

# Contrasting Impacts of Two Invasive Plant Species on Soil Carbon Transformation Function in Temperate Forests

Erwan Le Jeune

[erwan.le.jeune@u-picardie.fr](mailto:erwan.le.jeune@u-picardie.fr)

Universite d'Amiens: Universite de Picardie Jules Verne <https://orcid.org/0009-0007-5916-6514>

Annie Guiller

University of Picardy Jules Verne: Universite de Picardie Jules Verne

Mattéo Dorvillé

University of Picardy Jules Verne: Universite de Picardie Jules Verne

Redhouane Al Kharrat

University of Picardy Jules Verne: Universite de Picardie Jules Verne

Jérôme Duclercq

University of Picardy Jules Verne: Universite de Picardie Jules Verne

Hélène Horen

University of Picardy Jules Verne: Universite de Picardie Jules Verne

---

## Research Article

**Keywords:** P Serotina, R Ponticum, Indicators, Process, Temporal Dynamics, Soil Health

**Posted Date:** September 24th, 2026

**DOI:** <https://doi.org/10.21203/rs.3.rs-10985946/v1>

**License:**  This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

---

# Abstract

Plant invasions can impact the carbon cycle in forest ecosystems, notably through vegetation structure, which alters environmental conditions and through litter inputs that differ quantitatively and qualitatively from those of native species. This study compares invaded and uninvaded forest plots along an invasion chronosequence, revealing that *Rhododendron ponticum* (an invasive shrub) significantly altered the forest soil micro-environment particularly by reducing light availability and temperature, whereas *Prunus serotina* (an invasive tree found in both shrub and tree layers) caused more limited environmental changes. These environmental shifts, combined with species-specific traits, such as the deposition of recalcitrant litter by *R. ponticum* versus labile litter by *P. serotina*, resulted in contrasting effects on carbon processing. *R. ponticum* promoted organic matter accumulation in the surface organic horizons, while *P. serotina* stimulated microbial activity and reduced litter thickness. The duration of the invasion accentuated these contrasting trajectories, leading to progressive organic matter accumulation under *R. ponticum* and increasing microbial activity under *P. serotina*. These results highlight that those invasive plants can alter forest carbon processing through the combined influence of plant functional traits, vegetation structure, and the duration of the invasion. Integrating various indicators operating at different time scales allows for a better characterization of the long-term changes in soil functioning induced by biological invasions.

## Highlight

- Exotic litter input and abiotic changes both affect the carbon transformation function
- The vertical structure of invasive plant species strongly determines their capacity to modify forest microenvironmental conditions
- Contrasting effects of *R. ponticum* and *P. serotina* on soil carbon cycling are mainly explained by their functional traits
- The combination of short-term and long-term indicators provides a simultaneous picture of the current state of soil function and legacy effects

## 1 - Introduction

Soils constitute the largest terrestrial reservoir of organic carbon and therefore play a major role in regulating the global carbon cycle and climate. Among the global changes affecting soil functioning, plant invasions are increasingly recognized as important drivers of biogeochemical alterations (Liao et al. 2008; Sardans et al. 2017). By modifying plant community composition, litter inputs, and environmental conditions, invasive alien plants can profoundly alter soil carbon transformation processes. Plant functional traits and soil properties form a continuum (Wardle et al. 2004; Reich 2014). So-called economic traits, associated with nutrient uptake, nutrient-use efficiency, and resource conservation, play a key role in how plants modify soil functioning (Wardle et al. 2004; Bruehlheide et al. 2018), notably through the quantity and quality of organic matter they return to the soil (Sardans et al.

2017). In turn, soil decomposes dead plant material and indirectly regulates plant growth and community composition by modulating nutrient availability. These interactions are well documented in forest ecosystems, where differences in litter quality produced by coexisting tree species explain the heterogeneous distribution of soil organisms and variation in process rates resulting from tree-specific effects (Saetre and Bååth 2000). Thus, the introduction of invasive alien plants can profoundly alter these processes by introducing organic inputs that differ both quantitatively and qualitatively from those of native species.

In general, invasive plants are characterized by fast acquisitive traits. They typically exhibit high nitrogen content, low leaf construction costs, rapid growth, and high nutrient plasticity (Liao et al. 2008; Sardans et al. 2017). These acquisitive traits generally promote the production of nutrient-rich and labile litter, stimulating microbial activity and accelerating carbon and nutrient cycling (Wardle et al. 2004; Allison and Vitousek 2004). These conditions can favour positive feedbacks that reinforce invasion success (Allison and Vitousek 2004). In contrast, some invasive alien plants exhibit conservative traits associated with highly efficient nutrient use, long lifespan, and strong tolerance to nutrient-poor environments (Sardans et al. 2017). These species can slow decomposition processes and promote the accumulation of organic matter in soils. For example, Tamura et al. (2017) observed a 26% increase in soil organic carbon in abandoned fields invaded by *Polygonum cuspidatum*, which produces recalcitrant litter rich in plant polymers. In addition, some invasive plants may release secondary metabolites, such as polyphenols, which can further slow decomposition.

In addition to altering the quality and quantity of litter inputs in forest soils, invasive alien plants can modify local environmental conditions by changing the physical structure of forest stands. Understorey density, vertical vegetation stratification, and light interception directly influence temperature, humidity, and therefore decomposition at the soil level (Kemppinen et al. 2024; Garcia and Clusella-Trullas 2025). However, this environmental influence on forest ecosystem functioning remains relatively underappreciated (De Frenne et al. 2013). Several studies even suggest that micro-environmental effects may influence decomposition more strongly than litter quality itself (Prescott 2005). During the temporal evolution of an invasion, the structure of invasive plants and their associated litter inputs also change, potentially increasing their impacts over time (Frouz 2024; Haubrock et al. 2026). For example, the impact of *Prunus laurocerasus* invasion on several soil enzymatic activities intensifies over time across a 17-year chronosequence (Rusterholz et al. 2018). However, the impacts of invasive alien plants do not follow a single temporal trajectory. Depending on the species and processes under consideration, these impacts may increase gradually, reach a new equilibrium state, fluctuate over time, or even decline after a period of intensification (Haubrock et al. 2026). This diversity of trajectories results from multiple mechanisms, such as environmental changes linked to shifts in the structure of exotic and native vegetation, or changes in soil communities that may gradually alter ecosystem processes (Le Jeune et al. 2026; Haubrock et al. 2026). The temporal dynamics of invasion impacts highlight the need for integrative approaches considering multiple temporal scales.

The set of disturbances induced by invasive plants can be assessed using soil functional approaches. Soil health is defined as the capacity of soil to sustain its ecological functions over time (Karlen et al. 1997; Heepngoan et al. 2021). Among these functions, carbon transformation is particularly sensitive to changes in plant composition, as it directly depends on the quantity and quality of organic matter inputs as well as local environmental conditions. It encompasses the processes involved in carbon decomposition, storage, and fluxes within and between soil compartments (Raheem et al. 2024). In this context, plant invasions altering both biotic and abiotic conditions can strongly and persistently affect this function. While some effects may occur rapidly, notably through root exudates, others result from the gradual accumulation of litter inputs and humus transformations over several years or decades (Frouz 2024). The integration of processes occurring at different temporal scales is consistent with the methodological framework for assessing ecosystem functionality proposed by several reviews (Manning et al. 2018; Garland et al. 2021). While these authors propose using both short-term process indicators and medium- to long-term process indicators, they exclude the physical or chemical properties of ecosystems—such as soil pH—from the framework of functional indicators and suggest considering them solely as explanatory variables.

In this study, we use multiple complementary biological indicators that integrate processes operating over different temporal scales to assess the contrasting impacts of two invasive alien plants on soil carbon transformation. As these impacts strongly depend on litter quality and on environmental modifications induced by invasive species, we expect contrasting effects between *Rhododendron ponticum* and *Prunus serotina*. *R. ponticum* produces recalcitrant litter and exhibits a shrub growth form (Casati et al. 2022) whereas *P. serotina* produces labile litter and has a tree growth form (Kušková et al. 2026). We suspect that these differences in functional traits and vegetation structure simultaneously modify micro-environmental conditions and soil carbon transformation processes. Our study therefore aims to determine how these two species modify soil environmental condition, how they influence carbon transformation function, and how the intensity of these disturbances varies with invasion age. Based on this, we formulate the following hypotheses:

**H1:** *Prunus serotina* and *Rhododendron ponticum* alter forest soil environmental conditions through changes in vegetation structure. **H2:** Both species have contrasting effects on soil carbon cycling. *Prunus serotina* is expected to accelerate soil carbon turnover, resulting in faster organic matter decomposition, greater microbial activity, and reduced soil carbon storage. In contrast, *Rhododendron ponticum* is expected to slow soil carbon turnover, leading to reduced organic matter decomposition, lower microbial activity, and increased soil carbon storage.

### H3

The effects of *R. ponticum* and *P. serotina* on soil carbon transformation are expected to follow contrasting temporal trajectories as invasion progresses because the two species progressively modify forest structure and resource inputs according to their contrasting functional traits.

## 2. Materials and methods

### 2.1 Study sites and sampling design

We conducted a comparative study between invaded plots and control plots in several forest areas in northern France. Between April and June of 2023, we assessed the effects of *R. ponticum* on soil carbon transformation processes in 15 paired plots across six forests (Supplementary table 6). Between April and June of 2024, we similarly evaluated the effects of *Prunus serotina* in 15 paired plots located in three forests (Supplementary table 6). The invaded plots were characterized by dense, continuous stands of the focal invasive species, forming a continuous cover, whereas the paired control plots showed no invasion by the target species. Within invaded plots, *P. serotina* occurred as both shrubs and trees, whereas *R. ponticum* was exclusively present as shrubs. To isolate the effect of the invasive species, we ensured that the both invaded and control plots had similar range of tree stands and soil types. Each plot measured 20 metres by 20 metres, and four sampling points separated by at least 3 metres were established for environmental and soil functional measurement.

### 2.2 Soil functional indicators

At each sampling point, soil carbon transformation was characterized using complementary indicators describing 3 major processes: organic matter decomposition, microbial activity and carbon storage. The process of degradation of organic matter was assessed using the Tea Bag Index protocol (Keuskamp et al. 2013). This protocol yields two indicators: the decomposition rate constant ( $k$ ), reflecting the rapid breakdown of the labile fraction, and the stabilization factor ( $S$ ), corresponding to the stabilized portion of green tea material that resists decomposition. The process associated with microbial activity was evaluated using two complementary approaches which provided 3 indicators. Basal respiration (BR) was measured using the SituResp protocol (Thoumazeau et al. 2017). After litter removal, soil was sampled from the 0–10 cm layer and incubated at 30°C for 24 h under controlled laboratory conditions. Microbial functional activity was additionally characterized using Biolog EcoPlates™ (Garland and Mills 1991), from which two indicators were derived: average well color development (AWCD) and functional richness (FR) the number of substrates metabolized among the 31 available substrates. The process of carbon storage was estimated using four complementary indicators. First, permanganate oxidizable carbon (POXC) (Weil et al. 2003) allowed us to quantify the labile soil carbon pool. A 1 g sample of air-dried, sieved soil was oxidized with potassium permanganate ( $\text{KMnO}_4$ ), and the decrease in  $\text{KMnO}_4$  concentration was quantified spectrophotometrically. Second, organic matter accumulation was approximated by measuring the thickness of the humic (O) horizons using a measuring tape in centimetres. Thirdly, the thickness of the litter layer (OL) was measured in centimeters. This horizon corresponds to fresh and partially decomposed litter, in which plant residues remain identifiable. Fourth, we calculated an additional indicator (resid) derived from the relationship between labile carbon (POXC) and basal respiration (BR), following the framework proposed by (Hurisso et al. 2016). For each dataset (i.e. plots invaded by *R. ponticum* and their associated control plots, and plots invaded by *P. serotina* and their associated controls), we fitted a linear regression model relating BR to POXC with forest stand

identity included as a fixed effect. The residuals of these models were extracted and used as an additional indicator of carbon transformation. They represent deviations from the expected relationship between labile available carbon and microbial respiration. For a given amount of labile carbon, negative residuals indicate higher microbial respiration than expected, suggesting enhanced short-term mineralisation of soil organic carbon., whereas positive residuals reflect lower than expected respiration, consistent with reduced mineralisation or greater stabilisation of the labile carbon fraction. These indicators reflect processes occurring on varying time scales (Garland et al. 2021). Indicators of microbial activity, carbon transformation, and available carbon (BR, AWCD, FR, k, S, POXC, and resid) reflect short-term responses in soil functioning (ranging from a few days to a few weeks), whereas storage indicators such as the O and OL horizons incorporate longer-term changes resulting from the accumulation and transformation of organic matter (ranging from several years to several decades).

## 2.3 Environmental variables

On each plot, we installed HOBO temperature sensors (UA-001-08) at a depth of 5 cm, allowing automatic temperature recording temperature hourly. The data was retrieved using HOBOWare® software, which enabled us to calculate the average daily temperature (T) and the daily temperature range (DeltaT). At each point, the pH was measured using a field soil stick (Extech-pH100) at a depth of 10 cm. Cylindrical cores 10 cm deep and 8 cm in diameter were also taken to quantify the bulk density (BD) of the soil. From these same soil samples, we quantified the water content (WW) by comparing the mass of the fresh soil to that of the same sample after one week of drying at ambient conditions. Light availability in the understory was estimated using the diffuse non-interceptance index (DIFN), derived from hemispherical photographs processed in R using the *hemispher* package. Higher DIFN values indicate greater canopy openness and increased light transmission to the forest floor. The circumference at breast height (CBH) of the largest individual of the focal invasive species within each plot, was used as a proxy for invasion age. A strong relationship between trunk diameter and age was evidenced for *R. ponticum* in a previous work including our study plots (Casati et al. 2023) indicating that our chronosequence ranges from 16 to 153 years. For *P. serotina* the diameter-age relationship was established based on data from several Netherlands sites with similar climatic conditions (Vanhellemont et al. 2009). However, since soil conditions and stands are not identical, the interpretation of diameters in terms of age should be used with caution. Based on the average relationship they achieve in an oak-pine stand, our chronosequence would range from 27 to 143 years.

## 2.4 Statistical analyses

A paired comparative analysis was conducted between invaded and control plots. Because each plot contained four sampling points, observations were not independent. Linear mixed-effects models were therefore used to account for the hierarchical sampling design. In all models, invasion status (invaded vs. control) was included as a fixed effect and two random effects were included: plot identity, to account for the non-independence of the four sampling points within each plot, and the invaded–control pair identity to account for the paired sampling design. To determine whether invasion modified local environmental conditions, linear mixed-effects models were first fitted for each environmental variable

(DIFN, pH, BD, Tmean, DeltaT, and WW). Invasion status was included as a fixed effect, together with the same random-effects structure described above. To assess the effects of invasion and invasion age on soil functional indicators (k, S, BR, AWCD, FR, O, OL, and POXC), two model structures were fitted for each response variable. The first model included invasion status as a fixed effect and was used to evaluate the overall effect of invasion on soil functional indicators. To disentangle the direct effects of invasive plants from indirect effects mediated by invasion-induced environmental changes, a second set of models additionally included environmental covariates. These covariates were selected using redundancy analysis (RDA), which served as a variable reduction approach to identify the main environmental gradients associated with multivariate variation in soil functioning. Variable collinearity was checked beforehand. Soil functional indicators (k, S, POXC, O, OL, BR, AWCD, FR, and resid) were used as response variables, whereas environmental variables (DIFN, pH, BD, Tmean, DeltaT, and WW) were included as explanatory variables. The significance of the global RDA model was assessed using permutation tests. Significant environmental variables were then selected using a forward selection procedure based on adjusted  $R^2$  values and retained as covariates in the adjusted mixed-effects models. To evaluate whether invasion effects varied with time since invasion, additional mixed-effects models were fitted including the interaction between invasion status and invasion age. Control plots were assigned the same invasion age as their corresponding invaded plots in order to preserve the paired structure and evaluate temporal changes relative to local reference conditions. A significant interaction between invasion status and invasion age indicated that invasion effects changed with time since invasion. Model assumptions were assessed by visual inspection of residual distributions, residuals *versus* fitted values plots, and quantile–quantile plots. Collinearity among explanatory variables was evaluated using variance inflation factors (VIF). All analyses were conducted using R version 4.4.1. Linear mixed-effects models were fitted using the lme4 package, with significance tests obtained using lmerTest. Redundancy analyses were performed using the vegan package, and figures were produced using ggplot2.

## 3. Results

### 3.1 Environmental differences between invaded and control sites

No significant differences in environmental variables were detected between invaded plots and control plots for *P. serotina* plots. However, a tendency towards higher pH values was observed in invaded plots, without reaching statistical significance ( $p = 0.114$ , Fig. 1 and Table 1). In contrast, plots invaded by *R. ponticum* were associated with a significant decrease in incident light ( $p = 0.002$ ), average soil temperature ( $p = 0.003$ ) and a tendency towards a decrease in temperature range ( $p = 0.061$ ). The soils of the invaded plots are also on average more acidic ( $p = 0.039$ ) and have lower bulk densities ( $p = 0.011$ ).

Table 1  
Results of linear mixed-effects models associated with Fig. 1 evaluating the effect of invasion status on environmental variables.

| Variable      | <i>Prunus serotina</i> |                |         | <i>Rhododendron ponticum</i> |                |              |
|---------------|------------------------|----------------|---------|------------------------------|----------------|--------------|
|               | N                      | Estimate       | P value | N                            | Estimate       | P value      |
| <b>DIFN</b>   | 119                    | -1.253 ± 1.528 | 0.426   | 113                          | -6.434 ± 1.723 | <b>0.002</b> |
| <b>Tmean</b>  | 26                     | 0.162 ± 0.204  | 0.444   | 27                           | -0.445 ± 0.118 | <b>0.003</b> |
| <b>DeltaT</b> | 26                     | 0.096 ± 0.120  | 0.440   | 27                           | -0.508 ± 0.242 | 0.061        |
| <b>WW</b>     | 120                    | 6.68 ± 6.540   | 0.324   | 115                          | 5.633 ± 11.995 | 0.646        |
| <b>BD</b>     | 120                    | 0.000 ± 0.051  | 0.999   | 115                          | -0.133 ± 0.045 | <b>0.011</b> |
| <b>pH</b>     | 120                    | 0.262 ± 0.155  | 0.114   | 111                          | -0.234 ± 0.102 | <b>0.039</b> |

### Legend

The table shows the environmental variable considered (Variable), the ordinate at the origin of the model (Estimate), corresponding to the mean difference between invaded and control sites (I – T), the number of observations (N).

## 3.2 Effect of *Prunus serotina* and *Rhododendron ponticum* on functional variables.

*P. serotina*-invaded plots showed a significantly thinner OL horizons compared with control plots ( $p = 0.034$ ) (Fig. 2, Table 2) and an increase in FR that was close to the significance threshold ( $p = 0.059$ ). Conversely, *R. ponticum*-invaded plots were characterized by thicker organic horizons, with an O horizon 1.77 times thicker than in control plots ( $p = 0.038$ ), and a similar trend was observed for the OL horizon ( $p = 0.069$ ). The invaded plots also exhibited higher levels of oxidizable carbon (POXC;  $p = 0.007$ ) as well as higher values for the resid variable ( $p = 0.027$ ).

Table 2  
Results of linear mixed-effects models associated with Fig. 2 evaluating the effect of invasion status on soil functional variables.

| Variable | <i>Prunus serotina</i> |                  |              | <i>Rhododendron ponticum</i> |                   |              |
|----------|------------------------|------------------|--------------|------------------------------|-------------------|--------------|
|          | N                      | Estimate         | P value      | N                            | Estimate          | P value      |
| k        | 82                     | 0.003 ± 0.002    | 0.189        | 95                           | 0.000 ± 0.001     | 0.848        |
| S        | 104                    | 0.009 ± 0.011    | 0.442        | 95                           | -0.012 ± 0.014    | 0.411        |
| BR       | 104                    | 0.206 ± 0.859    | 0.812        | 98                           | 0.153 ± 0.193     | 0.444        |
| AWCD     | 104                    | 4.475 ± 7.598    | 0.567        | 97                           | 1.818 ± 11.868    | 0.881        |
| FR       | 104                    | 0.820 ± 0.429    | 0.059        | 97                           | 0.652 ± 1.878     | 0.735        |
| POXC     | 104                    | 82.074 ± 111.977 | 0.478        | 98                           | 630.21 ± 189.203  | <b>0.007</b> |
| O        | 104                    | -0.621 ± 0.407   | 0.155        | 99                           | 4.457 ± 1.921     | <b>0.038</b> |
| OL       | 104                    | -0.649 ± 0.267   | <b>0.034</b> | 99                           | 0.538 ± 0.267     | 0.069        |
| resid    | 104                    | 69.951 ± 91.332  | 0.459        | 97                           | 502.221 ± 194.942 | <b>0.027</b> |

## Legend

The table shows the environmental variable considered (Variable), the ordinate at the origin of the model (Estimate), corresponding to the mean difference between invaded and control sites (I – T), the number of observations (N).

The RDA revealed that mean temperature (Tmean) was the most influential variable structuring soil functional indicators, explaining 23.71% of the total variance. Soil pH (8.67%) and water content (WW; 8.17%) explained an additional 8.67% and 8.17% of the variance, respectively. The model left 59.43% of the variance unexplained (Table 3).

Table 3  
Summary of RDA results.

| Model                                       | Variable  | Variance | P value | Adjusted R <sup>2</sup> | F Statistic |
|---------------------------------------------|-----------|----------|---------|-------------------------|-------------|
| Soil Variable ~ All environmental variables | Tmean     | 1.660    | < 0.001 | 0.37                    | < 0.001     |
|                                             | pH        | 0.607    | < 0.001 |                         |             |
|                                             | WW        | 0.573    | < 0.001 |                         |             |
|                                             | Residuals | 4.160    |         |                         |             |

Legend

The table includes the following variables, explained variance, P-value, adjusted R<sup>2</sup>, and F-statistic. Temperature mean (Tmean), pH (pH), Water Weight (WW).

After accounting for environmental covariates (Tmean, pH, and WW), the decrease in OL horizon thickness and the increase in FR in *P. serotina*-invaded plots were no longer statistically significant, although similar trends remained (p = 0.121 and p = 0.079, respectively) (Table 4). In contrast, the effects observed in plots invaded by *R. ponticum* remained broadly similar, with consistently higher values for O, OL, POXC, and resid (p = 0.050, p = 0.053, p = 0.009, and p = 0.011, respectively). Finally, the stabilization coefficient S showed a trend toward lower values in *R. ponticum*-invaded plots after accounting for environmental covariates (p = 0.090).

Table 4  
Results of linear mixed-effects models evaluating the effect of invasion status on soil functional variables and accounting for the environmental covariates identified by the RDA (Tmean, pH and WW).

| Variable | <i>Prunus serotina</i> |                  |              | <i>Rhododendron ponticum</i> |                   |              |
|----------|------------------------|------------------|--------------|------------------------------|-------------------|--------------|
|          | N                      | Estimate         | P value      | N                            | Estimate          | P value      |
| k        | 82                     | 0 ± 0.002        | 0.910        | 95                           | 0 ± 0.001         | 0.715        |
| S        | 104                    | 0.009 ± 0.012    | 0.453        | 95                           | -0.022 ± 0.012    | <b>0.090</b> |
| BR       | 104                    | 0.148 ± 0.891    | 0.869        | 98                           | 0.15 ± 0.175      | 0.409        |
| AWCD     | 104                    | 1.484 ± 7.337    | 0.843        | 97                           | 2.971 ± 12.705    | 0.820        |
| FR       | 104                    | 0.831 ± 0.467    | <b>0.079</b> | 97                           | 1.048 ± 1.999     | 0.611        |
| POXC     | 104                    | 87.289 ± 124.755 | 0.498        | 98                           | 529.504 ± 197.902 | <b>0.009</b> |
| O        | 104                    | -0.397 ± 0.408   | 0.347        | 99                           | 4.034 ± 1.864     | <b>0.050</b> |
| OL       | 104                    | -0.413 ± 0.251   | 0.121        | 99                           | 0.6 ± 0.276       | <b>0.053</b> |
| resid    | 104                    | 90.487 ± 101.427 | 0.389        | 97                           | 483.088 ± 186.198 | <b>0.011</b> |

Legend

The table reports the response variable (Variable), the estimated effect of invasion status (Estimate ± SE), the number of observations (N) and the associated p-value.

3.3 Invasion age-related changes in functional variables

For *P. serotina*, invasion age effect was significantly associated with AWCD values (p = 0.013), indicating that microbial metabolic activity increased with invasion age (Fig. 3, Table 5). In contrast, the thickness of the OL horizon decreased significantly along the invasion age gradient, suggesting a progressive

reduction of litter accumulation over time ( $p = 0.002$ ). For *R. ponticum*, invasion age was significantly associated with an increase in O horizon thickness, indicating a progressive accumulation of organic material with increasing invasion duration ( $p = 0.013$ ) (Fig. 3, Table 5).

Table 5  
Results of linear mixed-effects models evaluating the effect of invasion age relative to control plots.

| Variable | N                      | Estimate $\pm$ SE  | P value      | N                            | Estimate $\pm$ SE  | P value      |
|----------|------------------------|--------------------|--------------|------------------------------|--------------------|--------------|
|          | <i>Prunus serotina</i> |                    |              | <i>Rhododendron ponticum</i> |                    |              |
| k        | 82                     | $0 \pm 0$          | 0.598        | 95                           | $0 \pm 0$          | 0.466        |
| S        | 104                    | $0 \pm 0$          | 0.479        | 95                           | $-0.001 \pm 0.001$ | 0.349        |
| FR       | 104                    | $0.012 \pm 0.011$  | 0.279        | 97                           | $0.078 \pm 0.101$  | 0.462        |
| AWCD     | 104                    | $0.429 \pm 0.156$  | <b>0.013</b> | 97                           | $0.43 \pm 0.662$   | 0.524        |
| BR       | 104                    | $-0.023 \pm 0.022$ | 0.308        | 98                           | $0.008 \pm 0.008$  | 0.390        |
| O        | 104                    | $-0.005 \pm 0.011$ | 0.671        | 99                           | $0.204 \pm 0.068$  | <b>0.013</b> |
| OL       | 104                    | $-0.017 \pm 0.004$ | <b>0.002</b> | 99                           | $-0.002 \pm 0.014$ | 0.899        |
| POXC     | 104                    | $-3.729 \pm 3.382$ | 0.283        | 98                           | $10.551 \pm 9.412$ | 0.266        |
| resid    | 104                    | $-1.649 \pm 2.721$ | 0.551        | 97                           | $5.633 \pm 9.142$  | 0.539        |

## Legend

The table reports the response variable (Variable), the number of observations (N), the estimated effect of invasion status (Estimate  $\pm$  SE) and the associated p-value.

## 4. Discussion

1. *Prunus serotina* and *Rhododendron ponticum* alter soil microclimatic conditions in different ways depending on their plant structure.

Plant invasions are often associated with modifications of habitat structure and soil properties (Lone et al. 2019), and our results indicate that these environmental changes strongly depend on the growth form and structural characteristics of the invasive species. This pattern was particularly evident for *R. ponticum*, whose presence was associated with significant changes in soil environmental conditions, whereas the effects observed for *P. serotina* appeared weaker and more dependent on invasion age and local environmental context. These differences are consistent with the contrasting structural traits of the two species, with *R. ponticum* rapidly forming a dense evergreen shrub layer, whereas *P. serotina* progressively integrates into the tree canopy. One of the most pronounced disturbances concerns the reduction in light availability within invaded plots (Fig. 1, Table 1). This decrease was particularly marked

in plots invaded by *R. ponticum*, consistent with previous studies (Cross 1975; Casati et al. 2022). We also observed lower light incidence in plots invaded by *P. serotina* at the earliest stages of invasion included in our chronosequence (Supplementary Fig. 4). However, this initial negative impact was followed by a gradual increase in light availability as invasion progressed, suggesting a different trajectory from that observed under *R. ponticum*. At the earliest stages sampled, *P. serotina* may still contribute to the structure of the understory, limiting the penetration of incident radiation (Hardwick et al. 2015; Kušková et al. 2026). As the invasion progresses, the expression of its tree-like character, specifically its ability to reach the canopy layer becomes increasingly pronounced. This progression into the tree layer is accompanied by a gradual thinning of the understory and an increase in light penetration (Supplementary Fig. 4). Regardless of the species, our results show a positive correlation between light intensity and average soil temperature (Supplementary Fig. 5, Pearson's  $r = 0.50$ ), suggesting that variations in light availability are an important factor in regulating the soil microclimate. This relationship is consistent with the lower soil temperatures in plots invaded by *R. ponticum*, where the density of shrubs is particularly high and considerably limits the incidence of radiation (Casati et al. 2022). The relation between the vertical structure, notably the density of shrub layers, and forest microclimate conditions is largely documented (Kovács et al. 2017; De Frenne et al. 2019; Stickley and Fraterrigo 2021; Gril et al. 2023; Terschanski et al. 2024). This relationship can be explained by variations in light penetration (Hardwick et al. 2015), as well as by the increased humidity and reduced air circulation under dense shrub cover, thereby contributing to a more buffered microclimate (Kovács et al. 2017; Terschanski et al. 2024). While soil temperature is influenced by air temperature, it is also influenced by local physical conditions: i) The litter thickness can moderate minimum and maximum temperature values by intercepting radiation and reducing evaporation from the soil surface (Sayer 2005; Fekete et al. 2016). Consistent with this mechanism, we found that the impact of invasive species on litter thickness (OL) was negatively correlated with their impact on microclimatic buffering (DeltaT) (Supplementary Fig. 5, Pearson's  $r = -0.47$ ), consistent with the results of Jo et al., (2017), ii) soils with a high proportion of air-filled pore space present a low thermal conductivity reducing heat transfer (Ochsner et al. 2001). Accordingly, there was a positive correlation between bulk density and daily soil temperature amplitude (Supplementary Fig. 5, Pearson's  $r = 0.5$ ), indicating that lower bulk density increases the soil's insulating capacity and reduces daily temperature fluctuations. Because soils invaded by *R. ponticum* were characterized by both thicker organic horizons and lower bulk density resulting from organic matter accumulation, these two mechanisms likely acted together to strengthen soil microclimatic buffering (DeltaT) (Fig. 1, Table 1). Overall, we show that the environmental disturbances associated with *P. serotina* are relatively minor compared with those caused by *R. ponticum*. This difference may be explained by their contrasting structural traits, particularly their growth forms. *R. ponticum* forms a dense shrub layer that is absent from control plots, whereas *P. serotina*, as a tree species, primarily competes with the native tree layer and gradually alters stand composition without creating a new dense understory. We therefore partially support Hypothesis I: the most pronounced environmental changes were associated with plots invaded by *R. ponticum*, while the effects of *P. serotina* appeared to depend more on the stage of infestation. These results suggest that the vertical structure of invasive plant species strongly determines their capacity to modify forest microenvironmental conditions. These

environmental changes are likely to influence soil carbon transformation processes, particularly through temperature, which emerged as the main environmental variable associated with carbon transformation indicators in our RDA analysis (Table 3). This finding is consistent with previous studies that have highlighted temperature as a key regulator of decomposition processes and microbial activity (Davidson and Janssens 2006; Prescott 2010).

#### 1. Contrasting effects of *Rhododendron ponticum* and *Prunus serotina* on soil carbon cycling based on their functional traits

Beyond their effects on environmental conditions, *R. ponticum* and *P. serotina* also differed in the way they altered soil carbon transformation, consistent with their contrasting resource-use traits. Plots invaded by *R. ponticum* showed higher levels of oxidizable carbon (POXC) and significantly thicker O and OL horizons. The “resid” indicator also suggested a dynamic of organic matter accumulation in invaded plots (Fig. 2, Table 2). These patterns remained significant after accounting for environmental covariates, suggesting that organic matter accumulation was strongly associated with the presence of *R. ponticum* itself rather than solely with local abiotic conditions (Table 4). This result is consistent with a previous study, which reported that organic horizons were on average twice as thick in invaded plots (Le Jeune et al. 2026). These impacts are consistent with the conservative functional trait of *R. ponticum*, which is considered a resource-conservative species. The litter produced by *R. ponticum* contains high concentrations of polyphenolic compounds in both leaves and fine roots (Jones et al. 2019; Casati et al. 2023), compounds that are particularly resistant to decomposition. In addition, the roots form a dense mat within the superficial soil layers (Cross 1975), associated with melanin-rich ericoid mycorrhizae, a feature known to promote organic matter accumulation in forest soils (Clemmensen et al. 2013; Ward et al. 2022). However, contrary to our expectations, this accumulation of organic matter was not associated with reduced microbial activity (BR, AWCD, FR) or lower decomposition rates (k) (Fig. 2, Table 2). Interestingly, despite the cooler and more acidic conditions associated with invaded plots, accounting for environmental covariates revealed lower stabilization coefficient values (S), suggesting that organic matter was more completely decomposed than expected in invaded soils (Table 4). These results contrast with those of Jones et al. (2019), who reported significantly lower soil respiration beneath *R. ponticum*. One possible explanation is a gradual adaptation of microbial communities to *R. ponticum* litter, as previously suggested by Le Jeune et al. (2026). Such adaptation could increase the capacity of microbial communities to degrade recalcitrant organic matter, a phenomenon commonly described as a home-field advantage and previously reported for other species of the Ericaceae family (Joanisse et al. 2018). In contrast, plots invaded by *P. serotina* were rather associated with an acceleration of the soil carbon cycle. Invaded soils exhibited significantly thinner litter layers (OL) and a tendency towards greater functional capacity for organic matter degradation (FR), close to the statistical significance threshold (Fig. 2, Table 2). These results are consistent with previous studies reporting increased microbial activity and accelerated decomposition rates in soils invaded by this species (Lorenz et al. 2004; Aerts et al. 2017; Desie et al. 2020). Indeed, *P. serotina* leaves are rich in nutrients and characterized by lower C:N ratios than those of native species, which may explain the faster litter decomposition observed in invaded plots (Lorenz et al. 2004; Aerts et al. 2017). These patterns are

consistent with the acquisitive resource-use strategy of *P. serotina*, characterized by nutrient-rich litter and faster nutrient cycling (Wardle et al. 2004). However, these effects appeared to be partly mediated by local environmental conditions. In particular, litter thickness (OL) was sensitive to temperature and pH, suggesting that abiotic context partly drives the effects of *P. serotina* on litter dynamics (Table 4). Together, these results suggest that differences in functional traits between the two invasive species largely determine the direction of soil carbon dynamics, with *P. serotina* favouring carbon release through enhanced decomposition, whereas *R. ponticum* promotes carbon storage through organic matter accumulation.

## 4.3 Contrasting temporal trajectories revealed by the complementarity of functional indicators

Our results show that the effects of invasions on the soil forest carbon dynamics evolve over time, following contrasting temporal trajectories between *R. ponticum* and *P. serotina* that are consistent with the distinct functional traits of the two invasive species. Increasing invasion age was associated with a gradual increase in the thickness of the organic layer in plots invaded by *R. ponticum* (Fig. 3, Table 5), in contrast to plots invaded by *P. serotina*, which show a gradual decrease in litter thickness (OL) and an increase in microbial metabolic activity (AWCD), suggesting an acceleration of the soil carbon cycle (Fig. 3, Table 5). These contrasting trajectories support hypothesis 3 and indicate that invasive plants do not induce a uniform temporal response of soil functioning. Instead, the direction and magnitude of ecosystem changes depend on the functional traits of each species and on the way they progressively modify forest structure and resource inputs. Our results also highlight the complementary nature of the various indicators describing carbon transformation. Indicators related to material stocks, such as organic horizons or carbon pools, exhibit high inertia and are therefore relevant for assessing long-term trends in soil functioning (Bünemann et al. 2018; Garland et al. 2021). Other indicators, such as soil respiration or the functional activity of microbial communities, conversely respond rapidly to environmental changes (Garland et al. 2021). Their combined interpretation therefore allows for the simultaneous characterization of the current state of soil functioning and the cumulative consequences of disturbances over time, which constitute a long-term legacy (Frouz 2024).

In plots invaded by *R. ponticum*, the gradual accumulation of organic matter observed within the O horizon may result from a persistent imbalance between carbon inputs and outputs. The higher concentrations of oxidizable carbon (POXC) and increased litter depth (OL) observed in the invaded plots suggest increased inputs of organic matter, while the decomposition rate ( $k$ ) remains stable. This imbalance between carbon inputs and outputs may therefore contribute to a gradual accumulation of organic matter in the organic horizon (O). Although POXC and OL values were higher in the invaded plots, the lack of a temporal increase in these parameters suggests that these changes likely occurred during the early stages of the invasion, before the youngest stages represented in our chronosequence (before 16 years). After this initial phase, these indicators may have reached a new equilibrium state and remained relatively stable. In contrast, the thickness of the O horizon reflects the cumulative

consequences of prolonged imbalances between organic matter inputs and losses, resulting in a gradual accumulation of organic matter over several decades. In contrast, plots invaded by *P. serotina* appear to follow a different trajectory, characterized by a gradual increase in microbial activity. As *P. serotina* progressively becomes dominant within the tree layer, its nutrient-rich litter represents an increasing proportion of total litter inputs, gradually stimulating microbial metabolism and carbon turnover. By producing litter that is richer in nutrients and more readily decomposable (Aerts et al., 2017), *P. serotina* could thus gradually stimulate microbial metabolism and accelerate the soil carbon cycle through a priming effect (Kumar Rai and Singh 2020). However, despite these functional changes, we do not observe a significant long-term decrease in the O horizon up to an estimated age of 143 years. This difference between rapid-response indicators (AWCD and OL) and slower indicators (O) suggests that changes in soil carbon transformation processes have started but have not yet translated into measurable losses of accumulated organic matter. The contrasting trajectories of the two species can also be explained by differences in their structural development. The shrubby architecture of *R. ponticum* rapidly creates an additional vegetation layer that strongly modifies forest microclimatic conditions and resource availability shortly after its establishment. These structural modifications are consistent with the physical ecosystem engineering effects described for invasive species that alter habitat structure and abiotic conditions, thereby reshaping ecosystem functioning (Haubrock et al. 2026). Conversely, *P. serotina* progressively replaces the native tree layer, resulting in a slower and more gradual reorganization of forest structure. This interpretation is consistent with the gradual changes in light availability observed along the *P. serotina* chronosequence. Consequently, the two invasions appear not only follow contrasting functional trajectories, but their impacts may also manifest at different rates due to their contrasting structural characteristics.

## 5. Conclusion

This study highlights that the invasive alien plants *R. ponticum* and *P. serotina* alter soil carbon transformation processes through both their specific functional traits and the microenvironmental changes they induce within forest ecosystem. *R. ponticum*, by forming a dense shrub layer, significantly altered soil environmental conditions by reducing light availability and limiting both mean and variation in soil temperatures. Conversely, the effects of *P. serotina* on the microenvironment were weaker and exhibited more complex temporal dynamics. This trend can be explained by the transition from the shrub layer to the tree layer along our chronosequence, which resulted in an initial decrease followed by an increase in light incidence. These results highlight the importance of changes in vegetation structure induced by invasive alien species in shaping soil functioning. Our results also support the hypothesis that invasive alien species with contrasting ecological traits exert opposing effects on soil carbon transformation processes. In line with the “economic spectrum of plants”, the conservative traits of *R. ponticum* were associated with the accumulation of organic matter, whereas the acquisitive traits of *P. serotina* were associated with increased microbial activity through a priming effect. These effects changed differently over time as invasion progressed. While *R. ponticum* led to a gradual accumulation of organic matter in the O horizon, *P. serotina* was characterized by increasing microbial activity and

decreasing litter thickness, highlighting an intensification of impacts over time with distinct trajectories depending on the species. Overall, our research demonstrates the interest of a multi-indicator approach for better understanding the long-term impacts of invasive species on soil carbon dynamics.

## Declarations

### Declaration of interests

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.

### Annie Guiller

Conceptualization, Writing (review and editing).

### Mattéo Dorvillé

Investigation (field and laboratory data collection).

### Redhouane Al Kharrat

Investigation (field and laboratory data collection).

### Jérôme Duclerc

Investigation, Methodology (training and supervision of biological assays).

### Hélène Horen

Conceptualization, Supervision, Funding acquisition, Writing (review and editing).

## Funding

This work was supported by a doctoral fellowship from the Région Hauts-de-France. Additional support was provided by the Université de Picardie Jules Verne (UPJV) and the Centre National de la Recherche Scientifique (CNRS) through the funding and operating resources of the UMR 7058 EDYSAN laboratory.

## Author Contributions

**Erwan Le Jeune:** Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Writing (original draft).

# Acknowledgments

We would like to thank the «Office national des forêts » (ONF) and private forest owners for granting us access to the study sites. We would also like to thank Tristan Ubaldi for his assistance during the fieldwork campaign in the Compiègne Forest. This work was funded by the Hauts-de-France region.

## References

1. Aerts R, Ewald M, Nicolas M et al (2017) Invasion by the Alien Tree *Prunus serotina* Alters Ecosystem Functions in a Temperate Deciduous Forest. *Front Plant Sci* 8. <https://doi.org/10.3389/fpls.2017.00179>
2. Allison SD, Vitousek PM (2004) Rapid nutrient cycling in leaf litter from invasive plants in Hawai'i. *Oecologia* 141:612–619. <https://doi.org/10.1007/s00442-004-1679-z>
3. Bruehlheide H, Dengler J, Purschke O et al (2018) Global trait–environment relationships of plant communities. *Nat Ecol Evol* 2:1906–1917. <https://doi.org/10.1038/s41559-018-0699-8>
4. Bünemann EK, Bongiorno G, Bai Z et al (2018) Soil quality – A critical review. *Soil Biol Biochem* 120:105–125. <https://doi.org/10.1016/j.soilbio.2018.01.030>
5. Casati M, Kichey T, Closset D et al (2023) Is the invasive *Rhododendron ponticum* L. an emergent threat to mainland Atlantic forests? A population dynamics approach. *Ecol Manag* 549:121463. <https://doi.org/10.1016/j.foreco.2023.121463>
6. Casati M, Kichey T, Decocq G (2022) Monographs on Invasive Plants in Europe N°7: *Rhododendron ponticum* L. *Bot Lett* 169:213–236. <https://doi.org/10.1080/23818107.2022.2052182>
7. Clemmensen KE, Bahr A, Ovaskainen O et al (2013) Roots and associated fungi drive long-term carbon sequestration in boreal forest. *Science* 339:1615–1618. <https://doi.org/10.1126/science.1231923>
8. Cross JR (1975) *Rhododendron ponticum* L. *J Ecol* 63:345–364. <https://doi.org/10.2307/2258859>
9. Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440:165–173. <https://doi.org/10.1038/nature04514>
10. De Frenne P, Rodríguez-Sánchez F, Coomes DA et al (2013) Microclimate moderates plant responses to macroclimate warming. *Proc Natl Acad Sci USA* 110:18561–18565. <https://doi.org/10.1073/pnas.1311190110>
11. De Frenne P, Zellweger F, Rodríguez-Sánchez F et al (2019) Global buffering of temperatures under forest canopies. *Nat Ecol Evol* 3:744–749. <https://doi.org/10.1038/s41559-019-0842-1>
12. Desie E, Vancampenhout K, van den Berg L et al (2020) Litter share and clay content determine soil restoration effects of rich litter tree species in forests on acidified sandy soils. *Ecol Manag* 474:118377. <https://doi.org/10.1016/j.foreco.2020.118377>
13. Fekete I, Varga C, Biró B et al (2016) The effects of litter production and litter depth on soil microclimate in a central european deciduous forest. *Plant Soil* 398:291–300.

<https://doi.org/10.1007/s11104-015-2664-5>

14. Frouz J (2024) Plant-soil feedback across spatiotemporal scales from immediate effects to legacy. *Soil Biol Biochem* 189:109289. <https://doi.org/10.1016/j.soilbio.2023.109289>
15. Garcia RA, Clusella-Trullas S (2025) Microclimatic changes caused by plant invasions and warming: uncovering thermal costs and benefits to a tortoise. *Conserv Physiol* 13:coaf016. <https://doi.org/10.1093/conphys/coaf016>
16. Garland G, Banerjee S, Edlinger A et al (2021) A closer look at the functions behind ecosystem multifunctionality: A review. *J Ecol* 109:600–613. <https://doi.org/10.1111/1365-2745.13511>
17. Garland JL, Mills AL (1991) Classification and characterization of heterotrophic microbial communities on the basis of patterns of community-level sole-carbon-source utilization. *Appl Environ Microbiol* 57:2351–2359. <https://doi.org/10.1128/aem.57.8.2351-2359.1991>
18. Gril E, Laslier M, Gallet-Moron E et al (2023) Using airborne LiDAR to map forest microclimate temperature buffering or amplification. *Remote Sens Environ* 298:113820. <https://doi.org/10.1016/j.rse.2023.113820>
19. Hardwick SR, Toumi R, Pfeifer M et al (2015) The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: Forest disturbance drives changes in microclimate. *Agric Meteorol* 201:187–195. <https://doi.org/10.1016/j.agrformet.2014.11.010>
20. Haubrock PJ, Everts T, Abreo NAS et al (2026) The impacts of biological invasions. *Biol Rev* 101:1255–1310. <https://doi.org/10.1002/brv.70124>
21. Heepngoen P, Thoumazeau A, Renevier M-S et al (2021) Relationships between physico-chemical, biological and functional approaches for soil quality assessment. A case study along a gradient of disturbance. *Eur J Soil Biol* 104:103300. <https://doi.org/10.1016/j.ejsobi.2021.103300>
22. Hurisso TT, Culman SW, Horwath WR et al (2016) Comparison of Permanganate-Oxidizable Carbon and Mineralizable Carbon for Assessment of Organic Matter Stabilization and Mineralization. *Soil Sci Soc Am J* 80:1352–1364. <https://doi.org/10.2136/sssaj2016.04.0106>
23. Jo I, Fridley JD, Frank DA (2017) Invasive plants accelerate nitrogen cycling: evidence from experimental woody monocultures. *J Ecol* 105:1105–1110. <https://doi.org/10.1111/1365-2745.12732>
24. Joannis GD, Bradley RL, Preston CM (2018) The spread of *Kalmia angustifolia* on black spruce forest cutovers contributes to the spatial heterogeneity of soil resources. *PLoS ONE* 13:e0198860. <https://doi.org/10.1371/journal.pone.0198860>
25. Jones GL, Scullion J, Worgan H, Gwynn-Jones D (2019) Litter of the invasive shrub *Rhododendron ponticum* (Ericaceae) modifies the decomposition rate of native UK woodland litter. *Ecol Indic* 107:105597. <https://doi.org/10.1016/j.ecolind.2019.105597>
26. Karlen DL, Mausbach MJ, Doran JW et al (1997) Soil Quality: A Concept, Definition, and Framework for Evaluation (A Guest Editorial). *Soil Sci Soc Am J* 61:4–10. <https://doi.org/10.2136/sssaj1997.03615995006100010001x>

27. Kemppinen J, Lembrechts JJ, Van Meerbeek K et al (2024) Microclimate, an important part of ecology and biogeography. *Glob Ecol Biogeogr* 33:e13834. <https://doi.org/10.1111/geb.13834>
28. Keuskamp JA, Dingemans BJJ, Lehtinen T et al (2013) Tea Bag Index: a novel approach to collect uniform decomposition data across ecosystems. *Methods Ecol Evol* 4:1070–1075. <https://doi.org/10.1111/2041-210X.12097>
29. Kovács B, Tinya F, Ódor P (2017) Stand structural drivers of microclimate in mature temperate mixed forests. *Agric Meteorol* 234–235:11–21. <https://doi.org/10.1016/j.agrformet.2016.11.268>
30. Kumar Rai P, Singh JS (2020) Invasive alien plant species: Their impact on environment, ecosystem services and human health. *Ecol Indic* 111:106020. <https://doi.org/10.1016/j.ecolind.2019.106020>
31. Kušková K, Kutlvaš J, Stanek M et al (2026) *Prunus serotina* in Europe: A comprehensive review of ecology, impacts and management of an invasive tree. *Perspect Plant Ecol Evol Syst* 71:125932. <https://doi.org/10.1016/j.ppees.2026.125932>
32. Le Jeune E, Guiller A, Spicher F, Horen H (2026) How does the invasion of forests by *Rhododendron ponticum* disrupt the transformation of carbon in soils? *Biol Invasions* 28:43. <https://doi.org/10.1007/s10530-025-03745-8>
33. Liao C, Peng R, Luo Y et al (2008) Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytol* 177:706–714. <https://doi.org/10.1111/j.1469-8137.2007.02290.x>
34. Lone P, Dar J, Kothandaraman S et al (2019) Impact of plant invasion on physical, chemical and biological aspects of ecosystems: A review. *Trop Plant Res* 6:528–544. <https://doi.org/10.22271/tpr.2019.v6.i3.067>
35. Lorenz K, Preston CM, Krumrei S, Feger K-H (2004) Decomposition of needle/leaf litter from Scots pine, black cherry, common oak and European beech at a conurbation forest site. *Eur J Res* 123:177–188. <https://doi.org/10.1007/s10342-004-0025-7>
36. Manning P, van der Plas F, Soliveres S et al (2018) Redefining ecosystem multifunctionality. *Nat Ecol Evol* 2:427–436. <https://doi.org/10.1038/s41559-017-0461-7>
37. Ochsner TE, Horton R, Ren T (2001) A New Perspective on Soil Thermal Properties. *Soil Sci Soc Am J* 65:1641–1647. <https://doi.org/10.2136/sssaj2001.1641>
38. Prescott CE (2005) Do rates of litter decomposition tell us anything we really need to know? *Ecol Manag* 220:66–74. <https://doi.org/10.1016/j.foreco.2005.08.005>
39. Prescott CE (2010) Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? *Biogeochemistry* 101:133–149. <https://doi.org/10.1007/s10533-010-9439-0>
40. Raheem A, Yohanna P, Li G et al (2024) Unraveling the ecological threads: How invasive alien plants influence soil carbon dynamics. *J Environ Manag* 356:120556. <https://doi.org/10.1016/j.jenvman.2024.120556>
41. Reich PB (2014) The world-wide ‘fast–slow’ plant economics spectrum: a traits manifesto. *J Ecol* 102:275–301. <https://doi.org/10.1111/1365-2745.12211>

42. Rusterholz H-P, Schneuwly J, Baur B (2018) Invasion of the alien shrub *Prunus laurocerasus* in suburban deciduous forests: Effects on native vegetation and soil properties. *Acta Oecol* 92:44–51. <https://doi.org/10.1016/j.actao.2018.08.004>
43. Saetre P, Bååth E (2000) Spatial variation and patterns of soil microbial community structure in a mixed spruce–birch stand. *Soil Biol Biochem* 32:909–917. [https://doi.org/10.1016/S0038-0717\(99\)00215-1](https://doi.org/10.1016/S0038-0717(99)00215-1)
44. Sardans J, Bartrons M, Margalef O et al (2017) Plant invasion is associated with higher plant–soil nutrient concentrations in nutrient-poor environments. *Glob Change Biol* 23:1282–1291. <https://doi.org/10.1111/gcb.13384>
45. Sayer EJ (2005) Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. *Biol Rev* 81:1–31. <https://doi.org/10.1017/S1464793105006846>
46. Stickley SF, Fraterrigo JM (2021) Understory vegetation contributes to microclimatic buffering of near-surface temperatures in temperate deciduous forests. *Landsc Ecol* 36:1197–1213. <https://doi.org/10.1007/s10980-021-01195-w>
47. Tamura M, Suseela V, Simpson M et al (2017) Plant litter chemistry alters the content and composition of organic carbon associated with soil mineral and aggregate fractions in invaded ecosystems. *Glob Change Biol* 23:4002–4018. <https://doi.org/10.1111/gcb.13751>
48. Terschanski J, Nunes MH, Aalto I et al (2024) The role of vegetation structural diversity in regulating the microclimate of human-modified tropical ecosystems. *J Environ Manag* 360:121128. <https://doi.org/10.1016/j.jenvman.2024.121128>
49. Thoumazeau A, Gay F, Alonso P et al (2017) SituResp®: A time- and cost-effective method to assess basal soil respiration in the field. *Appl Soil Ecol* 121:223–230. <https://doi.org/10.1016/j.apsoil.2017.10.006>
50. Vanhellemont M, Verheyen K, De Keersmaecker L et al (2009) Does *Prunus serotina* act as an aggressive invader in areas with a low propagule pressure? *Biol Invasions* 11:1451–1462. <https://doi.org/10.1007/s10530-008-9353-8>
51. Ward EB, Duguid MC, Kuebbing SE et al (2022) The functional role of ericoid mycorrhizal plants and fungi on carbon and nitrogen dynamics in forests. *New Phytol* 235:1701–1718. <https://doi.org/10.1111/nph.18307>
52. Wardle DA, Bardgett RD, Klironomos JN et al (2004) Ecological Linkages Between Aboveground and Belowground Biota. *Science* 304:1629–1633. <https://doi.org/10.1126/science.1094875>
53. Weil R, Stine M, Gruver J, Samson-Liebig S (2003) Estimating active carbon for soil quality assessment: A simplified method for laboratory and field use. *Am J Altern Agric* 18:3–17. <https://doi.org/10.1079/AJAA200228>
54. Statements & Declarations

## Figures

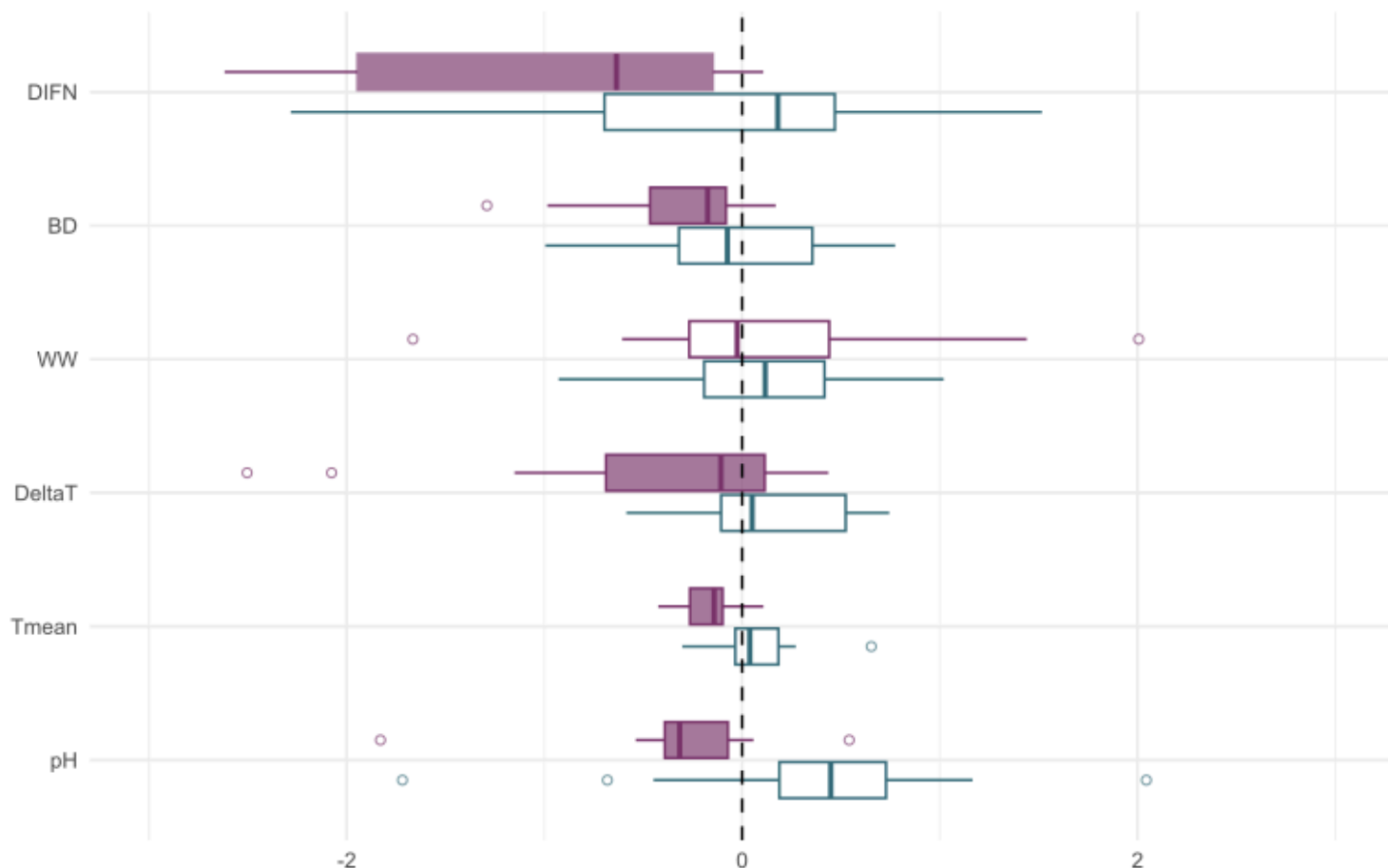


**Figure 1**

Effect of invasion on environmental variables. Values represent invaded sites minus control sites. Purple boxplots correspond to the effect of *R. ponticum*, and green boxplots correspond to the effect of *P. serotina*. Filled boxplots indicate statistically significant differences between invaded and control sites ( $p < 0.05$ ) based on linear mixed-effects models. Environmental variables include light availability (DIFN), bulk density (BD), water content (WW), thermal amplitude (DeltaT), mean temperature (Tmean), and soil pH (pH).

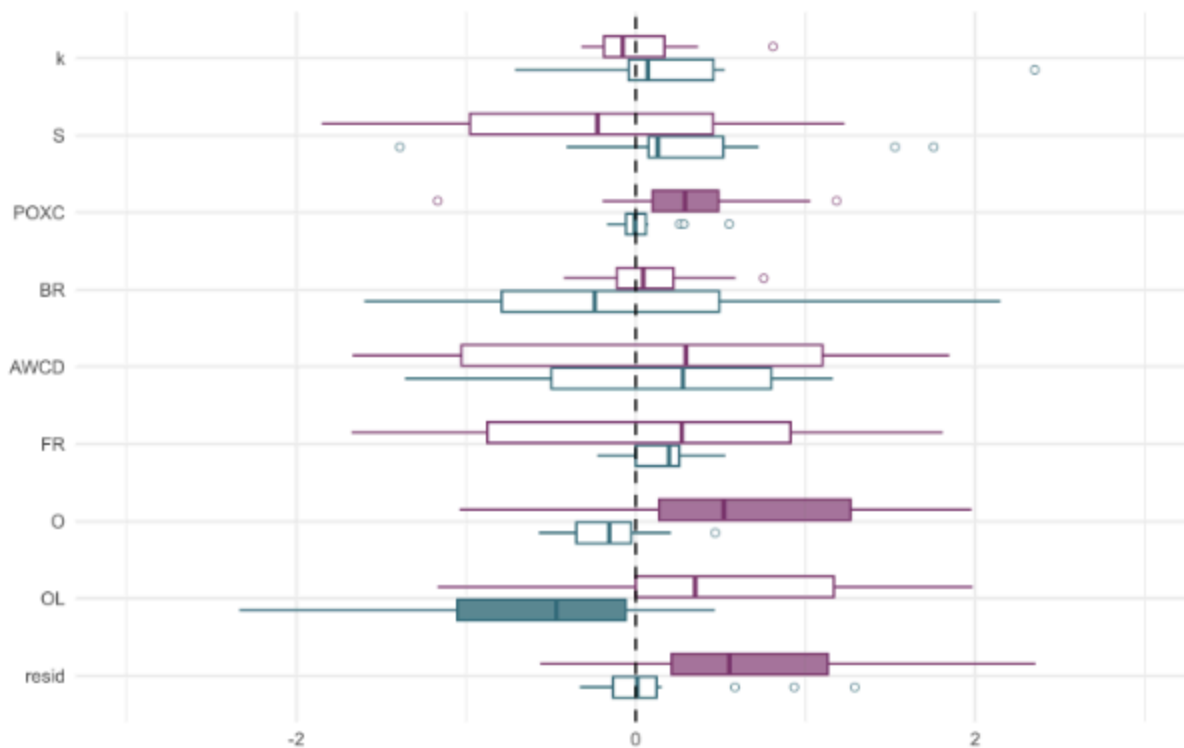


**Figure 2**

Effect of invasion on forest soil functional variables. Boxplots show the values of invaded sites minus control sites. Filled boxplots indicate statistically significant differences between invaded and control sites ( $p < 0.05$ ) based on linear mixed-effects models. Functional variables include the decomposition rate (k), stabilization factor (S), labile carbon content (POXC), basal respiration (BR), model residuals (resid), average well color development (AWCD), functional richness (FR), thickness of the humic horizon (O) and litter accumulation (OL).

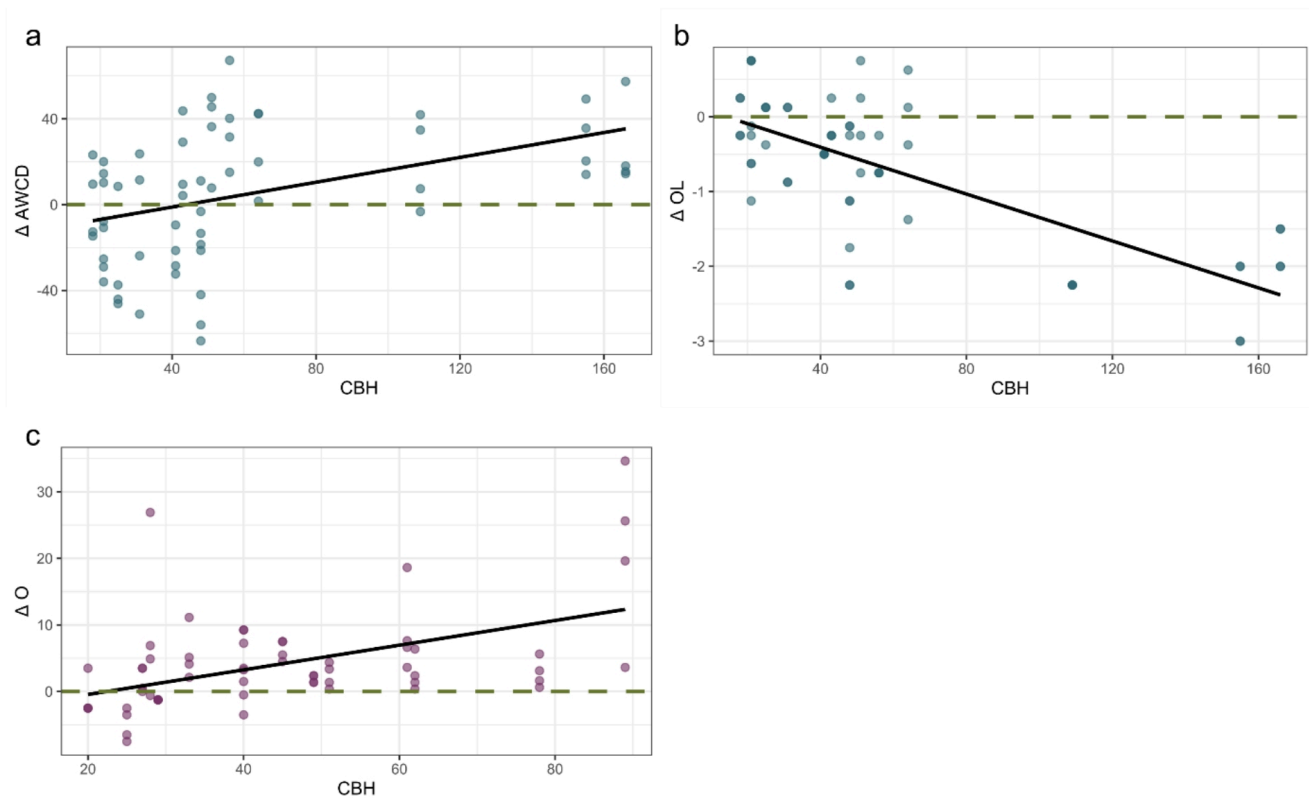


**Figure 3**

Relationship between the circumference in cm used as proxy of age of invasion (CBH), expressed in centimeters and differences between invaded and control plots for various functional and environmental variables. For *P. serotina*, relationship between: CBH and metabolic footprint AWCD (a), CBH and litter thickness (OL) (b). Within sites invaded by *R. ponticum*, relationship between CBH and organic horizon thickness (O) (c). Each point represents the mean difference between an invaded plot and its matched control plot. The green dotted horizontal line indicates no effect of invasion.

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Graphicalabstract.pdf](#)
- [Appendix.docx](#)