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Response-effect trait overlap and correlation in riparian plant communities suggests sensitivity of ecosystem functioning and services to environmental change

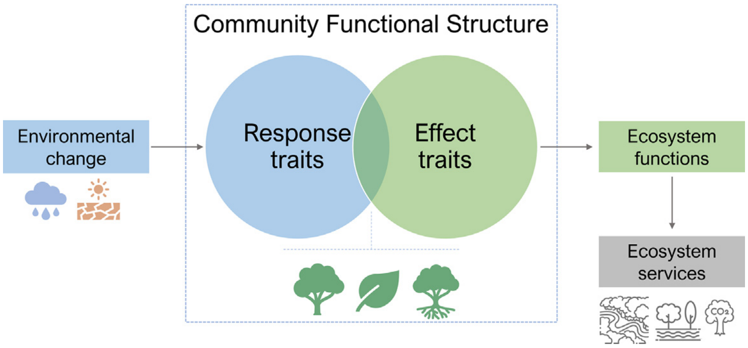
Ana Paula Portela [a,b,c,*], Isabelle Durance [d], Cristiana Vieira [e], João Honrado [a,b,c]

[a] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, 4485-661 Vairão, Portugal
[b] Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, 4099-002 Porto, Portugal
[c] BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, 4485-661 Vairão, Portugal
[d] Water Research Institute and School of Biosciences, Cardiff University, The Sir Martin Evans Building, Museum Avenue, Cardiff CF10 3AX, United Kingdom
[e] Museu de História Natural e da Ciência da Universidade do Porto (MHNC-UP/UPorto/PRISC), Praça Gomes Teixeira, 4099-002 Porto, Portugal.

HIGHLIGHTS

- We linked riparian plant traits, drivers, ecosystem function and services.
- Environmental response traits largely overlapped with functional effect traits.
- Correlations among trait community weighted means reinforced traits linkages.
- Community trait structure is most sensitive to precipitation and aridity.
- Regulation ecosystem services likely most affected by change in drivers and traits.

GRAPHICAL ABSTRACT



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ABSTRACT

Environmental changes and biodiversity loss have emphasized the need to understand how communities affect ecosystem functioning and services. In riparian ecosystems, integrative, generalizable, broad-scale models of ecosystem functioning are still required to fulfill this need. However, few studies have explored the links between functional traits, ecosystem functions, and the services of riparian vegetation. Here we adapt the response-effect trait framework to link drivers, traits, ecosystem functions, and services in riparian ecosystems and assess ecosystem functioning sensitivity to environmental changes. The response-effect trait framework distinguishes between traits related to responses to the environment (response traits) and effects on ecosystem functioning (effect traits). The framework predicts that if response and effect traits are tightly linked, shifts in environmental drivers may alter communities' traits and ecosystem functioning.

We adapted the response-effect trait framework for riparian plant communities and used it to assess the overlap between response and effect traits. We tested for correlation among traits identified in the framework and for community functional responses to climatic, topographic, soil, and land cover factors using riparian plant communities along a Temperate-Mediterranean climate gradient in North Portugal.

We found a high overlap between response and effect traits, with seven out of thirteen traits identified as both response and effect. Additionally, we found trait linkages in four groups of positively correlated community mean traits.

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* Corresponding author at: CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Campus de Vairão, Universidade do Porto, 4485-661 Vairão, Portugal.
E-mail address: apportela@fc.up.pt (A.P. Portela).

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Precipitation and aridity were the most predictive drivers of community functional structure, and life form and leaf area were the most responsive traits.

Overall, our findings suggest riparian plant communities are likely to propagate the effects of environmental changes to ecosystem functioning and services, affecting several regulation ecosystem services.

This work highlights the sensitivity of riparian ecosystems to environmental changes and how it can affect ecosystem services. Similar functional approaches can be useful for adaptive ecosystem management to sustain biodiversity and ecosystem services.

1. Introduction

Habitat degradation, flow modification and species invasions have altered riparian vegetation causing shifts in community composition, abundance, functional diversity, and structure (Kominoski et al., 2013; Tonkin et al., 2018; Stella and Bendix, 2019). These changes may impact multiple ecosystem functions and a range of provisioning, regulating, and cultural ecosystem services, which riparian vegetation provides at disproportionally high levels relative to its surface area (Capon et al., 2013; Riis et al., 2020). Therefore, it is critical to understand the sensitivity of riparian ecosystem functioning and service supply to ongoing environmental change processes, namely climate and land cover change (Stromberg et al., 2012; Capon et al., 2013; Kominoski et al., 2013).

Ecosystem functions are defined here as the proximal biological processes (e.g., productivity, nutrient cycling) that determine the supply of ecosystem services (Oliver et al., 2015). Ecosystem services are defined here as outputs from ecosystem functions that provide benefits to humans or human well-being (e.g., timber, crops, water quality regulation) (Millennium Ecosystem Assessment, 2005; Oliver et al., 2015). The ecosystem service supply corresponds to the ecosystem capacity to generate those benefits (Burkhard et al., 2012).

Functional traits, defined as the morphological, physiological, or phenological features of organisms (Violle et al., 2007), influence dispersal, establishment, competitive ability, as well as ecosystem functions, thus shaping responses to environmental changes, ecosystem functioning, and service supply (Lavorel and Garnier, 2002; de Bello et al., 2010; Hanisch et al., 2020).

Hence trait-based approaches can contribute to predicting the impacts of environmental change by linking biodiversity to ecosystem functioning and services (de Bello et al., 2010; Hevia et al., 2017; Gutiérrez-Cánovas et al., 2021). Functional traits can be classified into response traits – an organism characteristic that is associated with the response to environmental factors such as disturbances and resources, and effect traits – traits that determine the effects of species on one or several ecosystem functions (Lavorel and Garnier, 2002; Suding et al., 2008). The response-effect trait framework uses this trait classification to determine how environmental change affects plant community traits, which in turn, may impact ecosystem functioning (Lavorel and Garnier, 2002; Suding et al., 2008). If response and effect traits are the same or are tightly linked, the impacts of environmental change on community functional structure (distribution of traits within a community) may also propagate to ecosystem functioning (Lavorel and Garnier, 2002; Suding et al., 2008; de Bello et al., 2021b). If the two types of traits do not overlap, the communities may buffer the impacts of environmental changes, maintaining similar levels of ecosystem functioning despite changes in community functional structure (de Bello et al., 2021b). Consequently, the degree of overlap and correlation between response and effect traits is an indicator of the sensitivity of ecosystem functioning to environmental changes (Sterk et al., 2013; Hevia et al., 2017; de Bello et al., 2021b).

The sensitivity of riparian functional structure to environmental drivers and change processes has been explored mostly using functional groups (or guilds – groups of co-occurring species with similar traits) at reach to watershed scales (Lozanovska et al., 2018). Riparian functional studies have largely focused on species response traits and response trait functional groups to assess the effects of flow regime, hydrology, flow regulation, and land cover change (Merritt et al., 2010; Aguiar et al., 2018; Lozanovska et al., 2018). Riparian functional groups with large leaf area, taller stature, and low wood density have been found to be replaced by functional groups with smaller leaf areas, stature, and higher wood density, with declining water availability (Stromberg and Merritt, 2016; Aguiar et al., 2018; Scott and Merritt, 2020).

In comparison, fewer studies have linked the functional changes in riparian communities with impacts on ecosystem functioning, hence much less is known about the capacity of riparian communities to buffer the effects of environmental change on ecosystem functioning (Lozanovska et al., 2018; Riis et al., 2020). One study using species richness of effect trait functional groups as an indicator of riparian resilience found it declined with catchment-scale flow regulation, drought duration, and agriculture in a Mediterranean river basin (Bruno et al., 2016). Two other studies applied the response-effect framework to riparian vegetation in arid rivers to understand the implications of hydrological change for biogeomorphological processes in two river reaches (Diehl et al., 2017) and for key ecosystems services at catchment scale (Hough et al., 2018). Both studies identified traits that acted as response and effect traits, with implications for erosion-deposition dynamics in the first study (Diehl et al., 2017) and for habitat provision, tourism, and flood attenuation services in the second study (Hough et al., 2018). However, research is still needed to link riparian vegetation traits to ecosystems functions and ecosystem services, and to understand whether ecosystem functioning and ecosystem service supply are sensitive to environmental changes. In particular, this integrative model of riparian functioning is lacking for larger geographical regions and it is the comprehensive sets of drivers and ecosystem services which would allow a broader assessment of the sensitivity of riparian ecosystems to environmental change and the development of adaptive management strategies (Dufour et al., 2019; Gonzalez Del Tanago et al., 2021).

Here we aim to investigate, at a regional scale, the sensitivity of riparian ecosystem functioning and services to environmental changes in climatic and land cover drivers based on the response-effect trait framework. Specifically, we aim to investigate if riparian plant communities will propagate or buffer the effects of environmental changes on ecosystem functioning, and which climatic and land cover factors are the main drivers of change in community functional structure. To achieve this, we ask:

(i) Do riparian response and effect traits overlap and are they correlated?
(ii) Which are the main environmental drivers shaping the functional structure of riparian communities? And conversely, which traits are most influenced by drivers?
(iii) Which functions and services are most likely to be affected by environmental changes considering the main drivers and linkages between response and effect traits?

We hypothesise that riparian response and effect traits overlap, since previous studies considering particular sets of functions (e.g., biogeomorphological processes) have identified some overlap (Bruno et al., 2016; Diehl et al., 2017; Hough et al., 2018). Consequently, we expect environmental change impacts on communities are likely to propagate to ecosystem functioning. We expect riparian functional structure will be most sensitive to changes in the amount and seasonality of precipitation, as well as aridity, based on previous studies on the effects of variables related to water availability on riparian functional groups (Bruno et al., 2016; Stromberg and Merritt, 2016). We expect community height and leaf area to be the most sensitive traits, based on previous studies on riparian response traits (Merritt et al., 2010; Aguiar et al., 2018; Lozanovska et al., 2018). We also expect primary productivity, evapotranspiration, and the supply of regulating services to be the most affected, since these functions are known to relate to the aforementioned traits (de Bello et al., 2010).

We use a community-level functional structure approach, based on trait distributions within the community, instead of a species or functional group approach. The community-level was selected since it is more strongly related to ecosystem functioning (Balvanera et al., 2006; Suding et al., 2008). Moreover, ecosystem functioning is determined by the traits of the dominant species (mass ratio hypothesis), and by non-additive effects (effects not predictable by sum of single species) associated with functional divergence (complementarity hypothesis) (Díaz et al., 2007). The use of trait distributions to characterize community functional structure reflects both of the above hypothesis (Díaz et al., 2007), and ensures the functional structure metrics are independent of a priori classification and/or clustering of traits into response and effect (de Bello et al., 2021a).

We use the response-effect trait conceptual framework to identify environmental drivers, traits, ecosystem functions, and key ecosystem services in riparian ecosystems to assess the overlap between response and effect traits. We assessed the correlation among traits and tested for functional structure responses to environmental drivers using riparian plant communities from a Temperate-Mediterranean gradient in North Portugal. Finally, we discuss the sensitivity of ecosystem functioning and service to environmental change.

The novelty of this study lies in (i) the use of the response-effect trait framework to link traits, functions, and key provisioning and regulating services, (ii) using a community-level functional structure approach based on trait distributions instead of functional groups and (iii) using a regional scale riparian vegetation dataset to test for linkages between response and effect traits and for the effect of climatic, topographic and land cover drivers on functional structure.

2. Methods

2.1. Riparian conceptual response-effect trait framework

We used the response-effect trait framework to understand if environmental change will affect riparian vegetation communities and consequently ecosystem functions and services (Suding et al., 2008; de Bello et al., 2010). To apply the response-effect trait framework to riparian vegetation we used existing research to identify key drivers, traits, ecosystem functions, and services. In the first stage, we compiled information from the literature on the association of traits and environmental drivers and the association of traits to ecosystem processes, and when available ecosystem services. We collected information from riparian vegetation functional ecology papers that used response effect frameworks or classifications (Bruno et al., 2016; Diehl et al., 2017; Hough et al., 2018), described the responses of specific traits to environmental factors (Merritt et al., 2010; Stromberg et al., 2012; McCoy-Sulentic et al., 2017; Lozanovska et al., 2018; Lozanovska et al., 2020), and linked traits with functions and services (O'Hare et al., 2016; Capon and Pettit, 2018). We also collected information on the links between traits, ecosystem processes, and services from general review papers (de Bello et al., 2010; Garnier et al., 2015).

After this initial literature screening, the second stage consisted of summarizing and harmonizing the information compiled into a conceptual framework. The environmental drivers listed in the literature were grouped into broader categories to facilitate the framework interpretation. The drivers were grouped into climate (e.g., average temperature, precipitation), water availability (e.g., aridity, water table depth), hydrological regime (e.g., amount and timing of river flows), topography (e.g., elevation, slope), soil (e.g., soil nutrient content), and anthropogenic disturbance (e.g., land cover change). Traits were classified into response, effect, or both, based on information collected in the literature. Traits were considered both response and effect when consistently identified as being responsive to a driver(s) and influencing ecosystem process(es). We only kept traits for which it was possible to gather sufficient species data for further tests (see the section on Trait Data for details). The ecosystem functions and services found in the literature were standardized to a common nomenclature. We focused on provisioning and regulating services since they are more directly linked to environmental factors and functional traits (Riis et al., 2020). Cultural services were not considered since existing knowledge gaps hinder even general expert assessments (Riis et al., 2020). The selected ecosystem services were: (i) standing crop biomass for energy and fibres, which includes woody and herbaceous biomass used for fuel and fibres; (ii) carbon sequestration, which includes carbon capture and long-term storage in vegetation; (iii) hydrological cycle and water flow regulation, which includes the capacity of vegetation to retain water and slowly release it mitigating extreme flows; (iv) microclimate regulation, which includes air and water temperature control through shading and evaporative cooling; (v) regulation of physical and chemical condition of freshwaters, which includes the removal of nutrients, pollutants and sediments from runoff; (vi) stabilization and control of erosion, which includes the reduction of soil weathering through the stabilizing effect of vegetation; (vii) buffering and attenuation of mass movements, which includes prevention of landslides; and (viii) maintenance of nursery populations and habitats, which includes providing habitat and reproduction sites for other organisms (Riis et al., 2020). The associated ecosystem functions were categorized into: primary productivity, evapotranspiration, surface water flow and run-off, fluvial biogeomorphological dynamics, light and temperature control, nutrient filtration, and cycling, sediment retention, riverbank or bed stabilization, trophic subsidies, terrestrial or aquatic habitat (de Bello et al., 2010; Capon and Pettit, 2018).

2.2. Study sites

We used 99 study sites across a large Temperate-Atlantic to Mediterranean environmental gradient to test correlations among traits and the links between environmental factors and riparian vegetation functional structure. The sites are located across the North Portugal hydrographic region and were sampled for macrophytes and riparian vegetation in the scope of Water Framework Directive monitoring (Fig. 1). The sites span a sharp west-east climatic gradient corresponding to the transition between Temperate-Atlantic and Mediterranean climates due to the influence of the Atlantic Ocean and the barrier effect of mountain ranges. In the northwest watercourses, annual average temperatures are relatively low (12 °C, at 413 m mean elevation and lower), especially in mountain areas (11 °C, 506 m mean elevation), and annual average precipitation is high, over 1900 mm in the mountains and around 1200 mm in the lowlands (INAG IP, 2008b). In the northeast, annual average temperatures are slightly higher (13 °C) and annual average precipitation is substantially lower and more seasonal, with an average of 670 mm at medium-high elevations (432 m mean elevation) and 600 mm in lowlands (300 m mean elevation) (INAG IP, 2008b). In the northwest mountains, rivers have steep slopes, small catchment areas (<100 km^2), and high runoff (600–2200 mm) (INAG IP, 2008b). In the northwest lowlands, smaller rivers have runoff values between 100 and 1800 mm, while the medium to large rivers (>100 km^2) have runoff values between 100 and 2200 mm. In the northeast, the smaller rivers have runoff values between 25 and 600 mm, and the medium-large rivers have runoff values between 25 and 400 mm (INAG IP, 2008b). The land cover across the study area is also heterogeneous with mosaics of urban, agricultural, and forestry areas in the northwest and forest, scrubland, and rain-fed agriculture in the northeast (Supplementary Material).

2.3. Species data

Riparian species composition and abundance data were obtained from the North Regional Water Administration and correspond to data generated in the scope of the Water Framework Directive monitoring in the North Portugal Hydrographic Region. Macrophyte and riparian vegetation sampling were carried out during the first cycle of the River Basin Management Plans between April and June 2010 following EU standardized methods (INAG IP, 2008a; Comité Européen de Normalisation, 2014). For each site, a 100 m longitudinal transect was surveyed for vascular plants, and all the species from the watercourse channel and the margins up to the

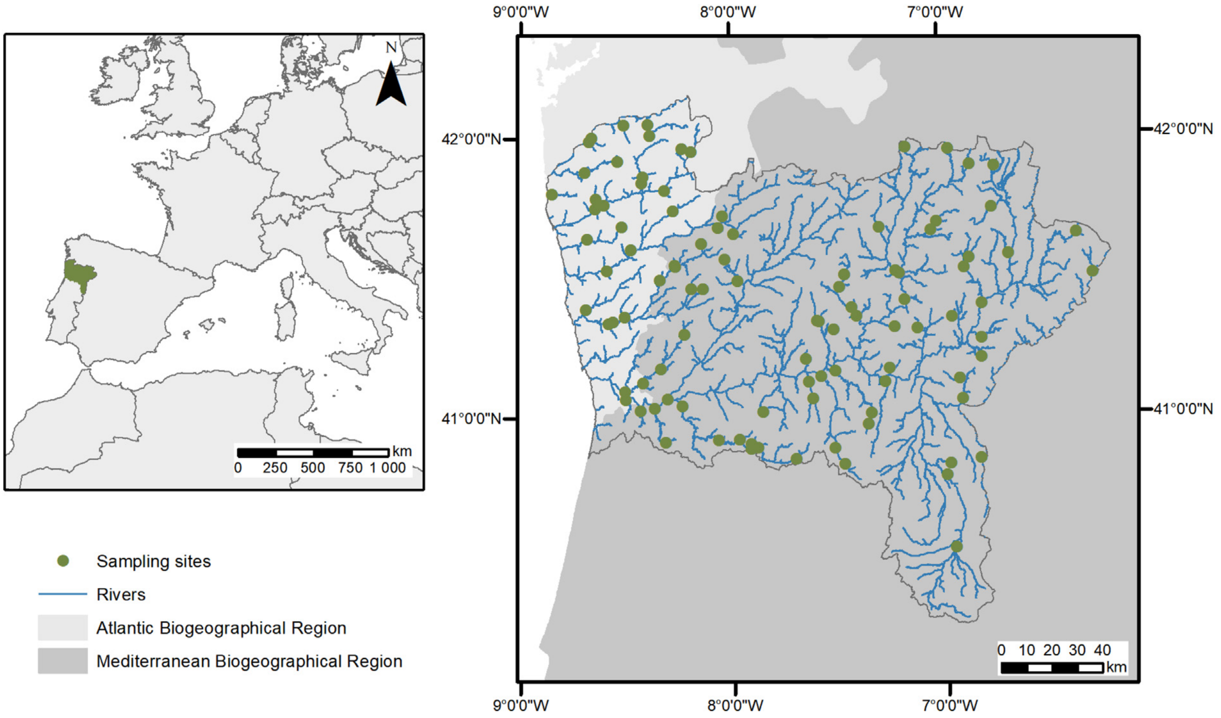

Fig. 1. Location of the study sites in the North Portugal hydrographic region shown over the European biogeographical regions (right rectangle), and the geographical setting of the study region in Southern Europe (green in the left rectangle).

line corresponding to the average annual flooding were recorded (INAG IP, 2008a). Species abundance was estimated by the percentage of cover occupied by each species relative to the transect (INAG IP, 2008a). Since this study focuses on riparian vegetation, particularly vascular plants, species recorded in the river channel, hydrophytes, and helophytes were excluded from the dataset. Species taxonomy was matched to accepted names using the taxonomic database The Plant List (2013), synonyms were combined, and infraspecific ranks were merged to the species level. Due to the high species richness across sites (420 species) and low frequency of a large proportion of species, only those with frequency ≥ 5 % across sites were maintained for functional structure analysis. The final dataset included 171 vascular plant species reflecting the most frequent and representative species of riparian plant communities in the study area, as well as >80 % of the total regional pooled abundance as assessed with R traitor package (Majekova et al., 2016; R Core Team, 2018).

2.4. Trait data

We compiled data for traits identified during the development of our conceptual framework as response and/or effect traits. The trait selection included traits identified in the development of the conceptual framework and reflects traits that underpin key trade-offs in plant strategies, influencing dispersal, establishment, and competitive ability as well as known effects on relevant ecosystem processes (Westoby, 1998; Wright et al., 2004; de Bello et al., 2010; Catford and Jansson, 2014; Laughlin and Wilson, 2014; Hevia et al., 2017). The final set of traits includes Leaf area (LA), Specific leaf area (SLA), Leaf Nitrogen content (LeafN), Life form (LifeForm), Plant height (Height), Root morphology (RootMorph), Root Depth (RootDep), Nitrogen fixation capacity (NFix), Seed bank longevity (SeedLong), Seed mass (SeedMass) and Dispersal syndrome (DispSynd). The trait selection was constrained by data availability and the completeness of the trait dataset relative to species presences and abundances in study sites. Only traits that met a threshold of ≥70 % of the regional pooled abundance were kept in the conceptual framework and in further tests to ensure missing data did not significantly affect the sensitivity of the statistical analysis (Borgy et al., 2017a; Borgy et al., 2017b).

We obtained trait data from online databases (Kleyer et al., 2008; Aguiar et al., 2013; Tavşanoğlu and Pausas, 2018; Kattge et al., 2020; Royal Botanic Gardens Kew, 2020) and complemented it with information from the literature and floras (Castroviejo, 1986-2012; Mediavilla and Escudero, 2003; Cerabolini et al., 2010; Plantureux and Amiaud, 2010; Milla and Reich, 2011; Bejarano et al., 2012; Domínguez et al., 2012; Pierce et al., 2012; Rodríguez-Gallego et al., 2015; Bejarano et al., 2016; de la Riva et al., 2016; Aguiar et al., 2018; Pan et al., 2020). Trait data from regional databases and studies, focused on the Mediterranean or Europe, were favoured in trait search when possible. Duplicate entries were removed when it was possible to identify overlap between databases. Continuous and categorical trait values were converted to standard units based on existing guidelines for trait data (Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2016) and common categories. Final species traits were obtained from the arithmetic mean of available trait values for continuous traits and the most frequent category for categorical variables considering the phenotype of species in the study area.

Since the final set of traits presented different levels of species coverage, in the statistical analyses for each trait we considered only sites where ≥80 % of the species abundance was covered by trait data. We applied this additional filtering of trait data since functional indices are sensitive to missing data and abundance distribution (Pakeman and Quested, 2007; Majekova et al., 2016). The completeness of the species traits dataset relative to the regional and site pooled abundances was assessed using the traitor package in R environment (Majekova et al., 2016; R Core Team, 2018).

2.5. Functional structure indices

We used three types of metrics to characterize community functional structure, including trait means, range, and divergence. Two community trait mean metrics were calculated: the community weighted mean (CWM) where the community trait mean is weighted by species relative abundances and the community arithmetic mean (CAM) where the trait mean is calculated with equal weight for all species present (the weight of each species present equals one). Trait range (Range) was calculated as the interval between minimum and maximum trait values. Two community divergence metrics were also calculated: Rao Quadratic entropy (Rao) weighted by species relative abundances and Rao quadratic entropy with equal weights for all species (Rao_{Pres}). We calculated standardized effect sizes to ensure that divergence metrics (Rao and Rao_{Pres}) were not correlated to species richness. The standardized effect sizes (SES = Observed Value − Mean Simulated Values / Standard deviation of Simulated Values) measured the deviation of the divergence metrics from random expectation estimated using 1000 simulated communities for each site (Gotelli and McCabe, 2002). Rao was compared to random expectation using randomization of abundances within sites (Mason et al., 2013) and Rao_{Pres} using a matrix-swap (Mason et al., 2013; de Bello et al., 2021a).

All metrics were calculated for each trait within each community, which correspond to study sites (one community per study site). CWM, CAM, Range were calculated in R using package FD (Laliberte and Legendre, 2010) and code adapted from (Götzenberger et al., 2021). Rao and Rao_{Pres} were calculated with R function “melodic” (de Bello et al., 2016). Null models were constructed in the R environment using the function “randomizeMatrix” available in the package “picante” (Kembel et al., 2010) and code adapted from Götzenberger et al. (2021).

2.6. Statistical analysis

To assess the association between traits at the community level we calculated the Pearson correlation for the traits' CWM. The correlation was calculated with R package “Hmisc” (Harrell, 2018) and the package “corrplot” was used to visualise the correlation matrix (Wei and Simko, 2021). The correlation matrix was ordered using hierarchical clustering, and based on that clustering, four groups were identified.

A range of environmental drivers including climatic, topographic, soil and land cover variables, was compiled to test for trait-environment relationships in our study area and identify key environmental drivers of functional structure. Climatic variables included annual mean temperature, minimum temperature of the coldest month, annual precipitation, and precipitation seasonality and were obtained from WORLDCLIM 2.0 (Fick and Hijmans, 2017). Potential evapotranspiration and an aridity index were obtained from Trabucco and Zomer (2019). The aridity index measures water surplus, therefore the index is higher for more humid conditions and lower for more arid conditions (Trabucco and Zomer, 2019). Elevation was obtained from the EU Digital Elevation Model (25 m spatial resolution, European Environment Agency (2016)) and used to calculate topographic and hydrographic indices including Terrain Wetness Index and Strahler's order in geographic information systems software SAGA GIS (Conrad et al., 2015) and ArcMap (ESRI, 2012), respectively. Soil textural classes were obtained from the European Soil Data Centre topsoil (20 cm depth) physical properties for Europe (Ballabio et al., 2016). The percentage of agriculture and urban land cover was calculated for the site using a 100 m buffer, for the site and vicinity using a 200 m buffer, and in the watershed, in ArcMap based on the national land cover classification for 2010 (DGT, 2010). Due to spatial mismatches between gauging stations and study sites and gaps in hydrological time series, it was not possible to include flow regime variables in our analysis.

We used linear regression to relate environmental drivers to functional structure metrics. We also tested for non-linear relationships by including a quadratic term in the linear model. The best fit was selected using the Akaike Information Criteria. For the significant models we verified the residual and quantile plots and used the Breusch–Pagan test to ensure the models met statistical assumptions of homoscedasticity. The regressions

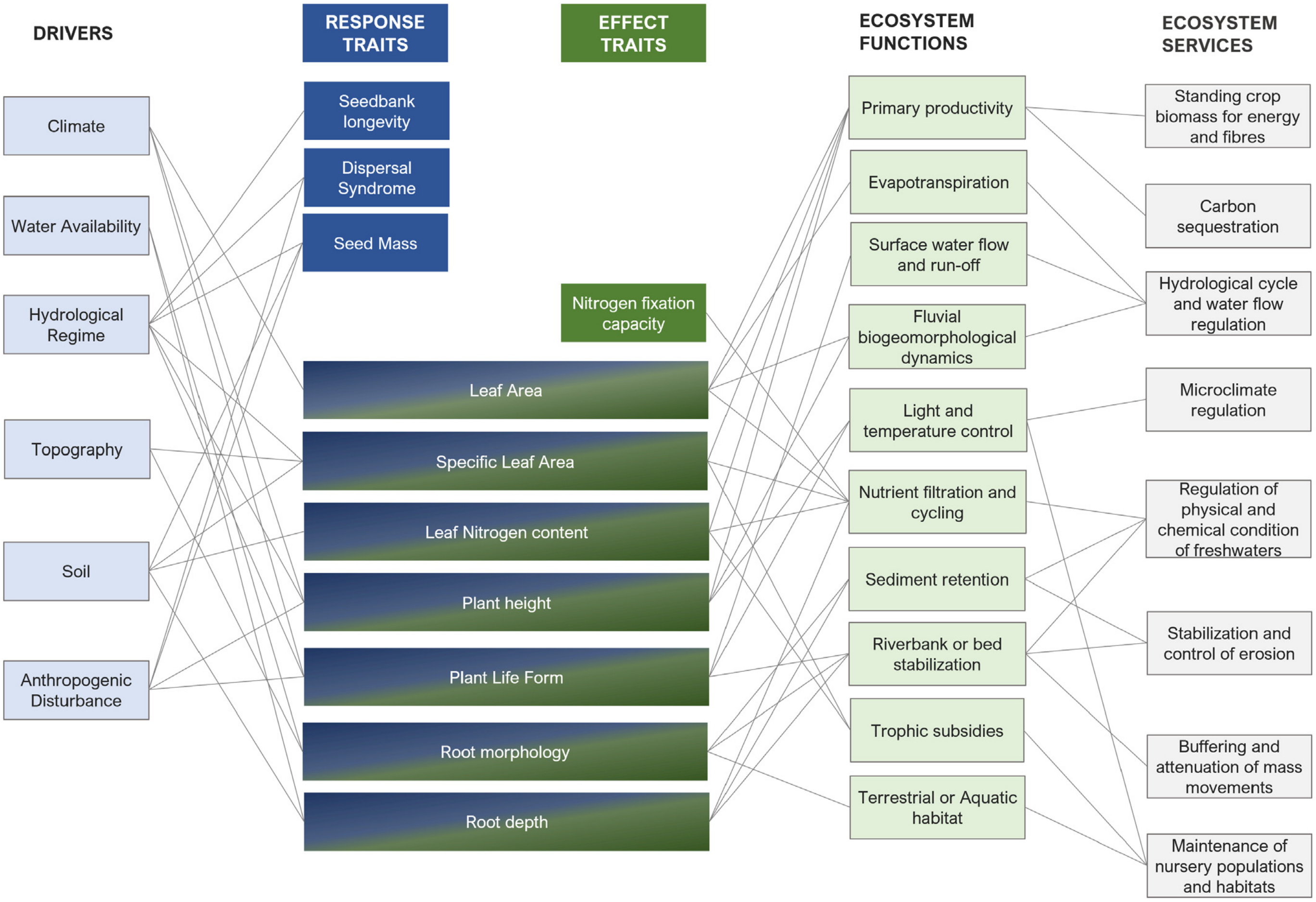

Fig. 2. Conceptual response-effect trait framework for riparian ecosystems based on the literature and restricted to traits with sufficient species coverage allowing statistical analysis. Response traits colored in blue and effect traits in green, traits that were identified as both response and effect traits present the two colors.

were calculated with "stats" package (R Core Team, 2018) and the Breusch–Pagan test with "car" package (Fox and Weisberg, 2019).

We used network analysis to visualise the links between the environmental drivers and the functional structure metrics using the R^2 of the significant regressions to create the links in the network (Blumenthal et al., 2020). The "igraph" package was used to construct the network (Csardi and Nepusz, 2006) and the package "ggraph" to visualise the network (Pedersen, 2021). To further identify groups of drivers and response traits we calculated the sum of R^2 by trait and driver and used the package "bipartite" to identify groups using the Dormann & Strauss method and 20 interactions (Dormann et al., 2008).

3. Results

3.1. Overlap between response and effect traits

For seven traits out of the eleven included in the conceptual framework we found information supporting classification as both response and effect traits (Fig. 2). Only three traits were categorized in our conceptual framework exclusively as response traits – seed bank longevity, dispersal syndrome, and seed mass- and only one as effect trait – nitrogen fixation capacity.

Based on the conceptual framework seed mass, specific leaf area, and plant height are linked to the highest number of environmental drivers including climatic, water availability and hydrological regime variables listed in the literature (Fig. 2). Conversely, leaf area and leaf N content appear to influence the highest number of ecosystem processes. Leaf area was linked to primary productivity, evapotranspiration, fluvial biogeomorphological processes, and nutrient filtration and cycling. Leaf N content was linked to primary productivity, nutrient filtration and cycling, and trophic subsidies.

Our conceptual framework suggests primary productivity is shaped by the highest number of traits including leaf area, specific leaf area, leaf N content and plant height, and affects two different services – standing biomass and carbon sequestration.

Regulating services namely hydrological cycle and water flow regulation, and regulation of physical and chemical conditions of freshwater were found to depend on the largest number of individual ecosystem processes and a wide range of effect traits.

3.2. Correlation between traits

The correlation analysis identified three main groups of correlations in traits CWM (Fig. 3). The first group includes high positive correlations

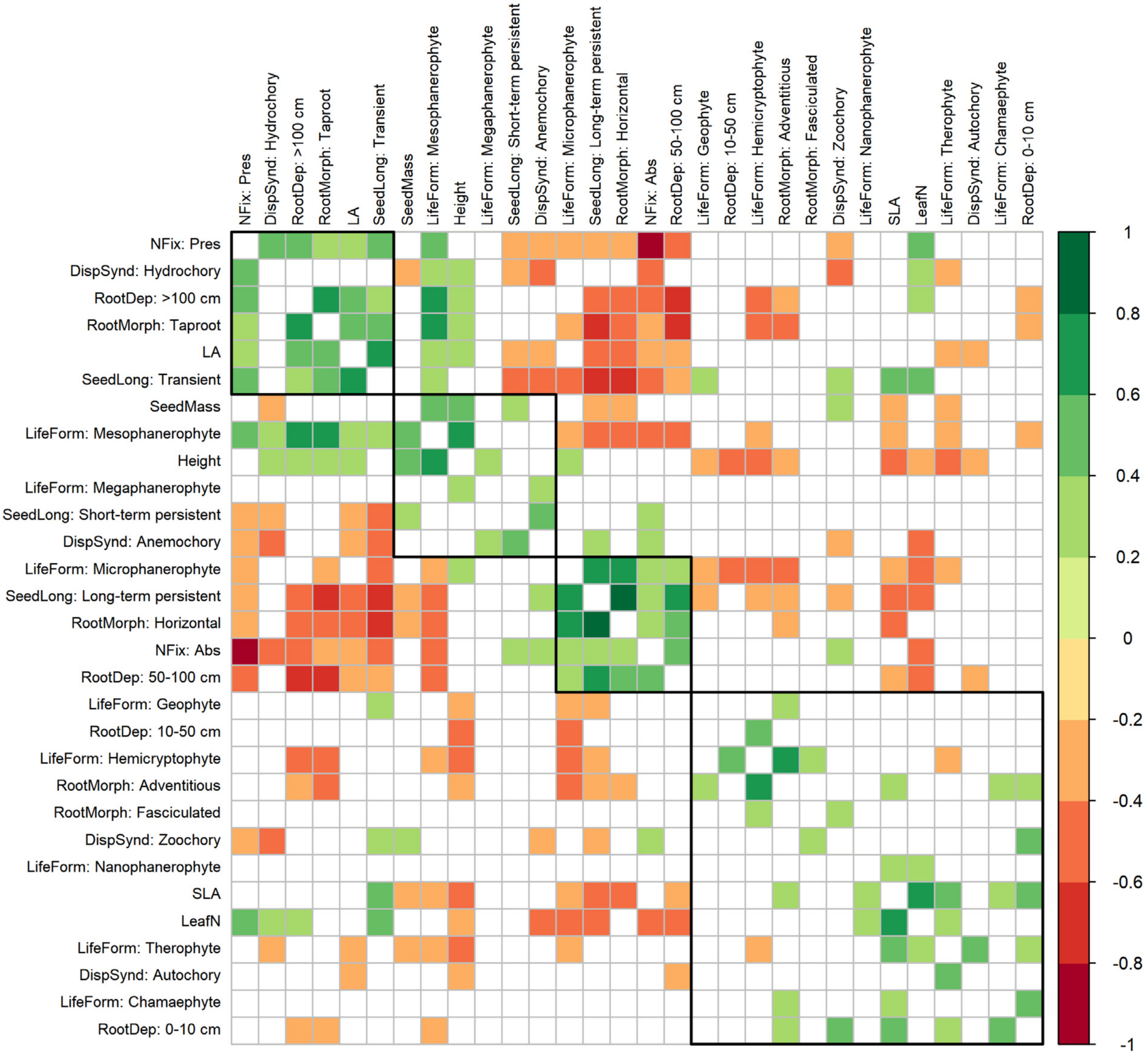

Fig. 3. Correlogram of CWM metrics Pearson correlation. Only significant correlations ($p < 0.05$) are colored. Groups of traits were identified using hierarchical clustering, using a predefined number of groups ($n = 4$). Note that for categorical traits the CWM is expressed as the percentage of each category, hence, for each categorical trait there are several entries in the correlogram.

between taproot and root depth > 100 cm percentage, leaf area and transient seed banks, and other lower but significant correlations with hydrochory and N fixation ability. The second group shows high positive correlations between height and percentage of mesophanerophytes, and other lower but significant correlations with seed mass, anemochory, short-term persistent seed bank and megaphanerophyte presence. The third group shows high positive correlations between microphanerophyte percentage, horizontal roots, long-term persistent seed bank, and lower correlations with rooting depth between 50 and 100 cm, and absence of N fixation. A fourth group was also identified, aggregating many insignificant and low correlations across a variety of traits, nevertheless, a positive correlation between specific leaf area and Leaf N was identified. An additional low but significant correlation was also identified between specific leaf area and N fixation presence.

3.3. Environmental drivers of functional structure

Generally, the environmental factors presented a higher explanatory power (R^2) for unweighted functional structure indices, CAM and Rao_{Pres}, than for abundance weighted indices, CWM and Rao (Fig. 4 and Supplementary Material). Some of the few exceptions include the effects of agriculture on life form and specific leaf area CWM, and aridity and precipitation on plant height CWM.

CAM presented the highest explanatory power for leaf area regressions with aridity ($R^2 = 0.35$, $p < 0.01$), evapotranspiration ($R^2 = 0.32$, $p < 0.01$) and precipitation ($R^2 = 0.28$, $p < 0.01$) (Fig. 4 and Supplementary Material). CWM presented the highest R^2 for Rooting Depth 10–50 cm percentage and precipitation seasonality ($R^2 = 0.21$, $p < 0.01$), followed by leaf area and aridity ($R^2 = 0.17$, $p < 0.01$), Rooting Depth > 100 cm percentage and temperature ($R^2 = 0.16$, $p < 0.01$), and hemicryptophyte percentage and temperature ($R^2 = 0.16$, $p < 0.01$) (Fig. 4). Trait range regressions had overall low explanatory power, with the highest R^2 for leaf N and elevation ($R^2 = 0.1$, $p = 0.02$), followed by height and precipitation seasonality ($R^2 = 0.09$, $p < 0.01$), and height and evapotranspiration ($R^2 = 0.07$, $p = 0.01$) (Fig. 4 and Supplementary Material).

SESRao regression also had low explanatory power, with leaf area presenting the highest R^2 for evapotranspiration and aridity ($R^2 = 0.1$, $p = 0.02$), followed by minimum temperature ($R^2 = 0.09$, $p = 0.02$) (Fig. 4 and Supplementary Material). $\text{SESRao}_{\text{Pres}}$ presented the highest explanatory power for life form and temperature ($R^2 = 0.22$, $p < 0.01$), followed by root morphology and agriculture in the basin ($R^2 = 0.21$, $p < 0.01$), and leaf N and precipitation seasonality ($R^2 = 0.2$, $p < 0.01$) (Fig. 4 and Supplementary Material).

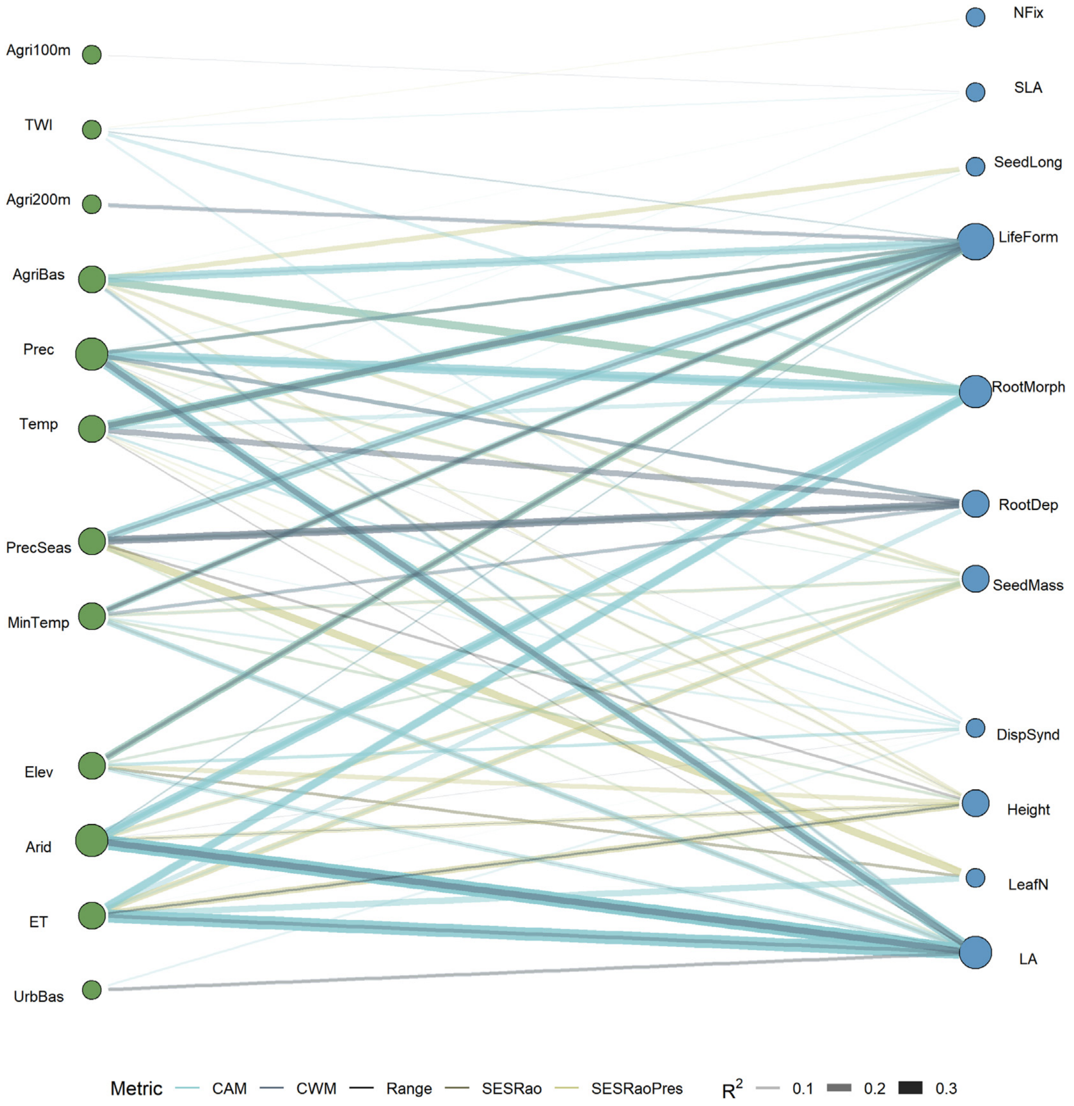

Fig. 4. Driver-trait network graph based on the explanatory power (R^2) of regressions between environmental drivers and individual trait metrics. The size of each node (circle) corresponds to the sum of R^2 for each trait and environmental factor. Line widths reflect R^2 values and line colors represent different functional structure metrics for each trait. Only significant regressions ($p < 0.05$) are shown.

The environmental driver with the highest combined explanatory power across all functional metrics and traits was precipitation closely followed by aridity and evapotranspiration (Fig. 4 and Supplementary Material). The trait most influenced by environmental factors across all functional metrics and environmental drivers was life form, followed by leaf area, and root morphology (Fig. 4 and Supplementary Material).

We identified three groups of driver-trait associations reinforcing the results of the network analysis (Fig. 5). The group with the highest combined explanatory power includes correlations between aridity, precipitation, evapotranspiration and community leaf area and height functional structure. The second group with the highest explanatory power includes correlations between temperature, elevation and minimum temperature and life form. The third group includes the correlation between precipitation seasonality and root depth.

4. Discussion

Research is still needed to understand how riparian vegetation functional structure shapes ecosystem functions and services and whether environmental change impacts will compromise the supply of key ecosystem services, particularly at larger scales and for comprehensive sets of drivers and services (Dufour et al., 2019; Gonzalez Del Tanago et al., 2021). Addressing this research gap is critical to adaptively managing ecosystems to sustain biodiversity and ecosystem services.

The response-effect trait framework used here for riparian ecosystems synthesized knowledge on the traits that underpin ecosystem services, enabled the assessment of the sensitivity of ecosystem functioning to environmental changes, and the construction of generalizable larger-scale frameworks on riparian ecosystem functioning.

Our synthesis of the literature and our results support the hypothesis that riparian response and effect traits present high overlap and correlation, and consequently riparian communities are likely to propagate the impact of environmental change to ecosystem functioning. This finding is in line with previous work that concluded that riparian ecosystems are highly sensitive to climate change and that services are likely to be affected (Capon et al., 2013). Our results also support the hypothesis that precipitation-related variables are the main drivers of functional structure, that leaf area is among the most responsive traits, and that regulation services are among the most sensitive.

4.1. Links between response and effect traits

Overall, the high overlap between response and effect traits indicates a high interdependence between ecosystem responses and ecosystem functioning. In line with our results, a recent review found indirect evidence of high overlap between response and effect traits across biological groups, reaching 90.4 % for vegetation traits (Hevia et al., 2017). Riparian vegetation studies have considered lower numbers of traits as response and effect, with one study considering eight out of 30 traits (25 %) (Bruno et al., 2016), and another considering only three out of 16 (18 %) (Diehl et al., 2017). However, there are key traits which are consistently identified as response and effect in different studies namely leaf area, leaf N, height, root depth, and architecture (Bruno et al., 2016; Diehl et al., 2017; Hevia et al., 2017). The main limitation of this overlap assessment is in the classification of traits into response and effect traits which relies on the literature. Most studies also rely on the literature and expert knowledge to classify traits, often opting to classify traits as one type or the other (Lavorel and Garnier, 2002; Bruno et al., 2016; Diehl et al., 2017). However, this classification is not always straightforward or well supported by empirical data,

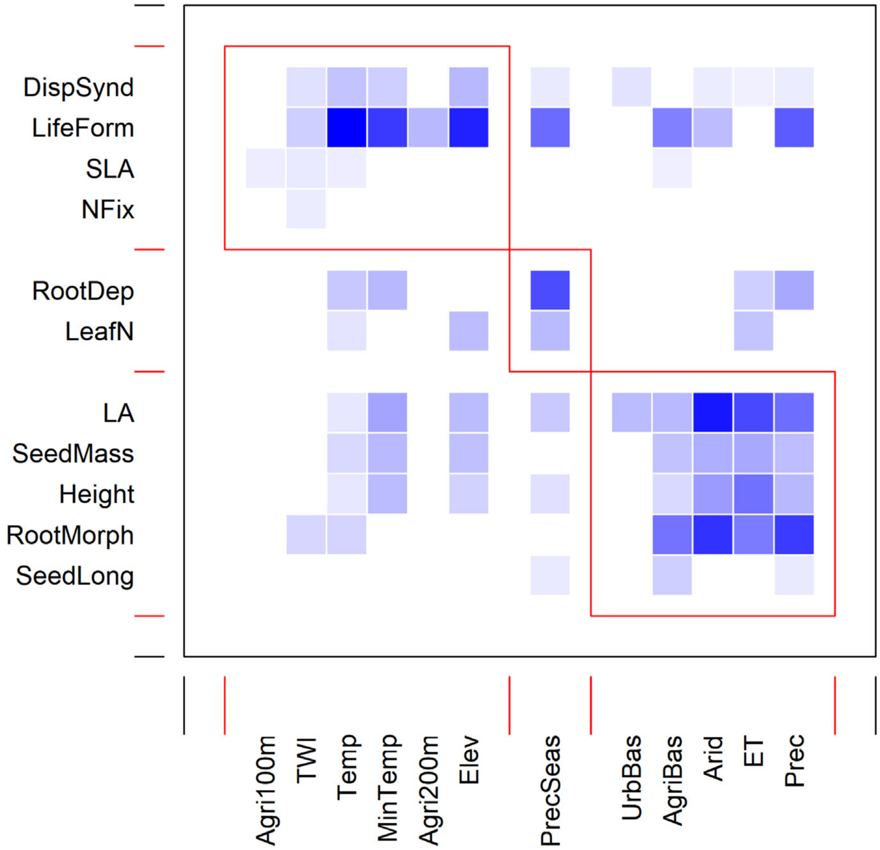

Fig. 5. Driver-trait bipartite network based on the explanatory power (R^2) of regressions between environmental variables and trait metrics. Darker blues represent higher explanatory power of the environmental variables, quantified by the sum of R^2 by trait and environmental variable. Only significant regressions ($p < 0.05$) were considered in R^2 sum. Red rectangles and lines in the axis represent groups of driver-trait associations, obtained after 20 interactions.

since it depends for instance on drivers analyzed and focal organisms or species (Hevia et al., 2017; de Bello et al., 2021a).

The significant correlations between community-weighted means of traits reinforced the interdependence between ecosystem responses and ecosystem functioning. For instance, we found a positive correlation between microphanerophyte percentage and a long-term persistent seed bank. Microphanerophyte species in the study area include riparian pioneer species, such as willows (*Salix atrocinerea* Brot., *S. salviifolia* Brot.), which have several traits adapted to the colonization of exposed riparian surfaces, such as persistent seed banks (Catford and Jansson, 2014; Politti et al., 2018). These traits and species are important for riparian recruitment, colonization and geomorphic processes since they are related to disturbance response strategies (avoidance vs resistance), recolonization of disturbed sites, and stabilization of landforms (Diehl et al., 2017; Martínez-Fernández et al., 2018).

The correlation between community height and mesophanerophytes suggests that ecosystem functions positively associated with community height will depend mainly on the presence and abundance of mesophanerophytes, which include key riparian species such as common alder (*Alnus glutinosa* (L.) Gaertn.) and narrow-leaved ash (*Fraxinus angustifolia* Vahl) in the study area. Other studies have confirmed the correlation between height and life form in riparian ecosystems and identified several other correlated traits including rooting depth, leaf area, wood density and growth rate (Stromberg and Merritt, 2016; Diehl et al., 2017).

Additional correlations between leaf area and N fixation ability, taproots with > 100 cm, and transient seed bank suggest a link to a keystone riparian species in the study area. The positive correlation between these traits is probably driven by the abundance of common alder in the communities, which is the only riparian tree in the study area with N fixation ability. This finding, shows the importance of common alder, a keystone riparian species, in nitrogen fixation, nutrient cycles, and bank stabilization (Claessens et al., 2010). A recent study showed that the loss of common alder can negatively affect leaf litter decomposition in streams (Alonso et al., 2021), highlighting the important role of this species in nutrient cycling and leaf litter inputs to aquatic systems.

Moving forward in the application of response-effect trait frameworks requires improving the coverage of commonly measured traits and less studied response and effect traits. During the development of our conceptual framework, we had to limit the traits we included based on the extent of the species trait coverage so we could use them in the statistical analysis (Majekova et al., 2016; Borgy et al., 2017b). We encountered several gaps in species trait coverage for riparian plants such as the Iberian endemic *Salix salviifolia* Brot. along with varying degrees of coverage in woody and non-woody species. Additionally, traits such as xylem vulnerability to cavitation or stem specific density could be useful response or effect traits (Griffin-Nolan et al., 2018), however, they remain underrepresented in databases for the studied riparian species hindering their use.

4.2. Environmental drivers of communities functional structure

As expected, annual precipitation and aridity gradients were the most predictive drivers of riparian functional structure. This finding suggests riparian vegetation is sensitive to large-scale gradients of water availability and evaporative stress, similarly to local water availability and upland vegetation. A study in semi-arid rivers found interactive responses of riparian vegetation composition to hydrology and climate, supporting the similar effects on vegetation of regional climatic gradients and local hydrological gradients of water availability (Butterfield et al., 2018). Another study evaluating the relative contributions of environmental, hydrological, and land use variables on the abundance of riparian woody functional groups found a larger effect of climate and geomorphological variables than local hydrological variables (Aguiar et al., 2018). We cannot exclude the possibility that local hydrological variables (e.g., water table depth) would be equally important drivers, however, it was not possible to test this in our study due to lack of data. This finding is particularly relevant since climate change scenarios predict lower annual precipitation and summer precipitation for the study area and in the Mediterranean (Cramer et al., 2018). Hence, riparian functional structure is expected to shift to more conservative functional strategies, characterized by lower leaf area and height, as currently observed in Mediterranean and arid regions in response to local water availability gradients (Stromberg and Merritt, 2016; Aguiar et al., 2018; Scott and Merritt, 2020). Considering that the study area is in a transition zone between the Atlantic and Mediterranean climates this trend may represent significant shifts from the current functional structure depending on the magnitude of change.

Precipitation and aridity were the most predictive drivers of leaf area mean metrics, showing the positive effect of precipitation and water availability on leaf size traits. Leaf area has been reported to strongly decline in riparian plant guilds with distance to groundwater (Stromberg and Merritt, 2016). This also follows known patterns of reduced leaf size under water limitation (Li et al., 2020). These findings underline the need to integrate regional climatic and water availability drivers in a hierarchical approach to study riparian functional structure and suggest leaf area may be a suitable response trait to study functional structure along precipitation and water availability gradients (Lozanovska et al., 2018; van der Plas et al., 2020).

Nevertheless, life form was the trait for which drivers were the most predictive. Life form average metrics and species divergence metrics were influenced by a wide range of drivers. Life form classification aggregates information from species' growth form, life-span and adaptation to unfavourable conditions, therefore it is expected to respond to several drivers and for different life forms to present different responses (Merritt et al., 2010; Laughlin and Wilson, 2014). The results showed an important effect of minimum and annual temperature associated with elevation, increasing the number and cover of hemicryptophytes, decreasing the cover of microphanerophytes, and decreasing the divergence between species life forms. Minimum temperatures are known to limit plant distributions due to the physiological effects of freezing temperatures and recent studies have shown that minimum temperature influences riparian vegetation composition in semi-arid rivers (Palmquist et al., 2018). The results also showed agricultural land use increased the cover and percentage of therophytes, while decreasing the cover of mesophanerophytes. These findings are consistent with the introduction of ruderal and annual species by agricultural practices and the reduction or complete removal of tree cover along the river (Hanna et al., 2020).

4.3. Sensitivity of ecosystem services to environmental change

Overall regulation services and standing biomass appear to be the most sensitive to environmental change, namely increased aridity, and watershed-scale agriculture. The high overlap between response and effect traits, and the dependence of ecosystem services on multiple functions and traits, renders many of these services sensitive to environmental change. Considering only the effects of precipitation and agriculture percentage on leaf area and plant life form we expect effects on primary productivity, evapotranspiration, fluvial biogemorphological dynamics, nutrient filtration and cycling, and almost all the key riparian ecosystem services.

Based on the above and information from the literature we expect changes in functional structure associated with large increases in aridity or agriculture to cause declines in the supply of several regulation services relative to current baselines (Hough et al., 2018; Hanna et al., 2020). This is supported by information from other studies which reported declines in surface water or water tables led to increases in annual species and shorter canopies affecting geomorphic processes such as sediment stabilization (Stromberg et al., 2010), or a lower supply of habitat provisioning and recreation services (Hough et al., 2018). Agricultural practices have also been shown to significantly decrease the amount of carbon stored in riparian forests by reducing the abundance of trees (Hanna et al., 2020). Nevertheless, the trends may be context and service dependent as evidenced by a study that reports the maintenance of supply of several regulating services due to the replacement by non-native species (Hough et al., 2018). Further studies and integration of knowledge are needed so that we can link riparian functional structure, service supply levels, and synergies and trade-offs between services (e.g. Hanisch et al. (2020)).

In this work we evaluated the sensitivity of riparian ecosystem functioning to environmental changes based on impacts via functional structure, however, it should be noted that abiotic and local factors may be equally important (van der Plas et al., 2020). For instance, the effects of abiotic change, such as increased drought intensity or duration, may impact primary productivity before functional change (Li et al., 2020; van der Plas et al., 2020). Local factors including stream geomorphology, riparian structure and width also shape riparian ecosystem functioning (Feld et al., 2018). However, integrating the effects of such a wide array of factors in a complex system like riparian areas remains challenging (Dufour et al., 2019; Gonzalez Del Tanago et al., 2021).

The combination of high sensitivity to environmental change with a range of key ecological functions and important ecosystem services reinforces the need for adaptive riparian management (Capon et al., 2013; Capon and Pettit, 2018). For instance, the microclimate regulation effect will be increasingly important to mitigate the effects of droughts and heatwaves for aquatic and terrestrial organisms as well as for people in urban areas (Capon et al., 2013; Capon and Pettit, 2018; Riis et al., 2020). To address these concerns, riparian management will need to continue to protect multifunctional riparian ecosystems and restore impaired ones (e.g., due to agriculture) to improve ecosystem functioning and service supply and build resilience to environmental change (Capon et al., 2013; Capon and Pettit, 2018). In this context, functional approaches can be instrumental in ensuring riparian ecosystems continue to satisfy ecological and societal needs under environmental change by linking riparian communities with ecosystem functioning and services.

5. Conclusion

Our findings suggest riparian plant communities are likely to propagate the effects of environmental change to ecosystem functioning, affecting several regulation ecosystem services. Aligned with our main hypothesis, we found that riparian vegetation displays a high overlap between response and effect traits, as well as significant linkages between traits. Our results also supported the hypothesis that functional structure is most sensitive to the total amount of precipitation and aridity. The most sensitive traits are also largely in accordance with our hypothesis as leaf area was one of the most sensitive followed by life form, which is related to height. Regulation services were also confirmed as likely to be affected by environmental changes.

Further research into trait and ecosystem service synergies and trade-offs would further improve our ability to predict the trajectories of ecosystems and their services. Nevertheless, this research highlights the sensitivity of riparian ecosystems to environmental changes and suggests that functional approaches may help guide adaptive management strategies to sustain biodiversity and ecosystem services.

CRediT authorship contribution statement

Ana Paula Portela: Conceptualization, Data curation, Methodology, Formal analysis, Writing – original draft, Writing – review & editing. **Isabelle Durance:** Conceptualization, Methodology, Writing – review & editing. **Cristiana Vieira:** Methodology, Writing – review & editing. **João Honrado:** Methodology, Writing – review & editing.

Data availability

The authors do not have permission to share data.

Declaration of competing interest

The authors have no conflict of interest to declare.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.160549.

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