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ORIGINAL PAPER

Canopy species composition drives seasonal soil characteristics in a Mediterranean riparian forest

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Abstract

Mediterranean riparian ecosystems provide key ecosystem services, such as climate regulation, water quality, and flood protection. Forest degradation and exotic species are among the main human-mediated impacts in these ecosystems, yet little is known about their interacting effect on the dynamics of soil characteristics. Here, we studied the effect of species canopy on monthly soil characteristics during one year in a riparian ecosystem in Central Spain. Soil chemical and microbiological properties were monthly recorded in five vegetation types: (1) forests dominated by the N_2-fixing *Alnus glutinosa*, (2) shrublands dominated by *A. glutinosa*, (3) poplar plantations of the exotic *Populus* × *hybrida*, (4) mixed forests dominated by *Fraxinus angustifolia* and *Salix alba*, and (5) grasslands. Canopy areas showed much higher soil organic C, total N, nitrate and ammonium contents than the grassland areas. *A. glutinosa* forests had the highest total N, organic C, ammonium, and most probable number (MPN) of aerobic and anaerobic microorganisms followed by *A. glutinosa* shrublands, while mixed forests and poplar plantations had the highest nitrate content. Poplar plantations showed the lowest soil N and C content likely due to the recalcitrant litter of *Populus* × *hybrida*. N_2 fixation peaked in months that differed among vegetation types. Temporal changes in soil characteristics were mostly driven by soil moisture, although the magnitude of these changes varied between canopy species. Our study highlights the importance of protecting forested areas and planting native tree species in afforestation programmes to keep the ecological integrity of riparian ecosystems. *A. glutinosa* is suggested as an appropriate species to improve soil fertility and stability in restoration projects.

Keywords *Alnus glutinosa* · Ammonium · N_2 fixation · Microbial abundance · Nitrate · Organic carbon · *Fraxinus angustifolia* · *Populus* × *hybrida*

Introduction

Riparian areas are the interfaces between terrestrial and aquatic environments, naturally characterized by a forested strip along freshwater ecosystems. These areas occupy a small proportion of the land, but represent an important ecological component of the landscape providing a plethora of ecosystem services (Gregory et al. 1991; Hanberry et al. 2015; Tockner et al. 2002). They naturally held high biodiversity levels boosted by a mosaic of habitats created by a high rate of natural disturbances (Décamps et al. 2009). Riparian vegetation may show different physiognomy, structure, growing phase, and composition because of local variability in physical conditions (e.g. flow velocity during floods, elevation above the water level and substrate), landform age, and land use (Dufour and Rodríguez-González 2019). Besides, riparian forests play a crucial role in carbon

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and nutrient cycles, regulating the effects that freshwater processes produce in terrestrial ecosystems and vice versa. On the one hand, riparian forests can modify, incorporate, dilute, or concentrate substances in ground waters before they enter waterways (Décamps et al. 2009; Osborne and Kovacic 1993). On the other hand, they can retain water-suspended sediments, uptake and sequester nutrients, and pollutants, which are essential regulatory processes (Décamps et al. 2009; Osborne and Kovacic 1993; Roy et al. 2007). In fact, riparian forests are considered as biological "buffers" and the interest for their preservation has become widespread.

Riparian forests, however, have been historically subjected to high anthropogenic disturbances exacerbating the natural perturbation regime and compromising the resilience of such as valuable ecosystems. In fact, 90% of riparian forests in Europe have disappeared and the remaining patches are extremely degraded due to channelling, intensive agricultural exploitation, or industrial uses (Hughes 2003). Additionally the plantation of fast-growing exotic and hybrid trees, and the colonization by invasive plant species contribute to landscape homogenization and can especially alter the characteristics and functioning of the forested freshwater ecosystems by modifying the direct input of nutrients, organic matter, and large wood (Décamps et al. 2009; Hughes 2003; Valett et al. 2002; Warren et al. 2007). Increasing our understanding of plant–soil interactions in riparian forests can guide conservation and management priorities as well as restoration practices in these threaten ecosystems.

Species that characterize the tree canopy strongly influence soil physical–chemical characteristics (e.g. soil humidity, acidity, organic matter, or nutrient pools) (Andivia et al. 2015; Augusto et al. 2002; Ayres et al. 2009; López-Marcos et al. 2019; Medina-Villar et al. 2016; Prescott 2002; Waring et al. 2015), soil biological communities (Dukunde et al. 2019; Gutiérrez-López et al. 2014; Medina-Villar et al. 2016), and soil ecological processes, such as litter decomposition, microbial activities, or nutrient mineralization rates (Castro-Díez et al. 2009; Medina-Villar et al. 2016; Pérez-Corona et al. 2006). The involved mechanisms included plant interspecific differences in plant functional traits, such as the ability to fix nitrogen (Dawud et al. 2017; De Deyn et al. 2008; van Miegroet and Cole 1984), the uptake of exchangeable cations and anions, nutrient use efficiency and growth rates (Aerts and Chapin 2000; Read 2001), as well as differences in the timing, quantity, and quality of the litter produced (Kamei et al. 2009; Medina-Villar et al. 2015a; Xiong and Nilsson 1999; Xu et al. 2013). Furthermore, it has been largely reported that different tree species determine different soil properties, which in turn may influence the plant nutrient uptake and the species composition of the understory plant community (Barbier et al. 2008; López-Marcos et al. 2019; Rhoades et al. 2001; Su and Zhao 2003).

Other aspects that may influence soil properties and microbial activities in riparian forests are the plant taxonomic and functional diversity, tree density, and the structure of ages and heights of the dominant woody species (Bauhus et al. 1998; Dawud et al. 2017; Hanif et al. 2019; Lucas-Borja et al. 2019; Su and Zhao 2003; Teixeira et al. 2020; Zheng et al. 2017). In this sense, soil carbon (C) and N have been reported to increase as tree age and height increase both in native and afforested forests (Su and Zhao 2003; Teixeira et al. 2020). Indeed, afforestation with different tree or shrub species in adjacent grasslands and degraded areas is one of the most common and efficient measures for the restoration of riparian forests (Sweeney and Czapka 2004). Revegetation of these areas can similarly modify soil properties, generally increasing soil fertility, but the intensity of the changes depends on the functional characteristics of the planted woody species (Chirino-Valle et al. 2016; Diallo et al. 2019; Kahle et al. 2005). Exotic tree plantations are also able to highly modify soil properties regarding native forests (Boothroyd-Roberts et al. 2013; Jeddi and Chaieb 2012; Turner and Lambert 1988).

The strength of the idiosyncratic effect of tree species on soil properties also depends on the ecosystem type and seasonality (Borken et al. 2002; Patel et al. 2010; Rhoades et al. 2001 2004). Mediterranean riparian forests are exposed to high intra-annual variability of flooding events coupled with seasonal drought that strongly affect nutrient cycles and soil properties (Bernal et al. 2013). However, little is known about the seasonal influence that riparian vegetation (differing in species composition, diversity, and demographic structure of woody species) may have on soil characteristics and processes.

This study aims to evaluate the effect of canopy species composition on the temporal dynamics of physical–chemical and biological soil parameters in Mediterranean riparian forests. For this, we monthly evaluated along one-year soil moisture, pH, contents of total N, ammonium, nitrate and organic C, most probable number of aerobic and anaerobic microorganisms, and acetylene reduction activity (as an estimate to the effective N_2 fixation) in different riparian vegetation-type zones in a riparian ecosystem in Central Spain: (1) forests dominated by native alder trees [*Alnus glutinosa* (L.) Gaertn], (2) shrublands dominated by young native alder shrubs [*Alnus glutinosa* (L.) Gaertn], (3) monospecific poplar (*Populus* × *hybrida* Moench) plantations, (4) mixed forests formed by alder [*Alnus glutinosa* (L.) Gaertn], poplar (*Populus alba* L. and *Populus* × *hybrida* Moench), ash (*Fraxinus angustifolia* Vahl) and willow (*Salix alba* L.) trees, and (5) humid grasslands (open area) without canopy species (tree or shrub). Based on previous literature, we hypothesized: (H1) more organic C and nutrients in canopy zones than in grassland due to greater leaf litter inputs (Kahle et al. 2005; Diallo et al. 2019); (H2) higher N and organic C contents in alder forests than in other zones due to the ability of alder to fix N_2 and the high N content of its litter (Chauvet 1987; Clein and Schimel 1995); and (H3) more ability of adult than young alder trees to increase soil C and N (Su and Zhao 2003; Lucas-Borja et al. 2019).

Material and methods

Study area and species

Field sampling was conducted in a riparian ecosystem alongside Sorbe river, in the vicinity of Humanes de Mohernando (Central Spain, N 40°50′46.8″, W3 °8′52.4″). A detailed description of the study area can be found in Pérez-Hernández (1996). The climate of the area is characterized as mild Mediterranean. Mean annual rainfall is 397.4 mm, and mean annual temperature is 13 °C. The mean temperature of the coldest and hottest months is 4 and 23 °C, respectively. The soils are brown ferrisialitic or calcareous soils and rendzinas with calcareous crust (Portero et al. 1990). Terrace levels and quaternary alluvial deposits form the soil substrate. Soil texture is sandy loam (mean granulometric values: 65.80% of sand, 21.00% of lime, and 13.25% of clay).

Within the study area, we identified five vegetation types (thereby called as canopy species): (a) monospecific native alder forests of *Alnus glutinosa* (Betulaceae), where alder trees ranged from 8 to 20 m in height, tree density was 0.7 trees/m^2, and the understory was mainly constituted, by *Urtica urens* L., *Scirpus holoschoenus* L., *Geranium robertianum* L., *Brachypodium sylvaticum* (Hudson) Beauv., among others; (b) shrublands dominated by alder shrubs that ranged from 0.5 to 3 m in height with an understory dominated by *S. holoschoenus* and *G. robertianum*; (c) monospecific plantations of the exotic poplar species, *Populus* × *hybrida* (Salicaceae) clone I-214, where trees ranged from 4 to 6 m in height, tree density was 0.87 trees/m^2, and the understory vegetation was dominated by herbaceous species, such as *Avena sterilis* L., *Trifolium* spp., and *Poa pratensis* L.; (d) dense mixed forests formed by willow (*Salix alba* L.; Salicaceae), ash (*Fraxinus angustifolia* Vahl; Oleaceae), alder and poplar (*Populus* × *hybrida* and *Populus alba* L.) trees with a dense understory dominated by *Rubus ulmifolius* Schott, and (e) humid grasslands (open area) without canopy species (tree or shrub) and with a floristic composition similar to that of the poplar plantation plus *Genista scorpius* (L.) DC. and *Hypericum perforatum* L.

The tree species *A. glutinosa* and *F. angustifolia* are very sensitive to changes in hydrological regimes, such as extreme events of droughts and floods (Rodríguez-González et al. 2014; Mikac et al. 2018). Moreover, the Habitats Directive of European Commission in its article 17 (2013–2018) considered Alluvial forests with *A. glutinosa* (91E0), as well as Thermophilous *F. angustifolia* forests (which include *Salix* spp.) (91B0) as priority habitats with unfavourable-inadequate status. *Populus* × *hybrida* is an exotic species, created by mixing the exotic *Populus deltoides* Bartram ex Marshall with the native *Populus nigra* L., and it has been widely planted in Western Europe, leading to biotic homogenization (Kominoski et al. 2013).

Sampling design

For each canopy species, we randomly selected five sampling plots (1 × 1 m) along the study area. At each sampling plot, four subplots (15 × 15 cm) were randomly settled. Under aseptic conditions, the upper litter layer of the soil was taken out with a hoe previously flamed and then the soil underneath till 10 cm depth was taken. The four soil subsamples for each sampling plot were mixed, homogenized, and divided into three parts: one for physical–chemical analysis, one for microbiological analysis, and one for soil N fixation measurements. Samples were conserved at 2–4 °C. This procedure was monthly repeated from June to May of 1987.

Physical–chemical analyses

Soil moisture content was gravimetrically measured as the difference between the initial fresh weight and dry weight (110 °C until constant weight) of the soil samples. For the rest of the analyses, soil samples were dried out at 55 °C and sieved through a 2.0 mm mesh size. pH was measured using a mv/pH meter (CRISON digit 501) in a mixture of 20 g of soil with 20 mL of deionized water (Allen et al. 1974). Total nitrogen and ammonium contents were measured by Kjeldahl digestion, and the produced ammonia was quantified with a selective electrode (Orion 95–10-00) connected to a mv/pH meter CRISON digit 501. Nitrate was extracted with a solution containing $Al_2(SO_4)_3$, H_3BO_3, Ag_2SO_4, and NH_2SO_3H (Milham et al. 1970) and determined with a nitrate selective electrode (ORION 93-07-00). Organic carbon was determined using the Walkey and Black method (1934).

Microbiological analyses

For microbiological analyses, soil samples were dried out at room temperature on filter papers. Then, they were sieved through 2.00 mm mesh size previously sterilized. Sieved samples were stored on glass bottles in the dark between 2 and 4 °C until use. Most probable number (MPN) of aerobic and anaerobic microorganisms (Aerobic Moos and Anaerobic Moos, respectively) was measured using the plating dilution soil method described by Pochon and Tardieux (1962) in a selective culture medium. Acetylene reduction activity (ARA) was used to screen the soil samples for effective N_2 fixation by soil free-living microorganisms, i.e. nitrogen fixation potentiality of the soil (Hardy et al. 1973; Siczek and Lipiec 2011; Yong et al. 2018). In total, 50 g of soil sample was weighted and introduced in glass vials sealed with a rubber lid. Then, 15 ml of air was extracted from the flasks and an equal amount of acetylene was introduced in them. Vials were incubated at room temperature during 24 h under natural photoperiod (Knowles 1982). The ethylene produced was measured in a gas chromatograph (KONIK, Cromatik KNK) with flame-ionization detector (Hardy et al. 1973). Christiansen and Graham (2002) reported that acetylene assay is useful to assess changes in N_2 fixation over time and among treatments.

Statistical analysis

We used linear mixed models (LMM) to evaluate the main effect of canopy species, collecting date and their interaction on soil physical–chemical and microbiological parameters. The identity of the sampling plot was considered as random term to account for lack of independence resulted for repeated measures at the same points. We used the Bonferroni post hoc test to evaluate differences between levels of significant factors. To achieve homoscedasticity and normality assumptions, we log-transformed some response variables. To analyse relationships between variables, we performed correlograms (Pearson correlations) at different scales: the whole study area (time and vegetation variation) and each vegetation-type area (time variation). We also performed a principal component analysis (PCA) with depicted ellipses for each canopy species. Non-overlapping ellipses indicate significant differences ($p < 0.05$) among different canopy species considering all soil variables along time. All statistical analyses were performed in R software 3.4.3 (R Core Team 2017). We used “lme” function (nlme package, Pinheiro et al. 2020) for the LMM analyses, “emmeans" (emmeans package, Lenth 2020) for post hoc pairwise comparisons, the functions “prcomp” and “autoplot” for the PCA plot (Tang et al. 2016), and the functions “rcorr” and “corrplot” (Hmisc package, Harrell and Frank 2020) for correlograms.

Results

Effect of canopy species on soil variables

All the studied soil parameters, except for C/N, showed significant differences among canopy species and collection time, being the interaction between canopy species and collection time significant in all parameters except ammonium and organic C (Table 1). Grasslands showed the lowest values of nitrate, ammonium, total N, and organic C contents during the whole year (Fig. 1). From canopy areas, nitrate content was higher in poplar plantations and mixed forests than in alder areas (Bonferroni post hoc test, $p < 0.05$; Fig. 1). In some months, nitrate content was higher in mixed forests than in plantations (winter months) and in alder forests than in alder shrublands (late spring and summer months) (Bonferroni post hoc test, $p < 0.05$; Fig. 1). From higher to lower ammonium content, canopy species ranked alder forests > alder shrublands > mixed forests > poplar plantations > grasslands. Total N and organic C showed similar species ranking but with small differences (Fig. 1). Total N content in mixed forests was similar to that in poplar plantations from September to February while similar to that in alder areas from May to July (Bonferroni post hoc test, $p < 0.05$; Fig. 1). Alder shrublands and mixed forests showed similar organic C. In the case of C/N, the lowest values were found in grasslands during summer and in alder shrublands during winter with no clear differences in temporal pattern between canopy species (Bonferroni post hoc test, $p < 0.05$; Fig. 1). In relation to the temporal evolution of nutrient contents, ammonium and nitrate had the lowest values in winter months in all vegetation types, whereas total nitrogen and organic C showed different seasonal dynamics in each vegetation type (Fig. 1).

Overall, pH values were lower in alder shrublands and grasslands compared to the other canopy species, with the lowest values in winter months (Bonferroni post hoc test, $p < 0.05$; Fig. 2). Soil moisture was the highest in alder forests, followed by mixed forests, and the lowest in grasslands and poplar plantations (Bonferroni post hoc test, $p < 0.05$; Fig. 2). Intra-annual variability of soil moisture was high in alder and mixed forest areas, with the highest values in late autumn and winter and the lowest in summer (Fig. 2).

Table 1 Two-way repeated-measures ANOVA results for different soil variables between canopy tree species, time, and interaction between them

Soil variables	Canopy	Time	Interaction
Nitrate (µg/g)	< 0.0001	< 0.0001	< 0.0001
Ammonium (µg/g)	< 0.0001	< 0.0001	0.983
Total nitrogen (mg/g)	< 0.0001	< 0.0001	< 0.0001
Organic C	< 0.0001	< 0.0001	0.0935
C/N	0.2327	< 0.0001	< 0.0001
pH	< 0.0001	< 0.0001	< 0.0001
Soil moisture (%)	< 0.0001	< 0.0001	< 0.0001
Aerobic microorganisms (MPN)	< 0.0001	< 0.0001	< 0.0001
Anaerobic microorganisms (MPN)	< 0.0001	< 0.0001	< 0.0001
ARA	< 0.0001	< 0.0001	< 0.0001

Fig. 1 One-year temporal changes of soil ammonium, nitrate, total nitrogen soil organic carbon, and C/N in different riparian vegetations: alder forest—Alder, alder shrubland—Alder (shrub), mixed forest, poplar plantation—Poplar, and grassland. Values are means ± standard error

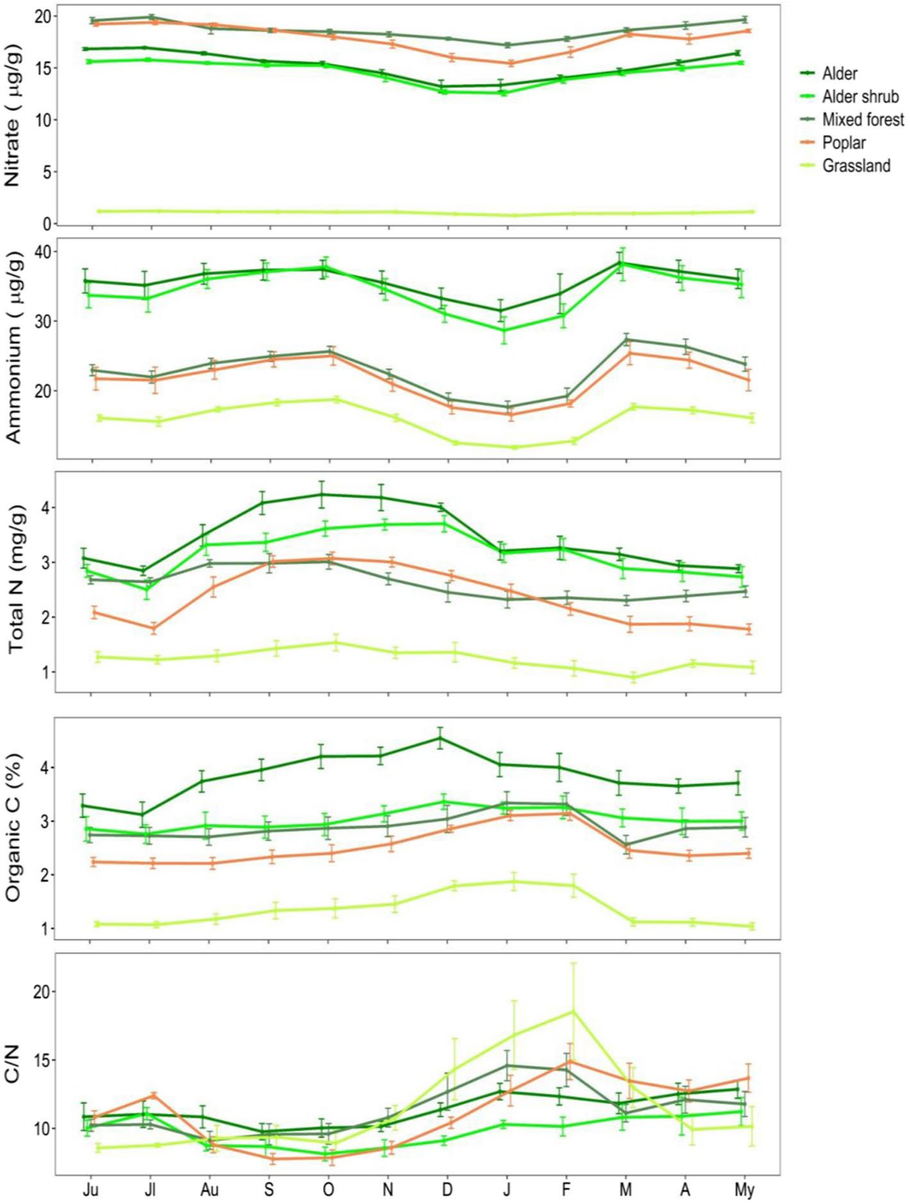
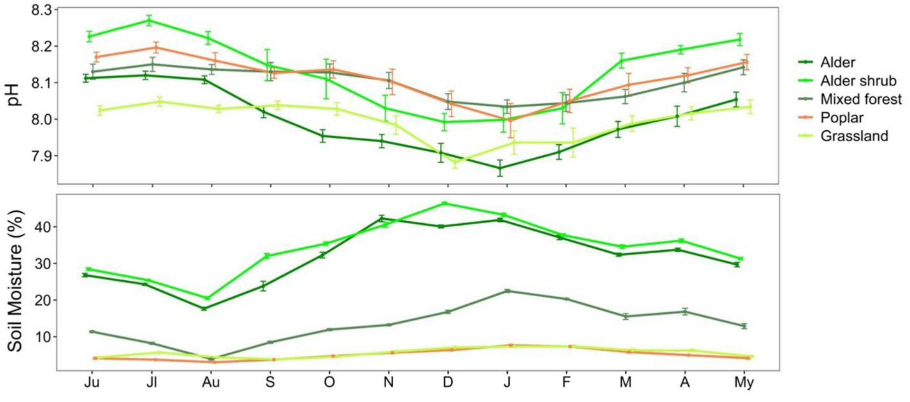


Fig. 2 One-year temporal changes of pH and soil moisture in different riparian vegetations: alder forest—Alder, alder shrubland—Alder (shrub), mixed forest, poplar plantation—Poplar, and grassland. Values are means ± standard error



ARA values peaked in February and November in mixed forests, in January in grasslands, in October and January in alder forest, and slightly in October and March in alder shrublands (Fig. 3). The number of aerobic and anaerobic microorganisms in the soil showed a similar pattern along the year, showing both biological parameters the highest values in alder areas, peaking in May, June, and October (Fig. 3).

Relationships between soil parameters

The correlation analysis revealed that soil parameters were rather correlated between them (60% of the correlations were significant; $p < 0.05$; Fig. 4) although correlations values did not show very high r (only 11% showed $r > 0.7$). Significant correlations considering all vegetation types were mostly positive (85%) except for C/N that was negatively correlated with pH, ammonium and total N, and soil moisture that was negatively correlated with pH (Fig. 4). Positive and strong correlations were found between N compounds (ammonium, nitrate, and total N), organic C, and soil moisture. The correlation strength between soil chemical and microbiological variables (ARA, aerobic, and anaerobic microorganisms) was low (Fig. 4). All soil microbiological variables were positively correlated with soil moisture (Fig. 4). The MPN of aerobic and anaerobic microorganisms was positively correlated between them and with C and ammonium (Fig. 4). The MPN of aerobic microorganisms was also positively correlated with total N and ammonium (Fig. 4).

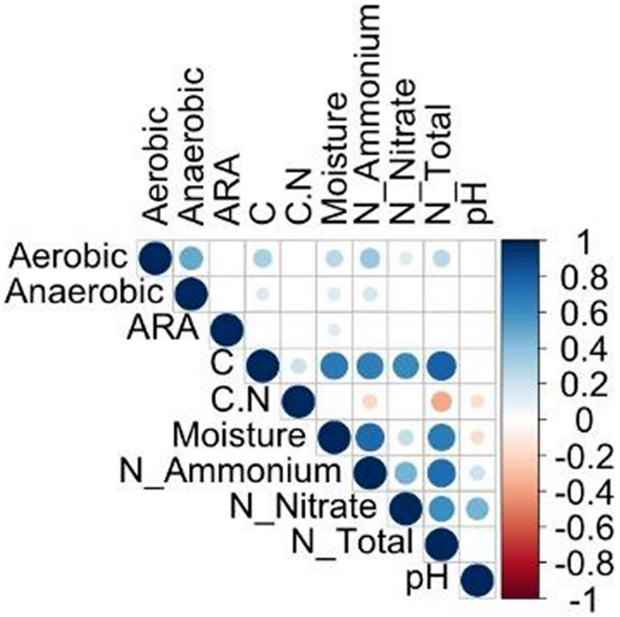
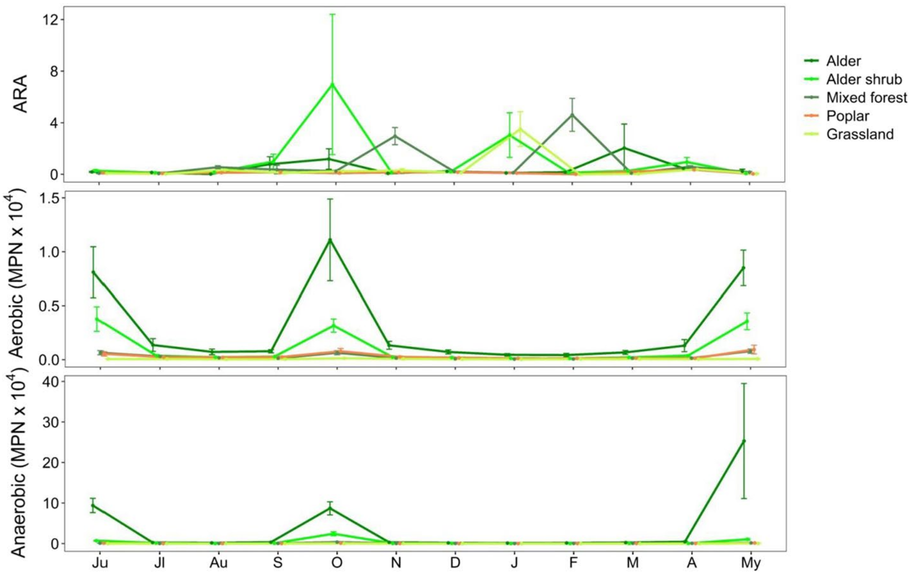


Fig. 4 Correlogram showing correlations between dependent variables: pH, total N, nitrate, ammonium, soil moisture, C/N, organic carbon (C), ARA, and aerobic and anaerobic most probable number of microorganisms. Colour intensity and the size of the circle are proportional to the correlation coefficients. The legend (right side of each correlogram) shows the correlation coefficient and the corresponding colour: blue circles mean positive correlations and red circles negative correlations. Blank spaces without circle are non-significant correlations ($p > 0.05$)

Correlation patterns were different between vegetation types, with the exception of alder forests and shrublands (Fig. 5). While soil moisture was positively correlated with N compounds at the study area scale, soil moisture was negatively correlated with inorganic N (ammonium and nitrate) in all vegetation types. MPN of aerobic microorganisms was positively correlated with pH in all vegetation types except grasslands and with nitrate in alder and mixed forests. Some correlations between studied variables were specific for each vegetation type. For instance, MPN of anaerobic

Fig. 3 One-year temporal changes of acetylene reductase activity (ARA), most probable number of aerobic and anaerobic microorganisms. alder forest—Alder, alder shrubland—Alder (shrub), mixed forest, poplar plantation—Poplar, and grassland. Values are means ± standard error



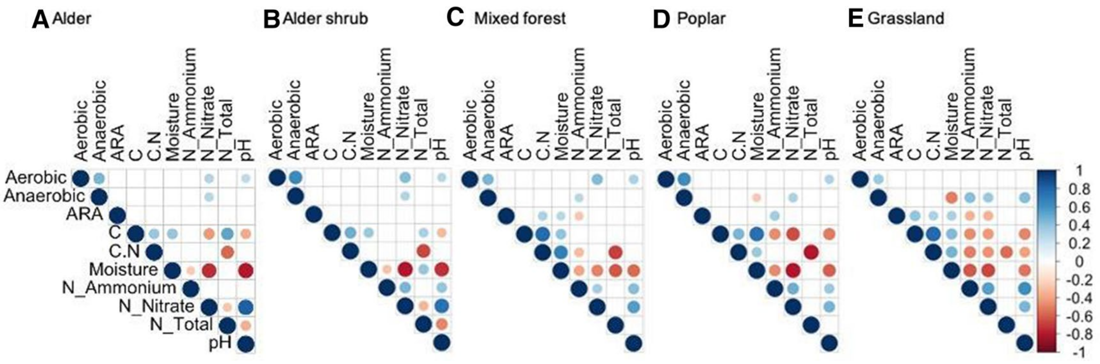


Fig. 5 Correlogram showing correlations for each vegetation area between dependent variables: pH, total N, nitrate, ammonium, soil moisture, C/N, organic carbon (C), ARA, and aerobic and anaerobic most probable number of microorganisms. Colour intensity and the size of the circle are proportional to the correlation coefficients. The legend (right side of each correlogram) shows the correlation coefficient and the corresponding colour: blue circles mean positive correlations and red circles negative correlations. Blank spaces without circle are non-significant correlations ($p > 0.05$)

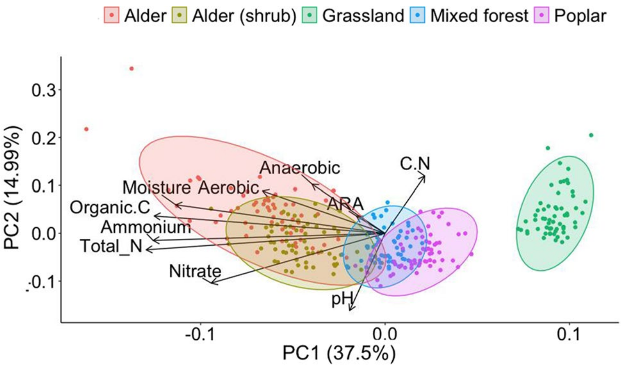


Fig. 6 Results of the PCA for the different soil variables: total N, nitrate, ammonium, pH, C/N (C.N) organic C, moisture, most probable number of aerobic, and anaerobic microorganisms and ARA. Colour ellipses represent different vegetation types

microorganisms was negatively correlated with soil moisture in poplar and grassland areas and positively correlated with nitrate in alder, poplar, and grassland areas, and with ammonium in grasslands and mixed forests. ARA also showed vegetation-specific correlations with chemical variables: i.e. the correlation between ARA and soil ammonium content was significant and positive ($p < 0.05$) in poplar plantations while negative in grasslands and mixed forests. In alder areas, ARA was not correlated with any chemical variable. Total N was negatively correlated with pH in alder areas but not in other areas. Organic C was negatively correlated with pH in all areas except mixed forests and negatively correlated with mineral N in poplar plantations and grasslands.

Principal component analysis (PCA)

PCA axes explained 37.5% and 14.99% of the total variance, respectively (Fig. 6). There was a clear spatial ordination of the observations with respect to the first PCA axis. From the negative to the positive extreme of the axis, the observations are ranked in the following order: alder forests, alder shrublands, mixed forests, poplar plantations, and grasslands. However, statistical differences regarding all soil variables were only significant between grassland and canopy zones (alder forests, alder shrublands, mixed forests, and poplar plantations). Grasslands showed the lowest values of soil nitrate, total N, ammonium, organic C, moisture, ARA, and MPN of aerobic and anaerobic microbes, while alder forests were characterized by high amounts of total N, ammonium, and organic C.

Discussion

Our study shows that riparian areas with tree canopy species had higher soil fertility (soil organic C, total N, ammonium, and nitrate) than grassland open areas, which support our hypothesis H1. This effect was more evident in the case of soil nitrate, which was more than 15 times higher in canopy areas than in grasslands. Our results are similar to those previously reported for alder in the study area (Pozuelo Gonzalez et al. 1995), for mixed forests (Rhoades et al. 2004), and for other riparian forests dominated by different species, such as *Alnus crispa* (Rhoades et al. 2001), *Populus* and *Salix* spp. (Kahle et al. 2005), and other woody species (Diallo et al. 2019). Soil fertility, in terms of organic C and total N, was higher in areas dominated by the N_2-fixing species, *Alnus glutinosa,* than in other canopy areas, supporting our H2. This result agrees with recent studies showing that tree identity and the functional group (e.g. the ability to fix N_2) seem more important factors influencing soil properties than forest structure and tree diversity (Dawud et al. 2017; Zheng et al. 2017). In addition, we also showed that the ability of alder to increase soil organic C and total N was higher in areas dominated by adult trees when compared to younger and smaller shrubs (H3), as it was also reported in alder and other N_2-fixing species (Pozuelo Gonzalez et al. 1995; Staska et al. 2014; Su and Zhao 2003).

Canopy N represents an important nutrient input to soil in natural and artificial systems, which may improve the nutrition of under-canopy plant species (Rhoades et al. 2001) and promote soil biological activity, and abundance of soil microbes (Birkhofer et al. 2012; Wang et al. 2018; Yevdokimov et al. 2005). In fact, correlations at the study area scale showed positive correlations between N compounds and the abundance of aerobic and anaerobic microorganisms. The highest abundance of total N and ammonium in the soil under alder canopies can be explained by the ability of alder to symbiotically fix N_2 from the atmosphere into ammonium in its radical nodules (Marschner and Rengel 2007), and the higher litter decomposition rates associated with N-rich and easily decomposable leaf litter that characterized these species (Clein and Schimel 1995; Paschke 1997; Pérez-Corona et al. 2006). N conversion in soil organic matter is mediated by soil non-specific aerobic and anaerobic microorganisms, which transform organic N to ammonium and nitrate through mineralization (Marschner and Rengel 2007). The positive influence of alder species on soil N content and availability and on the abundance of soil microbes has been previously reported (Hart et al. 1997; Homann et al. 1994; Pozuelo Gonzalez et al. 1995; Rhoades et al. 2001).

On the other hand, the lowest fertility in canopy areas was found in poplar plantations, overall in spring and summer. This is in accordance with a recent meta-analysis comparing soil properties between natural and planted forests (Liao et al. 2012) and could be explained by: (i) lower decomposition rates of leaf litter from *Populus* spp. than those from *A. glutinosa* and *F. angustifolia* (Abelho 2014; Casas et al. 2013; Horodecki et al. 2019; Martínez et al. 2013; Medina-Villar et al. 2015b); (ii) lower net primary production, litterfall inputs, soil nutrient conservation, and fine root biomass in plantations than in natural forests (Cai et al. 2019; Liao et al. 2010; Pandey et al 2007; Yang et al 2005); and (iii) tree harvesting and other management practices in productive plantations (Liao et al. 2010).

Despite higher contents of total soil N and ammonium, alder forests showed lower nitrate content compared to mixed forests and poplar plantations (Pozuelo Gonzalez et al. 1995). Nitrate can be easily lost from the soil system by leaching and denitrification as soil moisture increases (Marschner and Rengel 2007). The proximity of alder canopies to the river bank in the study area may explain their higher soil moisture, which could have determined higher rates of nitrate leaching and denitrification and thus lower soil nitrate contents in alder areas than in poplar plantations and mixed forests. Moreover, the strongly negative correlation between soil nitrate and soil moisture supports these results. Besides, some authors also pointed to the ability of N_2-fixing plant species to allelopathically inhibit nitrifying microorganism (Llinares et al. 1993; Pozuelo Gonzalez et al. 1995). Lastly, Schnabel et al. (1997) showed that grasslands had greater denitrification rates than woodlands and thus lesser retention for nitrate, which is also in accordance with our results showing lower nitrate content in grassland than in forested areas.

Contrasting correlations between abundance of soil microorganisms and mineral N between canopy species may indicate different dominance of functional groups of microorganisms. For instance, increases in the abundance of soil microorganisms with increasing nitrate in alder and mixed forests may indicate dominance of denitrifying bacteria (Marschner and Rengel 2007). On the contrary, the abundance of soil microorganism was positively correlated with both, nitrate and ammonium in mixed forests and grasslands, which might indicate dominance of microorganisms using both inorganic N forms (Marschner and Rengel 2007). Further studies are needed to better understand the relationship between species canopy, soil fertility, and the abundance of different groups of microorganisms. The potential nitrogen fixation (ARA) peaked in different months in alder areas, mixed forest, and grasslands. Several factors may regulate soil-free nitrogen fixation activity. For instance, the abundance and activity of free-living N_2-fixing microorganisms (diazotrophs) may increase with soil organic matter and water content, while decreasing with soil pH, N availability, and oxygen content (Chen et al. 2019; Smercina et al. 2019). Actually, we showed that ARA was correlated positively with organic C and soil moisture and negatively with inorganic N in grasslands. At a study site scale, we found that the soil characteristic that better explained ARA was soil moisture, according to Maggs and Hewet (1986).

Tree species has been identified as the main factor explaining C/N variations in European forest soils, being the forests dominated by N_2-fixing species (*Alnus glutinosa* and *Robinia pseudoacacia*) those showing the lowest C/N values (Cools et al. 2014). However, in the present study, C/N values were very similar between canopy species, yet forests dominated by alder shrubs showed the lowest C/N values. C/N showed a low correlation with physical soils variables indicating a low dependence of C/N with soil or ecosystem variability. Values of pH ranged from 7.99 in alder forests and open grasslands areas to 8.13 under alder shrubs. These results were similar to those for alder forests in Rhoades et al. (2001). Soil pH is highly determined by soil type. In our study site, soil is sandy with calcareous influence; thus, cation retention is lower compared to loamy or clay soils (Moore et al 1998). Differences in pH between canopy species can be mainly attributed to vegetation characteristic because soil type was rather homogeneous. For instance, differences in the production of organic acids from decomposing litter of the different plant species may affect the relative quantities of exchangeable base and acid cations in the soils (Finzi et al. 1998). High organic acid production and low soil pH have been noted in sites dominated by species whose litter is relatively recalcitrant, i.e. litter that decompose slowly (Konova 1966). That is not the case of the study tree species *A. glutinosa*, *F. angustifolia*, and *Populus* × *hybrida* that had elevated decomposition rates (Pérez-Corona et al. 2006). We showed that pH was highly correlated with soil moisture in all vegetation types according to Zhang et al. (2019).

Seasonal dynamics of soil parameters highlight different soil activities along the year. Decreases in soil ammonium and nitrate content during winter months were related to increases in soil moisture, which can favour denitrification and leaching processes (Pastor et al. 1984). Besides, low winter temperatures decrease microbial activity, such as the activity of soil ammonificant bacteria (Qiu et al. 2005). The number of microorganisms increased in late spring and in autumn in alder areas probably favoured by proper environmental conditions (mild temperatures and suitable soil moisture) and also due to high availability of nitrogen-rich autumnal litter (Facelli and Pickett 1991).

Implications for management

Riparian vegetation has been highly threatening by human activities, such as agriculture, road constructions, mining, channelling, and natural diseases and increased aridity due to climate change (Hughes 2003). Afforestation programmes using mixed native tree species, such as *A. glutinosa*, *F. angustifolia*, *P. alba*, and *Salix alba* are highly recommended, not only to restore degraded riparian areas but also to improve soil fertility (in terms of organic C, nitrate, and total N) and to reduce opportunity windows for the colonization by alien exotic species (Carvalho et al. 2010; Shea and Chesson 2002).

Exotic species are main drivers affecting native riparian plant communities (Décamps et al. 2009; Kominoski et al. 2013). Exotic poplar plantations have less ecological impacts than annual crops and high economic and social value, contributing to rural development (Heilman 1999; Neumann et al. 2007; Testa et al. 2014). Even so, monospecific plantations with exotic poplar hybrids with little or no vertical structure have largely contributed to species homogenization, ultimately affecting native fauna and flora (Godreau et al. 1999; Twedt et al. 1999). In addition, the replacement of native alder forests by *Populus* × *hybrida* plantations implies the introduction of low-quality litter that in turn can affect detritivore activity and thus the incorporation of soil nutrients from litter to soil through the decomposition process (Cai et al. 2019; Casas et al. 2013; González and Graça 2003). As we stressed, poplar plantations contributed to decrease soil fertility, being unlikely the recovery to values found in natural forest, which emphasizes that the replacement of native riparian forests by plantations should be avoided (Liao et al. 2012). Plantations could be placed in abandoned agricultural fields or no forested lands instead in order to preserve the socio-economic benefits. Besides, planting native species, such as *A. glutinosa*, among the poplar trees, would help to improve species diversity, soil fertility, and tree productivity (Sayyad et al. 2006). In fact, litter decomposition is accelerated in mixed forests regarding monoculture stands, leading to higher soil development (Horodecki et al. 2019). Management practices for poplar plantations should prioritize those minimizing harmful effects on biodiversity (Archaux et al. 2010). Finally, the presence of poplar plantations should not be at the expense of replacing native riparian forests and specific regulations should ensure poplar plantations for socio-economic development but also preserve native riparian forests by promoting conservation practices, such as afforestation programmes with native trees.

Conclusions

Overall, our study shows the ecological significance of forested riparian zones (especially, alder forests and shrublands) to improve soil fertility (N and C). From forested areas, plantations with the exotic *Populus* × *hybrida* showed the lowest soil fertility. Alder mature forests (i.e. higher tree age and size) show higher capacity to improve soil conditions than young alder forests. The highest soil ammonium values were found under alder canopies likely due to the ability of alder to symbiotically fix atmospheric N_2 into ammonium. Conversely, nitrate was the lowest in alder areas probably due to high soil moisture and thus high rates of denitrification and leaching. The highest abundance of aerobic and anaerobic microorganisms in alder areas matched the highest levels of soil N. Soil moisture highly influences seasonal differences in soil characteristics in riparian forested zones, especially soil nitrate, pH and abundance of microorganisms. Our results support planting native trees, e.g. *A. glutinosa* and *F. angustifolia* as restoration measures to improve soil fertility, ecological integrity, and productivity of riparian areas and poplar plantations.

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Authors' contributions María Esther Pérez-Corona helped in formal analysis, visualization, writing original draft preparation, writing—review and editing. María del Carmen Pérez-Hernández involved in conceptualization, methodology, investigation. Silvia Medina-Villar helped in visualization, formal analysis, writing— review and editing. Enrique Andivia contributed to formal analysis, visualization, writing—review and editing. Francisco Bermúdez de Castro involved in conceptualization, methodology, supervision.

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Availability of data and material Data will be provided upon request.

Declarations

Conflict of interest The author declares that they have no conflict of interest.

Consent to participate Authors consent to participate.

Informed consent Authors consent for publication the present manuscript.

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