



Drivers of vascular species diversity on floodplain poplar stands: An integrated approach for ecological and functional assessment

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ABSTRACT

Biodiversity restoration is pivotal to enhance natural ecological processes in riparian ecosystems, affected by intensive human impact. Improving the riparian area functionality through new plantations is an effective Nature-based Solution. Poplar plantations have great potential for preventing soil erosion and providing habitats, but their impact on biodiversity has been little studied. Aims of this study were to: (1) investigate the effect of different poplar woodland management on vascular species diversity; (2) define the main drivers of vascular plant species richness, community composition, invasiveness and functional strategies. In three sites (Po river, Italy), an integrated survey protocol was applied to assess vascular species diversity, stand structure and soil properties. For each site, three stands with different management (cultivated, semi-natural and natural) were surveyed. Differences among all stand structural parameters and the management types were found. Tree diameter did not change between natural and seminatural stands but mean quadratic diameter of seminatural stands (28.1 cm) was similar to cultivated ones (26.8 cm). While cultivated stands showed the highest species richness (mean 28 species), semi-natural stands showed the highest number of native species (82 %) and an efficient soil N cycle (microbial N limitation, MNL < 0). The total Ca and MNL in soil resulted the main drivers of species diversity in the studied poplar stands. Semi-natural stands highlighted the best trade-off amongst vascular plant species diversity, invasiveness and soil process. The used integrated approach was effective and extendable to ecological and functional assessment of poplar riparian forests under different management gradients.

1. Introduction

Although floodplains offer important ecosystem services, including water purification and regulation, control erosion, and nature conservation, these ecosystems are ones of most degraded areas in Europe mainly due to land use changes, river regulation, dam buildings, pollution and presence of invasive species (Vanneuille et al., 2016; El

Hourani and Broll, 2023). Within this natural environment, the European black poplar (*Populus nigra* L.) together with the related willows (*Salix* spp.), dominate the early successional stages of riparian forests in temperate ecoregions in Western and Central Europe (Corenblit et al., 2014). The succession towards mature or climax forests is hindered because *P. nigra* seedlings are unable to establish below their own canopy (Tinschert et al., 2020). At the same time, exotic poplar plantations

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have been widespread in the last decades for productive purposes (i.e., plywood veneer and other wood-based panels); they often consider a single hybrid clone (*Populus x canadensis* Moench or other species), thus limiting the genetic diversity (Smulders et al., 2008). Nevertheless, exotic *Populus* pose severe threats to native black poplar since they replaced former natural woodlands, they are planted in the vicinity of wild relatives with whom they compete in colonizing restored habitat and may suffer genetic introgression (Vanden Broeck et al., 2021).

Vascular species are often used as general indicators of overall biodiversity in forest ecosystems (Lindenmayer et al., 2000; Gao et al., 2015) as they determine the integrity and conservation value within plant communities. Therefore, the monitoring of this aspect is crucial in these highly disturbed ecosystems where biodiversity is influenced by a plethora of variables, from anthropogenic disturbances (Seifert et al., 2015) to environmental factors that act at site (e.g., floodplain, river morphology, land use, González et al., 2016) and stand level (e.g., periods of drought, soil quality and properties). Although it is often claimed that plantations deplete the ecosystems they replace (Brockerhoff et al., 2008), several studies have shown that poplar plantations for productive purposes may have a more balanced effect on biodiversity than is typically thought (Martín-García et al., 2016; Chiarabaglio et al., 2023). The systematic evaluation of biodiversity in planted poplar forests highlighted the potential of these habitats to harbour a significant diversity of vascular plants (Baum et al., 2012), hosting also species under threat (Delarze and Ciardo, 2002) or with high conservation values such as orchids (Süveges et al., 2022). Other key drivers of plant community are soil properties (e.g., soil nutrients), which are critical in poplar plantations (Archaux et al., 2010). In particular, nitrogen (N) is one of the major soil nutrients in supporting plant growth. However, the determination of available N in soil, such as nitrates and ammonia, can be a poor indicator of nutrient limitations due to the rapid turnover in the environment (Kunito et al., 2024). The evaluation of soil enzyme ratios (i.e., the coenzymatic stoichiometry) is a suitable approach to estimate the long-term soil nutrient availability in ecosystem in which the energy and nutrient sources for microorganisms are represented by plant-derived organic matter (Das and Varma, 2010; Moorhead et al., 2023). The quantification of microbial limitations in specific environmental conditions and spatial scale contributes to evaluating and predicting microbial process, carbon and nutrient cycling as well as nutrient availability (Zechmeister-Boltenstern et al., 2015; Cui et al., 2023a; Kunito et al., 2024). The estimation of microbial limitations can be an indicator of soil ability as a vital living ecosystem (soil health) to provide ecosystem services (e.g., carbon stock, nutrient cycle efficiency, Nolan et al., 2021; El Hourani and Broll, 2023). In addition, soil enzymes are effective indicators of biogeochemical cycles, as they are involved in organic matter degradation and they are sensitive to environmental changes (Kunito et al., 2024; Moorhead et al., 2023; Cui et al., 2023b). The determination of soil enzymes is essential to define the proper forest management to preserve riparian ecosystems. In fact, soil enzymes can be suitable indicators of floodplain functioning such as global nutrient cycles and organic matter decomposition that occur after regular floodings and the subsequent organic material depositions (Martynov and Piletskaya, 2022).

Considering that the restoration and protection of riparian forests is one of the key priorities in biodiversity conservation and climate change adaptation strategies (e.g., EU Biodiversity Strategy 2030; EU Floods Directive 2007/60/EC), the determination of drivers for vascular species diversity is crucial to select the best management strategy of poplar plantation in a restoration plan perspective. Restoration plans that include the design of natural and semi-natural area network can promote environmental, social and economic benefits (Vanneuville et al., 2016). Poplar plantations for productive purposes are generally monoculture, with a homogeneous even-aged structure (same rotation period and tree spacing). Because poplar is a light-demanding species, these plantations are characterized by an open canopy with low cover and leaf area index (Chianucci et al., 2021; Romano et al., 2024), which may

increase light availability in the understory layer (Kremer et al., 2022), favouring ruderal and pioneer species and limiting the presence of forest specialist tree and shrub plant species (Brockerhoff et al., 2008). In contrast, natural woodlands or semi-natural plantations are characterized by minimal soil disturbances and a lack of intensive management which may results in higher diversity of microhabitats (e.g., deadwood, soil and tree bases) and larger variety of soil types than actively managed plantations. Non-native plant invasions are another factor affecting the composition of plant communities in riparian ecosystems with different degrees of management (Stella et al., 2013; Thomaz, 2022). In natural woodlands or semi-natural plantations, the spread of non-native species is favoured by the green eco-corridors along rivers which provide the perfect routes for several alien species such as *Amorpha fruticosa* L., *Acer negundo* L. and *Reynoutria japonica* Houtt. (Stella et al., 2013). On the other hand, disturbance, mainly by harvesting, is the key factor determining the structure of vascular plant communities in productive plantations (Martín-García et al., 2016), leading to the establishment of other non-native species (Slabejová et al., 2024).

Nevertheless, relatively few studies analysed the jointly effect of management, structural attributes, and soil properties on vascular plant species diversity (Baum et al., 2012; Martín-García et al., 2016; Süveges et al., 2022) albeit poplar plantations can have a key role in biodiversity conservation. Therefore, the individuation of sustainable management practices to integrate economic and biodiversity needs is a key aspect in poplar plantations (Archaux et al., 2010). This is particularly important in Italy, that represents - together with France - the main country in Europe providing areas for plantations. Here, more than fifty percent of plywood, packaging, pulp, paper, and wood-based panel enterprises source industrial hardwoods from poplar plantations; the vast majority of poplar stands is located in the Po Valley (N-Italy, Corona et al., 2020) and could represent a threat for ecological restoration. At the same time, the Po river area is subjected to a massive Renaturation Project (National Recovery and Resilience Plan, Italy – PNRR – M2C4, Investment 3.3) aiming at restoring and protecting biodiversity along the river, including reforestation.

The objective of this study is to understand the appropriate management of riparian zone of Po River that support high level of biodiversity. To do so, we addressed key gaps in the literature by evaluating how stand structural attributes and soil properties shape vascular plant species richness and community composition in poplar woodlands, while also considering plant invasiveness and functional strategies. By applying an integrated, site-level approach, we compared intensively managed (productive) poplar plantations with less intensively managed (semi-natural) and naturally evolving stands. As little is known about poplar stand biodiversity and community structure under different management and environmental conditions, in our study we hypothesize that a) semi-natural stands have an important role in supporting the highest vascular species diversity, due to intermediate disturbance levels and the retained structural complexity; b) poplar plantations host moderate but comparatively lower plant diversity, reflecting the simplification through intensive management; c) natural stands, shaped by long-term ecological processes, are more homogeneous in terms of species composition and harbour fewer non-native species. In addition, due to their key role in driving the biodiversity in cultivated plantation, the structural attributes, coupled with soil properties, has been evaluated as drivers of vascular species richness and community composition in natural and semi-natural stands.

2. Methods

2.1. Study area and sampling design

The study area is located in the Piedmont region, NW-Italy (Fig. 1a) and consists of three sites (i.e., *Isola Colonia'*, Palazzolo Vercellese, VC; *'Ghiaia Grande'*, Pontestura, AL; *'Valenza'*, Valenza, AL). The sites are

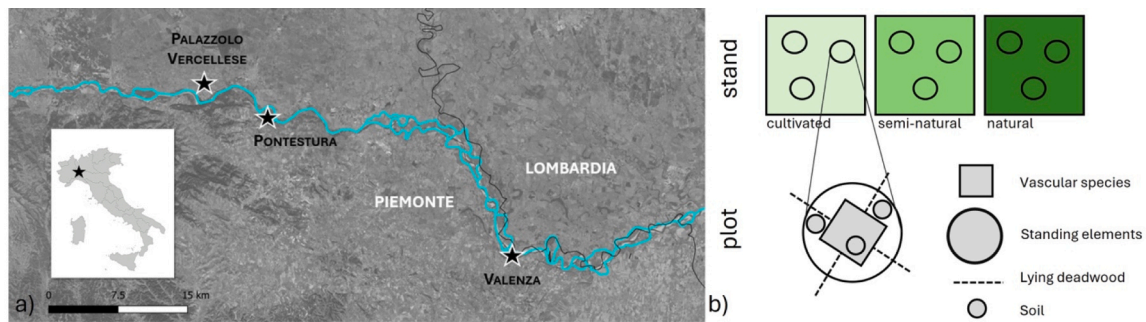


Fig. 1. (a) study sites and (b) field data collection protocol at site and plot level.

included in the Regional Protected Areas of Piedmont Po and in the Natura 2000 Network (i.e., SPA IT1180028 and IT2080501). For each site, three different poplar stand types were considered: cultivated, semi-natural (i.e., stand that were originally planted by the Management Body of the Regional Protected Areas of Piedmont Po for biodiversity restoration purposes and that are under spontaneous evolution since years) and natural (i.e., stand derived from spontaneous propagation). The cultivated stands (6–8 years) are subjected every year to harrowing activities and pruning interventions. The semi-natural stands (14–20 years) were characterised by minimal treatments (irrigation and weed control) in the first years after plantation. The natural woodland stand (18–35 years) has been affected by site-specific environmental (i.e., natural disturbances) dynamics. Within each site (size ranged between 21,751 and 142,400 m²), data were collected in three replicated plots (minimum distance among plots of 20 m) located within each managed type, for a total of 27 plots (i.e., 3 sites × 3 stand types × 3 plots). For stand attributes and soil properties, data were collected in a circular plot of 10 m in radius. Vascular species diversity was surveyed in a square area of 100 m² (10 × 10 m), centred in the circular plot (Fig. 1b).

2.2. Data collection and elaboration

Data on stand structure, vascular species and soil properties were collected between the end of May and mid-June 2024 in a single season sampling. Soil samples were collected at the end of the sampling period.

2.2.1. Stand structure

In each plot, stand structure data (living and deadwood elements) were collected using a standardized European protocol developed by Burrascano et al. (2021). Tree species, diameter at breast height (DBH ≥ 5 cm) and height of standing elements (snags, living trees and dead trees) were recorded using a tree caliper and an electronic hypsometer (Vertex IV-360 and Transponder T3). The number and volume of logs (larger diameter ≥ 10 cm) were assessed through the Line Intersect Method (Van Wagner, 1968; Marshall et al., 2000). Main stand structural parameters (i.e., mean diameter, tree density, basal area, tree volume) were calculated for living trees; deadwood volume was split into standing (snag, dead trees) and lying (logs) components. Volume of living trees and snags > 20 m was calculated through the volume functions developed for the Italian National Forest Inventory (Tabacchi et al., 2011). Volume of snags < 20 m was estimated according to the formula of an ellipsoid cone as in Brunet and Isacson (2009); volume of log was calculated using Van Vagner's formula (Van Wagner, 1968). The diameter variability of living trees was evaluated using the Gini index (Lexerød and Eid, 2006). The diversity of living tree species was calculated using the most common taxonomic indices based on the proportional abundances of species (Shannon, Simpson and Pielou, see Magurran, 2013). Diversity indices were calculated in R Statistical Software (v. 2024.9.1.394, R Core Team, 2024), using the *forestmangr* package (Braga et al., 2020); the Gini index was calculated using the *reldis* (Handcock, 2023) package. Living trees and dead trees volumes

were calculated using the *ForIT* package (Puletti et al., (2017)).

2.2.2. Soil properties

Topsoil layer (0–20 cm) was collected using a stainless auger (diameter 6 cm) in the same plots selected for stand structure. Three undisturbed core soil samples were collected using a known volume ring and the bulk density (BD) was determined after drying at 105 °C (ASA-SSSA, 1996). Three soil subsamples were mixed to obtain a composite sample in each plot. These samples were then air-dried and sieved using a mesh with a 2 mm size, before physical, chemical and enzymatic analyses. Soil texture and aggregate stability index (ASI) were determined using a laser granulometer Mastersizer 3000 (Malvern Panalytical Ltd., UK) equipped with a wet sample dispersion unit. Ultrasound was applied until the size distribution of dispersed particles was constant. The aggregate granulometric curve was compared to the curve obtained at the end of ultrasound application. ASI was calculated as the difference between the median diameter (d₅₀) of soil samples before and after sonication. Electrical conductivity (EC) and pH were determined using specific electrodes on water extract, 1:2 and 1:2.5 (w: v), respectively (ASA-SSSA, 1996). Total Organic Carbon (TOC) and Total Nitrogen (TN) were evaluated through dry combustion using a FlashSmart NC Soil elemental analyser (Thermo Fisher Scientific, Waltham, MA, USA). For TOC determination, soil samples were digested, using HCl:H₂O (1:1). For the determinations of total Ca, Mg, K and P concentrations, an amount of 0.30 g of soil sample was digested by a microwave (ETHOS 900, FKV, Torre Boldone, BG, Italy) using a HNO₃: H₂O₂ mixture (5:2 v:v) (EPA 3051). The total Ca, Mg and K concentrations were determined using inductively coupled plasma spectrometry (ICP-OES 5900 Agilent, Santa Clara, CA, USA). The available concentration of Ca, K, Mg for plants was also measured by ICP-OES after extraction with 1 M H₃COONH₄ at pH 7. Total phosphorous (TP) was determined spectrophotometrically (UV-1900i, Shimadzu, Kyoto, Japan), following the molybdenum blue method proposed by Murphy and Riley (1962). The hydrolytic enzyme activities were determined following the methods proposed by Marx et al. (2001) and Vepsäläinen et al. (2001), using fluorogenic methylumbelliferyl (MUF)-substrates. The enzymes analysed were β-glucosidase (BG; EC 3.2.1.21), phosphatase (P; EC 3.1.3.2), N-acetyl-β-D-glucosaminidase (NAG, EC 3.2.1.14), as proxies of soil C, P and N cycles, respectively. Specifically, the BG catalyses the hydrolysis of cellobiose residues in plant debris, producing glucose, a C energy source for microbial growth and activities. The P activities are related to the hydrolysis of esters and anhydrides of phosphoric acid, while NAG is a N-acquiring enzyme from chitin and peptidoglycan (Moorhead et al., 2016; Adetunji et al., 2017). The enzyme activities were calculated as μmol MUB g⁻¹ soil h⁻¹. The enzyme activities (BG, P and NAG) were normalised to TOC and log transformed. The estimation of microbial limitation for N (MNL), P (MPL) and C (MCL), were calculated at stand level following the threshold model of nutrient use efficiency-based proposed by Cui et al. (2023b). Specifically,

$$MNL = \ln(1.5 * (n_0 / EEA_{C:N}) / MPL = \ln(1.5 * (p_0 / EEA_{C:P})) \text{ and}$$

$$MCL = \ln((EEA_{C:N} * EEA_{C:P}) / (2.25 * (n_0 * p_0)))$$

where $EEA_{C:N}$ is the ratio amongst enzymes acquiring C and N, while $EEA_{C:P}$ is the ratio amongst enzymes acquiring C and P. Instead, $n_0 = e^{\text{intercept}}$ was calculated in the regressions for $\ln(\text{BG})$ vs. $\ln(\text{NAG})$ and $p_0 = e^{\text{intercept}}$ in the regression for $\ln(\text{BG})$ vs. $\ln(\text{AP})$. MNL, MPL and MCL values above 0 represent N, P and C limitations, respectively.

2.2.3. Vascular species diversity

Vascular plant species checklist was compiled for each plot to determine species richness. Species abundance was visually estimated by recording the cover percentage of each species within three vertical layers: herbaceous ($h < 1$ m), shrub ($1 \text{ m} \leq h < 5$ m), and tree ($h \geq 5$ m). Considering overlapping layers, total cover within each plot varied between 0 (i.e., bare ground) to > 150 %. Species nomenclature was harmonized and checked following Flora of Italy (PFI, 2025). We calculated true diversity (i.e., the effective number of species reflecting both species richness and evenness in species abundances; Hill, 1973) and the main taxonomic diversity indices (Shannon, Simpson and Pielou; Magurran, 2013) with the *diversity* function of the *Vegan* package (Oksanen et al., 2024) with R. To identify the ecological strategy of each species, the CSR (i.e., Competitor, Stress-tolerant, Ruderal) strategies *sensu* Grime (2001) were determined using the *Stratefy* application developed by Pierce et al. (2017), which is based on the leaf area, leaf dry matter content and specific leaf area. Based on their ecological strategies, plant species were categorized into seven groups, comprising three single dominant adaptation (i.e., Competitor (C), Stress-tolerant (S), Ruderal (R)) and four combinations of these traits, reflecting more complex ecological responses. Using the CSR scores, the secondary classification identified the following groups: Competitor-Stress-tolerant (CS), Competitor-Ruderal (CR), Stress-tolerant-Ruderal (SR) or a combination of all three strategies (CSR). Information on life-forms and invasiveness (i.e., native/non-native) for each species was also provided (data obtained from PFI, 2025), considering that groups of species sharing the same ecological properties (e.g., life-history traits, life-forms) might respond in a similar way to climate and disturbance, thus making generalization possible.

2.3. Data analysis

All statistical analysis was performed using R. Differences in stand structure, soil properties and vascular plant diversity (see Table S1 for response variables) data among stand types (cultivated, semi-natural, natural) and sites (Palazzolo Vercellese, Pontestura, Valenza) were firstly tested using the analysis of variance (ANOVA). Significance of differences between stand types and sites were assessed by Tukey's post-hoc (HSD) tests. Kruskal-Wallis test (Kruskal and Wallis, 1952) was used for non-normal data. The random part of the model accounted for the

Table 1

Mean (and standard deviation) of the main response variables (measuring unit) on stand structure in cultivated, semi-natural and natural stands. Parameters are shown with significance levels "****" $p < 0.001$, "***" $p < 0.05$; "n.s." $p \geq 0.05$. Lowercase letters highlight significant differences ($p < 0.05$) among stand types according to Tukey's post hoc test.

	Cultivated	Semi-natural	Natural	p-value
Tree density (n ha^{-1})	301 (43)	442 (119)	386 (216)	n.s.
Quadratic mean diameter (cm)	28.12 (3.40) b	26.76 (8.57) b	43.74 (15.75) a	***
Gini index	0.07 (0.05) b	0.24 (0.09) a	0.23 (0.08) a	***
Basal area ($\text{m}^2 \text{ ha}^{-1}$)	19.1 (6.3) b	24.9 (12.9) b	48.0 (18.2) a	***
Tree volume ($\text{m}^3 \text{ ha}^{-1}$)	83.2 (43.7) b	108.9 (78.7) b	250.4 (115.1) a	***
Dead wood volume ($\text{m}^3 \text{ ha}^{-1}$)	4.1 (6.9) b	88.1 (56.6) a	75.9 (93.1) a	***
Shannon index	0 b	0.90 (0.53) a	0.43 (0.35) a	***
Jentsch index	0.11 (0.01) ab	0.27 (0.13) c	0.24 (0.19) bc	*

nested site:stand data structure, which also account for pseudo-replication issues and relatively small sampling. Generalized linear mixed models (GLMM) were further fitted to select variables which explain the variability among stand type and site the most. To investigate patterns of ecological strategies across stand types, a Principal Component Analysis (PCA) was performed on the CSR values of plant species, weighted by their abundances. Characteristic predictors were pre-selected based on PCA correlation (variables centred and standardized, *Vegan* package), to keep the number of predictors (and their interactions) on a manageable level. Based on PCA results, representatives for correlated groups of variables were chosen. Multicollinearity issues were further evaluated, by retaining predictors having a correlation $r < 0.7$. After inspection, further multicollinearity issues were not found, as also confirmed by the variance inflation factor (VIF), calculated using the *car* package (Fox and Weisberg, 2019), and the $VIF < 4$ was checked (Zuur et al., 2013). GLMM was fitted using the *lme4* (Bates et al., 2015) and the *lmerTest* (Kuznetsova et al., 2017) packages. The random part of the model accounted for the nested site:stand data structure, which also account for pseudo-replication issues and relatively small sampling. As a response variable, the total species richness was considered, but two other independent GLMM models were also fitted considering native and non-native species richness only. The selected GLMM family function was Poisson for total and native species richness, and Gaussian for non-native species richness, as these distributions showed better fit to the data, based on model diagnostic test of overdispersion (*testDispersion()*) normality and uniformity (*testUniformity()*) using the *DHARMA* package (Hartig, 2024). From the full model fitted with the selected set of predictors, model selection was finally performed using the *dredge* function in the *MuMIn* package (Bartoń, 2024). This approach avoids the retention of overly complex models (i.e., models with additional parameters that result in minimal increases in model fit), using the corrected Akaike Information Criterion (AICc) to select the best model; AICc was used instead of AIC because sample size was small compared to the number of predictors (Burnham and Anderson, 2002). The final model averaged the models having an AICc delta < 2 (Burnham and Anderson, 2002). Conditional averages were taken from summary output. For all the selected models, conditional and marginal pseudo-R² were computed (Nakagawa and Schielzeth, 2013) with the *piecewiseSEM* package (Lefcheck, 2016).

3. Results

3.1. Stand structure characterisation

The DBH measures showed different distribution patterns depending on the management conditions (Fig. S1). In natural stands, tree DBH showed a larger size range, reaching in some cases a sort of multi-layered vertical structure (Table 1; Fig. S1). Natural and semi-natural stand composition was dominated (in terms of mean basal area, Fig. S2) by *P. nigra* followed by *P. alba*, with semi-natural stands characterized by a higher tree diversity. Moreover, significant differences

Table 2

Heatmap showing the results of the two-way ANOVA with site, stand type and their interaction with the response variables on stand structure, soil properties and vascular species diversity. Parameters are shown with significance levels: “****” $p < 0.001$, “***” $p < 0.01$, “**” $p < 0.05$; “ns” $p \geq 0.05$ (indicated in grey).

		Site	Type	Site x Type
Stand structure	Tree density	ns	ns	ns
	Mean diameter	ns	**	*
	Gini index	ns	***	*
	Basal area	ns	***	**
	Tree volume	ns	***	***
	Dead wood volume	ns	*	ns
	Shannon index	*	***	ns
	Jentsch index	ns	*	ns
Soil properties	Aggregate stability index	ns	ns	ns
	BD	*	ns	*
	pH	ns	ns	**
	Electrical conductivity	***	*	ns
	Total organic C	**	**	ns
	Total P	**	*	ns
	Total N	***	*	ns
	Total Ca	***	**	**
	Total Mg	***	ns	*
	Total K	***	ns	*
	Available Ca	***	**	**
	Available Mg	***	ns	*
	Available K	***	ns	*
	β -glucosidase	ns	ns	**
	Phosphatase	ns	**	ns
	N-acetyl- β -D-glucosaminidase	ns	ns	*
Vascular species diversity	Species richness	***	***	***
	True Diversity	***	ns	ns
	Shannon index	***	ns	*
	Simpson index	***	ns	ns
	Pielou index	***	ns	ns
	Invasiveness	ns	***	ns

among living trees' structural parameters were found according to the stand type, with the differences being not significant between semi-natural and cultivated stands (e.g., Vol ha⁻¹), except for the Gini index (Table 1). The site *per sé* has no significant effect on dead wood as well as on tree species diversity, but the interaction among site and stand has an influence on QMD, Gini index, G ha⁻¹, and Vol ha⁻¹ (Table 2). The deadwood volume showed significant differences among cultivated and the other two stand types (Table 2), with slightly higher values in semi-natural stands. Dead trees and snags are significantly higher in seminatural stands, while lying deadwood in natural one's (Table S2).

3.2. Soil properties

Soil data results are showed in Table 2. Soil texture showed a high percentage of sand, with the pH being slightly alkaline in all sites and stand types. Data regarding TOC, TN, TP, and EC were affected by stand type and site to a different extent, as highlighted by the one-way ANOVA. Specifically, TOC, TN and EC were significantly higher ($p < 0.01$) in the semi-natural while TP in the cultivated stands of Palazzolo Vercellese, while EC in the cultivated stand was lower compared to natural but like semi-natural stand in Valenza ($p = 0.027$). As reported in Table 2, the stand type and site interaction affected the total

Ca, Mg and K concentrations. Specifically, in Pontestura, Ca concentration in the cultivated stand had lower or similar values than in natural and semi-natural stands, respectively. Instead, in Palazzolo Vercellese, the semi-natural stand had similar Ca concentration to the natural one but higher values than cultivated. The available macronutrients were not affected by site and stand type interaction, while regarding the enzymatic activities a statistically significant interaction occurred for BG. In Pontestura, the BG in semi-natural stand had similar values to the cultivated one, but higher values than in natural stand. No significant interaction between stand type and site occurred for P, however the one-way ANOVA revealed differences amongst stands. In fact, P had higher values in cultivated than in natural and semi-natural stands in Valenza, while the lowest P was detected in natural stand rather than in semi-natural and cultivated stands in Pontestura ($p = 0.01$). No differences for NAG amongst stands were observed in all studied areas (Fig. S3, Table 2). The ecoenzyme stoichiometry, specifically the threshold model for the estimation of microbial nutrient and C limitations, revealed that all stands had negative values for MCL (Fig. 2a), indicating the absence of C limitation, however, natural stands had the lowest MCL while semi-natural stands the highest. The MNL (Fig. 2b) showed positive values for cultivated and natural stands, indicating a N limitation, while negative values were found for semi-natural stands. In all stands, MPL had

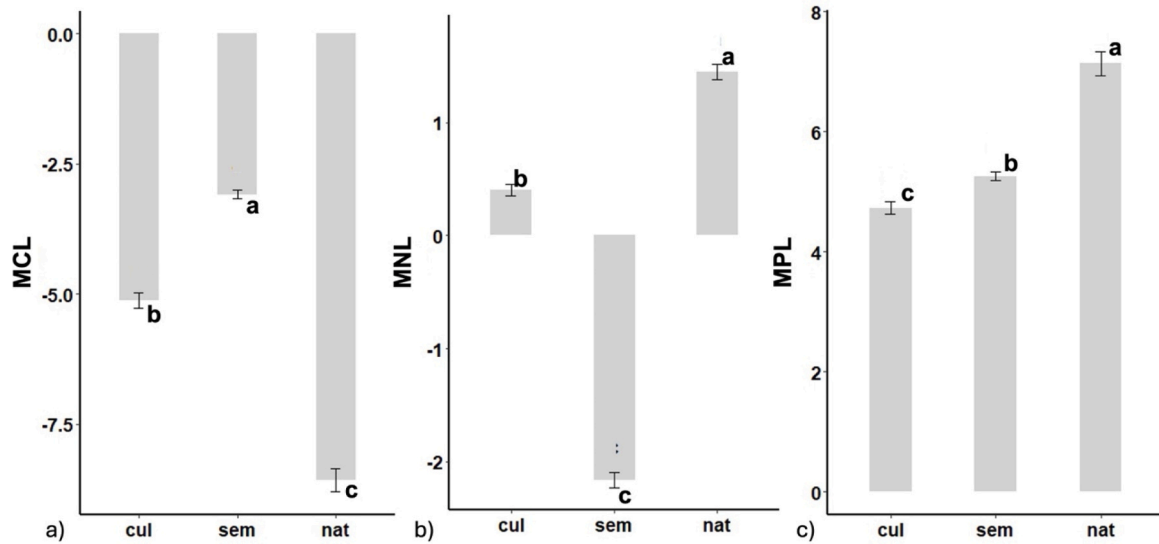


Fig. 2. Mean (and standard deviation) of the most representative soil properties variables in cultivated (cul), semi-natural (sem) and natural (nat) stands. (a) Microbial carbon (MCL), (b) nitrogen (MNL) and (c) phosphorus (MPL) limitations (unitless). Lowercase letters highlight significant differences ($p < 0.05$) among stand types according to Tukey's post hoc test. Values above zero for MCL, MNL and MPL indicated carbon, nitrogen and phosphorus limitations, respectively.

positive values and the lowest and the highest MPL were observed in cultivated and natural stands, respectively (Fig. 2c).

3.3. Vascular species diversity

The complete list of vascular plant species included 125 species belonging to 47 families, where the most diffuse were Asteraceae (17) and Poaceae (16; Table S4). Plant diversity was primarily affected by site, while stand type and the interaction between them had minor effects on the evaluated response variables (Table 2). In detail, species richness was significantly higher in Pontestura (mean 25 species), and, overall, in cultivated stands (mean 28 species; Table 2; Table S5). Nevertheless, the significant interaction between the explanatory variables mirrored differences in species richness among sites and management, with the highest number of species in Valenza observed in the semi-natural stand (28 species), while the highest species richness was observed in the cultivated stand in the Palazzolo Vercellese and Pontestura (24 and 39 species, respectively). True Diversity, Shannon index, Simpson index, and Pielou index were significantly affected by site (Table 2), highlighting that the vegetation community in Pontestura was more evenly distributed and heterogeneous compared to Palazzolo Vercellese and Valenza, which displayed a higher level of dominance of species, both rare and dominant (Table S5). However, stand type did not

influence the vascular flora composition. The interaction between stand type and site was slightly significant only for Shannon index (Table 2), which highlighted an increase in vascular species diversity with the decreasing of poplar management towards natural site in Palazzolo Vercellese while Valenza and Pontestura reported slightly higher diversity in the semi-natural and cultivated stands, respectively (Table S5).

The relative proportion of C, S and R selection among species varied across stand types. Specifically, the cultivated stand showed a higher proportion of ruderal species (57%), with lower percentages of competitor (24%) and stress-tolerant (19%) species (Fig. 3a). R (41%) and CR (19%) were the predominant strategies. Conversely, semi-natural and natural stands displayed a more balanced distribution of CSR primary strategies, with a lower proportion of stress-tolerant species (24% and 28%, respectively) compared to competitor (38% and 39%, respectively) and ruderal species (38% and 33%, respectively; Fig. 3). In the semi-natural stand, the predominant strategies were C and CR (both 19%), while CS and CR were more frequent in the natural stand (25% and 23%, respectively). Note that the percentages of the primary strategies (C, S, R) account for their occurrence both as pure strategies and within mixed combinations (CS, CR, SR, CSR). This trend was further confirmed by the PCA analysis weighted by species abundance (Fig. 4).

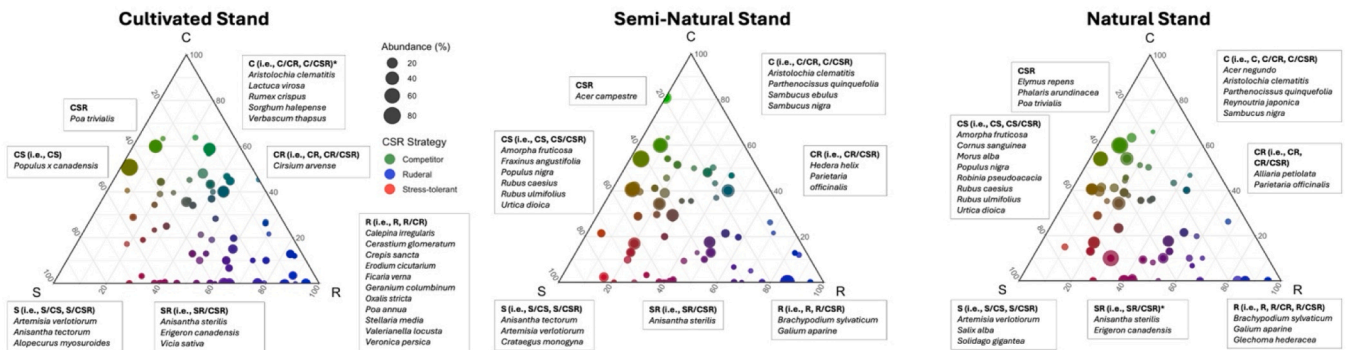


Fig. 3. Relative proportion (%) of C (Competitor), S (Stress-tolerant) and R (Ruderal) for the species detected in cultivated, semi-natural and natural stands according to the CSR Grime's strategy (2001). Species names (abundance > 10%; * abundance [1–5]) represent examples of the secondary CSR strategy classes which consider either individual (C, S and R), or combined (CS, CR, SR, CSR) values. The plots were generated using the globally calibrated CSR analysis tool *Stratefy*.

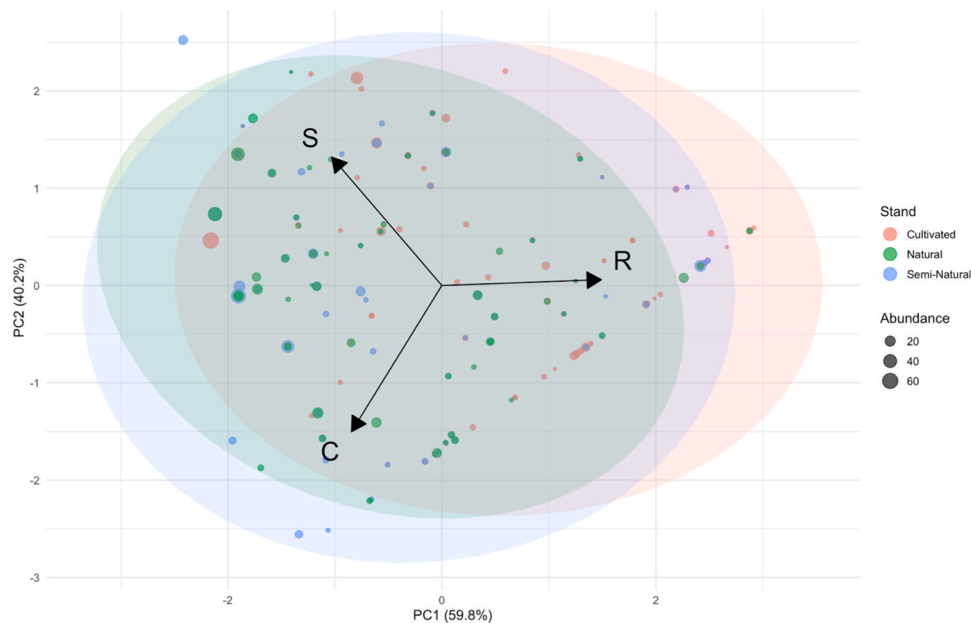


Fig. 4. Principal Component Analysis of CSR values of plant species recorded in each stand type (cultivated, semi-natural, natural), weighted by their relative abundance. Arrows indicate the primary CSR strategies: C = competitor, S = stress-tolerant, R = ruderal.

Table 3

Conditional estimates obtained from averaging across top model sets with a delta AICc < 2, for species (total, native, non-native) richness. Basis are linear mixed-effects models with site x stand as nested random factors, fit by maximum likelihood. Parameters are shown with significance levels “****” $p < 0.001$, “***” $p < 0.01$, “**” $p < 0.05$; “ns” $p \geq 0.05$. Pseudo-R2 calculated from the averaged models using the *piecwise* SEM package. For the description of abbreviations refer to Table S1.

	Total species richness	Native species richness	Non-native species richness
Intercept	3.38 (0.16) ***	3.09 (0.16) ***	5.93 (0.81) ***
Quadratic mean diameter	-1.05 (0.49) *	-1.35 (0.51) *	-
Total Ca	-1.04 (0.51) ns	-	-8.71 (2.05) ***
Stand age	-0.34 (0.29) ns	-	-
Microbial P Limitation	-	-0.37 (0.29)	-
Microbial N Limitation	-	-	4.38**
Family	Poisson (link:log)	Poisson (link:log)	Gaussian (link:identity)
R2 marginal	0.37	0.44	0.58
R2 conditional	0.72	0.69	0.62

Life-forms were not equally distributed within stand types and percentage varied significantly among categories ($p < 0.001$). On average, life-forms were mainly represented by hemicryptophytes (31 %) and therophytes (30 %), followed by phanerophytes (21 %) and smaller percentage of geophytes (14 %), nanophanerophytes (3 %) and helophytes (1 %), which notably occurred only in Palazzolo Verellese. The distribution of life-forms varied significantly among site ($p < 0.001$), stand type ($p < 0.001$) and their interaction ($p < 0.001$), with a smaller variety of life-forms in the cultivated stand (Fig. S4; helophytes and nanophanerophytes were absent) compared to the semi-natural and natural stands (Fig. S4; all life-forms were present). In detail, geophytes and hemicryptophytes did not vary significantly between site and stand type. Stand type influenced significantly the percentage of nanophanerophytes, phanerophytes and therophytes, with a higher percentage of nanophanerophytes and phanerophytes in the semi-natural site compared to the cultivated stand (Fig. S4). On the other side, therophytes were the dominant life-form in the cultivated stand. Invasiveness was significantly affected by stand type, with the highest percentage of non-native species in natural stand (36 %) compared to cultivated (28 %) and semi-natural (18 %) and one, which displays a higher number of native species (Table 2, Table S5).

3.4. Determinants of vascular flora diversity

The first three principal components of PCA explain 69 % of the variation (Fig. S5), with the highest representation of few structural (QMD, stand age, Gini index, living volume) and soil variables (Ca tot, K tot, Mg tot, MCL, MPL, TN, TOC) on the three first principal components (Fig. S6). Vascular plant data (species richness, both total as well as native and non-native), explained lesser variation. Results of the GLMM models are shown in Table 3. Total and native species richness were significantly affected by QMD, where higher tree diameter caused a reduced number of total and native species (Table 3; Fig. 5). Total species richness was also influenced by total Ca and stand age while native species richness by the MPL; however, the effect of those variables was not significant (Table 3). On the other hand, non-native species richness was significantly affected by both total Ca and MNL (Table 3; Fig. 5), with the number of non-native species decreasing with the increasing of total Ca and MNL.

4. Discussion

4.1. Forest structure and soil assessment

The structural homogeneity of cultivated stands of our study is consistent with European near-to-mature productive hybrid poplar

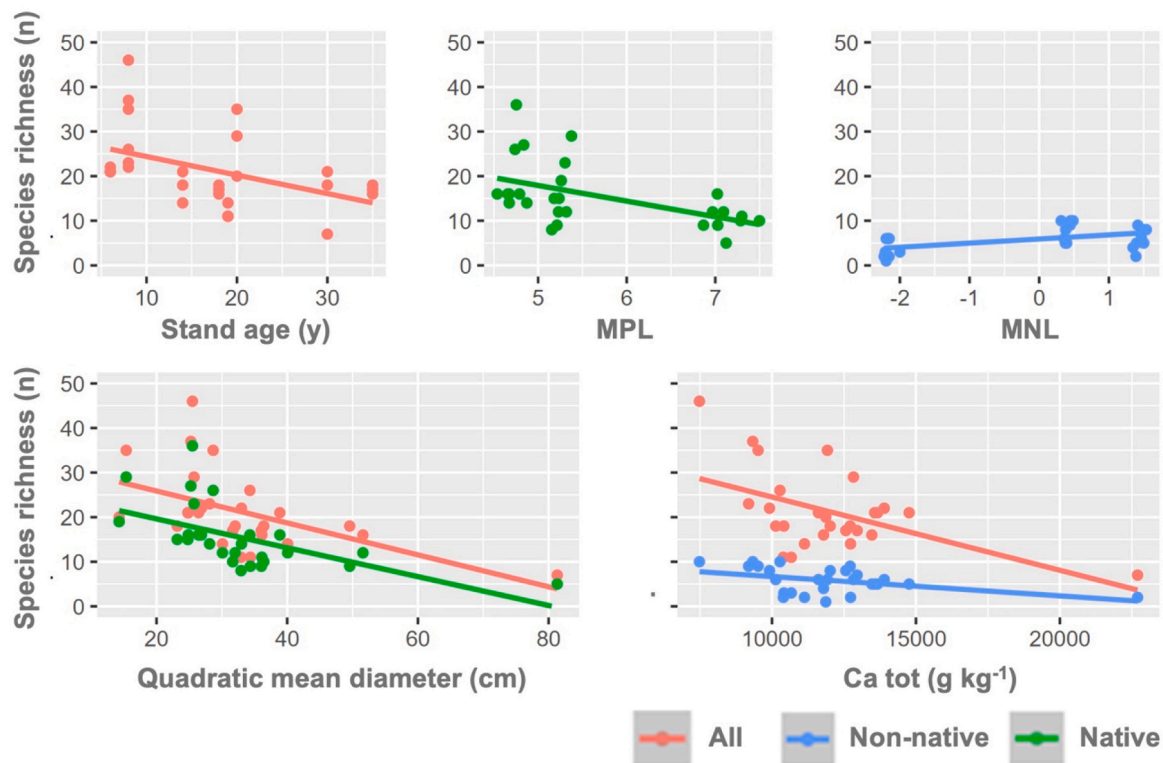


Fig. 5. Conditional variation in total (all), non-native and native species richness according to each explanatory variable (fixed effects) evaluated in the Generalized linear mixed model. Explanatory variables (measuring unit) are stand age, microbial phosphorous limitations (MPL), microbial nitrogen limitation (MNL), quadratic mean diameter and total Ca.

stands (Uhl et al., 2024) with similar planting density (i.e., 6×6 m) and rotation period (about 10 years). Living tree volume values of natural stands are comparable to those of Mediterranean riparian forests with *Populus* and *Salix* spp. subjected to periodic flooding events (de Groot et al., 2022). Interestingly, semi-natural stands are characterised by aboveground biomass levels comparable to natural poplar forests subjected to frequent flooding disturbances in Mediterranean areas (Cartisano et al., 2013; Shupe et al., 2021). This within-site variation determines the possibility for the oldest trees to reach considerable size only in Valenza and Pontestura. Interestingly, both natural and semi-natural stands reported a low diameter variability that might be due once more to the homogenization effect derived by flooding events that interrupt the growing dynamics of the natural sites. Similar levels of deadwood volume between natural and semi-natural stands can be explained by the high natural mortality of *P. nigra* in Pontestura and Valenza plantations; this is mainly because of climate change with a succession of extreme events (high winds) and periods of severe drought resulting in lowered water table. The deadwood amount and its variability among-sites can also be explained by the heterogeneous river morphological characters and the distance of the stands from the active channel, playing a significant role in deadwood accumulation (Oettel et al., 2022). As expected, tree diversity in riparian natural stands is very low, as Salicaceae are the only tree species that can colonize sites with recurring low-intensity flooding events, as well as temporary periods with swamp water (Alimpić et al., 2022). Semi-natural stands were planted for biodiversity enhancement purposes in sites that are less subjected to high intensity flooding events and thus can maintain high levels of tree biodiversity of the original plantation, coupled with new tree species encroachment.

The effect of stand type on soil properties was generally site-specific. This could be explained by the azonal dynamics of the riparian ecosystems, which are influenced by variation in vegetation, flooding regimes and human activities. These factors contribute to the spatial

heterogeneity of soil properties along the river and with increasing the distance from the watercourse (Xia et al., 2018; Zhang et al., 2021). Despite such variability, the soil microbial limitation approach revealed a different soil nutrient availability amongst stands, while C was not a limiting factor. When nutrients or carbon are limited in soil, microorganisms increase the release of specific extracellular enzymes over others, for guaranteeing the nutrient and carbon acquisition for their metabolism (Kunito et al., 2024). The ecoenzyme stoichiometry approach was a suitable tool for estimating both the nutrient and carbon availability as well as microbial use efficiencies. In fact, the presence of specific nutrient or carbon limitations affects the main environmental microbial-related processes, e.g., by increasing the microbial immobilisation over mineralization (Kunito et al., 2024), with consequences for nutrient and carbon cycling.

In our study, the management type did not lead to C limited condition, as highlighted by negative values for MCL in all stands, and the absence of C limitation may depend on substrate used by microorganisms (plant litter or soil organic matter) as energy source for their metabolism. When the plant litter is the dominant substrate, the microorganisms are not C limited as this element in plant litter is more available than in soil organic matter, e.g., due to the higher C:N ratio in plant litter and the soil organic matter protection in soil aggregates (Cui et al., 2023a). The high C availability can also occur when the vegetation productivity is high thanks to the release of root exudates that enhance the labile C inputs in soil (Cui et al., 2023a). Instead, the positive values of MPL suggested a high production of P-related enzymes by microorganisms, e.g., phosphatase, for P acquisition, indicating P limited condition in soil. The P is one of the most common limiting factors in terrestrial soils (Cui et al., 2023b) and the magnitude of this limitation depends on several factors (Zechmeister-Boltenstern et al., 2015), including stand maturity. In fact, the older the stand, the less P available is expected, due to changes in soil properties and plant development (Yan et al., 2018; Xu et al., 2022, Tie et al., 2024). This may explain the

differences in P availability, as highlighted by MPL, depending on management conditions: the natural stands (28 ± 8.7 y) had the higher soil P limitation, followed by semi-natural (18 ± 3.2 y) and cultivated (7 ± 1.2 y) stands. Concerning the N limitation, the semi-natural stands did not show a MNL, suggesting an efficient N cycle in these stands, probably thanks to a more control of C and N cycles by ecosystem traits (soil, vegetation, biota interaction) than other factors (e.g., climate). In fact, N and C cycles are strictly correlated and the dominance of ecosystem traits can lead to a balance between plant C input (plant litter) and microbial C output (microbial respiration) resulting in an efficient microbial processing in N acquisition, thus an equilibrium between nitrogen mineralization and immobilization (Cotrufo et al., 2021; Cotrufo and Lavallee, 2022).

4.2. Vascular flora diversity and drivers

Cultivated stands hosted the highest number of vascular plant species, particularly in Palazzolo Verellese and Pontestura, highlighting a notable level of biodiversity in poplar stands managed for productive purposes, in line with previous studies (Baum et al., 2012; Randriamananjara et al., 2025). Conversely, species richness decreased along the management gradient towards natural sites, possibly related to the increase in mean tree diameter and basal area. While some studies found no significant differences in vascular plant communities across management gradients (Martín-García et al., 2016), Archaux et al. (2010) reported a decline in species richness with increasing plantation age. Older stands often show denser shrub cover and reduced light availability, which can limit the establishment of herbaceous species. In this context, the development of a shrubby layer can be detrimental to tall herbs and meadow plants, which are generally shade-intolerant and negatively affected by shrub encroachment (Archaux et al., 2010), at the expense of shrubs and trees. Nevertheless, in our study the site characteristics - more than the stand type - were the main drivers of plant diversity, with different trends observed across sites. This could be explained by the site variability in riparian context. In fact, riparian site variability is mainly due to features of flooding events (e.g., recurrence period, maximum flow and volume) and it deeply influences edaphic environment and, subsequently, vascular flora turnover rates (Saint-Laurent et al., 2019; Gallardo, 2003). Moreover, fluvial dynamics triggered by previous land use (e.g., pasture, cultivation, river channel modification) shape micromorphology (such as terraces and micro-reliefs; Castellarin et al. (2011), diversify soil properties (hydro-physical and chemical; Ferré et al. (2014), and promote pedogenic processes (Banach et al., 2009) that affect vegetation colonization. This pattern was mirrored in the CSR strategies of plant species across the stand types. Cultivated stands, subjected to various disturbances (e.g., canopy openings, topsoil removal, and soil disturbance through harrowing and other agronomic practices), favoured shade-intolerant and ruderal species such as *Calepina irregularis* (Asso) Thell., *Ficaria verna* Huds., *Oxalis stricta* L., supporting the idea that physical disturbance plays a key role in early successional stages (Paillet et al., 2010). A similar pattern was observed in northern France, where ruderal or generalist species accounted for an average of 40.5 % of total species richness in poplar plantations (Archaux et al., 2010). In contrast, tall herbs and meadow plants were negatively affected in semi-natural and natural stands, confirming findings that riparian forests are primarily characterized by stress-tolerant and competitive species (Martín-García et al., 2016), such as *Amorpha fruticosa* L., *Rubus caesius* L., *Rubus ulmi-folius* Schott.

Life-form composition reflected general trends reported in the literature (Kremer et al., 2022; Randriamananjara et al., 2025), with a broader spectrum of life-forms present in semi-natural and natural stands compared to cultivated ones. Cultivated stands were mainly characterized by therophytes, hemicryptophytes, and geophytes, associated with a higher degree of disturbance (Paillet et al., 2010). The greater diversity of life-forms in semi-natural and natural stands

contributes to the functional diversity of these plant communities (Martín-García et al., 2016). Native species were significantly more abundant in semi-natural sites, while the proportion of non-native species increased in both cultivated and natural stands. The moderate presence of non-native species across these stands reflects both the vulnerability of riparian ecotones and the impact of disturbance commonly applied in poplar plantations (Martín-García et al., 2016).

Soil parameters resulted the main drivers for vascular species diversity in poplar plantations. In particular, the total soil Ca concentration was an indicator of plant invasiveness. Species richness, and particularly non-native species, decreased with increasing total Ca in the soil. Although a few studies addressed this aspect, such a relationship seems to be context-dependent, whose variation depends on other environmental factors. Generally, positive correlations have been reported in the literature between Ca and species richness (Cachovanová et al., 2012; Sekulová et al. 2012) with only Hettengergerová et al. (2013) reporting the same negative trend observed in the present study. In addition, the MNL was a good determinant for species richness, and for non-native species. In fact, the applied model showed a positive correlation between exotic species richness and N limitation, thereby the limited N availability determined a favourable ecological environment to accelerate exotic species invasion (Xu et al., 2021). This relationship could be related to differences in resource uptake and use efficiency between exotic and native species. Ren et al. (2021) observed a higher resource conservation strategy and rapid growth in invasive plants than native in low-N environment, conferring a competitive advantage to invasive plants.

5. Conclusion, study implications and perspectives

New plantations established on former agricultural land, and especially in most intensively managed monocultures, may provide significant opportunities for biodiversity conservation (Paquette et al., 2009; Pawson et al., 2010) and high-quality ecosystem services provision, especially throughout riparian ecosystems (Stoffers et al., 2024). The integrated approach of the study has proven to be effective and extendable to ecological and functional assessment of riparian forests. Results highlighted that soil total Ca concentration and microbial nitrogen limitation were the main drivers of vascular species diversity in floodplain poplar stands. Semi-natural stands under spontaneous evolution were the best trade-off amongst vascular plant species diversity, invasiveness and soil process (e.g., nutrient cycles). Respect to other works more focused on the impact of different management practices of poplar cultivated stands (Archaux et al., 2010; Antoniella et al., 2024), our work focuses on the stand origin (planted/not planted) and evolution (stand age and trees maturity) of poplar stands under different environmental gradients (i.e., the selected site across the river). Within the framework of Nature Restoration Law (Regulation EU 2024/1991), our approach could help for the implementation of management plans at different scale levels (e.g., from watershed scale to single river level). The sensitivity of the observed trade-offs to former land uses and river flood dynamics require further investigation to test the scalability of the woodland patterns across a broader range of riparian conditions, with the final aim of informing adaptive, landscape and site-specific restoration strategies.

CRediT authorship contribution statement

Silvia Traversari: Writing – review & editing, Resources, Methodology, Investigation. **Simone Orsenigo:** Methodology, Investigation, Data curation, Conceptualization. **Luca Cristaldi:** Writing – review & editing, Investigation. **Anna Corli:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis. **Giovanni Trentanovi:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Francesca Vannucchi:** Writing – original draft, Visualization, Methodology, Investigation,

Formal analysis, Conceptualization. **Francesco Chianucci**: Writing – review & editing, Formal analysis, Data curation. **Carlo Calfapietra**: Writing – review & editing, Project administration, Funding acquisition. **Alessio Giovannelli**: Writing – review & editing, Project administration, Methodology, Investigation, Conceptualization. **Pier Mario Chiarabaglio**: Writing – review & editing, Methodology, Investigation, Conceptualization. **Marco Carlo Mascherpa**: Writing – review & editing, Formal analysis. **Maria Laura Traversi**: Investigation, Conceptualization. **Andrea Scartazza**: Writing – review & editing, Formal analysis.

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Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2025.123000](https://doi.org/10.1016/j.foreco.2025.123000).

Data availability

Data will be made available on request.

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