Deep impact: invasive non-native trees alter the entire soil profile in montane forests invaded by Ligustrum lucidum

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Abstract

Background and Aims

Biological invasions modify the structure and functioning of the recipient ecosystems, including soil properties that determine plant development. To determine whether tree invasions affect soil properties across soil layers, we evaluated chemical and physical soil properties across multiple depths in subtropical mountain forests invaded by *Ligustrum lucidum* in northwestern Argentina.

Methods

We collected soil samples from native subtropical forests and forests invaded by *L. lucidum* at three soil depths (0-10, 11-30, and 31-50 cm). For each sample, we measured cation exchange capacity, pH, bulk density, and the concentrations of aN, C, P, Ca^{2+}, Mg^{2+}, Na^{+}, and K^{+}. We used Gamma regressions to estimate mean values for each soil property for each forest type (native vs invaded) and soil depth combination.

Results

L. lucidum invasion altered soil properties down to 50 cm depth. The most pronounced change occurred in the deepest layer sampled, where P increased markedly, whereas K^{+}, Na^{+}, and Mg^{2+} decreased relative to native forest soil. These patterns remained detectable across all soil layers. C, Ca^{2+}, and bulk density smoothly increased in invaded forest soil in different layers. N increased slightly in the upper layer of invaded forests, but decreased in the middle layer for the former. CEC and pH were not affected by *L. lucidum*invasion.

Conclusions

The effects of *L. lucidum* invasion go beyond the upper soil layer. By modifying nutrient availability and physical properties throughout the soil profile, invaded forests exhibit a distinct belowground environment with potential consequences for ecosystem functioning and native vegetation recovery.

Introduction

Invasive non-native species (INNS) are species that have established self-sustaining populations across multiple locations and can colonise areas outside their native ranges (Blackburn et al. 2011; Soto et al. 2024), impacting ecosystems, economies, and human societies (Roy et al. 2024). Impacts are particularly strong when INNS act as ecological engineers, altering ecosystem properties and triggering cascading effects on ecosystem processes and native biodiversity (Crooks 2002; Rilov et al. 2024).

Invasive ecosystem engineers can profoundly modify soil conditions, making invasion-driven soil alteration particularly important. Soil nutrients support all terrestrial life processes, and their dynamics are shaped by interactions between abiotic (e.g., moisture, pH, texture) and biotic factors, particularly

vegetation and soil biota (Guerra et al. 2022). Mountain soils in particular are highly dynamic systems. The combination of steep slopes, young parental materials, and active erosion limits the development of deep soil horizons, resulting in shallow, weakly developed soils (Egli and Poulenard 2016). In mountain forests, where slopes commonly reach 30–40%, vegetation cover plays a dual role: it influences soil composition through nutrient uptake and litter return, and it stabilises the soil by reducing water erosion. Consequently, changes in vegetation may affect the characteristics of the entire soil profile by altering dominant species nutrient-use strategies, root traits, and litter quality, leading to contrasting patterns of nutrient uptake, organic matter inputs, and microbial activity (Guerra et al. 2022).

Invasive non-native trees tend to exhibit growth and reproductive strategies that foster rapid capture of edaphic resources, thereby altering biogeochemical cycles and nutrient availability for co-occurring species (Afreen et al. 2023; Green et al. 2025). In particular, plant invasions can impact soil decomposer organisms that drive carbon and nutrient cycling by breaking down plant material, root exudates and soil organic matter, influencing soil physicochemical characteristics such as pH, organic matter content, soil water-holding and soil structure (Ehrenfeld et al. 2005; van der Putten et al. 2016). Plant invasions can further amplify such changes by disrupting microbial assemblages through the selection of certain microorganisms over others (Le Roux et al. 2018), leading to shifts in microbial composition and function that can alter nutrient cycling (Van Der Heijden et al. 2008). Such processes occur at different soil depths. While nutrient decomposition can alter litter and the upper soil layer, nutrient uptake and plant exudates occur in the rhizosphere, affecting the deeper soil layers. These alterations can adversely affect sensitive native species, potentially facilitating further invasions (e.g., invasion meltdown; Green et al. 2011). Even after the removal of invasive species, alterations in soil nutrient pools, microbial assemblages, and mutualistic soil networks can persist as legacy effects, constraining native species assemblages and disrupting plant successional trajectories toward undesirable alternative ecosystem states (Corbin and D'Antonio 2012; Albertson et al. 2024). Effective management of invasive trees acting as ecosystem engineers therefore requires an understanding of soil dynamics throughout the soil profile, as these processes can strongly influence the recovery of native forests.

The invasion of the non-native glossy privet (*Ligustrum lucidum*) represents a key threat to the conservation of the southernmost limit of Yungas mountain forests, which occur in the eastern foothills of the Andes, from Venezuela to Northwestern Argentina (Cabrera 1976; Oyarzabal et al. 2018; Nanni et al. 2020). The ecosystem engineer *L. lucidum* forms monodominant forests and progressively replaces native forests (Montti et al. 2017, 2021; Fernandez et al. 2020), affecting canopy structure and light availability (solar radiation), as well as litter depth and quality (including C: N ratio) and soil moisture (Ayup et al. 2014; Zamora Nasca et al. 2014; Aragón et al. 2014a). Invaded forests accumulate litter that decomposes faster than that of native species due to their lower cellulose and lignin content, thereby leading to faster decomposition rates (Aragón et al. 2014a). In addition, the replacement of native forests by glossy privet alters soil processes by changing fungal and faunal species composition (Aragón et al. 2014b; Fernandez et al. 2017) and modifying soil enzyme composition and concentration (Aragón et al. 2014b). Such alterations can accelerate nutrient uptake and overall nutrient cycling, particularly nitrogen cycling (Aragón et al. 2014b).

Many studies assessing the impacts of plant invasions, including those of glossy privet, have focused on the uppermost layers of soil (often the top 10 cm), potentially overlooking deeper soil changes where plant roots remain active and may influence vegetation recovery after glossy privet removal. To address this gap, we asked whether glossy privet alters soil physical and chemical properties beyond the top 10 cm of soil, and how these effects vary with depth up to 50 cm in Yungas forests in Tucumán, NW Argentina. We hypothesise that invasion by the exotic species would decrease exchangeable base cation concentrations (e.g., Ca, Mg, K, and Na) while increasing soil organic matter-related nutrient pools, particularly soil C and N, relative to native forests. These changes were expected to be strongest in the upper soil layer for C and N and in the lower soil layer for exchangeable cations.

Methodology

Study area

Our study sites were part of the Selva Tucumano-Boliviana, or Yungas ecoregion, which consists of montane, subtropical cloud forests in the eastern foothills of the Andes (Fig. 1A, Cabrera 1976; Olson et al. 2001; Brown et al. 2005). This ecoregion harbours high biodiversity due to its capacity to capture nutrients and water from global circulation regimes (Brown et al. 2005). It is characterised by a strong altitudinal gradient from 400 to 3,000 m.a.s.l., with steep slopes on which different vegetation units develop: lowland forests (upper limit 700 m.a.s.l.), lower montane forests (upper limit 1500 m.a.s.l.), and upper montane forests (upper limit 3000 m.a.s.l.). We conducted our study in the lower montane forests (Fig. 1B, 700m a.s.l.), characterised by a humid subtropical climate, a rainy season from October to April, and mean annual temperatures of around 19°C (Minetti 2005). Slope (ranging between 30–40%) is a limiting factor for soil development, producing shallow soils, with a dark upper layer and high levels of organic matter (Puchulu and Fernández 2004).

The vegetation of lower montane forests comprises a variety of plant life forms (trees, shrubs, herbs, epiphytes, and vines), with a canopy of evergreen and semi-deciduous tree species, with relatively high abundances of native tree species such as *Allophylus edulis*, *Blephalocalix salicifolius*, *Cedrela angustifolia*, *Cupania vernalis*, *Myrsine laetevirens*, *Ocotea porphyria*, and *Tecoma stans* (Brown et al. 2005; Blundo et al. 2012). Our study area has been subject to extensive logging, agriculture, and cattle grazing until the 1970s and 1980s, when the protected areas “Parque Sierra de San Javier” and “Reserva Experimental de Horco Molle" were established, respectively (Grau et al. 1997). Since then, spontaneous forest recovery has occurred. Importantly, this process has often been accompanied by the invasion of the INNS, *Ligustrum lucidum*, leading to the formation of monodominant invaded forests (Easdale et al. 2007; Montti et al. 2017; Jimenez et al. 2021).

Field surveys

We selected 13 previously established forest plots based on their tree composition to obtain a representative sample of invaded and native forests. Five of them were dominated by native tree species and belong to the Red Subtropical de Parcelas Permanentes (RSPP, Ceballos et al. 2022), whereas the remaining seven plots were dominated by glossy privet and belong to the CONTAIN project (Lambin et al. 2020). We considered a plot to be invaded when the relative abundance of glossy privet (individuals larger than 10 cm DBH) was greater than 50%. All our plots covered at least 1 hectare, and we are not aware of any forest fires, logging, or cattle presence in these plots in the last 30 years.

Within each forest plot, we established five to seven points at random, spaced at least 10 meters apart. At each point, we used a soil auger to collect soil samples from three depth layers: upper (0–10 cm), middle (11–30 cm), and deeper (31–50 cm). We took two separate soil samples per layer (one for chemical analysis and the other for bulk density). We stored soil samples in sealed plastic bags and transported them to the laboratory.

Laboratory analyses

We analysed a total of 209 soil samples in the laboratory, of which 134 were from invaded forests (64%). To determine bulk density, we used the soil core cylinder method (Blake and Hartge 1986; Campbell and Henshall 1991), except for cases with a high proportion of coarse material (e.g., stony soils). In these situations, we determined the soil bulk density using the excavation method (Blake and Hartge 1986).

We dried and sieved all samples (2 mm mesh) before chemical analyses. We determined the total carbon and nitrogen content of all soil samples by dry combustion (LECO CN 628). We determined soil extractable P using the Bray and Kurtz I method (Bray and Kurtz 1945), and we measured cation exchange capacity and exchangeable Ca^{2+}, Mg^{2+}, Na^{+} and K^{+} using the ammonium acetate at pH 7 method (Food and Agriculture Organization of the United Nations (FAO 2022). We measured soil pH in distilled water (1:2.5 soil-to-solution ratio). We repeated all analyses that had values outside the expected analytical range in the first measurement.

We conducted nitrogen and carbon analyses at the Instituto de Investigación Animal del Chaco Semiarido laboratory in Tucumán, Instituto Nacional de Tecnología Agropecuaria (INTA), and all other determinations at the Edaphology Laboratory of the Facultad de Agronomía y Zootecnia, Universidad Nacional de Tucumán, Argentina.

Statistical analyses

We modelled the value $V_{z,i,j,k}$ of each of the 10 physical and chemical soil characteristics, z, as a function of the survey plot, *i*, the type of forest (non-invaded vs invaded), j, and the sample depth, *k*, using a Gamma-log model parameterised by the mean and the standard deviation of the Gamma distribution:

$$log(\lambda_{z,i,j,k}) = \alpha_{z,i} + \beta_{z,k,j}, \quad (1)$$

$V_{z,i,j,k} \sim Gamma(mean = \lambda_{z,i,j,k}, standard\ deviation = \sigma)$, (2)

where $\lambda_{z,i,j,k}$ is the mean value of element *z* in plot *i* of forest type *j* at soil depth *k* (on the log-scale), $\alpha_{z,i}$ is a the plot-specific random effect (on the log scale) of element z that controls for plot-level effects, $\beta_{z,k,j}$ is the mean value (on the log-scale) of element z in forest type j and soil depth k, and σ is the standard deviation. A Gamma distribution has a support in the range of positive continuous values (i.e., between 0 and infinity, and including decimals) and, therefore, is an appropriate choice for analysing our data. Typically, the Gamma distribution is parameterised by its shape and scale rather than the mean and standard deviation (Thompson Hobbs and Hooten 2015). However, the mean and standard deviation can be derived using the method of moments (Thompson Hobbs and Hooten 2015), and this parametrisation is easier to understand and manipulate, and is available in existing R software packages (de Valpine et al. 2017). We do not provide the mathematical equivalences between the shape, scale, mean, and standard deviation of the Gamma distribution here; interested readers are referred to (Thompson Hobbs and Hooten 2015) for details.

We fitted the model in expressions 1 and 2 to each of the nine soil elements independently (i.e., we fitted one model per element *z*) using Bayesian methods implemented in the nimble and nimbleHMC packages for the R statistical software (R Core Team 2022). We used relatively uninformative priors for all model parameters. We specified an a priori distribution for the plot-level random effect as $\alpha_{z,i} \sim Normal(0, \sigma_{z,i}^2)$, $\sigma_{z,i}^2 \sim Uniform(0, 1000)$, $\beta_{z,k,j} \sim Normal(0, \sigma_{z,k,i}^2 = 1000)$ for the log-scale mean effects of forest type and soil depth, and $\sigma^2 \sim Uniform(0, 1000)$, $\sigma = sqrt(\sigma^2)$ for the standard deviation of the Gamma distribution in expression 2. All models were fitted to the data using Hamiltonian Monte Carlo methods via the No-U-Turn Sampler (NUTS) implemented in the package nimbleHMC (de Valpine et al. 2017). The nine models were run using three chains with 50,000 iterations each and retaining one in five iterations (thinning of five). We discarded the first 10,000 iterations of each chain as burn-in, resulting in 24,000 draws from the posterior distributions of the model parameters. We checked the convergence and mixing of the chains by visually inspecting trace plots and calculating the Gelman-Rubin diagnostic. These checks showed that the chains had converged and mixed adequately.

We evaluated the adjustment of our models to the data using Bayesian p-values (Thompson Hobbs and Hooten 2015). Bayesian p-values compare the scores of a goodness-of-fit test, the root mean square error in our case, obtained from the model fitted to the data to the scores expected under the assumption that the model can generate the data (Thompson Hobbs and Hooten 2015). Bayesian p-values can range from 0 to 1, with values > 0.05 and < 0.95 indicating an adequate adjustment of the model to the data.

Once we had verified that the fitted model was suitable for inference, we derived the differences in the means of each element at each depth in each forest type as (β value at a given depth in native forests - β value at a given depth in invaded forests). This approach produces a score that is negative when the mean value of an element is higher in invaded forests, positive if it is higher in native forests, and zero if there is no difference between forest types. To facilitate the interpretation of the results, we estimated

the proportion of times these comparisons between forest types were consistently positive or negative, akin to *p*-values in frequentist statistics. Low values of these proportions (e.g., < 0.05) will indicate a clear difference between the means being compared. We report the mean, standard deviation, and 95% credible intervals of all parameters. The annotated R scripts for fitting the Bayesian models are available in the Appendix.

Results

Our statistical analyses showed that chemical and physical properties changed between native and invaded forests, with differences mediated by soil depth (Table 1). The most notable change was in P concentrations, which increased on average 315% in the deepest soil layer (31–50 cm) of invaded forests, followed by a 42% mean increase in the intermediate soil layer of invaded forests relative to native forest (11–30 cm) (Table 1, Fig. 2). In contrast, K^+ and Mg^{2+} concentrations were lower in invaded than in native forests. These differences became more pronounced with soil depth (Table 1, Fig. 2). Na^+ followed a similar pattern, albeit with a smaller magnitude (Table 1, Fig. 2). CEC and Ca^{2+} decreased with increasing soil depth. Still, only Ca^{2+} was affected by forest type in the intermediate soil layer, with a slight increase in the invaded forest (Table 1, Fig. 2).

C and N concentrations showed minor differences between invaded and native forests, and these differences were not consistent across soil layers. C increased in invaded forests, with differences becoming more pronounced from the upper to the intermediate layer. On the other hand, N showed the opposite pattern: it increased in the upper layer, but it decreased slightly in the intermediate layer in invaded forests compared with native ones (Table 1, Fig. 2). Bulk density was higher in the invaded forest. Although bulk density increased with soil depth in both forest types, the magnitude of the differences between forests remained similar across all depths (Table 1, Fig. 2). In contrast, pH exhibited similar values across both forest types and all soil depths, with minor differences that could be attributed to measurement error (Table 1, Fig. 2).

Table 1: Estimated mean, standard deviation, and 95% credible intervals of soil properties by forest type and depth, proportion of times these comparisons between forest types were consistently positive (Pr > 0) or negative (Pr > 0). Differences between the means in native and invaded forests were derived from our Gamma model. Green rows indicate properties that decreased in invaded forests, while grey rows indicate properties that increased in invaded forests.

Discussion

Our results reveal that glossy privet invasions alter both the chemical and physical properties of Yungas mountain forest soils across the soil profile. Yet, these changes were variable in magnitude and direction, with invaded forests exhibiting increases in some properties and decreases in others compared to native forests. Notably, invasion-related differences were detected down to 50 cm, in the

deepest layer analysed, highlighting the importance of assessing soil properties beyond the surface level when studying the impacts of invasive tree species.

The increase in P availability in invaded forests may be explained by increased phosphatase activity (Aragón et al. 2014b). Similar patterns in other invaded systems have been attributed to enhanced root exudation that mobilises P and/or an increase in P-solubilising bacteria (Wang et al. 2021; Wu et al. 2025). For instance, INNS may overcome P-limitation by reshaping the soil microbiome to favour P-mineralising taxa, thereby increasing available P fractions through both biochemical (phosphatase) and chemical (gluconic acid/carboxylates) pathways (Yu et al. 2025). The decline in exchangeable cations such as K^+, Mg^{2+}, and Na^+, most of which are important for soil fertility and plant physiology (Guerra et al. 2022), may result from strong nutrient uptake, supported by elevated enzymatic activity and efficient nutrient resorption in invaded forests (Ostertag and Verville 2002; Ehrenfeld et al. 2005; Aragón et al. 2014a). Additionally, decreases in Na^+ may have functional implications, as Na^+ can partially substitute for K^+ under conditions of K^+ limitations for some plant species (Maathuis 2014).

Additionally, soil compaction, measured by bulk density, showed the greatest difference in the upper portion of the soil in invaded forests and decreased with depth. Higher soil bulk density in invaded forests represents another factor that potentially limits native plant establishment. Compacted soils could affect plant establishment and development because it hinder root penetration, reduce oxygen, nutrient movements, and water percolation (Peralta Ogorek et al. 2025). In consequence, soils of invaded forests are drier and show low nutrient concentrations (Zamora Nasca et al. 2014; Whitworth-Hulse et al. 2023).

Carbon increased slightly at the intermediate layer in invaded forests, relative to soils under native forests. Ca^{2+} and N exhibited a small, depth-dependent response to invasion: they increased slightly in the upper layer but decreased in the middle layer. The small increases in C and N differ from those reported in previous analyses in the same study area (Aragón et al. 2014b), which may reflect either methodological differences or temporal or seasonal effects (Sardans et al. 2017). More broadly, the increase in soil C and N has been identified as a global trend in plant-invaded ecosystems and is attributed to faster nutrient cycling in those environments (Sardans et al. 2017). In our case, these changes may be associated with faster decomposition rates of glossy privet litter relative to native species, as well as increased decomposition enzyme activity in invaded forests (Aragón et al. 2014b, b).

Although glossy privet invasion altered several soil chemical properties, soil pH and CEC remained stable across soil depths. This suggests that glossy privet invasion modified nutrient pools and their vertical distribution in the soil without substantially affecting the soil's overall buffering capacity or ion exchange potential.

In conclusion, our results support the role of the glossy privet as an invasive ecological engineer, affecting strongly the below-ground structure and processes of the subtropical mountain forest in Northwestern Argentina (Fernandez et al. 2017, 2020). Remarkably, the strong differences documented in the deeper soil layer measured (30–50 cm below ground) highlight that studies restricted to the

topsoil layer could underestimate the belowground invasion impacts. These below-ground invasion effects can affect native regeneration, leading to divergence from the native community after INNS control (Corbin and D'Antonio 2012; Cequinel et al. 2018). In consequence, additional actions to INNS control should be considered to enhance soil quality for restoration. Our findings call for a better integration of deep soil monitoring into management protocols to detect persistent invasion legacies in soils and guide a holistic targeted restoration.

Declarations

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Competing 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.

Author Contributions

Priscila Ana Powell: Conceptualisation, Methodology, Validation, Investigation, Resources, Data Curation, Writing- Original Draft, Writing-Review & Editing, Visualisation, Supervision, Project administration. Pablo García-Díaz: Conceptualization, Methodology, Software, Validation, Formal Analysis, Data Curation, Writing- Original Draft, Writing-Review & Editing, Visualisation, Funding acquisition; Roxana Aragón: Conceptualisation, Investigation, Writing- Original Draft, Writing-Review & Editing. Natalia Banegas: Methodology, Validation, Investigation, Resources, Data Curation, Writing -Original Draft, Writing-Review and editing. David Burslem: Conceptualisation, Methodology, Project administration, Funding acquisition. Romina Fernández: Conceptualisation, Writing- Original Draft, Writing- Review and editing, Visualisation. Florencia Yannelli: Conceptualisation, Writing- Review and editing, Visualisation. Lía Montti: Conceptualization, Methodology, Writing-Original Draft, Writing -Review and editing, Visualisation.

Data Availability

The dataset generated during the current study is available in the EIDC REPOSITORY (Powell et al. 2023).

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Table

Table 1 is available in the supplementary files section

Figures

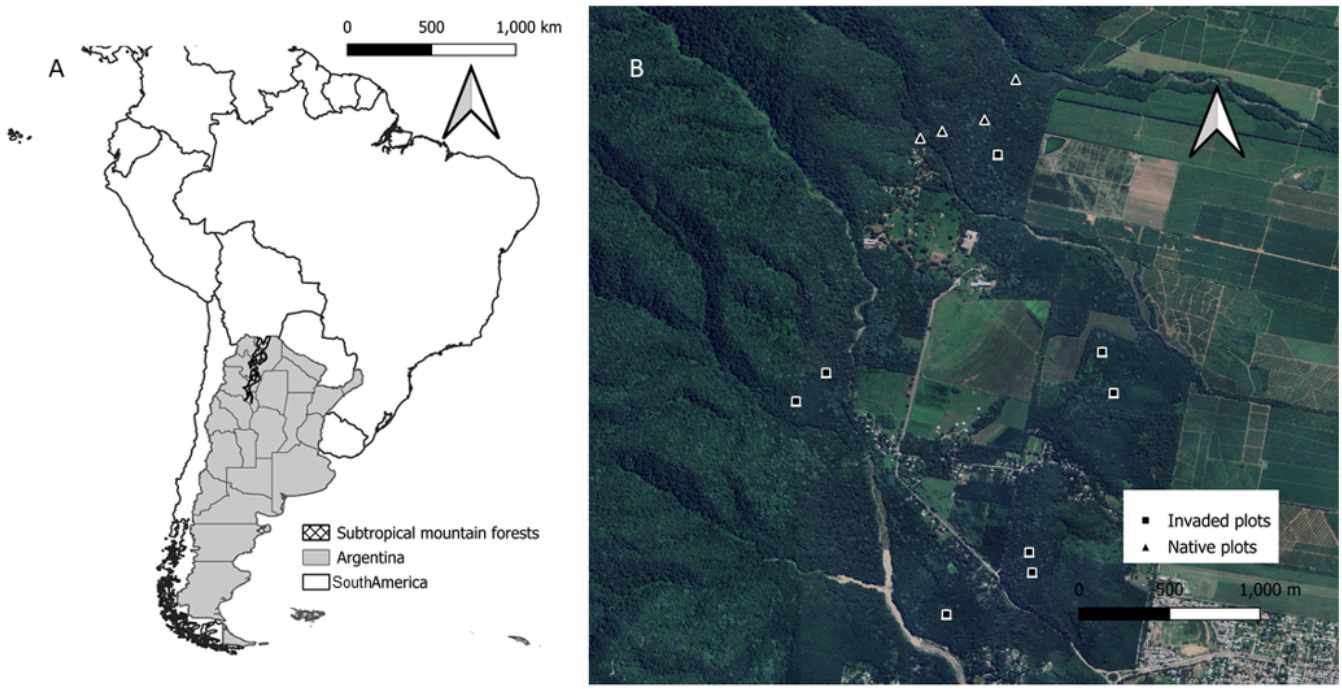

Figure 1

Study area. A. Distribution of Yungas subtropical mountain forests in Argentina (according to Olson et al. 2001). B. Location of our forest plots used to assess the effects of *L.lucidum*invasion on soil characteristics.

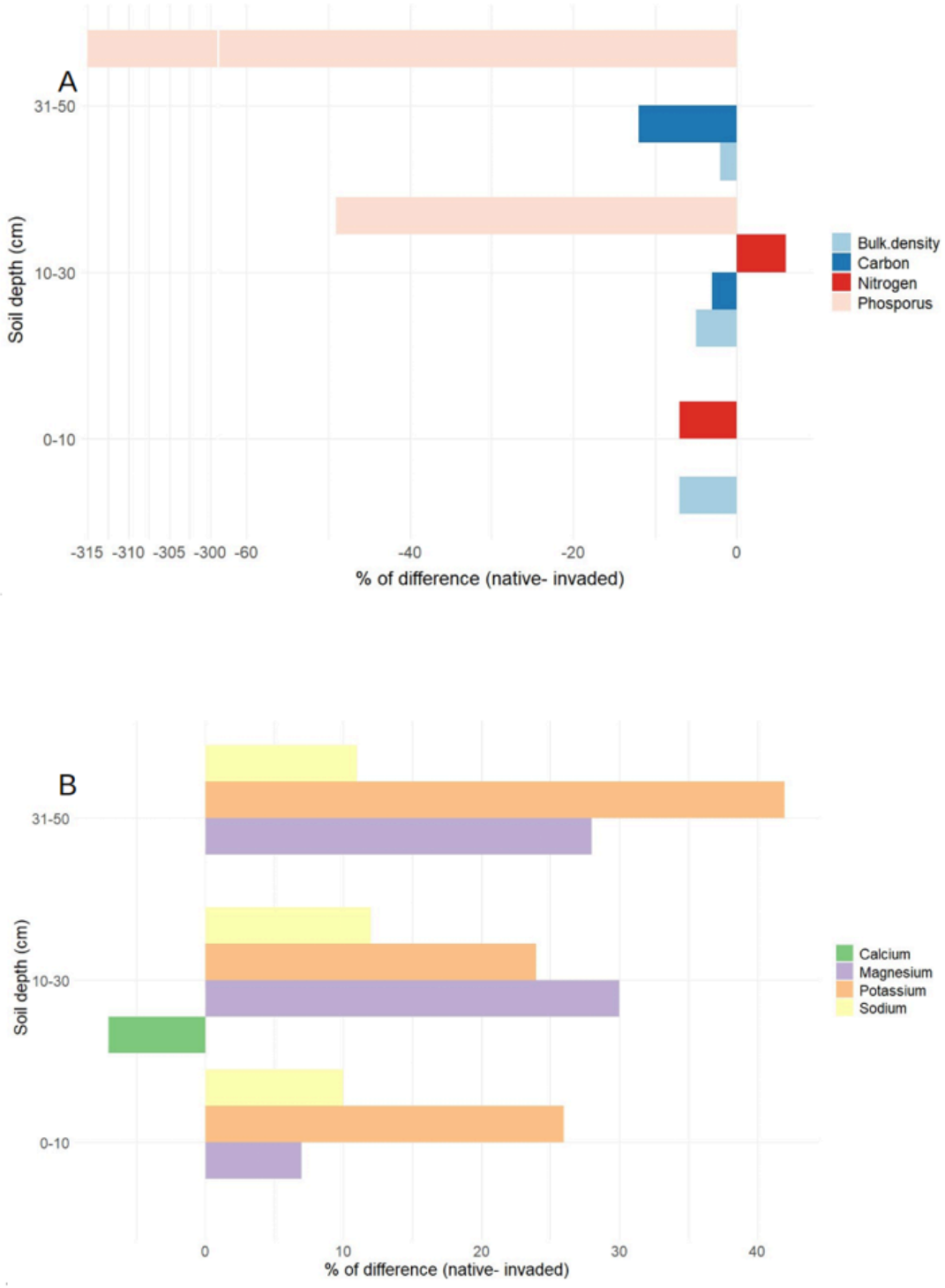

Figure 2

Percentage of differences in soil properties (Native minus Invaded, and considering the value of the soil property of Native forest as 100%) for the different soil layers. We present only important differences, defined as those for which the 95% credible interval did not overlap zero or overlapped it marginally. A- Bulk density, total carbon, total nitrogen and total phosphorus, B- Cations (Calcium, magnesium, potassium, sodium).

Supplementary Files

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

- Table1.xlsx
- M1CarbonSoilHMCGammaRegression.r
- M2NitrogenSoilHMCGammaRegression.r
- M3CalciumSoilHMCGammaRegression.r
- M4MgSoilHMCGammaRegression.r
- M5NaSoilHMCGammaRegression.r
- M6KSoilHMCGammaRegression.r
- M7phSoilHMCGammaRegression.r
- M8CECSoilHMCGammaRegression.r
- M9BDSoilHMCGammaRegression.r