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Asian knotweed's impacts on soil chemistry and enzyme activities are higher in soils with low-nutrient status

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ABSTRACT

Invasive alien plants such as *Reynoutria* spp. can drastically affect the composition of plant communities. Yet, whether and how these species also affect soil physicochemical properties and microbial functioning is still an unresolved question in the literature. Using a space-for-time substitution approach comparing invaded to uninvaded adjacent plots, we estimated the impacts of *Reynoutria* on soil biochemistry across nine contrasted sites in France by measuring soil carbon content, nutrient availability and enzyme activities. Soil under *Reynoutria* displayed higher carbon, nitrogen and phosphorus contents but no differences were detected regarding enzyme activities between invaded and uninvaded sites. Moreover, the magnitude of *Reynoutria*'s effects differed depending on local conditions, with greater effects when total carbon and phosphorus-related enzymes were relatively low. These data highlight that changes in soil nutrient availability might be primarily due to direct effects of *Reynoutria* on soil properties and microbial functioning. Higher impacts were observed in soils with low-nutrient status, suggesting a 'niche construction ability' of *Reynoutria*. Our results underscore the necessity of considering the context-dependency of *Reynoutria* on soil biochemistry and highlight that the impact of alien species belowground functioning depends on initial soil conditions.

1. Introduction

Biological invasions are major drivers of ecosystem degradation and biodiversity loss worldwide (Pyšek and Richardson, 2010). Among them, invasive alien plant species represent more than 50 % of all invasive taxa (McGeoch et al., 2010). The ecological impacts of invasive alien plants are manifold: (i) they affect native plant species assemblages and community structure through interspecific interactions, including allelopathy and competition (Vilà et al. 2011); (ii) they influence the structure of soil biota and trophic networks (McCary et al., 2016; Abgrall et al., 2019); and (iii) they modify plant-soil interactions and ecosystem processes such as decomposition and nutrient recycling (Liao et al., 2008; Vilà et al. 2011; Abgrall et al., 2018). While there is a growing acknowledgment that invasive alien plants can exert a significant 'legacy' effect that hinders the recovery of the original plant community (Corbin and D'Antonio, 2012; Tekiela and Barney, 2017; Ahmad et al., 2021), the direction and magnitude of these effects are inconsistent and may depend strongly on climate, habitat type and human activity (González-Moreno et al., 2014). Consequently, making broad generalizations about the impact of invasive alien plants is challenging

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(Ehrenfeld, 2003), and a greater emphasis on understanding the environmental context becomes imperative for the successful implementation of restoration strategies in diverse invaded ecosystems.

A well-known case of plant invasion affecting ecosystems is that of the *Reynoutria* species complex (Asian knotweeds, hereafter, *Reynoutria*). Composed of *Reynoutria japonica* Houttuyn [*Fallopia japonica* (Houttuyn) Ronse-Decraene], *R. sachalinensis* (F. Schmidt) Nakai [*F. sachalinensis* (F. Schmidt) Ronse-Decraene] and the hybrid *R.* x *bohemica* Chrtek & Chrtková [*F.* x *bohemica* (Chrtek and Chrtková) J.P. Bailey], these species outcompete native plant species and often come to dominate the plant community within a very short span of time (Lavoie, 2017). Originating from eastern Asia, *Reynoutria* have colonized numerous countries at the global scale and are now present on all the continents except Antarctica (Martin, 2019). An increasing body of literature has shown that *Reynoutria* decreased the biomass of native species and altered native community composition (Maurel et al., 2013; Lavoie, 2017; Woch et al., 2021; Holmes and Kuebbing, 2022). Yet, the impacts of *Reynoutria* on soil properties and microbial activity were highly variable among studies. For instance, several publications assessing differences in total and available carbon, nitrogen and phosphorus between invaded and reference plots have found either increasing (Urgenson et al., 2012; Tharayil et al., 2013), neutral (Dassonville et al., 2007, 2011; Kappes et al., 2007; Aguilera et al., 2010; Dommanget, 2014; Dommanget et al., 2014; Stefanowicz et al., 2017; Woch et al., 2021; Zhang and Suseela, 2021; Schmitz et al., 2023), or even decreasing effects (Stefanowicz et al., 2018, 2020). Similarly, enzymatic activities under *Reynoutria* can either increase, decrease or remain constant according to the enzymes or ecosystems considered and soil depth (Suseela et al., 2016; Min and Suseela, 2020; Stefanowicz et al., 2021, 2022). While the source of such variability remains unclear, Dassonville et al. (2011) suggested that *Reynoutria*'s effects on soil properties might be contingent upon the initial local conditions, and proposed a 'niche construction' mechanism. This mechanism entails *Reynoutria*'s ability to alter its local environment to promote its growth and fitness, but this hypothesis remains to be confirmed across various environments.

In this study, we tested the effects of the *Reynoutria* species on soil biochemical properties and enzyme activities in nine contrasted sites along three catchments in the French alpine foothills. The sites varied in terms of landscape context, bedrock composition and nutrient availability. Through a space-for-time substitution approach based on a paired-design (Barney et al., 2013; Pickett, 1989; Sax et al., 2005), we compared *Reynoutria*-invaded plots to neighbouring uninvaded riparian plots. First, we hypothesized (H_1) that *Reynoutria* would increase soil carbon (soil C) and nitrogen (soil N) concentrations due to the higher plant biomass in invaded plots combined with the production of litter with high C/N ratios (Urgenson et al., 2009; Dassonville et al., 2011; Mincheva et al., 2014; Suseela et al., 2016). Second, we hypothesized (H_2) that the enhanced soil C and N contents would increase soil enzymatic activities due to a stimulation of microbial communities (Fanin et al., 2014). Finally, we hypothesized (H_3) that the initial site conditions would influence soil responses to *Reynoutria* ingress. Specifically, we anticipated that *Reynoutria* would have more pronounced effects in sites characterized by low soil organic carbon and nutrient contents, as well as reduced enzyme activities (Dassonville et al., 2011).

2. Materials and methods

2.1. Experimental design and collecting soil sample

Our study was conducted in nine sites spread over three contrasted catchments in south-eastern France, in the Auvergne-Rhône-Alpes region where monthly mean temperatures range between 2.2 and 22.3 °C and mean annual precipitation reaches 1037 mm distributed over 143 rainy days (2000 – 2020; data from the closest MeteoFrance weather stations https://publitheque.meteo.fr). The three catchments (hereafter called "catchments" – Fig. 1) are located: (i) along the Isère river with a nivo-pluvial regime in a large densely urbanized and cultivated glacial valley (GRESIVAUDAN catchment), (ii) along the Bourne river with a pluvio-nival regime at the foot of the limestone Vercors Mountain range (ROYANS catchment), and (iii) along a small tributary of the Sonnant d'Uriage river in an acidic-soil rural valley at the foot of the crystalline Belledonne Mountain range (BELLEDONNE catchment). Within each catchment, we selected three sites with a distance between them ranging from 77 m to 466 m. Within each site, two plots were sampled (Fig. 1): one invaded by *Reynoutria* (REYN treatment) and one in an adjacent uninvaded riparian area (RIPA treatment). This space-for-time substitution approach (Pickett, 1989), also called comparative approach, is the most widely used method in invasion ecology for assessing the impact of non-native species (Barney et al., 2015; Parker et al., 1999; Ricciardi et al., 2013), and is typically used for the *in situ* study of *Reynoutria*'s effects on soil (Dassonville et al., 2008; De Almeida et al., 2022; Stefanowicz et al., 2016, 2020; Suseela et al., 2016; Tamura and Tharayil, 2014). Although this approach is often one of the few ways of studying the effects of invasive alien plant species over time in the wild (Barney et al., 2013), it may have some limitations, including the fact that adjacent plots may not represent exactly the same soil conditions before invasion. To overcome this issue, the paired-plots composed of *Reynoutria*-invaded and uninvaded riparian plots were carefully chosen from the same habitat and were on average 9 m apart (range [7;17 m]) in order to minimize differences in environmental conditions prior to invasion. Uninvaded plots were at least 5 m apart from the edge of a *Reynoutria*-patch to avoid any interference (Fennell et al., 2018; Dommanget, 2014). The coordinates and a description of all the sites are provided in the supplementary material section (Table S1). The invaded plots (REYN) were all characterized by an herbaceous layer dominated by *Reynoutria* (more than 80 %) and at the BELLEDONNE catchment, were located under an overstory dominated by *Acer* and *Fraxinus* trees. Uninvaded riparian plots (RIPA) were typical of local riparian forests and composed mainly by *Salix* and *Populus* species (ROYANS catchment), *Acer* and *Fraxinus* trees (BELLEDONNE catchment) and *Robinia*, *Fraxinus* or *Populus* species (GRESIVAUDAN catchment) (Table S1). Two sites at the GRESIVAUDAN catchment were regularly managed (mowing of the herbaceous layer) but sampling took place before any intervention and *Reynoutria* stands showed no difference in vigour from the unmanaged plots.

Using satellite images from Google Earth (Google Earth Pro – v7.3.4.8248) and the Geoportail website (https://remonterletemps.ign.fr), we estimated that *Reynoutria* had invaded the sites at the GRESIVAUDAN catchment between 5 and 10 years prior, and more than 10 years prior for sites at the ROYANS catchment. At the sites at the BELLEDONNE catchment, as the invaded plots had a thick overstory, it was not possible to date the invasion with aerial images. However, thanks to interviews with local residents, we determined that *Reynoutria* establishment was more than 5 years old (Table S1). From June 23rd to 26th 2020, we collected three soil samples per plot (=pseudo-replicates) with a soil corer (10 cm diameter, 20 cm depth). Each of the 54 soil samples was divided in three aliquots. One aliquot was kept at 4°C for the immediate extraction of available nutrients, a second was stored at −20°C for enzyme assays, and a third was air-dried and crushed to measure total macro- and micro-nutrients. During the entire sampling period, the weather was sunny and stable. In all, 54 soil samples were collected for nutrient and enzyme analyses (3 catchments × 3 sites × 2 paired-treatment plots × 3 pseudo-replicates – Fig. 1).

2.2. Available soil nutrients

Available ammonium (NH_4^+), nitrate (NO_3^-), and phosphate (PO_4^-) were measured in one aliquot of each soil sample. In brief, 4 g of dry weight soil was poured into 20 mL of ultrapure water and shaken for 16 h at 4°C. Then, the solution was placed vertically at ambient temperature for an hour to enable precipitation. The supernatant was

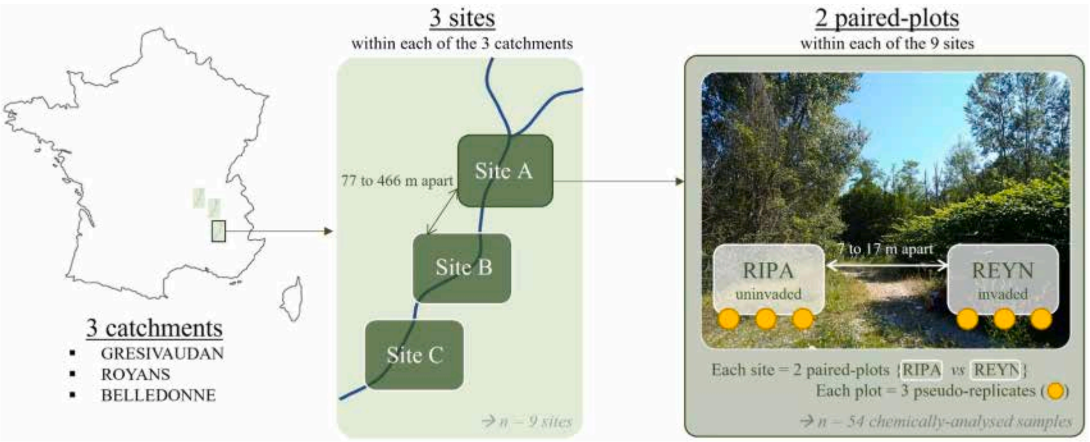

Fig. 1. Experimental design with catchments (GRESIVAUDAN, ROYANS and BELLEDONNE), sites, plots (REYN and RIPA) and pseudo-replicates. A total of 54 samples were analysed over the 18 paired-sites studied.

filtered through an 8 μm mesh size (Whatman filter). Then, the filtered solution was put through a second precipitation step (3 h at room temperature), and the supernatant was again filtered through a syringe equipped with a 5 μm mesh paper. The final solution was used to measure NO_3^-, NH_4^+ and PO_4^- by colorimetry (San++, Automated Wet Chemistry Analyzer, Breda, Netherlands). Total available mineral N (N_{avail}) was expressed as the sum of the mineral N from NO_3^- and NH_4^+ (μg N g^{-1} dry soil), and total available mineral P (P_{avail}) as PO_4^- (μg P g^{-1} dry soil).

2.3. Concentrations of macro and micro-nutrients in the soil

On one aliquot per soil sample, we measured the pH and concentrations in macro (carbon [C], nitrogen [N], phosphorus [P], potassium [K], calcium [Ca] and sulfur [S]) and micro-nutrients (copper [Cu], iron [Fe], manganese [Mn] and zinc [Zn]). Before the measurements, the soil samples were air-dried and finely milled (Planetary Ball Mill PM 400, Retsch). Total C (C_{total}) and N (N_{total}) were measured by dry combustion (NF [i.e., French standard] ISO [i.e., international standard] 10694 and 13878; AFNOR, 1999). Organic C (C_{org}) was measured with the same method after acidification of the soil samples. Total P (P_{total}) was assessed according to the malachite green colorimetric method (Vanveldhoven and Mannaerts, 1987). The elements K, Ca, S, Fe, Mn, Al, Cu, Zn were measured by inductively coupled plasma atomic emission spectrometry (Agilent Technologies, ICP-OES 5110, Santa Clara, CA, USA).

2.4. Soil enzyme assays

On the third aliquot soil sample, we measured the potential activity of seven hydrolytic soil enzymes. We focused on enzymes that catalyze the degradation of: (i) organic carbon, namely β-1,4-glucosidase [BGLU]), 1,4-β-D-cellobiohydrolase [CBH], α-1,4-glucosidase [AGLU] and β-xylosidase [XYL]; (ii) nitrogen, namely β-1,4-N-acetyl-glucosaminidase [NAG] and L-leucine aminopeptidase [LAP]; and (iii) phosphorus, namely alkaline phosphatase [AP] (Bell et al., 2013; Fanin et al., 2016). Briefly, 2.75 g from the aliquot soil sample (frozen and stored at −20°C) was homogenized in 91 mL of a 50 mM sodium acetate buffer in a blender for 1 min at room temperature. The resulting soil slurries were incubated with fluorometric substrates for 3 h at 25 °C (two measurement replicates per aliquot soil sample). The incubation of the substrates was conducted in 96-deepwell (800 μl) microplates with an eight-channel electronic pipette (Eppendorf Xplorer Plus, Hamburg, Germany). For each soil sample, we included additional quench control replicates of the soil slurry, 4-methylumbelliferone or 7-amino-4-methylcoumarin standard curves (200 μl of respectively 0–100 μM and 0–10 μM concentrations) and controls without substrate addition (soil + 200 μl water). After incubation, the plates were centrifuged for 3 min at 3000 rpm and, for each well, 250 μl of the supernatant was transferred to black flat-bottomed 96-well plates. Fluorescence was measured with an excitation wavelength of 365 nm and an emission wavelength of 450 nm with a microplate reader (Synergy H1 microplate reader, Biotek, Winooski, USA). A calibration step with standard curves enabled us to calculate enzyme activity. To express the enzymes as quantities, each enzyme activity was then converted into mmol kg^{-1}. The total amount of C-related enzymes (hereafter referred to as C_{enz}) was calculated as the sum of the BGLU, CBH, AGLU, and XYL quantities. Similarly, the total amount of N-related enzymes (hereafter referred to as N_{enz}) was calculated as the sum of the NAG and LAP quantities. The total amount of acid phosphatase (AP) reflects the single P-related enzyme (hereafter referred to as P_{enz}). To investigate ecological stoichiometry and microbial limitations (Sinsabaugh et al., 2002), we calculated the ratios of C_{enz}:N_{enz}, C_{enz}:P_{enz} and N_{enz}:P_{enz}.

2.5. Statistical analyses

In order to investigate initial site differences, we firstly conducted a Principal Component Analysis (PCA) on macro-nutrients characterizing RIPA sites, with the ratios C to N, C to P and N to P as supplementary variables using the ‘ade4’ and ‘factoextra’ packages (Dray and Dufour, 2007; Kassambara and Mundt, 2020). We conducted Kruskal-Wallis non-parametric tests to test for differences between RIPA sites on the basis of their coordinates along the first two axes of the PCA ($n = 9$).

We used a non-parametric test for pairwise analyses, the ‘sign test’, which needs no hypothesis on variable distribution, to test for differences between RIPA and REYN plots for all soil variables, using the ‘rstatix’ package (Kassambara., 2023). For pairwise analyses, mean data per plots were used in order to solve pseudoreplication issues ($n = 18$).

We expected *Reynoutria* effects would be contingent on the local conditions, as prior research had suggested that *Reynoutria* had the capacity to establish its own ecological niche. We calculated the Spearman correlation coefficient between the log response ratio $\ln(\text{Variable}_{REYN} / \text{Variable}_{RIPA})$ (Hedges et al., 1999) and the local uninvaded conditions Variable_{RIPA} to assess the relationships between the local uninvaded conditions and the effects of *Reynoutria* on soil properties and enzyme activities for each dependent variable. If the Spearman correlation coefficient was significantly different from zero, it means that *Reynoutria*’s effect was dependent on local conditions. Because a Spearman correlation coefficient close to zero can imply either the absence of a relationship between local conditions and *Reynoutria*’s impact or the presence of a non-monotonic relationship, we also carried out a visual assessment by plotting the log response ratio against the local uninvaded conditions for each relevant variable. As time since invasion could be a confounding factor affecting the effect of plant invasion on soil (Kou et al., 2016; Zavaleta and Kettley, 2006), we also tested for the effect of estimated time since invasion on the log response ratio ln($\text{Variable}_{\text{REYN}}$ / $\text{Variable}_{\text{RIPA}}$) for macro-nutrients through the same process (Spearman correlation coefficient and visual check of plots).

We used the 'ggplot2' package (Wickhame, 2016) for all plots. All of the statistical analyses were performed in the R software, version 4.3.1 (R Development Core Team, 2023).

3. Results

3.1. Variability in soil chemistry across sites without invasion

The PCA on macro-nutrients for RIPA plots represented 73.8 % of the variability across the different sites (Fig. 2). Sites differed between catchments along the second axis, mainly in relation to C_{total}, N_{total}, P_{total}, NO_3^-, K and Ca (Kruskal-Wallis chi-squared = 23.619, *p-value* = 0.002654); and within catchments along the first axis, mainly in relation to C_{org}, P_{avail}, S and NH_4^+ (Kruskal-Wallis chi-squared = 23.958, *p-value* = 0.00233). The sites on the ROYANS catchment showed overall greater C_{total} values (Fig. 2), likely primarily due to $CaCO_3$ contents, as indicated by the high levels of Ca at the catchment scale (Table 1). The three sites of this catchment were also globally the poorest in micro-nutrients (Table 1). Sites within the GRESIVAUDAN catchment were the more diverse ones as represented by the relatively high variation along the two first PCA axes (Fig. 2). They showed also the highest concentrations in most micro-nutrients, notably Cu and Zn (Table 1). Sites in the BELLEDONNE catchment were more homogeneous (Fig. 2) and displayed high values for C_{enz} activities (Table 1).

3.2. Differences between Reynoutria-invaded and uninvaded adjacent plots regarding soil chemistry

Soil samples collected in *Reynoutria* plots differed significantly from those collected in adjacent uninvaded riparian soil regarding macro-nutrients (Table 2). Under *Reynoutria,* soil samples displayed higher content of C_{total}, N_{avail} and P_{total} compared to paired uninvaded plots (Fig. 3). This pattern was observed at all the sites but one (Fig. 3). Statistical 'sign-test' was not significant for other macro-nutrients (C_{org}, N_{total}, P_{avail}, K, Ca and S) but C_{org} and N_{total} values were higher in REYN plots than in RIPA plots for seven of the nine sites studied. We also observed a decreasing trend for Ca in *Reynoutria*-invaded plots compared to adjacent riparian plots in seven of the nine sites, particularly those with initially higher Ca concentrations (Fig. 3H). By contrast, micro-nutrients did not differ significantly between *Reynoutria*-invaded plots and paired uninvaded ones (Table 2).

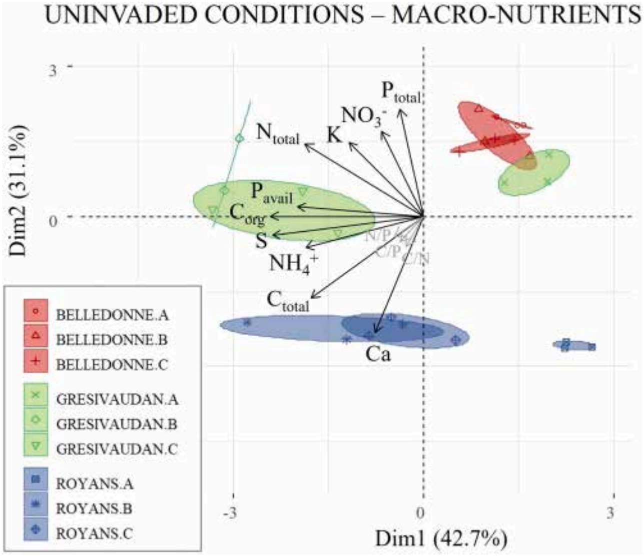

Fig. 2. Graphical results of the first two dimensions of the Principal Component Analysis ran on the macro-nutrients measured on control riparian plots (RIPA). Ellipses represent confidence interval around mean points for each of the nine sites. For abbreviations see text.

3.3. Differences between Reynoutria-invaded and uninvaded adjacent plots regarding soil enzyme activity

We found no significant difference between invaded and non-invaded plots for individual enzyme activity nor for the aggregated values reflecting C, N and P acquisitive enzymes or stoichiometry of enzyme activities (Table 2, Figure S1).

3.4. Linking local soil conditions to Reynoutria effects

No effect of time since invasion (ranging from 6 to 12 years) could be observed on the log response ratio ln($\text{Variable}_{\text{REYN}}$ / $\text{Variable}_{\text{RIPA}}$) for macro-nutrients. Spearman coefficients ranged from −0.523–0.364 and *p-values* were all higher than 0.148 (Figure S2).

The positive log response ratios for soil C_{total} content slightly depended on local uninvaded conditions (Spearman coefficient = −0.617; *P* = 0.086; Fig. 4A). The magnitude of the positive differences between *Reynoutria*-invaded and uninvaded adjacent plots was higher for sites with lower C_{total} (Fig. 4A). On the other hand, *P* values upper than 0.1 and the graphical check confirmed no dependence on local conditions for N_{avail}, N_{total}, $P_{avail,}$ P_{total}, C_{org}, K, Ca or S. However, on the plot for NO_3^- (Spearman coefficient = −0.567; *P* = 0.121), the high log response ratios at NO_3^--poorer sites seemed to be masked by the null effects at NO_3^--richer sites (Fig. 4B).

For soil enzyme activity, log response ratios depended on local conditions for P_{enz} (Spearman coefficient = −0.767; *P* = 0.021; Fig. 5A) and more slightly for C_{enz} to P_{enz} ratio (Spearman coefficient = −0.653; *P* = 0.057; Fig. 5B). In those cases, the log response ratios were positive at sites with low microbial activity related to P cycle, and then decreased progressively, becoming negative at sites with high local microbial activity (Fig. 5).

4. Discussion

This study compared soil chemical properties of plots invaded by *Reynoutria* spp, a well-known invasive alien plant species complex, to adjacent *Reynoutria*-free riparian plots. Using a space-for-time substitution approach, we analyzed soil macro-nutrients and their stoichiometry, micro-nutrients and potential activity of soil enzymes related to carbon, nitrogen and phosphorus cycling.

Our study demonstrated that soil under *Reynoutria* differed from adjacent uninvaded ones for different macro-nutrients and that some of these differences depended from local soil conditions. The observed differences in soil chemistry were mainly attributed to the presence of *Reynoutria* and the local plant community, but the magnitude of these effects was highly context-dependent.

4.1. Reynoutria alters soil chemical properties

In line with our first hypothesis H_1 and previous works (Lavoie, 2017), we found that under *Reynoutria* spp. (Asian knotweeds) macro-nutrients were globally higher in abundance and particularly for total carbon (+21 % on average), available nitrogen (+58 % on average), and total phosphorus content (+26 % on average). Despite the absence of a statistically significant signal, soil samples collected under *Reynoutria* also tended to display higher total nitrogen and organic carbon and lower calcium content for seven out of nine plots (+35 % and +39 % on average, respectively). The higher concentrations of C, N

Table 1

Mean values (and standard deviations in brackets) for macro- and micro-nutrients and enzyme activities for each two treatment plots (REYN and RIPA) of the three catchments. For abbreviations, see text.

Variables			BELLEDONNE		GRESIVAUDAN		ROYANS	
			REYN	RIPA	REYN	RIPA	REYN	RIPA
Macro-nutrients	$\mathbf{C_{total}}$	(mg g^{-1})	$31.16^{(10.29)}$	$24.26^{(4.69)}$	$69.10^{(26.17)}$	$53.47^{(25.62)}$	$70.52^{(21.29)}$	$69.5^{(11.90)}$
	$\mathbf{C_{org}}$	(mg g^{-1})	$23.12^{(7.92)}$	$17.84^{(3.60)}$	$49.68^{(29.06)}$	$31.46^{(15.38)}$	$24.93^{(12.83)}$	$22.52^{(15.09)}$
	$\mathbf{N_{total}}$	(mg g^{-1})	$2.18^{(0.78)}$	$1.78^{(0.17)}$	$3.24^{(1.83)}$	$2.17^{(1.11)}$	$1.39^{(0.68)}$	$0.99^{(0.48)}$
	$\mathbf{NO_3^-}$	(μg g^{-1})	$8.67^{(3.23)}$	$6.63^{(1.60)}$	$15.33^{(11.13)}$	$4.10^{(4.10)}$	$3.20^{(1.89)}$	$2.14^{(1.86)}$
	$\mathbf{NH_4^+}$	(μg g^{-1})	$3.91^{(1.48)}$	$3.11^{(0.63)}$	$6.83^{(3.61)}$	$5.39^{(3.12)}$	$4.41^{(1.90)}$	$4.61^{(2.39)}$
	$\mathbf{N_{avail}}$	(μg g^{-1})	$12.57^{(4.08)}$	$9.74^{(1.71)}$	$22.16^{(14.70)}$	$9.49^{(5.11)}$	$7.61^{(2.81)}$	$6.75^{(3.82)}$
	$\mathbf{P_{total}}$	(mg g^{-1})	$0.75^{(0.06)}$	$0.72^{(0.16)}$	$1.08^{(0.27)}$	$0.74^{(0.12)}$	$0.26^{(0.11)}$	$0.20^{(0.08)}$
	$\mathbf{P_{avail}}$	(μg g^{-1})	$1.78^{(1.84)}$	$2.17^{(1.35)}$	$15.86^{(12.29)}$	$3.81^{(2.75)}$	$6.99^{(4.14)}$	$2.51^{(2.06)}$
	K	(mg g^{-1})	$3.97^{(0.27)}$	$3.91^{(0.42)}$	$5.90^{(1.49)}$	$7.27^{(2.41)}$	$2.09^{(0.98)}$	$2.25^{(0.49)}$
	Ca	(mg g^{-1})	$3.87^{(0.74)}$	$3.34^{(0.50)}$	$65.05^{(9.20)}$	$79.56^{(20.61)}$	$155.14^{(17.5)}$	$166.24^{(10.6)}$
	S	(mg g^{-1})	$0.30^{(0.08)}$	$0.25^{(0.03)}$	$0.74^{(0.41)}$	$0.63^{(0.34)}$	$0.37^{(0.13)}$	$0.46^{(0.21)}$
	C/N		$10.72^{(1.12)}$	$10.01^{(1.80)}$	$15.01^{(3.44)}$	$15.41^{(5.68)}$	$18.07^{(6.23)}$	$21.28^{(9.01)}$
	C/P		$31.36^{(11.68)}$	$26.21^{(9.27)}$	$45.09^{(26.19)}$	$42.89^{(21.43)}$	$100.78^{(62.09)}$	$117.27^{(103.41)}$
	N/P		$2.95^{(1.13)}$	$2.58^{(0.63)}$	$3.00^{(1.75)}$	$3.001^{(1.64)}$	$5.68^{(3.14)}$	$5.07^{(3.04)}$
Micro-nutrients	**Cu**	(mg g^{-1})	$18.85^{(0.68)}$	$18.52^{(1.23)}$	$44.24^{(37.07)}$	$27.27^{(5.69)}$	$4.31^{(2.26)}$	$4.12^{(1.30)}$
	Fe	(mg g^{-1})	$25.21^{(0.87)}$	$25.56^{(0.80)}$	$32.11^{(22.06)}$	$25.84^{(3.61)}$	$6.37^{(2.59)}$	$6.75^{(0.74)}$
	Mn	(mg g^{-1})	$0.66^{(0.08)}$	$0.68^{(0.07)}$	$0.65^{(0.12)}$	$0.67^{(0.17)}$	$0.15^{(0.02)}$	$0.18^{(0.02)}$
	Zn	(mg g^{-1})	$0.07^{(0.007)}$	$0.06^{(0.005)}$	$0.16^{(0.10)}$	$0.10^{(0.04)}$	$0.03^{(0.01)}$	$0.02^{(0.005)}$
Aggregated enzyme activities	$\mathbf{C_{enz}}$	(nmol.g^{-1}.h^{-1})	$273.31^{(101.61)}$	$218.02^{(71.05)}$	$187.76^{(110.73)}$	$184.29^{(122.62)}$	$66.13^{(50.15)}$	$96.20^{(70.93)}$
	$\mathbf{N_{enz}}$	(nmol.g^{-1}.h^{-1})	$104.17^{(37.85)}$	$93.78^{(28.47)}$	$311.91^{(160.35)}$	$215.37^{(98.14)}$	$123.94^{(41.86)}$	$122.79^{(69.40)}$
	$\mathbf{P_{enz}}$	(nmol.g^{-1}.h^{-1})	$240.62^{(45.96)}$	$264.34^{(110.06)}$	$312.97^{(119.99)}$	$224.91^{(107.62)}$	$166.43^{(51.35)}$	$137.63^{(82.58)}$
	$\mathbf{C_{enz}/N_{enz}}$		$2.63^{(0.46)}$	$2.33^{(0.38)}$	$0.61^{(0.23)}$	$0.81^{(0.27)}$	$0.49^{(0.28)}$	$0.72^{(0.21)}$
	$\mathbf{C_{enz}/P_{enz}}$		$1.19^{(0.56)}$	$0.96^{(0.46)}$	$0.58^{(0.22)}$	$0.77^{(0.22)}$	$0.35^{(0.21)}$	$0.67^{(0.32)}$
	$\mathbf{N_{enz}/P_{enz}}$		$0.45^{(0.19)}$	$0.40^{(0.15)}$	$0.96^{(0.19)}$	$0.98^{(0.14)}$	$0.76^{(0.19)}$	$0.91^{(0.34)}$

Table 2

Results from non-parametric sign-test comparing soil properties and enzyme activities between *Reynoutria*-invaded plots (REYN) and paired-adjacent riparian plots (RIPA). If estimate is negative, RIPA plots have lower values than REYN ones and reversely if estimate is positive, RIPA plots have higher values than REYN plots. Significant tests are indicated in bold letters. Symbols under the 'significance' column indicate statistically significant differences between RIPA and REYN (****p-value* ≤ 0.001, ** *p-value* ≤ 0.01, * *p-value* ≤ 0.05, † *p-value* ≤ 0.10) after a sign-test was run. For abbreviations, see text.

		estimate	df	p-value	significance	conf.inf	conf.high
Macro-nutrients	$\mathbf{C_{total}}$	**−4.58**	9	**0.0391**	*	**−13.6**	**−2.57**
	$\mathbf{C_{org}}$	−5.67	9	0.18	-	−22.8	0.4
	$\mathbf{N_{total}}$	−0.393	9	0.18	-	−1.4	0.05
	$\mathbf{NO_3^-}$	**−1.76**	9	**0.00391**	**	**−0.67**	**−0.187**
	$\mathbf{NH_4^+}$	**−0.593**	9	**0.0391**	*	**−2**	**−0.0467**
	$\mathbf{N_{avail}}$	**−2.24**	9	**0.0391**	*	**−8.68**	**−0.21**
	$\mathbf{P_{total}}$	**−0.137**	**9**	**0.0391**	*	**−0.303**	**−0.0067**
	$\mathbf{P_{avail}}$	−1.36	9	1	-	−11.8	0.752
	K	0.0833	9	1	-	−1.02	1.38
	Ca	5.19	9	0.18	-	−1.03	14.9
	S	−0.06	9	0.18	-	−0.133	0.0267
	C/N	0.49	9	1	-	−1.74	2.72
	C/P	−4.27	9	0.508	-	−7.89	41.3
	N/P	−0.202	9	0.508	-	−0.977	0.349
Micro-nutrients	**Cu**	−0.64	9	0.508	-	−2.67	1.24
	Fe	0.653	9	0.508	-	−2.95	1.56
	Mn	0.04	8	0.289	-	−0.0167	0.0677
	Zn	−0.0067	6	0.219	-	−0.0533	0
Aggregated enzyme activities	$\mathbf{C_{enz}}$	−8.64	9	1	-	−159	65.8
	$\mathbf{N_{enz}}$	−18.5	9	0.508	-	−78.9	36
	$\mathbf{P_{enz}}$	−30.2	9	0.508	-	−109	89.7
	$\mathbf{C_{enz}/N_{enz}}$	0.113	9	0.508	-	−0.103	0.437
	$\mathbf{C_{enz}/P_{enz}}$	0.14	9	0.508	-	−0.437	0.763
	$\mathbf{N_{enz}/P_{enz}}$	0.01	9	0.508	-	−0.233	0.333

and P under *Reynoutria* compared to adjacent plots may be attributed to three non-exclusive mechanisms. First, *Reynoutria* produces 1.8–13 times more aboveground biomass than the native vegetation across various ecosystems (Dassonville et al., 2007; Aguilera et al., 2010; Stefanowicz et al., 2020). Such an increase in plant biomass ultimately increases the litter quantity returning to the soil (Ehrenfeld, 2003), notably because *Reynoutria* spp. are known to generate large amounts of aboveground litter during the autumn season (Maerz et al., 2005; Urgenson et al., 2009; Maurel et al., 2010). Furthermore, *Reynoutria* litter is characterized by low N content and high lignin content (Lecerf et al., 2007; Urgenson et al., 2009; Claeson et al., 2014), resulting in a relatively high C:N ratio, which generally contrasts with herbaceous native species litter (Aguilera et al., 2010; Mincheva et al., 2014). Larger amounts of litter with a different chemical composition may explain the increase in soil organic carbon, specifically in ecosystems where *Reynoutria* has rapidly become dominant (Claeson et al., 2014). In addition to the potential impact of litter, the accumulating effect of *Reynoutria* on soil N and P may also be attributed to *Reynoutria*'s ability to uplift nutrients from deeper soil horizons (as deep as 3 m) through a complex root network (Chiba and Hirose, 1993; Katayama et al., 2021). This

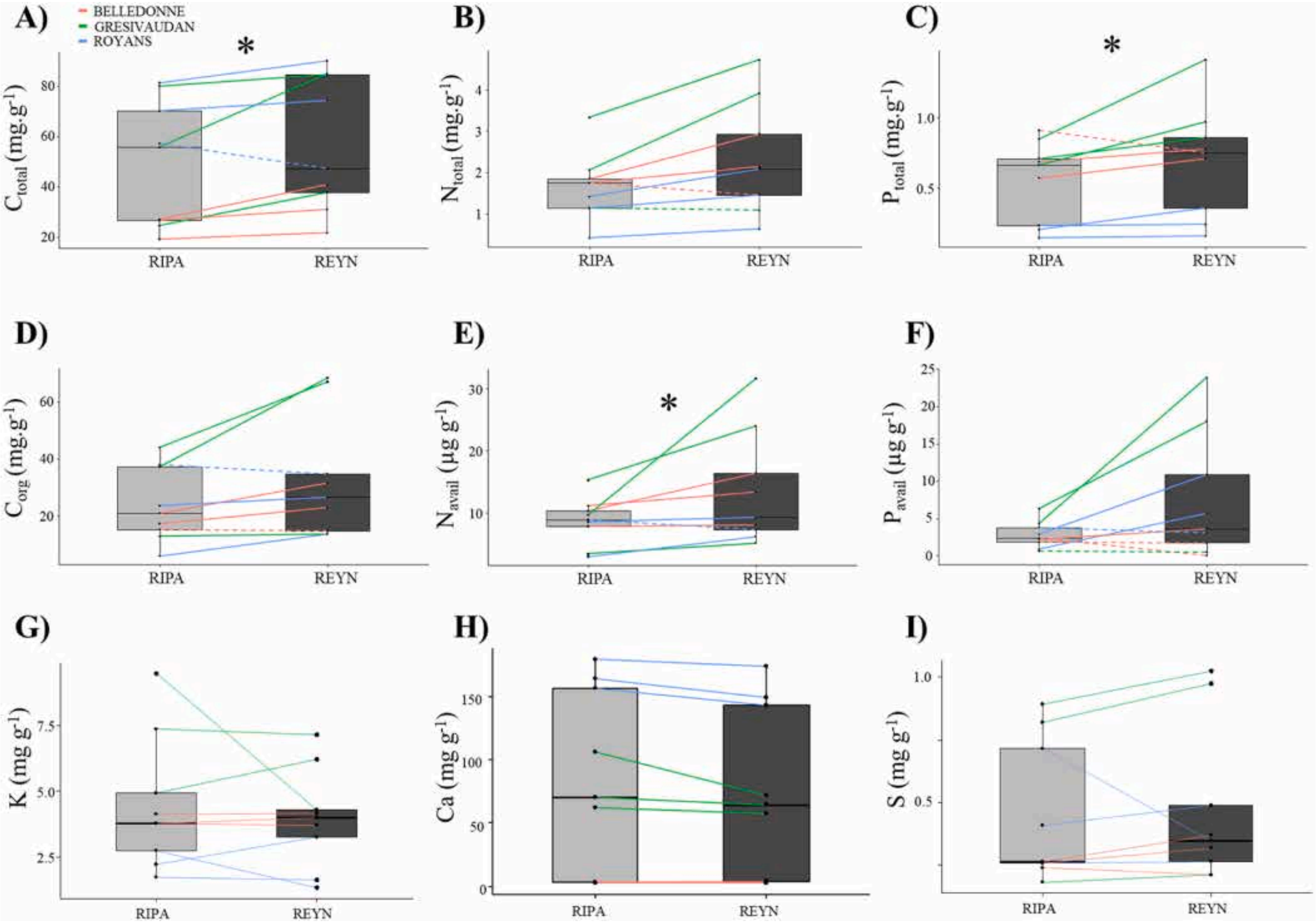

Fig. 3. Boxplots of the effects of plant invasion on soil chemistry: (A) total C, (B) total N, (C) total P, (D) organic C, (E) available N, (F) available P, G) potassium, H) calcium and I) sulfur. Lines inside each box represent the median. Coloured lines link the paired treatments within a site, each colour representing a catchment. Dashed lines indicate links which direction differs from the result of the sign-test. Symbols indicate statistically significant differences between RIPA and REYN (****p-value* $\leq$ 0.001, ** *p-value* $\leq$ 0.01, * *p-value* $\leq$ 0.05, † *p-value* $\leq$ 0.10) after a sign-test was run.

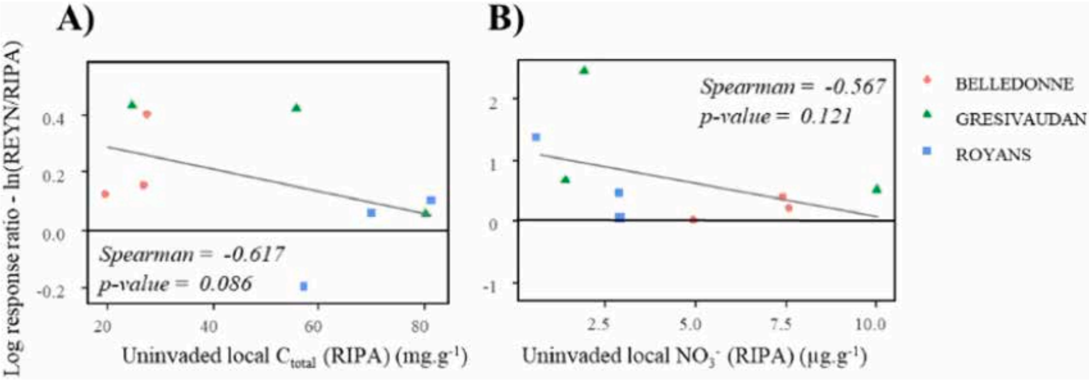

Fig. 4. Relationship between the log response ratio ln(REYN/RIPA) and uninvaded local conditions (RIPA) for (A) total C and (B) nitrate. Spearman coefficient and p-value are indicated.

mechanism has been observed for various exotic plant species including pines and eucalyptus (Jobbagy and Jackson, 2004). Greater N uptake from deeper soil horizons may contribute to explaining the greater N contents in the topsoil after invasion, despite the fact that *Reynoutria* presents relatively high leaf-tissue C:N:P ratios (Urgenson et al., 2009; Stefanowicz et al., 2020). Altogether, these results highlight that an invasion by *Reynoutria* can have important, long-term consequences on C and nutrient cycling through modifications in soil chemical properties.

4.2. *Reynoutria did not increase soil enzyme activity*

In contrast with our second hypothesis H_2, our results suggest that *Reynoutria* did not significantly increase soil enzyme activities. This lack of effect aligns with previous existing field studies showing that although *Reynoutria* invasion strongly alters microbial functional composition it only causes minor changes in soil enzymes activity (Stefanowicz et al., 2021, 2022). This can be due to the fact that soil

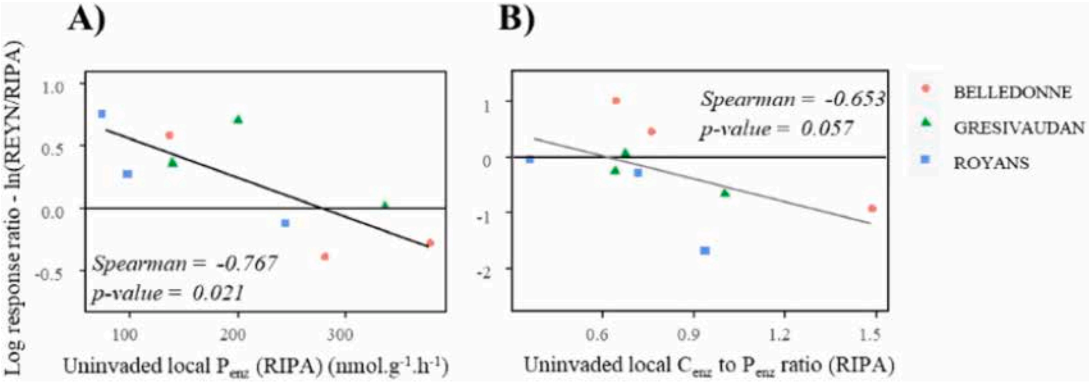

Fig. 5. Relationship between the log response ratio ln(REYN/RIPA) and uninvaded local conditions RIPA for (A) P-acquisitive enzyme (P_{enz}) and (B) C_{enz} to P_{enz} ratio (C_{enz} to P_{enz}). Spearman coefficient and p-value are indicated.

microbial communities depend more on other environmental conditions in these sites such as soil moisture (Maxwell et al., 2023) or because they are subjected to top-down effects through grazing effect by higher trophic levels and soil fauna (Fanin et al., 2019). The very weak effects of *Reynoutria* on soil enzymes in our study can also be explained by the sampling period. Specifically, Tharayil et al. (2013) showed that C and N-related enzymes were lower inside *Reynoutria* stands than outside the stands in spring (April), but they became null to higher during summer and autumn, respectively. Since our sampling took place in late June, i.e., which corresponds to the transition between spring and summer, and since enzymes are highly dynamics over time (Fanin et al., 2022), we may have captured only a transitional moment for the effect of *Reynoutria* on soil enzyme activity.

4.3. Magnitude and direction of effect are site-dependent

Despite the consistent cumulative effects of *Reynoutria* on C, N and P contents across different catchments, we found a strong heterogeneity among the different sites. Looking at the relationship between the log response ratio and local uninvaded conditions, we found that *Reynoutria* effects tended to be more important on sites with lower levels of total carbon and NO_3^-. Even though the relationships were relatively weak, these results partly support our third hypothesis H_3 and suggest that the effect of *Reynoutria* on soil properties are context-dependent and were driven by the initial habitat characteristics (Abgrall et al., 2019; De Almeida et al., 2022). These results are in line with previous studies showing that *Reynoutria* have higher effects on C and nutrient cycling in poorer soil conditions, in which nutrient availability is less favorable for microorganisms (Dassonville et al., 2007; Kappes et al., 2007). In line with this idea, we also found that *Reynoutria* switched P_{enz} activity and the ratio C_{enz}:P_{enz} from positive to negative with increasing local P_{enz} and C_{enz}:P_{enz} activity respectively. This result suggests that *Reynoutria* could potentially mitigate differences in microbial activity among diverse sites, which might help explain why we did not detect clear effects of *Reynoutria* on overall soil enzymes when examining all sites collectively. Finally, we did not find significant relationships between time since invasion (ranging from 6 to 12 years) and changes in soil chemistry. It has been previously shown that *Reynoutria*'s effects on soil properties are relatively rapid and observable usually after less than one year (Dommanget et al., 2014). Because the effects of plant invasions on soil C and N tend to stabilize after a few years, and notably at shallow soil horizons (Kou et al., 2016; Zavaleta and Kettley, 2006), these results support the idea that *Reynoutria* species are able to modify their environment and create their own favorable niche quickly after invasion (Dassonville et al., 2011), but that the magnitude of these effects depend on local soil conditions.

5. Conclusions

Our objective was to highlight the potential role of *Reynoutria* invasion on soil chemical properties and enzyme activities across nine contrasted sites. We found a higher content in C, N and P under *Reynoutria* compared to adjacent uninvaded plots, with important differences in the magnitude of differences among sites. These results have several implications for restoration ecology and soil management. First, they highlight that invasive alien species such as *Reynoutria* can have important consequences on organic matter stocks due to their greater productivity. Given that the potential impact on belowground soil C stocks contradicts the overall negative effects on the aboveground diversity and biomass of the native plant community, this finding warrants further scrutiny and necessitates more long-term investigations. Secondly, the substantial variation in soil chemistry and microbial activity following *Reynoutria* invasion highlights the importance of taking into account the specific local soil conditions, especially when striving to implement effective restoration strategies. Finally, our data suggests that the *Reynoutria* species' ability to create its own niche is realistic in line with the 'niche construction' mechanism suggested by Dassonville et al. (2011). Although it also remains to be explored whether the changes in soil physicochemical properties and microbial activity will be transient or stable in the long term, these findings collectively indicate that invasive plants can modify soil functioning to their advantage. We conclude that some ecosystems may be more prone to alteration by invasion, and presumably, more difficult to rehabilitate. Identifying the parameters that drive the variability of *Reynoutria* effects on soil biochemical properties could help to better define rehabilitation strategies after invasion.

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CRediT authorship contribution statement

Fanny Dommanget: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Camille Noûs:** Writing – original draft, Conceptualization. **Amandine ERKTAN:** Writing – original draft, Validation, Conceptualization. **Matthieu Chauvat:** Writing – original draft, Validation, Conceptualization. **Estelle FOREY:** Writing – original draft, Validation, Conceptualization. **Coralie Chesseron:** Formal analysis, Data curation. **Léa Daniès:** Methodology, Formal analysis, Data curation. **Nicolas Fanin:** Writing – original draft, Validation, Supervision, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: DOMMANGET Fanny reports financial support was provided by The French Biodiversity Agency. If there are other authors, they 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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Author contributions

The lead author, F.D., initiated the present study, carried out field sampling, as well as statistical analyses and participated in writing the manuscript. N.F. conducted all the chemical analyses with L.D and C.C., participated to statistical analyses and participated in writing the manuscript. A.E., E.F. and M.C. actively contributed to interpreting the results, and to writing and reviewing the manuscript. Funding acquisition was done by F.D. All authors have read and agreed to the published version of the manuscript.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.pedobi.2024.151002.

Data availability

Data will be made available on request.

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