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# Environmental Filtering of Leaf Traits, Spectral and Genetic Variation in *Phragmites australis*: Responses and Spatial Patterns

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## ABSTRACT

1. Intraspecific variation in plant phenotypes mediates responses to changing environmental conditions; however, a comprehensive analysis of factors influencing variation in plant species traits is still lacking in freshwaters. Here, we used *Phragmites australis*, a cosmopolitan foundation wetland species, to understand adaptation by plants to environmental conditions and spatial patterns in local adaptation by combining information on functional traits, including remote sensing-derived spectral traits and genetic diversity.
2. We measured eleven leaf functional traits, including four spectral traits related to leaf structure and pigments content, plus two genetic diversity indices in 48 plots of *P. australis* from eight wetland systems in Italy. We used GAMMs to model trait responses to water and sediment conditions. We also produced continuous maps of trait variation using very-high-resolution maps obtained by remote sensing and used trait-environment relationships to analyse plant responses at fine and large scales.
3. Ten out of eleven traits and genetic indices were significantly influenced by at least one environmental variable. Eutrophication and N/P ratio limitation led to a decrease in values of traits related to photosynthesis and productivity, especially for water phosphate concentration $> 40\,\mu g\,L^{-1}$, and to increased genetic diversity. Extreme conditions at specific sites (like high conductivity above 3000 $\mu S\,cm^{-1}$) also determined a marked increase in traits related to high resource-use efficiency.
4. Stressful conditions determined by P-limited eutrophication induced trait and genetic response of *P. australis*, shifting to more conservative strategies. Moreover, continuous maps of remotely sensed plant traits that respond strongly to environmental variables highlighted patterns of eutrophication and resource-use at the site scale, providing an innovative approach to monitoring sites densely covered by vegetation.
5. This study demonstrates that coordinating functional, spectral and genetic data can robustly describe factors influencing diversity and responses in plants, and shows that consistent intraspecific variation of a dominant species can influence ecosystem processes at different scales.

Paolo Villa and Rossano Bolpagni are to be considered joint senior authors.

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## 1 | Introduction

Plants can exhibit a remarkable capacity to adapt to heterogeneous and changing environments. While species-level phenotypic traits have long been used to explain patterns of plant performance and community assembly (Lebrija-Trejos et al. 2010; Díaz et al. 2016), growing evidence shows that phenotypic variation within species—intraspecific variation—can play an equally critical role (Violle et al. 2012; Rixen et al. 2022). Aquatic vegetation often forms extensive, visually uniform stands, represented by floating-leaved species or emergent vegetation (e.g., common reed). Despite their apparent homogeneity, these monospecific stands can harbour considerable intraspecific trait variation that is influenced by their genetic diversity as well as by their ecological interactions (Dalla Vecchia, Castellani, et al. 2024; Dalla Vecchia, Coppi, et al. 2024). Leaf traits, in particular, are informative of trade-offs in resource acquisition strategies (Wright et al. 2004), and therefore they are key in unravelling plant-environment relationships. However, a comprehensive understanding of how leaf functional variation and genetic differentiation interact across environmental gradients is hard to achieve as relationships are context-dependent, especially in freshwater environments (Alahuhta et al. 2019) and can vary within a few metres as well as at large scales.

Remote sensing is an invaluable tool to detect leaf functional variation patterns across scales, providing data from individual or canopy level to regional scale (Villa et al. 2017; Pinardi et al. 2018; Dalla Vecchia, Coppi, et al. 2024). These data can provide spatially continuous information, which is crucial in logistically complex environments like wetlands (Silva et al. 2008; Jetz et al. 2016; Gamon et al. 2019). Specific regions of the reflectance spectrum of plant leaves are associated with plant functions, such as water and pigments content and leaf mesophyll structure (Féret et al. 2017, 2021). In this sense, spectral features can be used as plant functional traits (spectral traits) related to plant fitness (*sensu* McGill et al. 2006), and they can be measured either directly from leaves using a spectroradiometer or derived from very-high-resolution (VHR) multispectral images. Starting from the relationships between (spectral) traits and environmental variables modelled with field-collected data, we can use spectral traits derived from multispectral images as predictors of environmental variation, mapping driver-response patterns at a larger scale. For example, this could allow the identification of eutrophication or pollution hotspots in cases when direct spectral analysis of water quality from remote is not possible, such as in areas with dense aquatic vegetation.

*Phragmites australis* (Cav.) Trin. ex Steud. (common reed) is a cosmopolitan wetland plant which forms dense, uniform stands that can dominate the plant community (Castellani, Coppi, et al. 2023). It is widely spread in a variety of conditions, from oligotrophic to eutrophic, including brackish water (Landucci et al. 2013), it positively influences the nutrient turnover and ecosystem stability, and provides a habitat to several wetland species (Saltonstall and Meyerson 2016; Milke et al. 2020). Its wide ecological amplitude makes this species an ideal model to study the drivers of intraspecific variation (Li et al. 2014; Ren et al. 2020; Castellani, Coppi, et al. 2023; Haldan et al. 2023). The factors and the interactions that drive leaf functional trait variation in *P. australis* are still not clear, and existing studies mainly investigate the effects of specific factors like soil moisture or salinity, or the genetic make-up of the plant, rather than the interaction of spatially variable factors within wetlands (like, for instance, nutrient availability in wetlands) that can vary considerably (Eller et al. 2014; Zhang et al. 2019, 2021; Zhou et al. 2021; Chen et al. 2024). *Phragmites australis* also presents high genetic diversity and has a high number of genotypes and lineages that respond differently to environmental factors, like salinity, nutrients and light (Hanganu et al. 1999; Hansen et al. 2007; Eller et al. 2014; Ren et al. 2019; Lambertini et al. 2020), suggesting that the distribution of the genotypes within a wetland is also influenced by spatially variable factors. However, compared to true hydrophytes, emergent species like *P. australis* may be less dependent on local water quality conditions and may behave more similarly to terrestrial plants (Zhou et al. 2022). Therefore, understanding the interplay between functional traits, genetics and environmental conditions could improve our knowledge of the processes underlying the variability of the performance and morphologic variation of this ecologically important species.

In this study, we aim to fill the gap around how local environmental conditions shape intraspecific variation in leaf traits of *P. australis*, by combining information on functional traits (including spectral traits) and genetic diversity. We analysed 48 stands of *P. australis* in eight distinct water bodies located in Central and Northern Italy where genetic variation in the common reed is known to occur (Castellani, Coppi, et al. 2023). With a remote sensing approach, we mapped the spectral trait variation measured in the field and at the water body scale with VHR images to identify the underlying spatial patterns of trait-environment relationships. We hypothesized that sediments have a stronger effect than water-related variables on leaf trait variation, as *P. australis* relies less on the aquatic environment than true hydrophytes. We also hypothesized that leaf trait and genetic variation are determined by site-specific conditions that are not directly captured by the water and sediment variables investigated in this study but may be influenced by the history of land use, climate and species interactions that characterize each study site.

## 2 | Materials and Methods

### 2.1 | Study Sites

This study was carried out in seven lakes and one wetland located in Central and Northern Italy covering a total area larger than 30,000 $km^2$ (Figure 1). The sites included natural and artificial lakes, a coastal brackish wetland, a shallow lake, a deep volcanic lake and a swamp (Table 1).

### 2.2 | Sampling Design

Sampling was carried out in July 2020 for lakes Chiusi and Martignano, and between July and early September 2021 for all other sites, during the flowering season of *P. australis*.

Overall, we sampled 48 plots of about 16 $m^2$ each from the 8 study sites, which were all dominated by *P. australis*. A variable number of plots were sampled within each site, depending on the size of the site and of the plant populations. All plots were at least 200 m apart.



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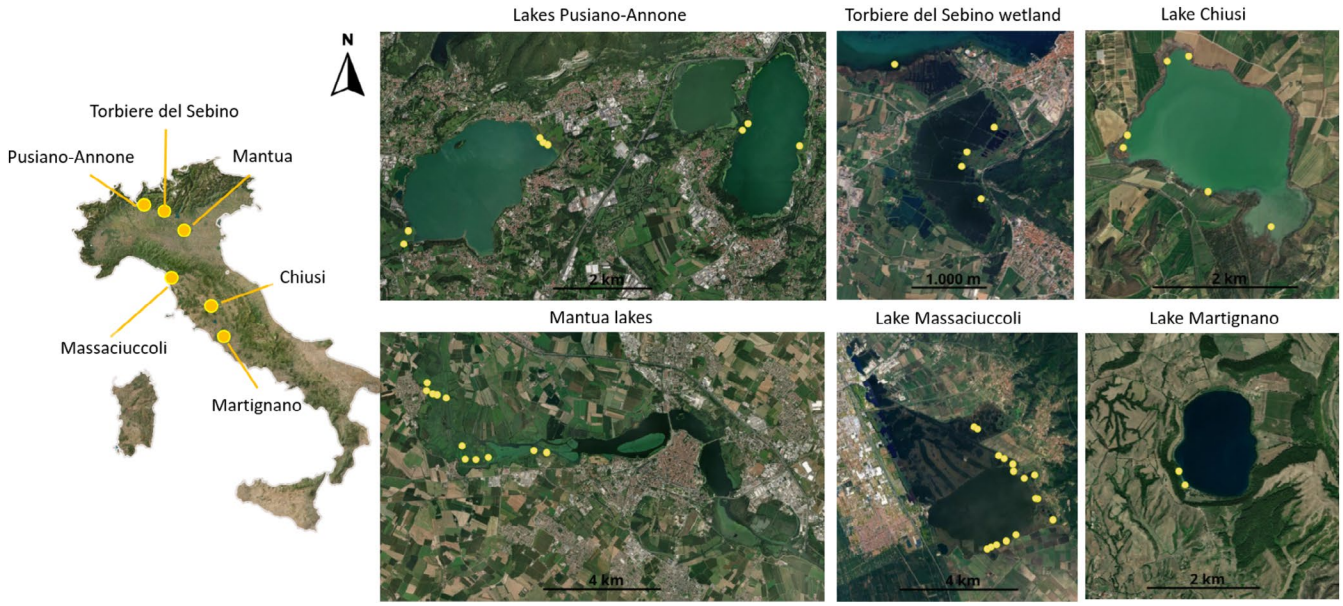



**FIGURE 1** | Map of the study sites in Italy. On the right panels the locations of each sampling plot are indicated in yellow.

**TABLE 1** | Location of the study sites and their habitat type.

| Site | Decimal latitude | Decimal longitude | Habitat type | Number of plots sampled |
|---|---|---|---|---|
| Annone | 9.3 | 45.8 | Sub-alpine lake | 3 |
| Pusiano | 9.3 | 45.8 | Sub-alpine lake | 5 |
| Iseo | 10.0 | 45.8 | Sub-alpine lake | 1 |
| Torbiere del Sebino | 10.0 | 45.6 | Swamp | 4 |
| Mantua | 10.7 | 45.2 | Artificial shallow lakes system | 11 |
| Chiusi | 12.0 | 43.1 | Shallow lake | 6 |
| Massaciuccoli | 10.3 | 43.8 | Brackish lake | 16 |
| Martignano | 12.3 | 42.1 | Deep volcanic lake | 2 |

Plots were selected from macrophyte maps derived from very-high-resolution (VHR) satellite images (2 m pixel) by drawing plots randomly within 3 m of the waterfront of stands that were larger than 100 $m^2$ and logistically reachable with a light boat. Plots were further selected by three levels of Water Adjusted Vegetation Index (WAVI; Villa et al. 2014), as a spectral proxy of canopy density, to ensure representativeness of within-site variation. A floristic survey was conducted in each plot to record species presence and percentage cover. Additionally, water, sediment and plant samples were collected for environmental characterization, as well as for the determination of leaf functional traits (including spectral traits) and genetic analyses.

## 2.3 | Environmental Characterization

In each plot we collected one measure of water electrical conductivity, pH, water nitrate, phosphate (Soluble Reactive Phosphorus—SRP), and dissolved reactive silica concentration, sediment organic matter content and sediment total phosphorus (Sed.TP) content (values for each plot provided in Table S1). Electrical conductivity and pH were determined in situ using a multiparameter probe (YSI 556 MPS), while site water was filtered with glass fibre filters (Whatman GF/F) and kept refrigerated. Phosphate and dissolved reactive silica were determined spectrophotometrically following Valderrama (1977) and Lienig et al. (1978), respectively. The remaining water was filtered with 0.2 μm pore size nylon filters, and nitrate concentration was determined with ion chromatography (883 Basic IC plus Metrohm, Herisau, Switzerland). A sample of 50 mL of sediment was collected from the upper 5 cm sediment layer—representing the most reactive sediment horizon in direct contact with the water mass—in each plot, and frozen as soon as possible after collection. Sediment samples were then homogenized, and a subsample was dried at 60°C for 24 h. An aliquot of ca. 0.3 g was incinerated at 450°C for 4 h. Sediment organic matter content was determined gravimetrically (Buchanan et al. 1984). Sed.TP includes both organic and inorganic P pool in the sediments, and was analysed spectrophotometrically from the ashes, after extraction in HCl (Aspila et al. 1976).

The sites covered a gradient of environmental conditions, with electrical conductivity ranging from 217 μS $cm^{-1}$



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**TABLE 2** | Environmental conditions of sampled sites.

| Site | pH | SPC | DRSi | SRP | Nitrate | Sed.OM | Sed.TP |
|---|---|---|---|---|---|---|---|
| | | $\mu S\ cm^{-1}$ | $\mu g\ L^{-1}$ | $\mu g\ L^{-1}$ | $mg\ L^{-1}$ | % | $\mu g\ g^{-1}$ |
| *Minimum* | 7.51 | 217 | 14.34 | < 4 | < 1 | 2.10 | 178.40 |
| *Median* | 8.46 | 406 | 860.55 | 6.32 | 0.10 | 31.00 | 835.45 |
| *Maximum* | 10.26 | 3470 | 1335.74 | 78.51 | 9.57 | 83.60 | 2278.30 |
| Annone | 7.96 (0.22) | 292 (2.45) | 603.46 (142.83) | 5.05 (3.55) | 0.07 (0.03) | 27.07 (22.08) | 616.43 (308.97) |
| Pusiano | 8.18 (0.38) | 221 (4.83) | 126.14 (81.66) | 10.09 (2.54) | 0.59 (0.10) | 33.46 (23.49) | 1069.70 (748.69) |
| Iseo | 8.28 (0.27) | 234 (13.73) | 270.11 (7.52) | 0.14 (0) | 1.82 (1.27) | 21.6 | 693.80 |
| Torbiere del Sebino | 9.97 (0.25) | 293 (5.35) | 892.46 (170.55) | 39.55 (5.07) | 0.89 (1.32) | 54.90 (14.09) | 895.48 (522.56) |
| Mantua | 7.86 (0.22) | 398 (6.21) | 1045.99 (133.16) | 51.90 (17.06) | 8.29 (0.97) | 21.28 (14.41) | 1048.00 (139.06) |
| Chiusi | 8.24 (0.42) | 558 (19.29) | 856.75 (60.45) | 6.50 (2.29) | 0.02 (0.02) | 25.95 (11.01) | 476.63 (182.39) |
| Massaciuccoli | 8.72 (0.21) | 2820 (491.74) | 963.39 (323.84) | 2.65 (2.94) | 0.01 (0.24) | 44.59 (19.74) | 819.88 (339.91) |
| Martignano | 8.93 (0.04) | 424 (1.41) | 18.15 (5.38) | 3.53 (3.95) | 0.03 (0.04) | 2.85 (1.06) | 463.10 (402.63) |

*Note:* Overall minimum, median and maximum values for each environmental variable are provided. For each site, mean and standard deviation (in brackets) are shown.
Abbreviations: DRSi, dissolved reactive silica; Sed.OM, sediment organic matter content; Sed.TP, sediment phosphorus content; SPC, water electrical conductivity; SRP, phosphate.

(Pusiano) to 3470 $\mu S\ cm^{-1}$ (Massaciuccoli), pH ranging between 7.5 (Pusiano) and 10.3 (Torbiere del Sebino), phosphate ranging between $< 4.0\ \mu g\ L^{-1}$ (Massaciuccoli) to $78.5\ \mu g\ L^{-1}$ (Mantua), while sediment organic matter content ranged between 2.1% in Martignano and 83.6% in Massaciuccoli (Table 2).

## 2.4 | Leaf Traits

In each plot, the first fully developed leaf from the apex of the plant of 8 healthy individuals (at least 1 m apart from each other and with no signs of herbivory or disease) was collected for the measure of functional traits (including spectral traits).

Reflectance spectra were measured from each leaf with a portable spectroradiometer (SR-3500, Spectral Evolution, Lawrence, USA; range covered: 350–2500 nm) within seconds from leaves detachment. Radiance reflected from the adaxial side of each leaf laid on dark background (black neoprene with absolute reflectance factor < 5%) was measured and converted to reflectance via readings taken over white standard panel (Spectralon, with absolute reflectance factor > 95%).

From the reflectance spectra we derived four specific spectral traits connected to pigment content and leaf structure. These traits were: (i) $r440_{rough}$ (i.e., the mean reflectance between 430 and 450 nm), related to leaf surface roughness and structure (e.g., presence of trichomes, Sims and Gamon 2002); (ii) $r515_{car}$ (i.e., the mean reflectance between 510 and 520 nm), related to the absorbance band of carotenoids and anthocyanins (Féret et al. 2017; Peters and Noble 2020); (iii) $r625_{chl}$ (i.e., the mean reflectance between 610 and 640 nm), inversely related to chlorophyll-*a* and -*b* content on a surface basis and their ratio (Villa et al. 2021); and (iv) $r800_{mesoph}$ (i.e., the mean reflectance between 780 and 820 nm), related to mesophyll structure complexity (Table 3) (Féret et al. 2017).

After reading the spectra, leaves were stored in sealed plastic bags and kept cool and moist until processing, within few hours. Five leaves per plot were used to determine the following structural traits: leaf area, specific leaf area and leaf dry matter content. The fully hydrated leaves were weighed (scale precision 0.0001 g) and scanned with a portable scanner at 300 dpi, and subsequently dried at 60°C for 48 h. Leaf area was calculated using the software imageJ (Schneider et al. 2012). Specific leaf area was derived as the ratio between leaf area and leaf dry weight, while leaf dry matter content was determined as the ratio between leaf dry and fresh weight (Pérez-Harguindeguy et al. 2013). Leaf pigments were analysed spectrophotometrically from the remaining three leaves after extraction of ground fresh leaf tissue in 80% acetone for 24 h (Wellburn 1994). From this analysis we derived leaf chlorophylls content, expressed as sum of chlorophyll-*a* and chlorophyll-*b* on a fresh weight basis, and ratio between chlorophylls and carotenoids. Leaf P content was measured in three replicates per plot using the same methodology described for sediments. Leaf nitrogen (N) content was determined by a combustion analysis with an elemental analyser (Thermo FlashEA 1112) on one sample per plot, pooling together all dried leaves.

## 2.5 | Genetic Analyses

A second healthy leaf was collected from the same culm selected to collect the previous leaves and immediately dried in silica gel for the genetic analyses. The AFLP protocol was conducted on 403 leaf samples (from seven to eight for each plot). DNA was extracted using a modified 2× cetyltrimethylammonium



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**TABLE 3** | List of functional traits (including spectral traits) and genetic diversity indices, with related abbreviations, units of measurements and ecological meaning.

| Trait/Index | Abbreviation | Unit of measurement | Meaning |
|---|---|---|---|
| Leaf Area | LA | $mm^2$ | Leaf size |
| Specific Leaf Area | SLA | $mm^2 mg^{-1}$ | Acquisitive resource-use strategy |
| Leaf Dry Matter Content | LDMC | $mg g^{-1}$ | Conservative resource-use strategy |
| Leaf Chlorophylls Content | Chl | $\mu g g^{-1}$ | Photosynthetic capacity |
| Chlorophylls/Carotenoids ratio | Chl/Car | ratio | Pigments balance |
| Leaf Phosphorus Content | P | % dry weight | Acquisitive resource-use strategy |
| Leaf Nitrogen to Phosphorous Ratio | N/P leaf | ratio | Nutrient balance and limitation |
| Leaf reflectance between 430 and 450 nm | $r440_{rough}$ | ratio | Surface roughness and composition |
| Leaf reflectance between 510 and 520 nm | $r515_{car}$ | ratio | Carotenoids and anthocyanins content |
| Leaf reflectance between 610 and 640 nm | $r625_{chl}$ | ratio | Chlorophylls content |
| Leaf reflectance between 780 and 820 nm | $r800_{mesoph}$ | ratio | Mesophyll structure complexity |
| Genetic Diversity | AGD | % | Average genetic diversity within plot |
| Percentage of Outlier Loci | OUTLIER | % | Percentage of loci falling out of a determined threshold in the plot |

bromide (CTAB) method previously described by Doyle and Doyle (1990). The quality and quantity of extracted DNA were assessed spectrophotometrically using a Bio-Photometer (Eppendorf). The AFLP analysis followed the standard procedure described by Vos et al. (1995), with modifications in the final amplification step described by Coppi et al. (2014) and associated references. Two primer pair combinations were used for the final PCR amplification: hex_EcoRI-ACG/MseI-TTA and fam_EcoRI-CTA/MseI-CTC. AFLP fragment profiles, obtained via capillary electrophoresis, were analysed using GeneMarker v1.5 software (SoftGenetics LLC, State College, PA, USA). Genetic variation within plots was evaluated using the average genetic diversity across loci (AGD), which reflects heterozygosity within the population (Nei 1987). The AGD calculations were performed with Arlequin v2.000 software (Schneider et al. 2000). Outlier loci percentages (OUTLIER) were identified using BayeScan v2.01 following the method of Yang et al. (2016). Loci were classified as outliers if their logarithm of posterior odds (LogPO) values exceeded a defined threshold (Foll 2012). The outlier loci were assessed to identify genomic sites potentially under non-neutral selection pressure, based on significant differences in allele frequencies between populations (Beaumont and Balding 2004). The analysis involved 20 pilot runs, each consisting of 10,000 iterations, following the protocol described by Coppi et al. (2018).

## 2.6 | Lake-Scale Satellite Data

Very high-resolution satellite data acquired during summer 2021 were gathered from the EU Copernicus Earth Observation programme over seven of the study sites: Chiusi (13 August 2021); Iseo and Torbiere del Sebino (10 July 2021); Mantua (11 July 2021); Massaciuccoli (11 August 2021); Pusiano and Annone (17 August 2021). VHR satellite data consisted of orthoprojected (L3) top of atmosphere (TOA) radiance scenes with 2 m spatial resolution and 4 spectral bands: blue (450–520 nm), green (520–580 nm), red (630–690 nm) and near infrared (NIR; 780–900 nm). The scenes were converted to surface reflectance through correction of atmospheric effects performed via ATCOR software (Richter and Schläpfer 2019).

From VHR satellite data bands, we derived the WAVI (Villa et al. 2014), a proxy of canopy density specifically designed for aquatic vegetation already used to characterize spectro-functional variation of *P. australis* stands by Castellani, Coppi, et al. (2023). From these data, we produced 2 m resolution maps of NIR reflectance of the areas covered by dense common reed stands (i.e., WAVI $\geq$0.5; Villa et al. 2014), broadly compatible with leaf reflectance measured around 800 nm, to convey spatial-wise information on variability in target *P. australis* variability within and across sites, to extend the analysis of common reed functional patterns beyond sampled plots.

## 2.7 | Data Analyses

To examine the relationships between leaf functional traits, genetic indices and environmental variables, we used GAMMs (Generalized Additive Mixed Models). This approach enables the detection of any non-linear patterns and includes random effects (Zuur et al. 2014).



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All models were built in R (R Core Team 2023). Environmental variables and traits, as well as genetic diversity indices, were tested for collinearity and collinear variables were omitted from the analysis (with Pearson's correlation coefficient $> |0.7|$, correlation plots provided in Figure S1A–C). Accordingly, we did not include water nitrate concentration, leaf P content and $r515_{car}$, as they were highly collinear, respectively, with water phosphate concentration, leaf N to P ratio, $r440_{rough}$ and $r625_{chl}$. The 11 remaining traits and genetic indices were tested in separate models (11 models in total) with six covariates (pH, electrical conductivity, phosphate, dissolved reactive silica, sediment organic matter content and Sed.TP), using the function {gam} of the package *mgcv* (Wood 2011). For functional traits (including spectral traits), we implemented the model using the Gamma family of distribution, as data were strictly positive, excluding zero. For genetic diversity indices, we used the Beta family of distribution, as data were constrained within zero and one hundred. Indeed, the heterogeneous distribution of plots among study sites did not allow for a direct statistical comparison of traits and genetic variation among sites. Therefore, we tested our second hypothesis including random effects for *Site* and *Plot* in the model (only *Site* for those response variables with one value per plot). We did not include year information in the models as this was already incorporated in the *Site* factor. Model selection was performed using the argument 'select = TRUE', which automatically indicates which covariates can be dropped from the model and which are better fitted with a linear or non-linear regression. Model validation was carried out checking for patterns in the residuals. The AIC (Akaike Information Criterion) was ultimately considered to select the final models. The partial effect of each significant covariate for every model was predicted setting all other covariates to their median values, and represented graphically using the package *ggplot2* (Wickham 2016).

## 3 | Results

Overall, in the field we collected 3909 leaf functional trait data (including 1536 spectral trait data) and 92 genetic diversity data, as genetic analyses were unsuccessful for two plots. Data for traits, including spectral traits and genetic indices at the plot level can be found in Table S2. Ten out of eleven variables among functional and spectral traits and genetic diversity indices showed significant relationships with at least one environmental variable (Table 4). The only trait that did not show any significant relationship was $r440_{rough}$, related to leaf roughness. At least one of the two random factors (*Site* and *Plot*) was significant in all models (except for leaf N to P ratio), indicating strong differentiation among sites and plots. Certain sites exhibited some extreme environmental variables: for instance, Massaciuccoli was distinct from the other sites for its high electrical conductivity. Torbiere del Sebino, too, was distinct for its high pH ($> 9.5$) and, together with Mantua, for high phosphate (mean phosphate 39.5 and 51.9 $\mu g\,L^{-1}$ in Torbiere del Sebino and Mantua, respectively).

### 3.1 | Leaf Functional Trait Variation

According to our models, leaf functional traits of *P. australis* were significantly related to both water and sediment features. Structural traits—leaf area, specific leaf area and leaf dry matter content—showed a positive response to Sed.TP, electrical conductivity and water phosphate, respectively, though some patterns were not linear (Figure 2a–c). Electrical conductivity also positively influenced chlorophylls and leaf N/P ratio (Figure 2e–i). However, the relationship with conductivity was mostly determined by the conditions in Massaciuccoli. Indeed, when removing the data from Massaciuccoli from the models, no significant relationship was observed between leaf traits and conductivity, except for leaf N/P ratio, which maintained a positive linear relationship also for lower values of conductivity. Sediment features and water silicon concentration were also related to pigments content in the leaves, with sediment-related variables having a negative effect, while silicon had a positive effect on chlorophylls (Figure 2d,f,g). Finally, we found that increasing phosphate concentration reduced the N/P ratio of leaves (Figure 2h).

### 3.2 | Leaf Spectral Trait Variation

Leaf spectral traits revealed strong relationships with silicon and phosphorus: $r625_{chl}$, inversely related to leaf chlorophyll content on a surface basis (and highly positively correlated with $r515_{car}$, related to leaf carotenoids and anthocyanins), showed a negative response to dissolved reactive silica (Figure 3a). $r800_{mesoph}$—related to mesophyll structure complexity—was strongly related to Sed.TP (Figure 3c), showing a positive relationship especially for Sed.TP $> 900\,\mu g\,g^{-1}$, and was negatively related to dissolved reactive silica (Figure 3b).

### 3.3 | Genetic Diversity Variation

Both genetic diversity indices showed a positive relationship with nutrient-related variables. Average genetic diversity showed a positive linear relationship with Sed.TP and a non-linear relationship with sediment organic matter content, which was positive for values $> 40\%$ organic matter (Figure 3d,e). Percentage of outlier loci showed a positive linear relationship with water phosphate (Figure 3f), although the confidence intervals were rather large for high values of phosphate ($> 40\,\mu g\,L^{-1}$, observed in Torbiere del Sebino and Mantua).

### 3.4 | Maps of Continuous Spectral Trait Variation

Continuous maps derived from VHR satellite data show spectral trait variation of *P. australis* at the site scale. In fact, maps of $r800_{mesoph}$ not only provide a snapshot of local variability in leaf mesophyll structure complexity, but can also inform about local environmental characteristics, such as Sed.TP and dissolved reactive silica—proxied by $r800_{mesoph}$ via calibrated GAMMs. Examples of the Mantua lakes and Lake Chiusi, based on $r800_{mesoph}$ maps, will be presented below (see Figure S2 for all $r800_{mesoph}$ maps and Figure S3 for WAVI maps as a proxy for reed canopy density).

*Phragmites australis* mapped in Mantua lakes show high local spectral variation in $r800_{mesoph}$ (Figure 4), with a median of 0.438 and an inter-quartile range of 0.063 [0.409–0.472]. The map highlights local differences within the site: (i) different $r800_{mesoph}$ values for reed stands lying on the two sides of the main river



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**TABLE 4** | Results of GAMM models run for each trait (rows), showing parameters for the covariates included in each model (columns).

| | | pH | SPC | SRP | DRSi | Sed.OM | Sed.TP | Site | Plot | $R^2$ | Dev. Exp. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| LA | est. | | | −0.0003 | | | **0.0002** | | | 0.624 | 68.30% |
| | edf | | | | 1.99 | | | **5.41** | **26.27** | | |
| | p | | | 0.9014 | 0.1927 | | **0.0082** | **< 0.0001** | **0.0001** | | |
| SLA | est. | | **0.00005** | | | | | | | 0.335 | 40.50% |
| | edf | | | | | | | **3.12** | **23.39** | | |
| | p | | **0.0065** | | | | | **0.0322** | **0.0004** | | |
| LDMC | est. | | | | | | | | | 0.395 | 43.10% |
| | edf | | | **1.98** | | | | **5.83** | 9.67 | | |
| | p | | | **0.0168** | | | | **< 0.0001** | 0.0713 | | |
| Chl | est. | | **0.0001** | | **0.0002** | | **−0.0001** | | | 0.405 | 38.50% |
| | edf | | | | | | | **6.26** | 1.52 | | |
| | p | | **0.0214** | | **0.0283** | | **0.006** | **< 0.0001** | 0.213 | | |
| Chl/Car | est. | | | | | | | | | 0.316 | 41.70% |
| | edf | | | | | **1.54** | | **4.27** | **15.2** | | |
| | p | | | | | **0.01** | | **0.0055** | **0.0308** | | |
| N/P leaf | est. | | | **−0.0026** | | | | | | 0.725 | 77.10% |
| | edf | 1.58 | **3.275** | | | | | **0.5952** | | | |
| | p | 0.0584 | **< 0.0001** | **0.0268** | | | | **< 0.0001** | | | |
| $r440_{rough}$ | est. | | | | −0.0001 | | | | | 0.543 | 59.30% |
| | edf | | | | | | 1.88 | **5.74** | **30.18** | | |
| | p | | | | 0.091 | | 0.1866 | **< 0.0001** | **0.0024** | | |
| $r625_{chl}$ | est. | | | | | | | | | 0.442 | 49.20% |
| | edf | | | | **1.57** | | | 3.16 | **34.17** | | |
| | p | | | | **0.0251** | | | 0.0983 | **< 0.0001** | | |
| $r800_{mesoph}$ | est. | | | | | 0.0003 | | | | 0.65 | 67.30% |
| | edf | | | | **1.43** | | **2.69** | **4.12** | **31.11** | | |
| | p | | | | **0.0075** | 0.148 | **0.0004** | **0.0065** | **< 0.0001** | | |
| AGD | est. | | | | | | **0.0002** | | | 0.539 | 64.30% |
| | edf | | | | | **1.99** | | **4.63** | | | |
| | p | | | | | **0.0478** | **0.0211** | **< 0.0001** | | | |
| OUTLIER | est. | | | **0.0111** | | | | | | 0.574 | 67.10% |
| | edf | | | | | | | **5.22** | | | |
| | p | | | **0.0272** | | | | **< 0.0001** | | | |

*Note:* Significant covariates are highlighted in bold (significance threshold $p < 0.05$). Estimates are provided for linear terms (est.), while degrees of freedom (edf) are provided for smooth terms. Site and plot are included as random factors. Model performance is indicated by adjusted *r*-squared ($R^2$) and deviance explained (Dev. Exp.). For traits and covariates names refer to Tables 2 and 3.

channel in the wetland area upstream of Superior Lake, 11.7% higher on the east shore than on the west shore (0.466 ± 0.043 vs. 0.417 ± 0.029; mean ± standard deviation; Figure 4a); (ii) high scores of $r800_{mesoph}$ for riparian reeds at the confluence of the lotic and lentic environments (0.485 ± 0.046; Figure 4b); and (iii) low-middle range $r800_{mesoph}$ scores in the upper portion of Superior Lake (0.424 ± 0.042; Figure 4c).

Considerable within-site variation in $r800_{mesoph}$ was observed also in Lake Chiusi (Figure 5), with a median score of $r800_{mesoph}$



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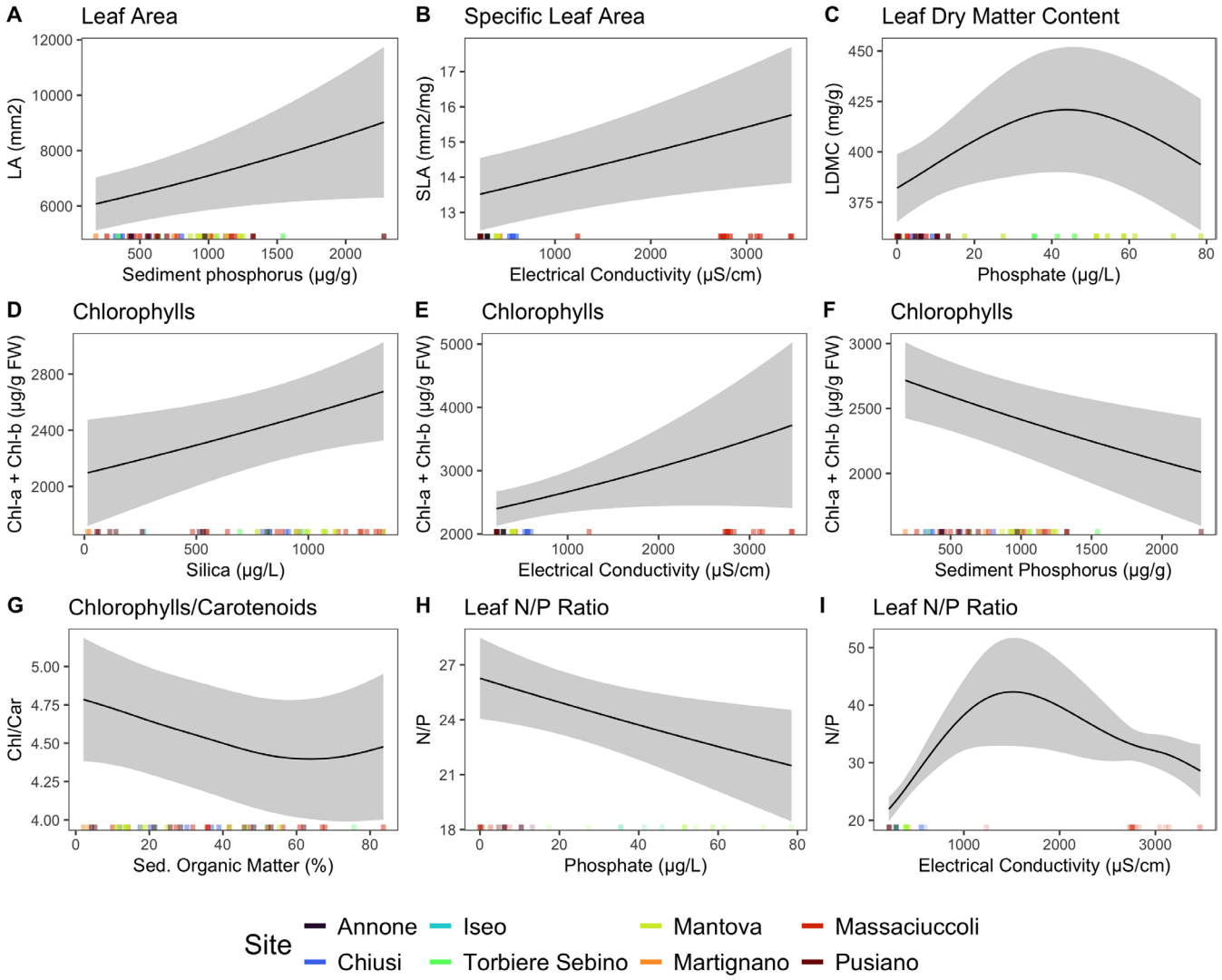



**FIGURE 2** | Partial effect of significant covariates on functional traits. The curves were obtained by predicting the partial effect of each covariate while setting the remaining covariates to their median values, so the relationship is plotted at the scale of the response variable. Grey shading indicates 95% confidence intervals, and rugs on the *x* axis indicate covariate values in each study site.

of 0.423 and an inter-quartile range of 0.094 [0.378–0.472]. The map shows areas of higher $r800_{mesoph}$ (0.460 ± 0.065) located in the eastern corner near the channel connecting Chiusi to a nearby lake (Figure 5a)—acting as an inlet or outlet depending on the season and dike management—and along the northern shore of the lake (0.457 ± 0.069; Figure 5b). In contrast, relatively low $r800_{mesoph}$ was observed for reed stands on the eastern (0.378 ± 0.054; Figure 5c) and south-eastern (0.402 ± 0.047; Figure 5d) shores of the lake, where the water is shallow and most of the inlets are located, including one coming from a local sewage treatment plant (Figure 5c,d). The map in Figure 5 shows that reed stands within 500 m from the lake inlets score an average $r800_{mesoph}$ lower by 6.6% than stands laying more than 500 m away (0.411 ± 0.059 vs. 0.440 ± 0.070).

## 4 | Discussion

Our results demonstrate that intraspecific functional trait variation and genetic diversity of *P. australis* are influenced by variation in environmental conditions, highlighting that the environment selects the population composition both for its genetic characteristics and for the intrinsic phenotypic variation within each genotype. Our first hypothesis was partially supported, as sediments had an important role in driving *P. australis* leaf traits variability and genetic diversity. However, water variables (phosphate concentration, dissolved reactive silica concentration and conductivity) had an even more prominent role as they were significant in 7 out of 11 models. Besides, as expected by our second hypothesis, the spatial pattern of variation that we observed was explained by more than just the water and sediment variables that we measured.

Concerning functional variation, P concentration in sediments and water was the most important factor in our study. P generally improves macrophyte performance, determining an increase in leaf area, specific leaf area as well as pigments content (Fan et al. 2013; Dalle Fratte et al. 2019; Zervas et al. 2019), and indeed in our study P was related to a higher leaf area and leaf dry matter content up to 40 µg SRP $L^{-1}$. This suggests that with increased availability of phosphate, *P. australis* is able to



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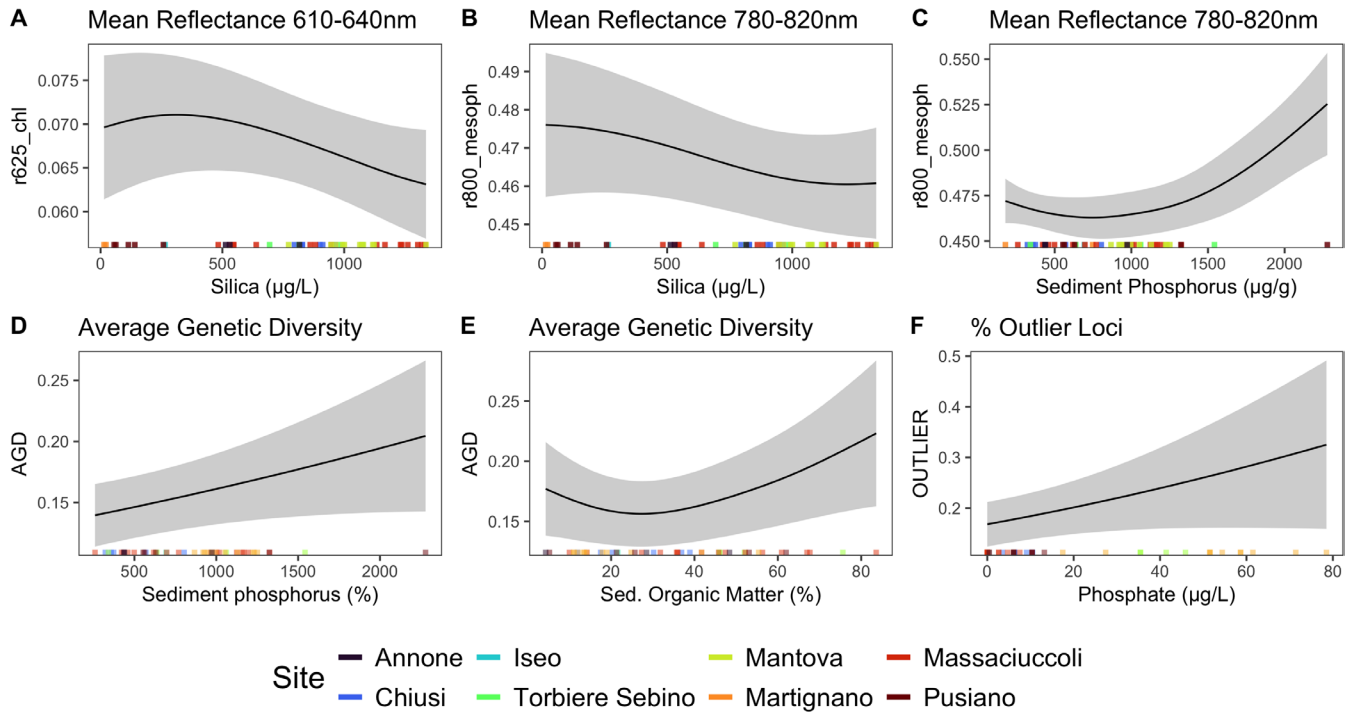



**FIGURE 3** | Partial effect of significant covariates on spectral traits and genetic diversity indices. The curves were obtained by predicting the partial effect of each covariate while setting the remaining covariates to their median values, so the relationship is plotted at the scale of the response variable. Grey shading indicates 95% confidence intervals, and rugs on *x* axis indicate covariate values in each study site.

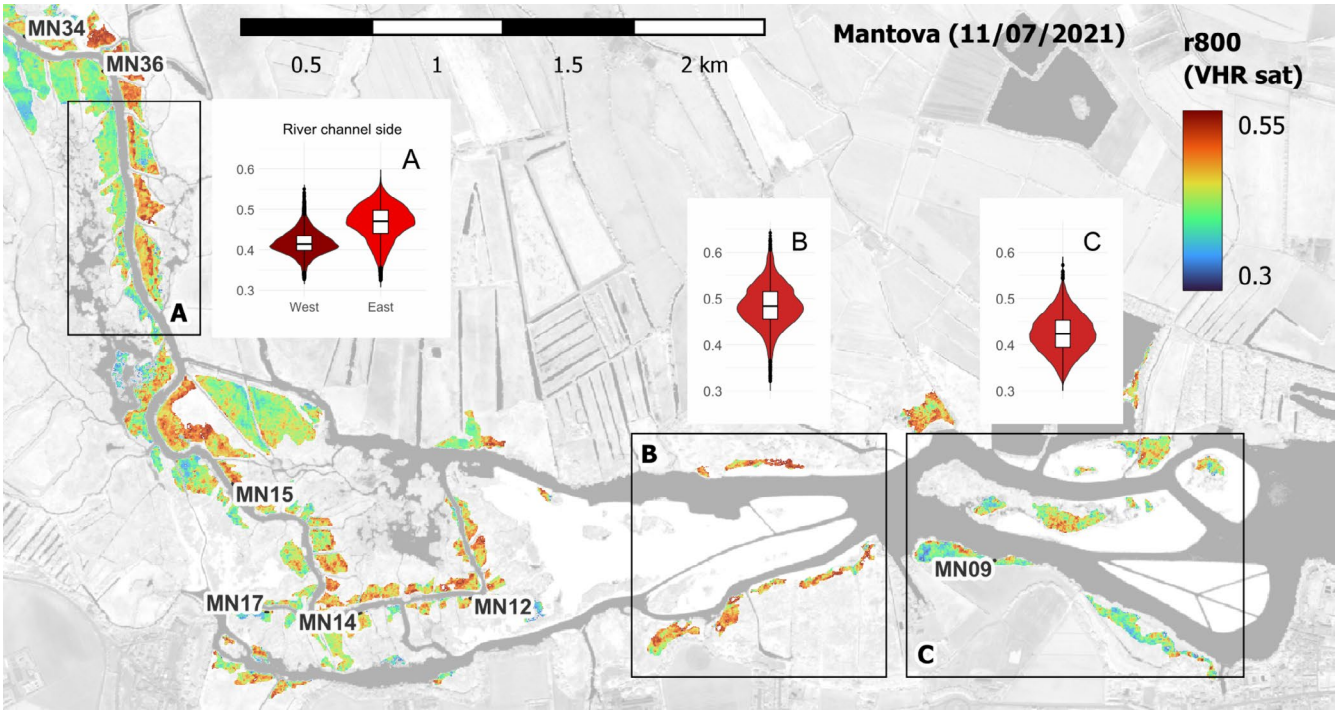



**FIGURE 4** | Map of $r800_{mesoph}$ variation of *P. australis* stands in the Mantua lakes site, as derived from VHR satellite data acquired on 11 July 2021; superimposed violin-box plots show the scores for local subsets (A–C) and selected plots sampled in situ are marked with black lettering.

invest more biomass in leaves. This, however, can be relevant up to a certain nutrient threshold, after which the plant builds relatively simpler leaves that can be more photosynthetically efficient (Pérez-Harguindeguy et al. 2013). Phosphate was negatively correlated with leaf N/P ratio, suggesting that with higher phosphate concentration, the plant could not incorporate much P in the leaves compared to the assimilation of N. Indeed, leaf N/P ratio was always above the 16:1 threshold (except for one plot in Mantua), indicating P limitation (Güsewell and Koerselman 2002; Güsewell 2004). Therefore, P limitation in eutrophic conditions, rather than P abundance, is likely the factor that most influenced leaf N/P ratio and the variation in



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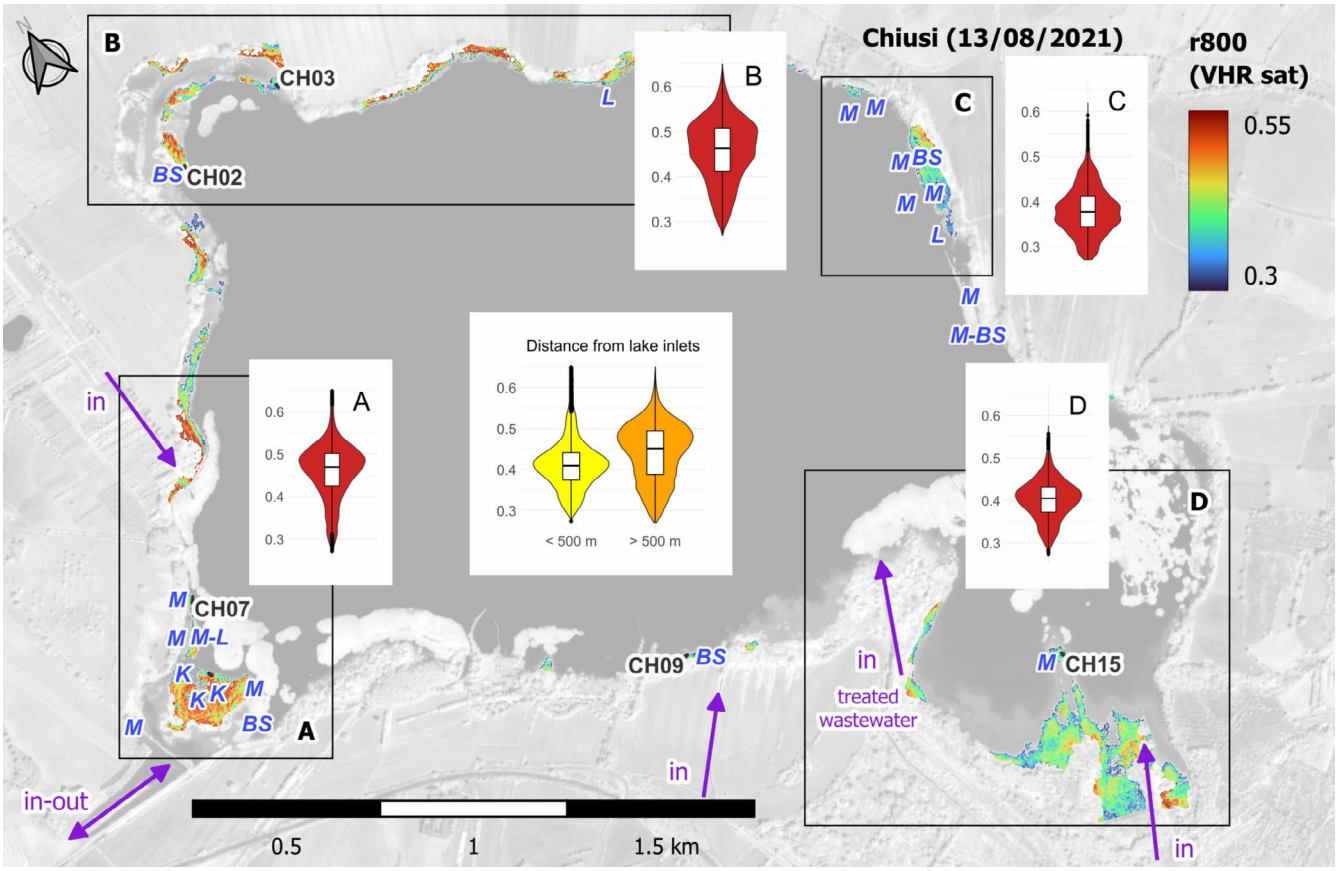



**FIGURE 5** | Map of $r800_{mesoph}$ variation of *P. australis* stands in the Lake Chiusi site, as derived from VHR satellite data acquired on 13 August 2021; superimposed violin-box plots show the scores for local subsets (A–D), selected plots sampled in situ are marked with black lettering, and blue lettering marks the location of sampled haplotypes from previous data (Castellani, Coppi, et al. 2023).

resource-use related leaf traits like chlorophylls and leaf area (Sorrell et al. 2011).

Eutrophic conditions had a negative effect on the photosynthetic performance of *P. australis* by decreasing the pigments content and increasing the complexity of leaf mesophyll ($r800_{mesoph}$). This could lead to lower competitiveness of *P. australis* compared to other emergent plants under eutrophic conditions (Peter and Burdick 2010; Tylová et al. 2013).

The effects of eutrophication were evident also on genetic diversity (both average genetic diversity and percentage of outlier loci), which increased with increasing phosphate, Sed.TP and sediment organic matter content. Some studies observed a negative effect of N on genetic diversity of *P. australis* (Patamsytė et al. 2023) and other plant species (Piqueras et al. 1999; Bai et al. 2009; Han et al. 2024), suggesting that non-stressful conditions derived from high nutrient availability favour clonal rather than sexual reproduction. However, our results suggest that eutrophication with a high N/P ratio may represent a stressful condition, since the plants exhibit less efficient traits (lower pigments and higher mesophyll complexity) at elevated nutrient concentrations. Under these conditions, multiple genotypes can provide larger overall genetic diversity and adaptive capacity. Impaired availability of N/P may, in fact, trigger sexual reproduction like in plants growing in nutrient-poor soils (Yang and Kim 2016). Interestingly, Castellani, Coppi, et al. (2023) found a high number of *P. australis* haplotypes in Chiusi and Massaciuccoli, which are the two sites of our study with the highest Sed.TP and leaf N/P ratio. Genetic diversity could partly support that the larger leaf trait variation observed at higher phosphorus concentrations and the increase in outlier loci (that by definition are those under selection) associated with increased genetic diversity may indeed reflect ongoing adaptive processes (Karbstein et al. 2020).

In contrast to phosphorus and nitrogen-related variables, dissolved reactive silica had a positive effect on the photosynthetic performance of *P. australis*. Silicon is known to promote plant growth (Conley and Carey 2015; Wu et al. 2024). Although not directly involved in photosynthesis, silicon can regulate the absorption and use of N and P in plants (Frazão et al. 2020; Pavlovic et al. 2021), and improve light interception (Klančnik et al. 2014), leading to increased photosynthetic capacity. In aquatic environments, silicon is usually abundant and readily available for plants, which use it to produce structural compounds (e.g., stem ridges, tough leaves), preferring it to more energy-consuming carbon-based compounds (Schoelynck and Struyf 2016; Wu et al. 2024). Moreover, silicon is also a key element in abiotic stress tolerance (Gharbi et al. 2025). Silicon can mitigate the damaging effect of salt on photosynthesis (Raihan et al. 2025), therefore, the ability of *P. australis* to efficiently accumulate silicon in the leaves (Kang et al. 2021; Wehrhan et al. 2021) may give this species a competitive advantage in saline conditions (in our study represented by Massaciuccoli site, which had the highest water conductivity).



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Spatial patterns of intraspecific trait variation were further supported by satellite data for $r800_{mesoph}$ (as well as for WAVI index), both within and among sites (Figures S2 and S3). These maps provide visual evidence of how intra-site trophic gradients can result in different *P. australis* leaf traits, and can be indirectly used to derive information on fine scale riparian trophic conditions. The patterns observed in Mantua lakes for $r800_{mesoph}$ show a clear differentiation between the two shores of the river system and at the confluence between the lotic and lentic environment. Areas with higher $r800_{mesoph}$ indicate higher Sed.TP and/or lower DRSi that may be due to the presence of different substrates and/or agricultural intensity on the two sides of the basin, as well as to increased deposition of P in areas with reduced water flow. The competition for nutrients between *P. australis* and the two invasive rooted macrophytes that have been expanding in this area for around two decades, *Nelumbo nucifera* and *Ludwigia hexapetala* (Pinardi et al. 2018, 2021), could also be a factor playing a role in this local variation.

A trophic gradient is evident also in Chiusi, where the $r800_{mesoph}$ map shows patterns from North-West to South-East, highlighting areas of unbalanced nutrient availability, with lower phosphorus in sediments and higher silica in water, possibly linked to the water inflow from numerous inlets. The substantial difference in $r800_{mesoph}$ in stands located within 500 m reach from main inlets from those that are more distant corroborates this correlation. Genetic diversity in chloroplast DNA markers can also have a role in explaining this variation in Chiusi (Castellani, Coppi, et al. 2023), where the phylogenetic lineage identified by chloroplast DNA as haplotype K scored high in $r800_{mesoph}$, indicating higher leaf structure complexity in haplotype K than in the other haplotypes L and M assessed in that study (Castellani, Dalla Vecchia, et al. 2023).

## 5 | Conclusions

This study demonstrates that coordinating functional, spectral and genetic data is useful to robustly describe factors influencing diversity and responses by macrophytes. P-limited eutrophication acted as a stressful factor in our study, influencing genetic and phenotypic variation of a key wetland species, altering its functional variation and, on a broader scale, ecosystem functioning. We show that intraspecific variation can be consistent even at the regional scale, and it is driven by local water and site-specific conditions. The ability of common reed to modulate its response at different scales was shown by remote sensing techniques, which specifically allowed us to visualize plant-environment relationships, highlighting fine-scale patterns in environmental conditions and functional responses by the plant. In future studies, to fully comprehend the adaptation of emergent vegetation and the variation of its ecological role in changing conditions, additional environmental aspects could be included, such as salinity, inter- and intraspecific species interactions as well as other traits than leaf traits, like reproduction and root traits.

### Author Contributions

Conceptualization, developing methods, conducting the research, data interpretation, writing: all authors. Data analysis: A.D.V., P.V., A.C. Preparing figures and tables: A.D.V., P.V., E.P.


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### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

The data on environmental variables, functional traits and genetic diversity are available in Supporting Information Tables S1 and S2.

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Environmental conditions of each study plot. DRSi, Dissolved Reactive Silica; Sed.OM, Sediment Organic Matter Content; Sed.TP, Sediment Total Phosphorus content; SPC, Electrical Conductivity; SRP, Soluble Reactive Phosphorus (phosphate). **Table S2:** Mean (and standard deviation in brackets) of leaf traits and genetic diversity indices for the study plots. No standard deviation provided for variables with only one observation per plot. Chl, Chlorophyll-a + Chlorophyll-b; Chl/Car, Chlorophylls to Carotenoids ratio; LA, Leaf Area; LDMC, Leaf Dry Matter Content; *N*, leaf Nitrogen content; N/P leaf, leaf Nitrogen to Phosphorus ratio; *P*, leaf Phosphorus content; r440rough, mean leaf reflectance between 430 and 450 nm; r515car, mean leaf reflectance between 510 and 520 nm; r625chl, mean leaf reflectance between 610 and 640 nm; r800rough, mean leaf reflectance between 780 and 800 nm; SLA, Specific Leaf Area. The genetic indices AGD (Average Genetic Diversity) and OUTLIER (percentage of outlier loci) were obtained from a matrix consisting of 341 loci in total: 130 from the primer combination hex_EcoRI-ACG/MseI-TTA and 211 from the primer combination fam_EcoRI-CTA/MseI-CTC. **Figure S1:** Correlation plots and Pearson's coefficients for covariates (A), functional traits (B), spectral traits (C) and genetic indices (D). **Figure S2:** Synoptic map of *P. australis* variation showing canopy near-infrared reflectance (connected to $r800_{mesoph}$ spectral trait) derived from VHR satellite data acquired, for the study sites not shown in the main manuscript except Martignano, with superimposed position of part of the study plots. **Figure S3:** Synoptic satellite map of *P. australis* variation showing WAVI index derived from VHR satellite data, for each study site except Martignano, with superimposed position of part of the study plots.



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