoochory
Quercus robur	40	3281	168	3378	Woody	Deep	Seeds	Seeds	Zoochory
Quercus suber	25	2406.25	168	3469	Woody	Deep	Seeds and/or vegetatively	Fruits	Zoochory
Ribes nigrum	1.25	5979	0.33	0.7	Woody	Deep	Seeds	Fruits	Anemochory, hydrochory, anemochory+hydrochory
Ribes rubrum	1.4	6172	0.33	4.1	Woody	Shallow	Seeds	Fruits	Zoochory
Robinia pseudoacacia	25	962	200	19.2	Woody	Deep	Seeds and/or vegetatively	Fruits	Anemochory, hydrochory, anemochory+hydrochory
Rosa canina	6	296	24	16	Semi-woody	Shallow	Seeds	Fruits	Zoochory
Rosa majalis	1.1	703.1	30	0.04	Woody	Shallow	Seeds and/or vegetatively	Fruits	Zoochory
Rosa pouzinii	3	750	36	11.17	Semi-woody	Shallow	Seeds	Fruits	Zoochory

Rubus brigantinus	2	1350	14	2.58	Semi-woody	Shallow	Seeds and/or vegetatively	Fruits	Anemochory, hydrochory, anemochory+hydrochory
Rubus genevieri	2	1750	14	2.58	Semi-woody	Shallow	Seeds and/or vegetatively	Fruits	Anemochory, hydrochory, anemochory+hydrochory
Rubus idaeus	1	3487.5	80	1.7	Semi-woody	Moderate	Seeds and/or vegetatively	Fruits	Zoochory
Rubus lainzii	2	3250	14	2.58	Semi-woody	Shallow	Seeds and/or vegetatively	Fruits	Anemochory, hydrochory, anemochory+hydrochory
Rubus radula	2	2300	14	1.84	Semi-woody	Shallow	Seeds and/or vegetatively	Fruits	Anemochory, hydrochory, anemochory+hydrochory
Rubus ulmifolius	2	1460	14	2.52	Semi-woody	Shallow	Seeds and/or vegetatively	Fruits	Zoochory
Rubus vagabundus	2	2244	14	2.58	Semi-woody	Shallow	Seeds and/or vegetatively	Fruits	Anemochory, hydrochory, anemochory+hydrochory
Salix alba	25	800	48	0.12	Woody	Shallow	Seeds	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Salix atrocinerea	12	992	48	0.001	Woody	Shallow	Seeds and/or vegetatively	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Salix aurita	1.5	936.5	0	0.08	Woody	Moderate	Seeds	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Salix caprea	10	900	0	0.25	Woody	Shallow	Seeds	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Salix cinerea	1.2	1349	129.5	0.17	Woody	Moderate	Seeds and/or vegetatively	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Salix glauca	2	489	148	0.16	Woody	Moderate	Seeds and/or vegetatively	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Salix hastata	1	401	0	0.02	Woody	Shallow	Seeds and/or vegetatively	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Salix herbacea	0.05	94.05	92.5	0.16	Woody	Deep	Vegetativley	Seeds	Anemochory, hydrochory, anemochory+hydrochory

Salix lanata	0.9	1133	0	0.08	Woody	Moderate	Seeds	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Salix lapponum	2	294.05	92.5	0.07	Woody	Deep	Seeds	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Salix myrsinites	0.6	323.24	74	0.34	Woody	Deep	Seeds and/or vegetatively	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Salix myrtilloides	0.4	122.5	0	0.45	Woody	Moderate	Seeds and/or vegetatively	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Salix neotricha	25	560	48	0.12	Woody	Shallow	Seeds and/or vegetatively	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Salix pentandra	8	1011	96	0.14	Woody	Shallow	Seeds	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Salix salviifolia	6	1200	48	0.001	Woody	Shallow	Seeds and/or vegetatively	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Salix triandra	6	952.25	0	0.02	Woody	Moderate	Seeds and/or vegetatively	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Sambucus nigra	5	11633	1	14	Woody	Deep	Seeds and/or vegetatively	Fruits	Zoochory
Sesamoides sufrruticosa	4.5	88.2	6	0.1	Woody	Shallow	Seeds and/or vegetatively	Seeds	Zoochory
Sorbus aucuparia	20	4000	6	7	Woody	Moderate	Seeds	Fruits	Anemochory, hydrochory, anemochory+hydrochory
Sorbus aucuparia	11.5	4000	6	7	Woody	Moderate	Seeds	Fruits	Anemochory, hydrochory, anemochory+hydrochory
Thymus mastichina	0.8	20.75	6	0.13	Semi-woody	Moderate	Seeds	Fruits	Zoochory
Ulex minor	1.5	5	1	3.2	Semi-woody	Deep	Seeds	Seeds	Anemochory, hydrochory, anemochory+hydrochory
Vaccinium microcarpum	0.35	6.3	2	0.22	Semi-woody	Shallow	Seeds and/or vegetatively	Fruits	Anemochory, hydrochory, anemochory+hydrochory

Vaccinium myrtillus	0.6	72	1	0.3	Woody	Shallow	Seeds and/or vegetatively	Fruits	Zoochory
Vaccinium myrtillus	0.5	72	1	0.3	Woody	Shallow	Vegetativley	Fruits	Zoochory
Vaccinium oxycoccos	0.5	15.5	4	0.48	Semi-woody	Shallow	Vegetativley	Fruits	Anemochory, hydrochory, anemochory+hydrochory
Vaccinium uliginosum	0.7	104	4	0.3	Woody	Shallow	Seeds and/or vegetatively	Fruits	Zoochory
Vaccinium vitis-idaea	0.17	48	4	0.3	Woody	Shallow	Vegetativley	Fruits	Zoochory
Vitis vinifera subsp. *vinifera*	35	8826	0.01	31	Semi-woody	Moderate	Seeds and/or vegetatively	Seeds	Zoochory

Table C6. Traits' mean, standard deviation (SD) and range in flow regime (free-flowing and regulated) in Portugal (PT) and Sweden (SW).

		PORTUGAL						SWEDEN					
		Mean		SD		Range		Mean		SD		Range	
Regime		Free-flowing	Regulated	Free-flowing	Regulated	Free-flowing	Regulated	Free-flowing	Regulated	Free-flowing	Regulated	Free-flowing	Regulated
Canopy height		2.65	2.68	1.10	0.85	3.77	3.47	3.48	2.38	0.59	1.10	2.63	3.67
Leaf area		394.66	410.76	183.47	188.63	726.91	736.79	421.59	287.11	173.39	178.82	637.34	678.46
Seed bouyancy		127.77	147.30	52.52	31.69	169.07	161.54	179.94	163.00	68.90	75.21	241.00	226.00
Seed weight		70.57	58.18	98.80	68.78	387.71	206.44	2.14	1.17	1.13	0.98	4.20	2.85
Stem flexibility	Woody	0.13	0.13	0.05	0.04	0.18	0.17	0.41	0.30	0.10	0.10	0.38	0.39
	Semi-woody	0.04	0.05	0.02	0.02	0.06	0.06	0.05	0.03	0.02	0.03	0.07	0.09
Rooting depth	Shallow	0.08	0.09	0.03	0.02	0.11	0.10	0.03	0.04	0.02	0.02	0.05	0.05
	Moderate	0.04	0.03	0.03	0.02	0.09	0.08	0.13	0.09	0.04	0.04	0.15	0.12
	Deep	0.06	0.07	0.03	0.03	0.11	0.14	0.30	0.20	0.07	0.09	0.27	0.34

Reproduction type	Seeds	0.07	0.08	0.02	0.02	0.09	0.09	0.15	0.13	0.04	0.04	0.16	0.15
	Vegetatively	0.00	0.00	0.01	0.00	0.02	0.02	0.11	0.07	0.03	0.05	0.11	0.16
	Seeds and/or vegetatively	0.10	0.10	0.03	0.03	0.14	0.10	0.20	0.13	0.05	0.05	0.23	0.18
Diaspore type	Seeds	0.07	0.07	0.03	0.03	0.12	0.11	0.18	0.13	0.05	0.06	0.18	0.23
	Fruits	0.10	0.10	0.04	0.03	0.12	0.09	0.26	0.18	0.07	0.06	0.28	0.25
Dispersal vector	Anemochory, hydrochory, anemochory+hydrochory	0.08	0.09	0.03	0.02	0.12	0.08	0.30	0.23	0.07	0.09	0.25	0.36
	Zoochory	0.09	0.08	0.04	0.03	0.13	0.14	0.16	0.10	0.05	0.04	0.20	0.16

Table C7. Analyses of variance (Two-way ANOVA) of river hydrological attributes (Indices of Hydrological Alternation, IHA) in countries (Portugal and Sweden) and in flow regimes (free-flowing and regulated).

	Df	SS	F	P-value
January				
Country	1	177442	29.97	<0.001
Regulation	1	144673	24.44	<0.001
Country:Regulation	1	157582	26.62	<0.001
February				
Country	1	168588	25.64	<0.001
Regulation	1	163880	24.92	<0.001
Country:Regulation	1	180473	27.45	<0.001
March				
Country	1	145795	24.90	<0.001
Regulation	1	130268	22.25	<0.001
Country:Regulation	1	147246	25.15	<0.001
April				
Country	1	168458	32.11	<0.001
Regulation type (ff/reg)	1	74635	14.23	<0.001
Country:Regulation	1	84276	16.06	<0.001
May				
Country	1	1093771	34.597	<0.001
Regulation	1	11433	0.362	0.549
Country:Regulation	1	6510	0.206	0.651
June				
Country	1	1523872	53.827	<0.001
Regulation	1	5088	0.180	0.672
Country:Regulation	1	3504	0.124	0.726
July				
Country	1	992260	67.892	<0.001
Regulation	1	2988	0.204	0.652
Country:Regulation	1	2805	0,192	0.662
August				
Country	1	649237	66.395	<0.001
Regulation	1	34246	3.502	0.0641
Country:Regulation	1	31154	3.186	0.0772
September				
Country	1	540514	63.232	<0.001
Regulation	1	43586	5.099	0.026
Country:Regulation	1	39916	4.670	0.033
October				
Country	1	428202	61.670	<0.001
Regulation	1	44951	6.474	0.0124
Country:Regulation	1	45094	6.494	0.0123
November				
Country	1	274172	47.74	<0.001
Regulation	1	74105	12.90	<0.001
Country:Regulation	1	86896	15.13	<0.001
December				
Country	1	210021	37.69	<0.001
Regulation	1	108674	19.50	<0.001
Country:Regulation	1	129887	23.31	<0.001
1-day minimum				
Country	1	22240	23.096	<0.001
Regulation	1	4655	4.834	0.030
Country:Regulation	1	4209	4.370	0.039

3-day minimum				
Country	1	27029	22.715	<0.001
Regulation	1	7408	6.226	0.014
Country:Regulation	1	6829	5.740	0.018
7-day minimum				
Country	1	34360	22.214	<0.001
Regulation	1	12084	7.812	0.006
Country:Regulation	1	11334	7.327	0.007
30-day minimum				
Country	1	50327	23.60	<0.001
Regulation	1	24006	11.26	0.001
Country:Regulation	1	22568	10.58	0.002
90-day minimum				
Country	1	84316	28.38	<0.001
Regulation	1	48224	16.13	<0.001
Country:Regulation	1	44914	15.12	<0.001
1-day maximum				
Country	1	3899340	33.753	<0.001
Regulation	1	135582	1.174	0.281
Country:Regulation	1	17877	0.155	0.695
3-day maximum				
Country	1	4212866	38.584	<0.001
Regulation	1	90552	0.829	0.365
Country:Regulation	1	3579	0.033	0.857
7-day maximum				
Country	1	4128598	42.952	<0.001
Regulation	1	48518	0.505	0.479
Country:Regulation	1	430	0.004	0.947
30-day maximum				
Country	1	2676619	50.336	<0.001
Regulation	1	2216	0.042	0.839
Country:Regulation	1	6573	0.124	0.726
90-day maximum				
Country	1	1473247	56.550	<0.001
Regulation	1	7270	0.279	0.598
Country:Regulation	1	24828	0.953	0.331
Number of zero day				
Country	1	108013	15.369	<0.001
Regulation	1	30334	4.316	0.040
Country:Regulation	1	24312	3.459	0.066
Base flow index				
Country	1	0.329	10.080	0.002
Regulation	1	0.377	11.545	<0.001
Country:Regulation	1	0.090	2.761	0.100
Low pulse count				
Country	1	1304	19.513	<0.001
Regulation	1	99	1.484	0.226
Country:Regulation	1	603	9.029	0.003
High pulse count				
Country	1	954.1	38.504	<0.001
Regulation	1	26.1	1.053	0.307
Country:Regulation	1	62.7	2.531	0.115
High pulse duration				
Country	1	9355	142.662	<0.001
Regulation	1	442	6.735	0.011
Country:Regulation	1	343	5.227	0.024

Rise rate				
Country	1	3225	25.992	<0.001
Regulation	1	912	7.353	0.008
Country:Regulation	1	348	2.803	0.010
Fall rate				
Country	1	1405	14.473	<0.001
Regulation	1	1474	15.182	<0.001
Country:Regulation	1	919	9.468	0.003
Number of reversals				
Country	1	45107	20.176	<0.001
Regulation	1	5106	2.284	0.134
Country:Regulation	1	149790	66.999	<0.001

Table C8. Post-Hoc Test (TukeyHSD) of river hydrological attributes in Portugal (PT) and Sweden (SW) and in flow regimes free-flowing (FF) and regulated (REG). The hydrological attributes are defined in Supplementary Table S4. This table presents the sign of the differences between means of each hydrological attribute for each pair of factor levels. Non-significant differences are denoted by “–“; positive and negative differences are denoted by “>0” and “<0”, respectively.

Hydrological attribute	SW:FF - PT:FF	PT:REG - PT:FF	SW:REG - PT:FF	PT:REG - SW:FF	SW:REG - SW:FF	SW:REG-PT:REG
January	-	-	> 0	-	> 0	> 0
February	-	-	> 0	-	> 0	> 0
March	-	-	> 0	-	> 0	> 0
April	-	-	> 0	-	> 0	> 0
May	> 0	-	> 0	< 0	-	> 0
June	> 0	-	> 0	< 0	-	> 0
July	> 0	-	> 0	< 0	-	> 0
August	> 0	-	> 0	< 0	-	> 0
September	> 0	-	> 0	< 0	> 0	> 0
October	> 0	-	> 0	< 0	> 0	> 0
November	> 0	-	> 0	< 0	> 0	> 0
December	-	-	> 0	-	> 0	> 0
1-day minimum	-	-	> 0	-	> 0	> 0
3-day minimum	-	-	> 0	-	> 0	> 0
7-day minimum	-	-	> 0	-	> 0	> 0
30-day minimum	-	-	> 0	-	> 0	> 0
90-day minimum	-	-	> 0	-	> 0	> 0
1-day maximum	> 0	-	> 0	< 0	-	> 0
3-day maximum	> 0	-	> 0	< 0	-	> 0
7-day maximum	> 0	-	> 0	< 0	-	> 0
30-day maximum	> 0	-	> 0	< 0	-	> 0
90-day maximum	> 0	-	> 0	< 0	-	> 0
Number of zero days	-	> 0	-	> 0	-	< 0
Base flow index	> 0	> 0	> 0	-	-	-
Low pulse count	< 0	< 0	< 0	-	-	-
High pulse count	< 0	-	< 0	> 0	-	< 0

High pulse duration	> 0	-	> 0	< 0	< 0	> 0
Rise rate	> 0	-	> 0	-	> 0	> 0
Fall rate	-	-	< 0	-	< 0	< 0
Number of reversals	< 0	< 0	< 0	-	> 0	> 0

Table C9. Indicators of Hydrologic Alteration (IHA) used in the study, reflecting the regime characteristics i.e., magnitude, time, duration, frequency and rate of change, and their ecological relevance (adapted from Richter et al., 1996). Short names used are highlighted in bold.

Category	Hydrological attribute (units)	**Ecological relevance**
Mean value of monthly water variations	**January mean flow** (mm) **February mean flow** (mm) **March mean flow** (mm) **April mean flow** (mm) **May mean flow** (mm) **June mean flow** (mm) **July mean flow** (mm) **August mean flow** (mm) **September mean flow** (mm) **October mean flow** (mm) **November mean flow** (mm) **December mean flow** (mm)	Magnitude of the water condition at any given time as a measure of the availability or suitability of habitat and defines wetted area or the position of a water table relative to wetland or riparian plant rooting zones. The timing of occurrence of particular water conditions can influence the degree of stress or mortality associated with extreme water conditions such as floods or droughts.
Duration of annual extreme water events	**1-day minimum**; annual minima, 1-day median (mm) **3-day minimum**; annual minima, 3-day median (mm) **7-day minimum**; annual minima, 7-day median (mm) **30-day minimum**; annual minima, 30-day median (mm) **90-day minimum**; annual minima, 90-day median (mm) **1-day maximum**; annual maxima, 1-day median (mm) **3-day maximum**; annual maxima, 3-day median (mm) **7-day maximum**; annual maxima, 7-day median (mm) **30-day maximum**; annual maxima, 30-day median (mm) **90-day maximum**; annual maxima, 90-day median (mm) **Number of zero days**; number of days with no flow (mm) **Base flow index** (=7-day minimum flow/average annual flow)	The duration of time over which a specific water condition exists may determine the degree to which stressful effects such as inundation or desiccation can accumulate.
Frequencies of high/low water pulses	**Low pulse count**; number of low pulses (=mean of the number of low flow pulses each year) **High pulse count**; number of high pulses (=mean number of high flow pulses each year)	The frequency of occurrence of specific water conditions such as droughts or floods may be tied to reproduction or mortality events, thereby influencing population dynamics.

	High pulse duration; mean duration of high pulses (days)	
Rate of change in water conditions	**Rise rate** (= median of all positive differences between consecutive daily values) (m^3s^{-1}) **Fall rate** (=median of all negative differences between consecutive daily values) (m^3s^{-1}) **Number of hydrologic reversals**; Number of hydrologic reversals (=mean of the number of flow variation between consecutive days)	The rate of change in water conditions may be tied to the ability of plant roots to maintain contact with phreatic water supplies.

Appendix D

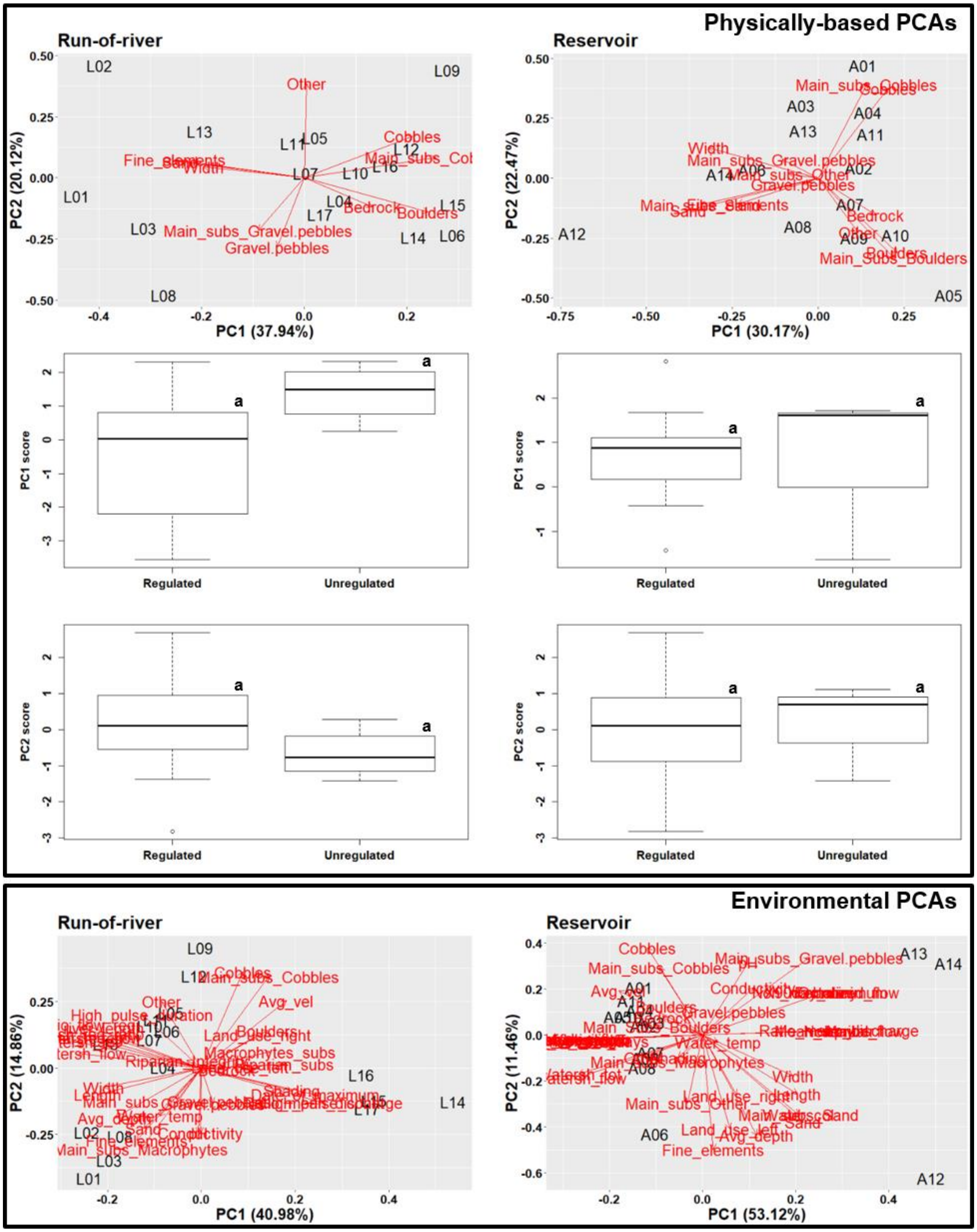


Figure D1. Principal Component Analyses (PCA) using abiotic variables to ensure similarities in the geomorphological settings between free-flowing sampling sites (reference) and regulated sampling sites in run-of-river and reservoir case studies (upper panel). Box-and-whisker plots for geomorphological differences between each principal component axes in the respective rivers. Same letters identify no significantly different values ($p < 0.05$) (lower panel).

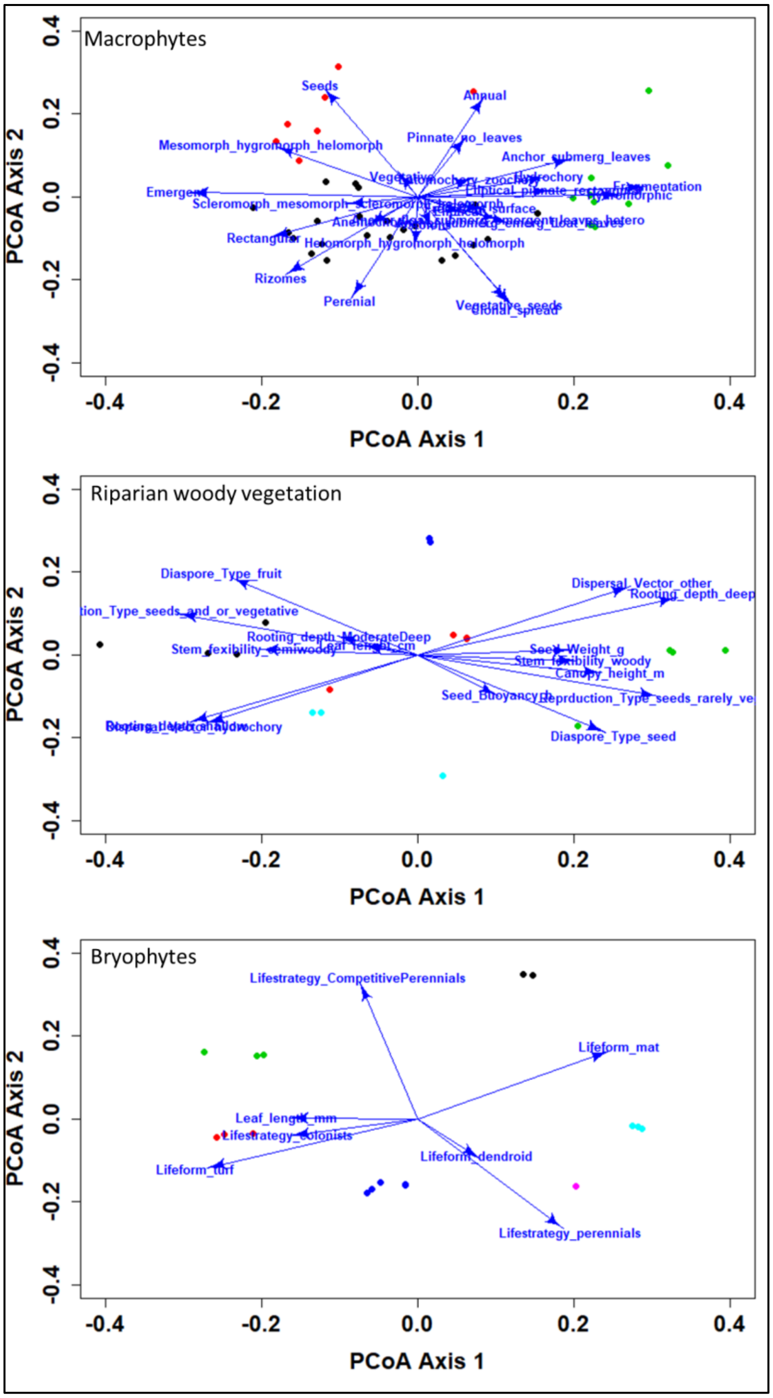


Figure D2. PCoA showing distances in traits for: macrophytes guilds (upper panel) - red dots Disturbance favored macrophyte, green dots “Disturbance-adapted macrophyte”, black dots Disturbance-resilient macrophyte; riparian woody guilds (middle panel) – light blue dots Disturbance-favored, dark blue dots Disturbance-resilient, green dots Poorly-disturbance adapted, red dots Disturbance-adapted, black dots Highly disturbance-adapted; and bryophytes guilds (lower panel) – black dots Hygrophilous lotic, green dots Heliophilous lenthic, red dots Hydrophilous lotic, dark blue dots Hydrophilous lentic, light blue dots Sciophilous lentic, purple dots Rheophilous. For hierarchical classification of the communities, see Figure 17.

Table D1. Characteristics of the case studies.

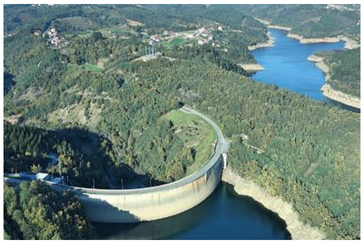
Case study	Run-of-river	Reservoir
Dam commissioning year	1993	1985
Hydropower plant name	Touvedo	Fronhas
River ID	River Lima	River Alva
Watershed (km^2)	1686	652
Mean annual flows (mm)	1216	962
Mean annual discharge (m^{3}s^{-1})	48.66	12.7
Mean annual runoff (hm^3)	1692	365
Aerial of the hydropower plants Photo credits: A Terceira Dimensão (http://portugalfotografiaaerea.blogspot.com/).		

Table D2. Species list, Family, Association to fluvial environment, Origin (biogeography), and Guilds assignment of all assessed species.

Table D2A. Macrophytes

Species	Family	Association to fluvial environment	Origin	Guild assignment
Agrostis stolonifera L.	Poaceae	Helophyte	Native	Disturbance-resilient
Apium nodiflorum Lag.	Apiaceae	Helophyte	Native	Disturbance-resilient
Bidens frondosa L.	Asteraceae	Hygrophyte	Exotic	Disturbance-favored
Bidens aurea (Aiton) Sherff	Asteraceae	Hygrophyte	Exotic	Disturbance-favored
Callitriche stagnalis Scop.	Callitrichaceae	Hydrophyte	Native	Disturbance-adapted

Carex pendula Huds.	Cyperaceae	Helophyte	Native	Disturbance-resilient
Carex elata Lam.	Cyperaceae	Helophyte	Native	Disturbance-resilient
Cyperus eragrostis Lam.	Cyperaceae	Helophyte	Exotic	Disturbance-resilient
Cyperus longus L.	Cyperaceae	Helophyte	Native	Disturbance-resilient
Dactylis glomerata L.	Poaceae	Hygrophyte	Native	Disturbance-favored
Elodea canadensis Michx.	Hyorocharitaceae	Hydrophyte	Exotic	Disturbance-adapted
Equisetum palustre L.	Equisetaceae	Hygrophyte	Native	Disturbance-resilient
Eupatorium cannabinum L.	Asteraceae	Helophyte	Native	Disturbance-resilient
Galium palustre L.	Rubiaceae	Hygrophyte	Native	Disturbance-resilient
Juncus effusus L.	Juncaceae	Hygrophyte	Native	Disturbance-resilient
Juncus acutiflorus Ehrh ex. Hoffm.	Juncaceae	Helophyte	Native	Disturbance-resilient
Juncus bulbosus L.	Juncaceae	Helophyte	Native	Disturbance-resilient
Hypericum elodes L.	Clusiaceae	Helophyte	Exotic	Disturbance-resilient
Iris pseudacorus L.	Iridaceae	Helophyte	Native	Disturbance-resilient
Lemna minor L.	Lemnaceae	Hydrophyte	Native	Disturbance-adapted
Lotus pedunculatus Cav.	Fabaceae	Hygrophyte	Native	Disturbance-favored

Lycopus europaeus L.	Lamiaceae	Helophyte	Native	Disturbance-resilient
Lythrum salicaria L.	Lythraceae	Helophyte	Native	Disturbance-favored
Lythrum portula (L.) D.A. Webb	Lythraceae	Hygrophyte	Native	Disturbance-favored
Mentha aquatica L.	Lamiaceae	Helophyte	Native	Disturbance-resilient
Mentha pulegium L.	Lamiaceae	Hygrophyte	Native	Disturbance-resilient
Myosotis secunda L.	Boraginaceae	Helophyte	Native	Disturbance-resilient
Myriophyllum spicatum L.	Haloragaceae	Hygrophyte	Native	Disturbance-adapted
Myriophyllum verticillatum L.	Haloragaceae	Hygrophyte	Native	Disturbance-adapted
Oenanthe crocata L.	Apiaceae	Helophyte	Native	Disturbance-resilient
Osmunda regalis L.	Osmundaceae	Hygrophyte	Native	Disturbance-favored
Panicum repens L.	Poaceae	Hygrophyte	Native	Disturbance-resilient
Paspalum paspalodes (Michx.) Scribner	Poaceae	Hygrophyte	Exotic	Disturbance-resilient
Polygonum hydropiper (L.) Delabre	Polygonaceae	Helophyte	Native	Disturbance-favored
Potamogeton polygonifolius Pourret	Potamogetonaceae	Hydrophyte	Native	Disturbance-adapted
Ranunculus peltatus Schrank	Ranunculaceae	Hydrophyte	Native	Disturbance-adapted
Ranunculus penicillatus (Dumort) Bab.	Ranunculaceae	Hydrophyte	Native	Disturbance-adapted

Ranunculus trichophyllus Chiax ex Vell.	Ranunculaceae	Hydrophyte	Native	Disturbance-adapted
Saponaria officinalis L.	Caryophyllaceae	Hygrophyte	Native	Disturbance-resilient
Sparganium erectum L.	Sparganiaceae	Helophyte	Native	Disturbance-resilient
Tradescantia fluminensis Vell.	Commelinnaceae	Hygrophyte	Exotic	Disturbance-resilient
Typha latifolia L.	Typhaceae	Helophyte	Native	Disturbance-resilient

Table D2B. Bryophytes

Species	Family	Association to fluvial environment	Origin	Guild assignment
Brachythecium rivulare Schimp.	Brachytheciaceae	Hygrophyte	Native	Hygrophilous lotic
Bryum capillare Hedw.	Bryaceae	Mesophyte/ xerophyte	Native	Heliophilous lentic
Bryum gemmiparum De Not.	Bryaceae	Hygrophyte/ amphiphyte	Native	Heliophilous lentic
Bryum pseudotriquetrum (Hedw.) P.Gaertn. et al.	Bryaceae	Hygrophyte	Native	Sciophilous lentic
Dicranella heteromalla (Hedw.) Schimp.	Dicranaceae	Mesophyte	Native	Heliophilous lentic
Fissidens crispus Mont.	Fissidentaceae	Mesophyte/ xerophyte	Native	Hydrophilous lotic
Fontinalis antipyretica Hedw.	Fontinalaceae	Hygrophyte/ rheophyte	Native	Hydrophilous lotic
Fontinalis hypnoides var. duriaei (Schimp.) Kindb.	Fontinalaceae	Hygrophyte	Native	Hydrophilous lotic
Fontinalis squamosa Hedw.	Fontinalaceae	Hygrophyte	Native	Hydrophilous lotic

Hygrohypnum ochraceum (Turner ex Wilson) Loeske	Amblystegiaceae	Hydrophyte/ hygrophyte	Native	Hydrophilous lentic
Kindbergia praelonga (Hedw.) Ochyra	Brachytheciaceae	Hydrophyte/ hygrophyte	Native	Hydrophilous lotic
Leptodictyum riparium (Hedw.) Warnst.	Amblystegiaceae	Hygrophyte/ amphiphyte	Native	Hydrophilous lentic
Plagiomnium affine (Blandow ex Funck) T.J.Kop.	Plagiomniaceae	Hydrophyte/ hygrophyte	Native	Sciophilous lentic
Platyhypnidium lusitanicum	Brachytheciaceae	Hygrophyte	Native	Hydrophilous lentic
Platyhypnidium riparioides	Brachytheciaceae	Hydrophyte/ amphiphyte	Native	Hydrophilous lentic
Scapania undulata	Scapaniaceae	Hydrophyte	Native	Hygrophilous lotic
Thamnobryum alopecurum	Neckeraceae	Hygrophyte/ rheophyte	Native	Rheophilous
Trichostomum brachydontium	Pottiaceae	Amphiphyte	Native	Sciophilous lentic

Table D2C. Riparian woody vegetation

Species	Family	Association to fluvial environment	Origin	Guild assignment
Acacia dealbata Link	Fabaceae	Facultative riparian	Exotic	Highly disturbance-adapted
Acer pseudoplatanus L.	Aceraceae	Nonriparian	Native	Disturbance-adapted
Ailanthus altissima (Miller) Swingle	Simaroubaceae	Facultative riparian	Exotic	Highly disturbance-adapted
Alnus glutinosa (L.) Gaertner	Betulaceae	Obligate riparian	Native	Poorly disturbance-adapted

Crategus monogyna Jacq.	Rosaceae	Facultative riparian	Native	Disturbance-resilient
Frangula alnus Mill.	Rhamnaceae	Obligate riparian	Native	Disturbance-adapted
Fraxinus angustifolia Vahl	Oleaceae	Preferential riparian	Native	Disturbance-adapted
Hedera hibernica (G. Kirchn.) Bean	Araliaceae	Facultative riparian	Native	Highly disturbance-adapted
Laurus nobilis L.	Lauraceae	Preferential riparian	Native	Disturbance-adapted
Platanus hispanica Miller	Plantaginaceae	Facultative riparian	Exotic	Poorly disturbance-adapted
Populus nigra Moench	Salicaceae	Preferential riparian	Exotic	Poorly disturbance-adapted
Quercus robur L.	Fagaceae	Facultative riparian	Native	Poorly disturbance-adapted
Rubus sp.	Rosaceae	Facultative riparian	Native	Highly disturbance-adapted
Salix alba L.	Salicaceae	Obligate riparian	Native	Disturbance-favored
Salix atrocinerea Brot.	Salicaceae	Obligate riparian	Native	Disturbance-favored
Salix salviifolia Brot.	Salicaceae	Obligate riparian	Native	Disturbance-favored
Sambucus nigra L.	Caprifoliaceae	Preferential riparian	Native	Disturbance-resilient

Table D3. Trait categories, trait classes, and respective plant groups.

Plant group	Trait	Classes
Riparian woody vegetation	Canopy height	Continuous (m)
	Leaf area	Continuous (mm^2)
	Stem flexibility	Woody Semi-woody
	Rooting depth	Shallow Medium-deep Deep
	Seed weight	Continuous (g)
	Seed buoyancy	Continuous (hours)
	Reproduction type	Seeds; rarely vegetative Seeds and/or vegetative
	Diaspore type	Fruit Seed
	Dispersal type	Hydrochory Other
		Zoochoric or entomochoric Other
		Anemochoric Other
Vascular macrophytes	Growth form	Emergent Anchored, submerged leaves Free-floating, surface Anchored, submerged and emergent leaves; or anchored, submerged and floating leaves Anchored, floating, submerged and emergent leaves/or heterophylly
	Life span	Annual Perennial
	Leaf anatomy	Hydromorphic Mesomorphic; or mesomorphic, hygromorphic; or mesomorphic, helomorphic Helomorphic; or hygromorphic, helomorphic Scleromorphic; mesomorphic; or scleromorphic, helomorphic
	Leaf shape	Elliptical Rectangular Pinnate or no leaves Elliptical and pinnate; or elliptical and rectangular
	Reproduction type	Seed Vegetative propagation Vegetative propagation and seeds
	Type of vegetative reproduction	Clonal spread Other

		Fragmentation Other
		Stolons Other
		Rhyzomes Other
	Diaspore type	Fruit Seed
	Dispersal type	Hydrochoric Non-hydrochoric
Bryophytes	Life form	Mat Turf Dendroid
	Leaf length	Continuous (mm)
	Life strategy	Perennials Competitive perennials Stress tolerant perennials Colonists

Table D4. Averaged functional trait values for each guild by plant group.

Table D4A. Macrophytes

Traits		Guilds		
Category	Classes	Disturbance-adapted	Disturbance-favored	Disturbance-resilient
Growth form	Emergent	0.0	87.5	80.0
	Anchored, submerged leaves	55.6	12.5	0.0
	Free-floating, surface	11.1	0.0	0.0
	Anchored, submerged and emergent leaves; or anchored, submerged and floating leaves	11.1	0.0	16.0
	Anchored, floating, submerged and emergent leaves/or heterophylly	22.2	0.0	4.0
Life span	Annual	33.3	50.0	0.0
	Perennial	66.7	50.0	100.0
Leaf shape	Elliptical	33.3	25.0	32.0
	Rectangular	0.0	37.5	52.0
	Pinnate or no leaves	33.3	37.5	16.0
	Elliptical and pinnate; or elliptical and rectangular	33.3	0.0	0.0
Leaf anatomy	Hydromorphic	88.9	0.0	8.0
	Mesomorphic; or mesomorphic, hygromorphic; or mesomorphic, helomorphic	0.0	62.5	28.0
	Helomorphic; or hygromorphic, helomorphic	11.1	25.0	48.0
	Scleromorphic; mesomorphic; or scleromorphic, helomorphic	0.0	12.5	16.0
Reproduction type	Seeds	0.0	100.0	0.0
	Vegetative propagation	22.2	0.0	20.0
	Vegetative propagation and seeds	77.8	0.0	80.0

Vegetative reproduction type	Clonal spread	100.0	0.0	100.0
	Fragmentation	100.0	0.0	4.0
	Stolons	0.0	0.0	24.0
	Rhizomes	0.0	0.0	72.0
Dispersal type	Hydrochory	88.9	25.0	28.0
	Anemochory	44.4	37.5	36.0
	Zoochory or entomochory	55.6	75.0	68.0

Table D4B. Bryophytes

Trait		Guild					
Category	Classes	Hygrophilous Lotic	Heliophilous Lentic	Sciophilous Lentic	Hydrophilous Lentic	Hydrophilous Lotic	Rheophilous
Life form	Mat	Yes	No	No	Yes	Yes	No
	Turf	No	Yes	Yes	Yes	No	No
	Dendroid	No	No	No	No	No	Yes
Life strategy	Perennials	No	No	No	Yes	Yes	Yes
	Competitive perennials	Yes	No	Yes	No	No	No
	Stress tolerant	No	No	No	No	No	No
	Colonists	No	Yes	No	No	No	No
Leaf length	Continuous (mm)	2.25	2.9	3.9	2.9	2	2

Table D4C. Riparian woody vegetation

Trait		Guild				
Category	Classes	Highly disturbance-adapted	Disturbance-adapted	Poorly disturbance-adapted	Disturbance-resilient	Disturbance-favored
Stem flexibility	Semi-woody	25.0	0.0	0.0	0.0	0.0
	Woody	75.0	100.0	100.0	100.0	100.0
Rooting depth	Shallow	75.0	25.0	0.0	0.0	100.0
	Medium-deep	25.0	0.0	0.0	0.0	0.0
	Deep	0.0	75.0	100.0	100.0	0.0
Reproduction type	Seeds; rarely vegetative	0.0	100.0	100.0	0.0	33.3
	Seeds and/or vegetative	100.0	0.0	0.0	100.0	66.7
Diaspore type	Fruit	100.0	100.0	0.0	100.0	0.0
	Seed	0.0	0.0	100.0	0.0	100.0
Dispersal type	Hydrochory	100.0	100.0	25.0	0.0	100.0
	Other	0.0	0.0	75.0	100.0	0.0

Table D5. Results of the linear models for macrophytes, riparian woody and bryophyte guilds with DOR (Degree Of Regulation) and DFD (Distance From Dam) in run-of-river and reservoir case studies.

RUN-OF-RIVER										
Guild	DOR					DFD				
	Coefficient determination	Intercept	Coefficient	Significant Response	Minimum DOR (%)	Coefficient determination	Intercept	Coefficient	Significant Response	Minimum DFD (m)
MACROPHYTES										
Disturbance-resilient	0.105754626	6.148	62.546	No	-	0.009090629	1.563e+01	2.985e-04	No	-
Disturbance-favored	0.006325455	7.083	5.171	No	-	0.074917908	11.2152048	-0.0002881	No	-
Disturbance-adapted	0.433130452	6.563	92.833	Yes	0.1509654	0.007874028	27.4162158	-0.0001606	Yes	17833.9
RIPARIAN										
Highly disturbance-adapted	1.432603e-01	2.47740	0.08068	No	-	5.425532e-07	8.602	1.811	No	-
Disturbance-adapted	1.863829e-06	18.1570762	-0.0009989	No	-	9.982248e-03	18.3110	-0.1058	No	-
Poorly disturbance-adapted	3.976483e-01	9.45321	0.08904	No	-	9.164922e-04	13.501	2.982	No	-
Disturbance-resilient	5.000265e-02	0.1444803	-0.0003356	No	-	8.775128e-02	0.15068	-0.01902	No	-
Disturbance-favored	2.586874e-01	31.37941	-0.05365	Yes	0.2190369	4.070153e-01	31.603	-2.763	Yes	10199.78
BRYOPHYTE										
Hygrophilous lotic	0.1908319277	-50.77	54.52	No	-	-	3.707	-4.180	-	-
Heliophilous lentic	-	-	-	-	-	-	-	-	-	-
Hydrophilous_lotic	-	-	-	-	-	-	-	-	-	-
Hydrophilous lentic	0.0371117638	-32.27	37.32	No	-	9.101859e-05	5.015	-2.850	No	-
Sciophilous lentic	0.0001359013	6.322	-4.397	No	-	1.267269e-02	1.8779	0.4121	No	-
Rheophilous	0.1908319277	-25.39	27.26	No	-	-	1.854	-2.090	No	-
RESERVOIR										
MACROPHYTES										
Disturbance-resilient	0.1194087	-0.006716	105.277280	Yes	0.1019996	0.26060307	23.92302	-0.00114	Yes	11273.42
Disturbance-favored	0.1546998	0.2554	8.4873	Yes	0.09224224	0.08000859	7.080e-01	4.321e-05	Yes	9364.942
Disturbance-adapted	0.1457686	0.3803	77.4623	Yes	0.09628237	0.24795171	16.8031494	-0.0007293	Yes	12243.05
RIPARIAN										
Highly disturbance-adapted	0.004505923	10.9344	0.1251	No		0.09679630	10.8344	0.2233	No	
Disturbance-adapted	0.120910055	3.367	0.693	No		0.33091464	2.813	1.236	No	
Poorly disturbance-adapted	0.519460373	9.590	2.103	Yes	0.09197149	0.08219133	7.909	3.752	Yes	5996.685
Disturbance-resilient	0.744179325	-0.3827	0.1694	Yes	0.1105711	0.08698157	18.508	-1.274	No	-
Disturbance-favored	0.271233109	17.938	-0.714	Yes	0.09804143	0.08386899	-0.5181	0.3022	Yes	12400.1

BRYOPHYTE										
Hygrophilous lotic	-	-	-	-	-	-	-	-	-	-
Heliophilous lentic	0.2459111	-0.07699	0.02737	No	-	3.295586e-02	0.028715	0.004542	No	-
Hydrophilous_lotic	0.2459111	-0.07699	0.02737	No	-	3.295586e-02	0.028715	0.004542	No	-
Hydrophilous lentic	0.1115527	0.77460	-0.05437	Yes	0.09975769	4.543883e-01	0.65175	-0.01556	Yes	12285.43
Sciophilous lentic	0.1633259	-0.09301	0.07998	No	-	6.641692e-06	-0.61165	0.07532	No	-
Rheophilous	-	-	-	-	-	-	-	-	-	-