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Worldwide comparison of carbon stocks and fluxes between native and non-native forests

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ABSTRACT

Climate change is one of the main challenges that human societies are currently facing. Given that forests represent major natural carbon sinks in terrestrial ecosystems, administrations worldwide are launching broad-scale programs to promote forests, including stands of non-native trees. Yet, non-native trees may have profound impacts on the functions and services of forest ecosystems, including the carbon cycle, as they may differ widely from native trees in structural and functional characteristics. Also, the allocation of carbon between above- and belowground compartments may vary between native and non-native forests and affect the vulnerability of the carbon stocks to disturbances. We conducted a global meta-analysis to compare carbon stocks and fluxes among co-occurring forests dominated by native and non-native trees, while accounting for the effects of climate, tree life stage, and stand type. We compiled 1678 case studies from 250 papers, with quantitative data for carbon cycle-related variables from co-occurring forests dominated by native and non-native trees. We included 170 non-native species from 42 families, spanning 55 countries from all continents except Antarctica. Non-native forests showed higher overall carbon stock due to higher aboveground tree biomass. However, the belowground carbon stock, particularly soil organic carbon, was greater in forests dominated by native trees. Among fluxes, carbon uptake rate was higher in non-native forests, while carbon loss rate and carbon lability did not differ between native and non-native forests. Differences in carbon stocks and fluxes between native and non-native trees were greater at early life stages (i.e. seedling and juvenile). Overall, non-native forests had greater carbon stocks and fluxes than native forests when both were natural/naturalised or planted; however, native natural forests had greater values for the carbon cycle-related variables than plantations of non-native trees. Our findings indicate that promoting non-native forests may

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increase carbon stocks in the aboveground compartment at the expense of belowground carbon stocks. This may have far-reaching implications on the durability and vulnerability of carbon to disturbances. Forestry policies aimed at improving long-term carbon sequestration and storage should conserve and promote native forests.

Key words: carbon cycle, carbon flux, carbon pool, carbon stock, exotic species, forest carbon, tree plantations, introduced species, native species, non-native species.

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I. INTRODUCTION

Forests play a pivotal role in the global carbon cycle and provide multiple services to society (Pan *et al.*, 2011). National and international agreements on climate change mitigation require an understanding of the capacity of forests to act as carbon sinks. Plants take up CO_2 and reduce it to carbohydrates, which constitutes the basis of ecosystem primary production. Part of this production (e.g. leaves and fine roots) may return rapidly to the atmosphere after being oxidised by consumers (herbivores, decomposers) to obtain energy. But another part may be stored long term in long-lasting biomass, such as wood. In addition, the forest soil – including roots, soil biota, and the soil organic carbon – may store high quantities of carbon, accounting for up to two-thirds of the carbon stock in forest ecosystems (Whitehead, 2011; Ruiz-Peinado *et al.*, 2017). Given the key role of forests as natural carbon sinks, administrations worldwide have launched broad-scale programs to promote forests, such as the European '3 Billion Tree Planting Pledge for 2030', the 'Great Green Wall' of Africa, the 'Grain for Green Programme' of China, or the 'One Billion Trees Programme' of New Zealand. Some of these programs promote both native trees (NTs) and non-native trees (NNTs). Yet, the relative abilities of NTs and NNTs to support native biodiversity and provide ecosystem services, including climate regulation, may differ widely (Castro-Díez *et al.*, 2019*a*).

NNTs have been introduced worldwide to promote fundamental services, such as timber provision, erosion control, soil fertility, and ornamental value (Brundu & Richardson, 2016; Castro-Díez *et al.*, 2019*b*; Lázaro-Lobo *et al.*, 2023*a*). On many occasions, NNTs naturalise and form new forests within the introduced regions (Brundu & Richardson, 2016). Given that NNTs may differ from NTs in structural and functional characteristics, the introduction and naturalisation of NNTs may have a profound impact on the functions and services of forest ecosystems, including nutrient cycling, decomposition rate, and carbon sink capacity, among others (Castro-Díez *et al.*, 2019*b*; Lázaro-Lobo *et al.*, 2023*a*). Many NNTs have been introduced for their rapid growth rate (Brundu & Richardson, 2016; Pötzelsberger *et al.*, 2020), an attribute used by some stakeholders to claim NNT forests as efficient carbon sinks (Ennos *et al.*, 2019; Nuñez *et al.*, 2021). However, the forest carbon sink efficiency in the long term depends on other factors beyond growth rate that are often neglected, such as lability of tree biomass or the amount of organic carbon stabilised in the soil (Ennos *et al.*, 2019; Suryaningrum *et al.*, 2022; Lázaro-Lobo *et al.*, 2023*b*). Several studies suggest that stands dominated by NNTs store more carbon in the aboveground biomass, but less in the soil (Wu *et al.*, 2020; Zarafshar *et al.*, 2020), and have more labile carbon stocks than NT forests (Suryaningrum *et al.*, 2022), but evidence is scattered across a few vegetation systems and climate types (Silva *et al.*, 2009; Paritsis *et al.*, 2018). Additionally, the potential superiority of NNTs over NTs in terms of carbon uptake rate may be modulated by the intensity of abiotic filters (e.g. temperature and water stress), being potentially higher in climates that allow for greater productivity (Martin, Newton & Bullock, 2017; Lázaro-Lobo *et al.*, 2023*b*). However, a holistic assessment of the multiple components of carbon sink efficiency across NT and NNT forests and across different contexts is lacking in the literature.

Research on carbon storage and sequestration has increased during the last few years, mainly in relation to global climate change (Gómez-García, 2020; Huang *et al.*, 2020). Previous research suggested that non-native introduced plants increase carbon stocks and primary production (Liao *et al.*, 2008; Vilà *et al.*, 2011; Xu *et al.*, 2022). However, such studies are generally conducted with invasive plants (a subset of non-native plants) and include species with different growth forms (e.g. trees, shrubs, herbs, and grasses). The heterogeneity of impacts of non-native plants on the carbon cycle may be explained by various factors, including species characteristics, abiotic conditions of the recipient environments, species life stages, and land use (Liao *et al.*, 2010; Martin *et al.*, 2017; Hua *et al.*, 2022; Lázaro-Lobo *et al.*, 2023*b*; Romero-Blanco *et al.*, 2023). Thus, generalising about the effects of non-native plants on carbon storage and sequestration is challenging (Martin *et al.*, 2017). Castro-Díez *et al.* (2019*b*) reviewed the effects of NNTs on ecosystem services, finding that NNTs increased climate regulation (*via* carbon uptake) and soil formation, which included several variables related to carbon storage and sequestration. However, there is no global synthesis quantifying the differences in above- and belowground carbon stocks and fluxes between NNT and NT forests, information which is crucial to developing forestry policies seeking to promote forest carbon sinks and their stability in the long term.

In this study, we conducted a global meta-analysis to provide concrete and empirical insights on the relative capacity of co-occurring NT and NNT forests to take up atmospheric carbon and store it in different compartments of the ecosystem. We used a comprehensive set of variables related to carbon stocks and fluxes, while accounting for the effect of climate, life stage, and stand type, to explain heterogeneity across case studies. Our general hypothesis was that NT and NNT forests differ in their carbon cycle. We expected that forests dominated by NNTs would store more carbon in aboveground biomass but less in the soil than NT forests, due to their early successional nature and rapid growth. We also expected NNT forests to have a faster carbon cycle, including faster CO_2 uptake, but also faster return of carbon to the atmosphere due to greater carbon lability. Additionally, we examined whether the potential differences in the carbon cycle between NT and NNT forests were associated with the climate of the area where the study was conducted, the age of the trees, and the stand type (planted *versus* natural or naturalised). We expected greater differences in climates that allow for greater productivity and in early life stages, when trees grow faster (i.e. seedling and juvenile). We also expected natural forests to have greater carbon stocks than tree plantations (at least in the belowground compartment) due to carbon losses associated with soil and stand management in plantations (Jandl *et al.*, 2007; Liao *et al.*, 2010; Lewis *et al.*, 2019).

II. MATERIALS AND METHODS

(1) Selection of variables

Based on the literature, we selected a set of quantitative variables that were associated with the forest carbon cycle, including carbon stocks and fluxes, and that allowed a comparison between NT and NNT forests (Table 1). A forest was considered as native or non-native when the dominant tree species were native or non-native, respectively, in the region where the study took place. This information was provided by the source articles. We included direct measurements of the carbon cycle (i.e. target variables; Table 1). However, when these were not provided by the article, we searched for related variables (i.e. proxy variables) that may be used as substitutes for the target variables. For example, litter C:N is a proxy for litter decomposition rate; if the article provided both litter C:N and litter decomposition rate, we only used the latter. All the target and proxy variables related to carbon stock and flux used in this study are shown in Table 1. Some of the variables were functional traits of the dominant forest-forming

Table 1. List of target variables and proxies for target variables grouped by categories.

Carbon cycle	Response variable category	Target variable[a]	Proxies for target variable[b]
Carbon stock	Total carbon stock	Total carbon stock +	Total biomass +
	Aboveground carbon stock (stem, branches); we do not include leaves as they have a relatively short lifespan	Aboveground carbon stock +	Aboveground biomass +
			Tree basal area +
			Tree DBH (diameter at breast height) +
			Tree height +
			Understory carbon +
	Belowground live carbon stock (in plant, fungal, and microbial tissues)	Belowground carbon stock in living tissues +	Belowground biomass +
		Root carbon +	Root biomass +
			Root length +
			Root depth +
			Root diameter +
		Microbial carbon stock +	Microbial biomass +
		Fungal carbon stock +	Fungal biomass +
			Hyphal length +
	Belowground soil carbon stock (in soil)	Soil organic carbon +	Soil organic matter +
	Forest floor carbon stock	Litter carbon stock +	Litter mass +
			Litter thickness/Litter depth +
		Dead wood carbon stock +	Dead wood mass +
Carbon flux	Carbon uptake rate	Carbon uptake rate +	Biomass increase +
			Stem growth rate +
			Root growth rate +
			Relative growth rate (RGR) +
		Soil organic matter increment rate +	
		Litter production rate +	
	Carbon loss rate	Carbon loss rate +	Biomass loss rate +
		Tree/stand respiration rate +	Leaf respiration rate +
			Soil respiration rate +
		Litter decomposition rate +	Litter mass remaining −
			Litter C:N −
			Litter N:C +
			Litter C:P −
			Litter P:C +
			Litter lignin content −
			Litter N:lignin +
			Litter lignin:N −
		Wood decomposition rate +	
		Organic matter decomposition rate +	Organic matter mineralisation rate +
	Carbon lability	Tree longevity −	
		Wood durability −	Wood density −
		Mortality after disturbance (only in field studies) +	Survival after disturbance (only in field studies) −

[a] The sign indicates whether the variable contributes to carbon stock or flux positively (+) or negatively (−).
[b] These variables are correlates or proxies of the target variable. Proxy variables were used when the article did not provide the target variable. If the article provided multiple proxy variables for a given target variable, we selected the most integrative one (based on expert knowledge). However, when we had no clear arguments to select one proxy variable over another, we retained more than one.

tree species (e.g. tree height, root biomass, relative growth rate, etc.), whereas other variables represented multiple properties and processes of the forest ecosystem (e.g. soil organic matter, litter mass accumulated in the forest floor, soil respiration, etc.).

There is a wide variety of techniques to estimate carbon stocks and fluxes. We included data on the carbon cycle generated using different methods. Some of these methods involve destructive harvesting of biomass (e.g. tree harvest, removal of soil organic matter, etc.), which is generally costly and complex (Ruiz-Peinado, Montero & del Rio, 2012). Other methods rely on indirect non-destructive estimations of carbon stocks and fluxes. For example, carbon stored in tree biomass may be quantified using allometric equations, which generally consider the diameter at breast height and the total height of the trees (Ameztegui, Rodrigues & Granda, 2022). These indirect methods are more prone to miscalculate the amount of carbon than direct ones, but they are more cost efficient and may be applied to larger spatial scales.

(2) Literature search

We conducted a comprehensive search for relevant articles comparing carbon stocks and fluxes between NT and NNT forests on the ISI *Web of Knowledge* and *Scopus* databases on 31 January 2022. We used the following query string and searched in the title, abstract, and key words article sections: '(exotic* OR alien* OR non-native* OR non-indigenous OR introduced OR naturalised OR naturalized OR neophyte* OR kenophyte* OR adventive* OR adventitious OR invas*) AND (native* OR indigenous OR autochthonous OR apophyte*) AND (tree* OR forest* OR wood* OR stand* OR thicket* OR grove* OR timber* OR coppice* OR copse* OR plantation* OR planted) AND (carbon OR "C" OR biomass OR mass OR product* OR (basal area*) OR (basal diameter*) OR DBH OR (organic matter*) OR grow* OR RGR OR mortalit* OR respir* OR decompos* OR litter* OR (dead AND wood*) OR debris OR detritus OR longevit* OR (densit* AND wood*) OR (persistence AND wood*) OR (durability AND wood*))'. We then screened the reference lists from all retrieved publications to include other potentially relevant articles in our research. This initial search provided a total of 19,537 potentially relevant articles (Fig. 1).

(3) Article screening and eligibility criteria

We examined each article retrieved above to assess its adequacy for our meta-analysis. First, we filtered out articles that were not quantitative comparisons of the variables shown in Table 1. This resulted in an initial set of 607 potentially suitable articles to conduct the meta-analysis (Fig. 1). Then, we set four selection criteria for data inclusion: (*i*) we checked whether the dominant NT and NNT species examined were trees, consulting different databases (e.g. BGCI GlobalTreeSearch; https://tools.bgci.org/global_tree_search.php) and USDA plants database (https://plants.usda.gov/). Trees were defined as perennial woody plants with many secondary branches supported clear of the ground on a single main stem or trunk with clear apical dominance (including palms) (Richardson & Rejmánek, 2011; Castro-Díez *et al*., 2019*b*). (*ii*) The NNTs were not archaeophytes (i.e. species introduced before 1492) because such species could not be clearly categorised as NT or NNT. (*iii*) The articles evaluated co-occurring NTs and NNTs (i.e. those occupying nearby areas or sharing environmental conditions, according to the criteria of the articles' authors). (*iv*) The articles compared trees/forests of similar age. We retained 317 articles after applying these criteria (Fig. 1).

(4) Data extraction and filtering

From the selected articles, we extracted one or more case studies (i.e. a quantitative comparison of the target (or proxy) variables between co-occurring NTs and NNTs; see online Supporting Information, Appendix S1). Data were extracted either from the main text, tables, and/or figures. Figures were digitised using WebPlotDigitizer, ImageJ, or TechDig, before data extraction. We ensured that each case study compared variables collected in the same way between NNT and NT forests (e.g. data collected at the same soil depth or volume). In some articles, several NNT forests were compared against a single NT forest or the reverse; in this case, each NNT–NT comparison was considered as a separate case study.

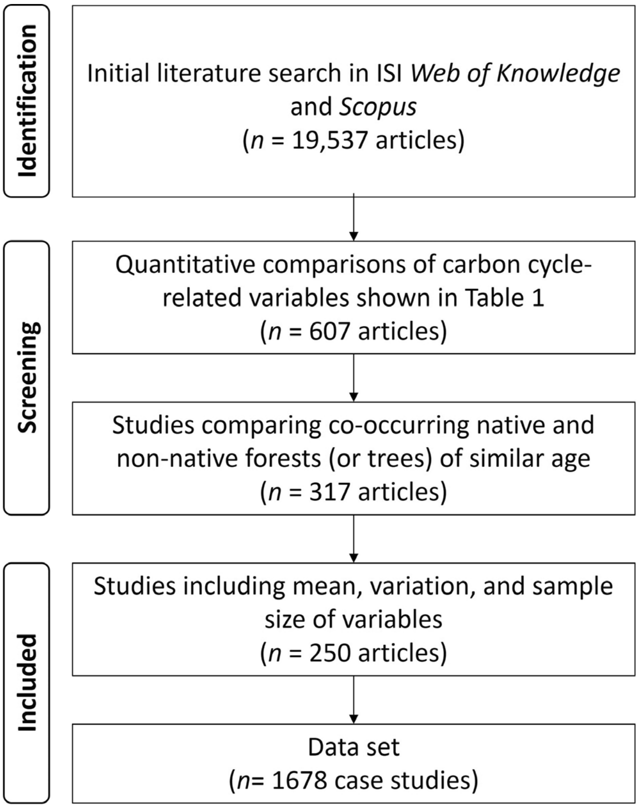

Fig. 1. Flow diagram explaining the filtering process from the initial literature search to the final number of articles and case studies.

For each case study, we extracted the reference of the publication, the name of the dominant NT and NNT species, the mean, the statistical dispersion (all measurements were converted to SD), and the sample size values for NNT and NT forests. Case studies where any of these variables were absent were discarded. This reduced the number of articles to 250 (Fig. 1; Appendix S2). To explain heterogeneity across case studies, we extracted a set of additional variables (moderators, see Table 2). The three first moderators hierarchically classified the variables related to the carbon cycle. First, they were classified into carbon stocks and carbon fluxes (variable category 1). Then, each category was subdivided (variable category 2): carbon stocks were divided into above and belowground stocks, forest floor stocks (litter and dead wood), and total carbon stock. Carbon fluxes were

Table 2. Variables (moderators) characterising each case study to be used in a structured meta-analysis to explain heterogeneity of effect sizes. NNT, non-native tree; NT, native tree.

Structure variable	Categories	Data source
Variable category 1	Carbon flux Carbon stock	Source study
Variable category 2	Carbon lability Carbon loss rate Carbon uptake rate Belowground carbon stock Forest floor carbon stock (litter/dead wood) Aboveground carbon stock Total carbon stock	Source study
Variable category 3	Carbon lability Carbon loss rate Carbon uptake rate Belowground soil carbon Belowground live carbon Forest floor carbon stock (litter/dead wood) Aboveground carbon stock Total carbon stock	Source study
Climate type (Köppen-Geiger)	Arid Warm temperate fully humid (Cf) Warm temperate summer dry (Cs) Warm temperate winter dry (Cw) Equatorial Snow	Geographical coordinates were obtained from each case study and subsequently used to obtain the Köppen-Geiger climate type
Study type	Controlled (laboratory, greenhouse, common garden) Field (no control over environmental variables) Mixed (field study manipulating one or more environmental variables)	Source study
Tree age (for NT and NNT)	Seedling (<1 year) Juvenile (1–10 years) Adult (>10 years)	Source study
Stand type (for NT and NNT)	Planted Natural or naturalised	Source study

divided into carbon lability, carbon loss rate and carbon uptake rate. An additional third subdivision (variable category 3) separated belowground carbon stock into belowground live carbon [carbon in living tissues, either roots, soil fauna, or microorganisms (bacteria and fungi)] and belowground soil carbon (carbon in the soil organic matter). The fourth moderator was the Köppen-Geiger climate zone where the studies were conducted. To obtain these values, we first retrieved the geographic coordinates of the sites of the source articles (either from the source paper or by searching in *Google Earth*). Then, we used the updated world map of the Köppen-Geiger climate classification (http://koeppen-geiger.vu-wien.ac.at/present.htm; Kottek *et al.*, 2006) to extract the main climates corresponding to the coordinates (equatorial, arid, warm temperate, and snow). Given that the majority of the articles fell into the category 'warm temperate', this was further divided into its three subcategories: fully humid, summer dry, and winter dry. The fifth moderator was the study type, which was classified into controlled (common garden studies controlling for environmental variables, or studies conducted in the laboratory or greenhouse), field (no control over environmental variables), or mixed (field studies in which one or more environmental variable was manipulated). The sixth moderator was the stand/tree age, which was divided into seedling (<1 year), juvenile (1–10 years), or adult (>10 years). Finally, the seventh moderator was the type of tree stand, either planted or spontaneous (natural for NT forest or naturalised for NNT forest).

Once the database was compiled, we performed a final exploration to reduce pseudo-replication. We identified case studies deriving from the same publication and providing the same variable or several variables in the same response variable category (see Table 1). For those cases, we made a reasoned decision on whether to keep all case studies or select any of them. For instance, when an article evaluated the effect of different treatments (e.g. N concentrations) on a target variable (e.g. tree growth), we collected data from the control treatment (the one that better represented natural conditions; e.g. no N addition); when a response variable was measured at different times, we considered the final measurement in time-series data (e.g. 10- instead of 5-year-old trees) or the season of maximum activity in annual series (e.g. spring rather than winter). When more than one variable was provided for the same target variable, we selected the most integrative one (e.g. if microbial biomass and belowground biomass were available as proxies for belowground live carbon stock, we selected belowground biomass; when tree height and tree diameter at breast height (DBH) were available as proxies for aboveground carbon stock, we selected DBH). Finally, we removed 79 case studies with variance values close to zero, either due to extremely large replication (e.g. LIDAR studies with millions of pixels as replicates), or pseudoreplication (i.e. several subsamples obtained from the same true replicate). The final filtering resulted in a data set of 1678 case studies from 250 published articles (Fig. 1, Appendix S1).

(5) Data analyses

(*a*) *Computation of mean effect sizes*

The effect sizes were derived from experimental and observational comparisons between NNT and NT forests (i.e. case studies). For each case study, we computed a standardised effect size with Hedges' *d* (Borenstein *et al.*, 2009) as the difference of mean variable values between NNT and NT forests, weighted by the number of replications and by the inverse of the variance. Hedges' *d* was computed using the *escalc()* command of the R package *metafor 4.6–0* (Viechtbauer, 2010). When the variable was negatively related to the response variable category (see Table 1), we changed the sign of Hedges' *d*. For example, the lignin:N ratio of the litter usually correlates negatively with litter decomposition rate and thus to carbon loss rate. Therefore, if the lignin:N ratio is larger in the NNT than in the NT forest, the NNT forest will have a positive effect size on this variable, but a negative effect on carbon loss rate. A positive value of *d* indicates that the variable category has a larger value in the NNT forest than in the NT one, while a *d* not different from zero indicates similar values between NNT and NT forests.

(*b*) *Meta-analysis models*

Meta-analysis databases on ecological systems usually present a great intrinsic variability and non-independence among case studies (Noble *et al.*, 2017). Accordingly, our database has several sources of non-independence among study cases: (*i*) shared study identity: the article provides values for the same NNT–NT comparison obtained from independent sampling units (problem #1); (*ii*) shared control/multiple control: when a single article provides values for a single NNT forest but several NT forests and the reverse, so that comparisons between every NNT–NT pair are possible (problem #2); and (*iii*) multiple outputs: the article provides more than one variable for the same response variable category and none of these is better suited than others (problem #3). Problem #1 induces dependency among effect sizes, but not among sampling variances, while problems #2 and #3 induce dependency also among sampling variances (Nakagawa *et al.*, 2023).

Non-independence may be dealt with by selecting one case study among the set of non-independent ones or by aggregating them into a single one (Borenstein *et al.*, 2009). However, this reduces the sample size and the statistical power. Alternatively, a multi-level meta-analysis model (MLMA) explicitly includes different hierarchical levels of random and fixed factors, similarly to mixed models (Konstantopoulos, 2011; Nakagawa & Santos, 2012). Our MLMA includes two levels of random variation [publication (identified by its bibliographic reference) and case study (identified by a correlative number nested within an article)] and none or one fixed factor (moderator) among those described in Table 2. This method solves the problem of dependency among effect sizes (problem #1 above), but not the problem of dependency among sampling variances (problems #2 and #3). To deal with the latter issue, we explicitly modelled this dependence by constructing a variance–covariance (VCV) matrix with sampling variances in its diagonal and sampling covariance in its off-diagonal (Nakagawa *et al.*, 2023). Given that exact covariance cannot be calculated in most cases, we fixed it at 0.5 and 0.8 (more conservative) and ran the MLMA twice (Nakagawa *et al.*, 2023).

MLMA models were fitted using the *rma.mv()* function in *metafor 4.6–0* (Viechtbauer, 2010; Senior *et al.*, 2016), with the method 'restricted maximum likelihood' (REML) to estimate model parameters. We first fitted the MLMA without moderators to obtain a grand mean effect size (Hedges' *d*) of NNT effects on carbon-cycle variables ±95% confidence intervals (CI) and a two-tailed parametric test indicating whether Hedges' *d* statistically differed from zero. To assess the heterogeneity of effect sizes across case studies, we used the estimated variance that cannot be attributed to sampling error, both in absolute (τ^2) and relative value (I^2) (Higgins *et al.*, 2003; Nakagawa *et al.*, 2023). Given the multi-level structure of our meta-analysis, both τ^2 and I^2 were partitioned into among-study variance (τ^2_{study} and I^2_{study}) and residual variance (τ^2_{res} and I^2_{res}) (Nakagawa & Santos, 2012; Senior *et al.*, 2016; Harrer *et al.*, 2021). Second, to explain heterogeneity, we fitted independent MLMAs with each of the moderators considered in Table 2 (structured MLMAs). In this case, we obtained: (*i*) the grand mean effect size ±95% CI for each moderator category, along with a two-tailed parametric test indicating whether each grand mean statistically differed from zero; (*ii*) an *F* test of moderators, indicating whether there were significant differences between groups; and (*iii*) the estimated components of variance among studies and residuals (τ^2_{study} and τ^2_{res}, respectively), and the proportion of total variation attributed to each component (I^2_{study} and I^2_{res}) (Borenstein *et al.*, 2009; Nakagawa & Santos, 2012; Harrer *et al.*, 2021). We did not include more than one moderator in each MLMA because the number of case studies in categories resulting from combinations of two or more moderators was often too small. However, to explore potential interaction between two significant moderators, we repeated the analysis of one moderator in the categories of the other with sufficient replication.

Differences in the fit across MLMAs were assessed using Akaike information criterion corrected for small sample sizes (AIC_c), with the more complex MLMA being favoured if it had an AIC_c that was two points lower than that of the less complex one (Senior *et al.*, 2016). This was particularly relevant to compare the models performed with variable categories 1, 2 and 3, as they represent three nested criteria for categorising the carbon cycle variables. All analyses were conducted using R software (version 4.3.1). The R code used to fit the MLMA models can be found in Appendix S3.

(*c*) *Publication bias*

Publication bias in data sets obtained from the literature may result either from the selective publication of articles finding larger effects over those with small effects ('small-study effect'), and/or from the earlier publication of studies with larger or more significant effects ('decline effect' or 'time-lag bias') (Borenstein *et al.*, 2009; Nakagawa *et al.*, 2023). If a small-study effect exists, we can expect that studies with low replication or large standard error of effect sizes are only published if they provide large effect sizes. With the decline effect, we can expect effect sizes to get closer to zero over time, as studies reporting small effect sizes take longer to be published.

To test for small-study effect, we visually explored asymmetry in a funnel plot, with effect sizes on the x-axis and standard error of effect sizes on the y-axis. In the absence of publication bias, this plot is expected to be a symmetrical funnel shape, with a larger dispersion of effect sizes for studies with smaller sample size and large standard errors of effect size (Borenstein *et al.*, 2009).

We performed additional analyses to detect and correct for both types of publication bias. We run a MLMA as explained above, including the variance of effect sizes and the publication year as moderators. A slope significantly different from zero in any of these moderators indicates publication bias (a small-study effect if the variance is significant or decline effect if the publication year is significant). The bias-corrected estimate of the overall effect size was calculated as the intercept of the MLMA. Thus, we first ran a model with only variance as moderator, so its intercept represents the overall effect size corresponding to a sampling error of zero or to an infinite sample size. Then, we ran a model with publication year as moderator, so its intercept represents the overall effect at year 2010 (this year was set as zero for the analysis). Finally, the intercept of the model with the two moderators represents the overall effect size after correcting for both sources of publication bias (Nakagawa *et al.*, 2023).

Given that our data set is expected to show great heterogeneity and that we test for the effects of the moderators of Table 2, we re-ran each structured MLMA adding variance of effect sizes and publication year as moderators. If their slopes do not differ from zero, we can consider that our results are not biased by small-study or decline effects (Nakagawa *et al.*, 2023). The R code used to evaluate publication bias can be found in Appendix S3.

The Preferred Reporting Items for Systematic reviews and Meta-Analyses (PRISMA) statement for this meta-analysis (O'Dea *et al.*, 2021) can be found in Appendix S4.

III. RESULTS

Results obtained with the two approaches (fixing covariances among sampling variances at 0.5 and 0.8) were very similar, although significance tended to be slightly lower with covariance = 0.8. Thus, we present here the results from the less conservative approach (covariance = 0.5). Results from the most conservative approach (covariance = 0.8) are shown in Table S1.

(1) Overview of the full data set

In total, we analysed 250 articles that met all the eligibility criteria, which provided a total of 1678 NT *versus* NNT comparisons (case studies; Appendix S1). Case studies covered 282 NT and 170 NNT forest dominant species (from 83 and 42 families, respectively). The best represented NNT species were *Ailanthus altissima* (81 case studies), *Tectona grandis* (56), *Robinia pseudoacacia* (48), and *Triadica sebifera* (48). Additionally, 16 NNT species were represented by 31–38 case studies: *Pinus patula*, *Eucalyptus globulus*, *Melia azedarach*, *Acer negundo*, *Broussonetia papyrifera*, *Ligustrum sinense*, *Acacia mangium*, *Albizia julibrissin*, *Cinnamomum camphora*, *Firmiana simplex*, *Paulownia tomentosa*, *Pyrus calleryana*, *Sonneratia apetala*, *Ulmus parvifolia*, *Pinus radiata*, and *Quercus rubra* (list arranged from largest to smallest number of case studies). At the other extreme, 27 NNT species were each represented by a single case study, and 74 NNT species by 2–5 case studies (Appendix S1).

There were more case studies regarding carbon flux (981) than carbon stock (697). Among carbon stock variables, aboveground carbon stock was the best represented (368 case studies), followed by belowground carbon stock (225). Regarding carbon flux variables, most case studies measured carbon loss rate (604), followed by carbon uptake rate (208) and carbon lability (169).

Most case studies were conducted in the field (1437), while controlled and mixed experiments were less represented (188 and 48 case studies, respectively). There were more case studies involving adult trees (1061) than juveniles (464) or seedlings (72). Data covered 55 countries from all continents except Antarctica (Fig. 2). Most case studies were conducted in North America (705), followed by Europe (330), Asia (266), and Africa (201). There were fewer case studies in South America (143) and Oceania (33). The warm temperate climate of the Köppen-Geiger climate classification accounted for most case studies (1015), followed by equatorial (282), arid (199), and snow (67) climates. Within the warm temperate

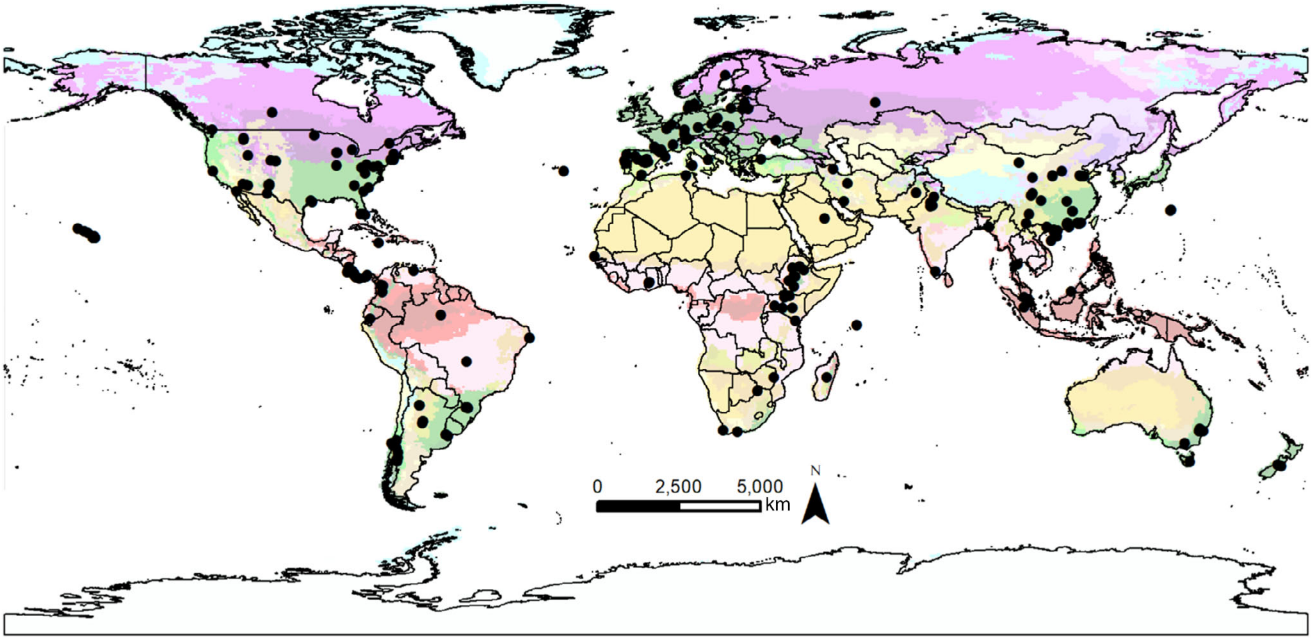

Fig. 2. Global distribution of study sites (black circles) used in this meta-analysis. The colours refer to the different climate types of the Köppen-Geiger climate classification (http://koeppen-geiger.vu-wien.ac.at/present.htm; Kottek *et al.*, 2006).

climate, the subcategory 'fully humid' was the most represented (634 case studies), followed by 'winter dry' (192) and 'summer dry' (189). The polar climate was not represented in our data set.

(2) Results of MLMAs

The simplest MLMA performed with no moderator and covariance among sampling variances fixed at 0.5 indicated that NNT forests have greater values of carbon cycle-related variables than NT forests (grand mean Hedges' *d* effect size = 0.2963, 95% CI = 0.0746 and 0.5180, $P = 0.009$, $n = 1678$, Table 3). The estimated residual variance (τ^2_{res}) was much greater than among studies (τ^2_{study}) (Table 3). A similar result was obtained by fixing covariance among sampling variances at 0.8 (grand mean Hedges' *d* effect size = 0.2612, 95% CI = 0.0469 and 0.4756, $P = 0.017$) (Table S1). Under both approaches, the sum of the two I^2 components (>95%) was indicative of high heterogeneity in the data set and suggests the existence of an underlying structure (i.e. heterogeneous effect sizes in different variable types or situations). Indeed, every MLMA including a moderator as fixed factor showed a lower AIC$_c$ than the MLMA without moderators (Tables 3 and S1).

(*a*) *Effects of response variable categories on the mean effect size*

When variable category 1 (which classifies the response variables between carbon fluxes and stocks) was added as a fixed factor to the MLMA, we found a significant effect of the moderator (see F_M in Tables 3 and S1), with slightly larger mean effect sizes for carbon fluxes than for carbon stocks (Fig. 3A). When variable category 2 (which split carbon fluxes and stocks into smaller categories) replaced variable category 1 as moderator, the significance of the moderator (F_M) increased, and the AIC$_c$ of the model declined (>50 units) despite the larger number of categories (Tables 3 and S1). This was due to the opposite sign of the effect that NNT forests had on aboveground carbon stock (positive), and on belowground carbon stock (negative) (Figs 3B and 4, Tables 3 and S1). Effects of NNT forests on the remaining categories were only significant for carbon uptake rate, which was greater for NNT forests.

The subsequent split of belowground carbon stock between live carbon and soil carbon (variable category 3), also improved the model in terms of AIC$_c$ decline (4 and 3 units for the 0.5 and 0.8 covariance, respectively; Tables 3 and S1). The effect of NNT forests on these two belowground compartments was negative, but only significant for soil carbon (Fig. 3C, Tables 3 and S1).

(*b*) *Effects of climate type on the mean effect size*

Climate type was not related to the NNT effect on carbon cycle variables (Tables 3 and S1). The NNT effect was only significant (and positive) for the equatorial climate type under the two approaches (Tables 3 and S1).

(*c*) *Effects of study type on the mean effect size*

We found a significant influence of the study type only when fixing covariance among study variances at 0.5 and at $\alpha = 0.10$ ($P = 0.052$). NNT effects were only significant in field studies, but not in controlled and mixed studies,

Table 3. Summary results of multi-level meta-analyses (MLMAs) performed with different moderators. Article (publication) and case study nested within article were included as random factors; different moderators were included as fixed factors. For each model we report the number of case studies (*n*) the grand mean effect size (Hedges' *d*) with its 95% confidence intervals (CI inf, CI sup), the significance of the two-tailed test checking for a significant difference of Hedges' *d* from zero, the *F* test of moderators and its significance (F_M; ·, $0.10 > P \geq 0.05$; *, $0.05 > P \geq 0.01$; **, $0.01 > P \geq 0.001$; ***, $P < 0.001$), the estimated variance proportion due to among-study variation (τ^2_{study}) and to within-study variation (τ^2_{res}), as well as the proportion of variance explained by each component (I^2_{study}, I^2_{res}), and the Akaike information index corrected for small samples (AIC_c). The variance–covariance (VCV) matrix, needed to account for non-independence among sampling variances of cases derived from the same study, was calculated setting rho = 0.5.

Moderator	Categories	*n*	Hedges' *d*	95% CI inf	95% CI sup	*P*	F_M	τ^2_{study}	τ^2_{res}	I^2_{study}	I^2_{res}	AIC_c
-	-	1678	0.296	0.075	0.518	0.009	-	1.22	5.13	18.58	78.39	8303.4
Variable category 1	Carbon flux	981	0.328	0.032	0.624	0.030	3.47*	1.23	5.13	18.77	78.20	8284.1
	Carbon stock	697	0.271	−0.003	0.544	0.052						
Variable category 2	Carbon lability	169	−0.060	−0.562	0.442	0.815	9.68***	0.95	5.02	15.39	81.39	8232.5
	Carbon loss rate	604	0.007	−0.354	0.368	0.970						
	Carbon uptake rate	208	0.796	0.386	1.207	<0.001						
	BG carbon stock	225	−0.613	−0.999	−0.227	0.002						
	Forest floor[1]	31	0.199	−0.710	1.107	0.668						
	AG carbon stock	368	1.099	0.748	1.451	<0.001						
	Total carbon stock	73	−0.137	−0.816	0.542	0.692						
Variable category 3	Carbon lability	169	−0.051	−0.554	0.451	0.841	8.73***	0.99	5.01	15.97	80.83	8228.4
	Carbon loss rate	604	0.015	−0.348	0.379	0.935						
	Carbon uptake rate	208	0.801	0.389	1.213	<0.001						
	BG soil carbon	117	−0.866	−1.369	−0.363	0.001						
	BG live carbon	108	−0.328	−0.858	0.202	0.225						
	Forest floor[1]	31	0.199	−0.710	1.107	0.668						
	AG carbon stock	368	1.109	0.755	1.463	<0.001						
	Total carbon stock	73	−0.130	−0.811	0.552	0.709						
Climate type	Arid	199	−0.173	−0.783	0.438	0.579	1.51 ns	1.22	5.11	18.71	78.25	7705.6
	Cf	634	0.378	−0.055	0.811	0.087						
	Cs	189	−0.099	−0.697	0.499	0.745						
	Cw	192	0.213	−0.405	0.830	0.499						
	Equatorial	282	0.554	0.056	1.051	0.029						
	Snow	67	0.273	−0.509	1.056	0.494						
Study type	Controlled	188	0.371	−0.159	0.901	0.170	2.958·	1.23	5.14	18.74	78.24	8267.5
	Field	1437	0.295	0.047	0.543	0.020						
	Mixed	48	0.502	−0.795	1.799	0.448						
Tree age[2]	Seedling (<1 year)	72	1.092	0.265	1.920	0.010	4.18**	1.25	5.28	18.54	78.48	7928.62
	Juvenile (1–10 years)	464	0.447	0.050	0.844	0.028						
	Adult (>10 years)	1061	0.159	−0.149	0.466	0.312						
Stand type	NNT(N)_NT(N)	767	0.423	0.062	0.783	0.022	5.26***	0.85	5.04	14.07	82.67	6890.77
	NNT(N)_NT(P)	21	0.902	−0.462	2.266	0.195						
	NNT(P)_NT(N)	92	−0.874	−1.479	−0.269	0.005						
	NNT(P)_NT(P)	525	0.399	0.060	0.737	0.021						

Abbreviations: BG, belowground; AG, aboveground; Cf, warm temperate fully humid; Cs, warm temperate summer dry; Cw, warm temperate winter dry; NNT, non-native tree; NT, native tree; (N), natural for NTs or naturalised for NNTs; (P), planted.

[1] Forest floor included carbon stored in debris deposited on the forest floor (e.g. litter and dead wood).

[2] Selected studies compared trees/forests of similar age [i.e. seedlings (<1 year), juveniles (1–10 years), or adults (>10 years)].

although this result may be due to greater replication in the former (Table 3; Fig. 5A). This uneven replication may involve a different proportion of case studies on variable categories where NNT forests showed a contrasting effect size (e.g. above- and belowground carbon stocks). Thus, we repeated the analysis separately for each of the three main variable categories (i.e. those with larger replication and the same Hedges' *d* sign: carbon flux, aboveground carbon stock and belowground carbon stock). Results confirmed the tendency of field studies to show larger effect sizes (positive for aboveground carbon stock or negative for belowground carbon stock), although the effect of the moderator was not significant for carbon flux (Table S2).

(*d*) *Effects of tree age on the mean effect size*

On average, effects of NNT forest on carbon cycle variables declined with increasing tree age, being greater in seedlings, followed by juveniles, and not different from zero in adults (Tables 3 and S1; Fig. 5B). To check whether this effect was due to different variable categories dominating each age group, we repeated the analysis for each of the main variable categories as before. The same trend of decreasing effects with age was found for carbon flux, but not for above- or belowground carbon stock (Table S3). This suggests that the effect of tree age may be due to different variables being assessed in each tree life stage.

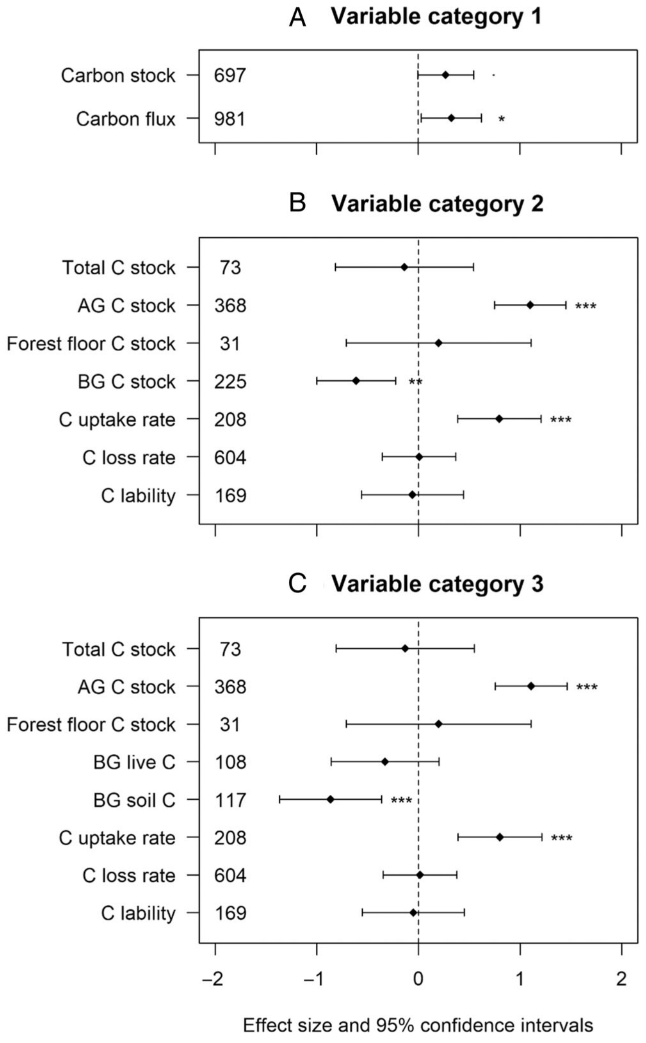

Fig. 3. Effects of non-native trees on the carbon cycle separated by category of variable: (A) separates variables related to carbon flux and carbon stock; (B) further separates carbon stock into total, aboveground carbon stock (AG C stock), forest floor carbon stock (litter and dead wood), and belowground (BG) carbon stock; carbon flux is separated into carbon uptake rate, carbon loss rate and carbon lability. In (C) the belowground carbon stock is further separated into carbon stock in living tissues (roots, bacteria, fungus, invertebrates) and carbon stock in soil organic matter. The mean effect size (Hedges' *d*) is indicated by a diamond, and the bars indicate the 95% confidence intervals. Significant effects (i.e. different from zero) are marked with asterisks (·, $0.10 > P \geq 0.05$; *, $0.05 > P \geq 0.01$; **, $0.01 > P \geq 0.001$; ***, $P < 0.001$). The number on the left side of the box is the number of case studies in each category.

(*e*) *Effects of stand type on the mean effect size*

The MLMA analysis assessing whether effect size of NNT forests on carbon cycle variables differed between stand types (natural/naturalised *versus* planted) showed a significant effect (Tables 3 and S1). Effect sizes were positive when the compared NNT and NT forests were both planted or both natural/naturalised, but negative for planted NNT *versus* natural NT (Fig. 5). The remaining category (naturalised NNT forest *versus* planted NT), with less replication, showed an effect size not different from zero. This result was consistent between the standard (covariance fixed at 0.5) and the conservative (covariance fixed at 0.8) approaches (Tables 3 and S1).

As for the previous moderators, we repeated the analysis for each of the three main variable categories (Table S4). The effect of stand type was significant in the three separated analyses. In the carbon flux data subset, the results followed a similar trend to the general analysis, but the effect sizes were only significant at $\alpha = 0.10$ ($P = 0.05$) when both NT and NNT forests were natural/naturalised (Table S4). In the aboveground carbon stock data subset, all stand type combinations showed greater values in NNT forests; the effects were significant when NNT forests were planted, but not when both forests were natural/naturalised. Finally, NNT forests only showed less belowground carbon stock than NT ones when the former were planted and the later natural (Table S4). This suggests an interaction between stand type and variable category.

(3) Publication bias

The funnel plot representing effect sizes against standard error of effect sizes showed asymmetry, with potentially missing points on the left side (negative effect) of the distribution (Fig. 6). However, in the MLMA with variance of effect sizes and publication year as moderators, neither showed a slope significantly different from zero, indicating the absence of small-study effect and decline effect (Table 4). Moreover, the bias-corrected estimates of the overall effect size did not differ in sign or in significance from the original estimate (Table 5), indicating that our initial results are robust.

Results of the structured MLMAs including variance of effect size and publication year along with the other tested moderators suggest the absence of small-study effect and decline effect in all analyses, as neither variance nor publication year showed a significant slope (Table S5). In only one case, the MLMA with stand type as moderator, publication year showed a negative slope significantly different from zero at $\alpha = 0.10$ ($P = 0.09$), which may be indicative of a decline effect.

IV. DISCUSSION

(1) The data set

Our study is the first comprehensive comparative global quantification of above- and belowground carbon stocks

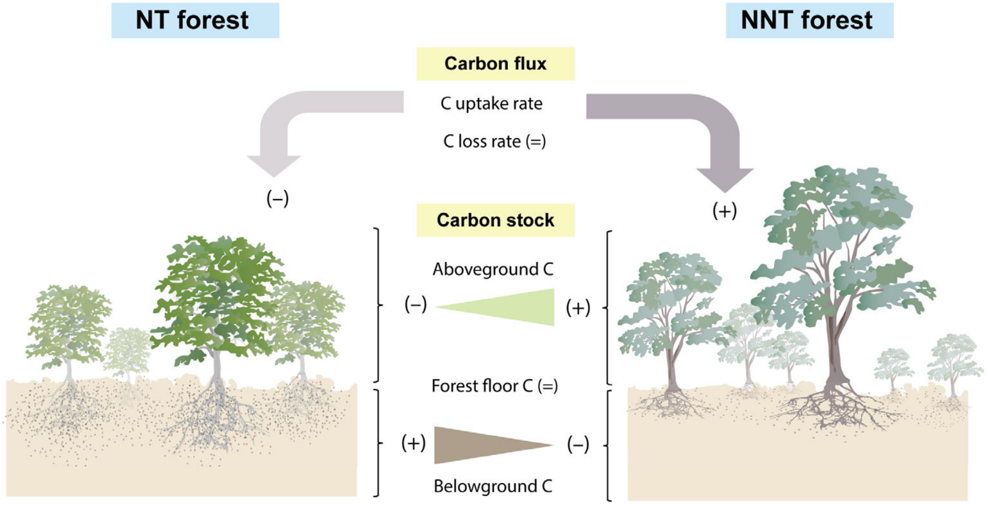

Fig. 4. Effects of native (NT) and non-native (NNT) forests on the carbon cycle, including carbon fluxes (carbon uptake and loss rates) and stocks (aboveground, forest floor, and belowground carbon). Positive, negative, and neutral effects are indicated with the symbols +, −, and =, respectively. The dots in the soil refer to soil carbon.

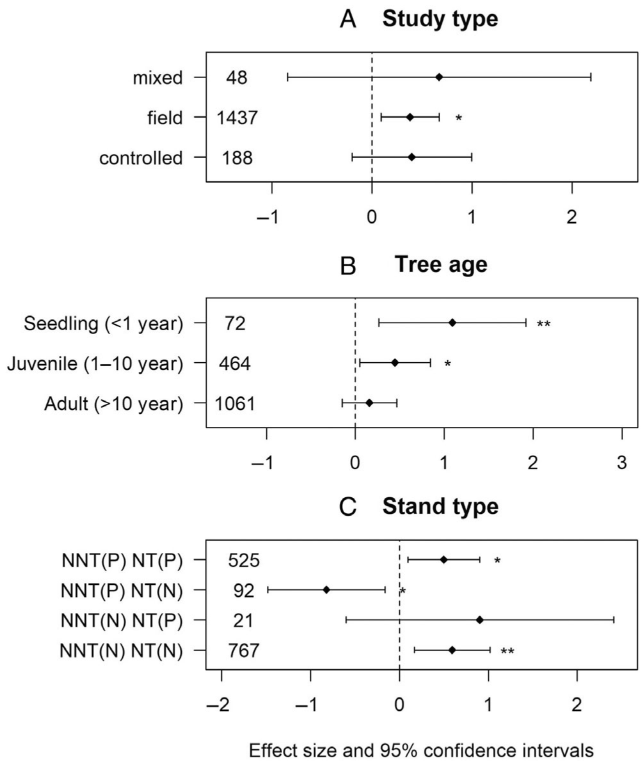

Fig. 5. Effects of non-native trees on carbon cycle variables separated by study type (A), tree age (B), and stand type (C). The mean effect size (Hedges' *d*) is indicated by a diamond, and the bars indicate the 95% confidence intervals. Significant effects (i.e. different from zero) are marked with asterisks (*, $0.05 > P \geq 0.01$; **, $0.01 > P \geq 0.001$). The number on the left side of the box is the number of case studies in each category. NNT, non-native tree; NT, native tree; (N), natural for NTs, naturalised for NNTs; (P), planted.

and fluxes between NNT and NT forests. Our results highlight differences in the capacity of these forests to capture and store carbon in different compartments, including above and belowground biomass, and soil organic carbon. Despite the global scope of our meta-analysis, most studies were conducted in developed countries with warm temperate climates. This geographical bias against research from low-income countries is well documented in the ecological literature (Pyšek *et al.*, 2008; Martin, Blossey & Ellis, 2012; Castro-Díez *et al.*, 2019*b*). Moreover, although our data set included 170 NNT taxa from 42 families, we found taxonomic bias towards a few species that show invasive behaviour and with global impacts, such as *Ailanthus altissima*,

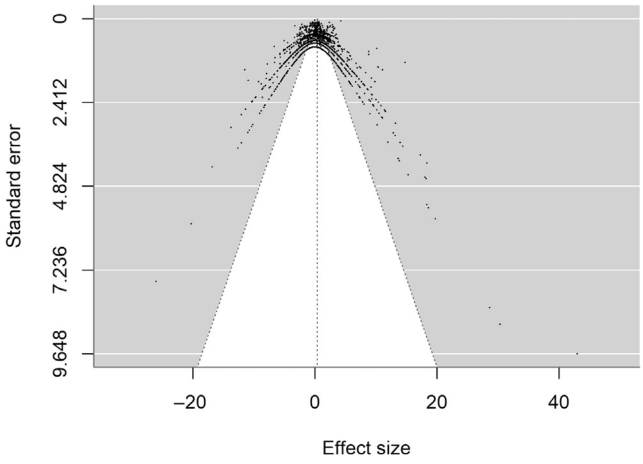

Fig. 6. Funnel plot showing the mean effect sizes of the data set (*x*-axis) plotted against the standard error of the effect size (*y*-axis). In the absence of publication bias, the dots are expected to distribute symmetrically around the overall mean effect size.

Table 4. Summary results of the structured multi-level meta-analysis (MLMA) assessing the effects of non-native trees (NNT) on carbon cycle variables. Article (publication) and case study nested within article were included as random factors in all models; publication year and effective sampling size variance (ess-variance) were also included as moderators to test for decline effect and small-study effect publication bias, respectively. The variance–covariance (VCV) matrix, needed to account for non-independence among sampling variances of cases derived from the same study, was calculated setting covariance at 0.5.

	Estimate	Standard Error	95% CI inf	95% CI sup	*P*
Intercept	0.538	0.203	0.140	0.936	0.008
Publication year	−0.019	0.015	−0.048	0.011	0.214
ess-variance	−0.661	0.512	−1.665	0.343	0.197

Tectona grandis, *Robinia pseudoacacia*, and *Triadica sebifera*. This taxonomic bias is also common within invasion science since research is often focused on species with known large impacts on social-ecological systems (Pyšek *et al.*, 2008; Hulme *et al.*, 2013). Lastly, our results do not seem to be significantly affected by two sources of publication bias (small-study effect and decline effect). Although the visual inspection of the funnel plot suggested that there might be some missing studies on the left side of the funnel, our bias-corrected estimates of the overall effect size were significant and positive, as for the non-corrected estimate. Thus, while the selective publication of favourable results is a widespread problem for meta-analyses (Thornton & Lee, 2000; Rothstein, Sutton & Borenstein, 2005), our results seem to be robust, offering the most complete and up-to-date analysis available of NNT impacts on the carbon cycle.

(2) Effects of non-native trees on carbon stock

Our multi-level meta-analysis showed that NNTs significantly increase overall carbon stock, through their higher aboveground carbon storage in tree biomass, as we initially hypothesised. This result is consistent with previous research on carbon storage (Liao *et al.*, 2008; Vilà *et al.*, 2011; Castro-Díez *et al.*, 2019*b*). High carbon storage in NNT stands may be linked to the high tree densities of productive NNT plantations, and to the large size that NNTs can reach (Vadell, de-Miguel & Pemán, 2016; Lázaro-Lobo *et al.*, 2023*b*). Thus, NNTs may enhance the ecosystem service of climate regulation in the short term by storing large amounts of carbon in their aboveground biomass. However, when productive NNT plantations are harvested, a great part of the carbon stock may be lost from the ecosystem, both in the form of wood and other by-products (of varying lifespan) and through enhanced soil respiration after soil disturbance (Jandl *et al.*, 2007). Finally, we highlight that increases in aboveground biomass associated with NNT forests also have the potential to alter other ecosystem services, such as fire hazard, which may increase due to fuel accumulation, or water supply, which may decline due to higher evapotranspiration (Le Maitre *et al.*, 1996; Levine *et al.*, 2003; Peltzer *et al.*, 2010; Martin *et al.*, 2017). Thus, it is pivotal to assess trade-offs between ecosystem services that may arise as a result of introductions of NNTs (Castro-Díez *et al.*, 2019*b*; Lázaro-Lobo *et al.*, 2023*a*).

Contrasting with the above, our results also indicate that forest belowground carbon stock, particularly soil organic carbon, is lower in NNT forests than in co-occurring NT ones, confirming findings of previous small-scale studies in forested ecosystems (Wu *et al.*, 2020; Zarafshar *et al.*, 2020). Two factors may have contributed to this result. First, many NNT species have been selected for rapid fast growth rate and/or low soil quality needs (Brundu & Richardson, 2016), and these early-successional trees tend to invest more carbon in shoots than in roots (Wright *et al.*, 2004; Díaz *et al.*, 2016). Second, many NNT stands are productive plantations, which are cyclically harvested using techniques that disturb the soil, alter its microclimate, and promote soil

Table 5. Original and bias-corrected estimates of the overall effect size of non-native trees (NNTs) on carbon cycle variables. The first column shows the original overall effect size obtained from the multi-level meta-analysis (MLMA) without moderators; the small-study effect correction is the intercept of the MLMA that includes variance of effect sizes as moderator; the decline effect correction is the intercept of the MLMA that includes publication year as moderator; and the small-study and decline effects correction is the intercept of the MLMA that includes both variance and publication year as moderators.

	Original	Small-study effect correction	Decline effect correction	Small-study and decline effects correction
Overall effect size	0.296	0.549	0.321	0.538
Standard error	0.113	0.204	0.114	0.203
P	0.009	0.007	0.005	0.008
Lower CI	0.075	0.149	0.098	0.140
Upper CI	0.518	0.948	0.543	0.936

CI, 95% confidence interval.

respiration (Jandl *et al.*, 2007; Ruiz-Peinado *et al.*, 2017). Indeed, the negative effect of NNT forests on soil carbon was the greatest when NNT forests were planted and NT forests were natural. This finding is key to explain the role of NNTs on the carbon cycle, since the forest soil stores high quantities of carbon, accounting for up to two-thirds of the carbon stock in forest ecosystems (Whitehead, 2011; Ruiz-Peinado *et al.*, 2017). In addition, carbon stored in the soil is more stable than carbon stored in tree trunks and branches, which are more vulnerable to disturbances, such as windstorms and fire events (Jackson *et al.*, 2017). Thus, promoting NT forests will be critical for stabilising atmospheric CO_2 concentrations within the forest soil, which is a key component of the carbon cycle.

(3) Effects of non-native trees on carbon flux

Our results indicate that NNT forests have faster carbon fluxes than NT ones due to higher carbon uptake rates, as suggested by previous research (Liao *et al.*, 2008; Castro-Díez *et al.*, 2019*b*). This is not surprising, given that many NNT species have been selected for their high productivity and rapid growth to satisfy increasing demands for timber or other wood-derived products, or for land reclamation (Richardson, 1998; Castro-Díez *et al.*, 2019*b*; Lázaro-Lobo *et al.*, 2023*a*). A rapid growth rate has also been shown to be a key trait in the naturalisation of NNT species (Richardson & Pyšek, 2006; Van Kleunen, Weber & Fischer, 2010).

We found that carbon loss rates did not differ between NT and NNT forests, suggesting similar decomposition rates of wood, litter, and organic matter. The collective assessment of the effect of native and non-native plants (not only trees) on litter decomposition rates across the globe has yielded mixed results, including increase in decomposition rate after plant invasions (Liao *et al.*, 2008), high heterogeneity of impacts on litter decomposition (Vilà *et al.*, 2011; Kennedy & El-Sabaawi, 2017), and inhibition of litter decomposition by non-native plants in the case of streams (Ferreira *et al.*, 2016). According to our results, there is no evidence that, on average, NNT species alter decomposition rates in a predominant direction. Thus, the effect of NNTs on decomposition rates may be species and ecosystem specific. Some species increase decomposition rates due to the production of easily decomposable litter (e.g. *Myrica faya*) (Vitousek & Walker, 1989; Liao *et al.*, 2008), while others produce litter that is poor in N or resistant to soil microbial decomposition, slowing down decomposition rates (e.g. *Acacia longifolia*, *Eucalyptus* spp. and *Pinus* spp.) (Castro-Díez *et al.*, 2019*b*; Marchante *et al.*, 2019).

Contrary to our initial expectations, we found that NNT forests do not have a higher carbon lability than NT forests, despite several studies showing that NNTs have a greater mortality than NTs after disturbances and that NTs are better adapted to stressful conditions in the recipient ecosystems (e.g. Oba *et al.*, 2001; Sher, Marshall & Taylor, 2002; Piotto *et al.*, 2003). Additionally, many NNTs used in forest plantations follow an acquisitive resource-use strategy, characterised by having higher carbon sequestration rates and lower carbon durability than the conservative strategy (i.e. slow growth, long life, and high investment in storage and defence) (Wright *et al.*, 2004; Díaz *et al.*, 2016; Lázaro-Lobo *et al.*, 2023*b*). Despite this evidence, we did not find significant differences in carbon lability between NNT and NT forests in our meta-analysis, possibly due to intrinsic differences among the evaluated forest types.

(4) Climate marginally affects differences in carbon cycle between NT and NNT forests

Although climate type did not significantly modify the effect of NNT on carbon cycle variables, we found that the differences in carbon stocks and fluxes between NT and NNT forests tended to be greater in climates that allow for greater productivity (i.e. equatorial climate). This result provides some support for our initial hypothesis. Previous research suggests that the size and productivity of plants can be limited by climatic filters (Moles *et al.*, 2009; Lázaro-Lobo *et al.*, 2023*b*). As a result, increased water stress may reduce the size and biomass attainable by NNT species, limiting carbon accumulation in aboveground stocks (Jakobs, Weber & Edwards, 2004; Stegen *et al.*, 2011; Martin *et al.*, 2017). Thus, the superiority of NNTs over NTs in terms of carbon storage and sequestration may decline as the abiotic filters become stronger, as found in the Iberian Peninsula (Lázaro-Lobo *et al.*, 2023*b*). Further research should be conducted in different climatic conditions to improve replication number and to corroborate this trend.

(5) Life stage may modify the carbon cycle differences between NT and NNT forests

Our results show that NNT forests had greater carbon stocks and fluxes at early life stages (i.e. seedling and juvenile) than NT ones, but this superiority diminishes as trees reach the adult stage and forests mature. This result could be due to the large size that many NNT selected in forestry reach in a short timeframe (Richardson, 1998; Castro-Díez *et al.*, 2019*b*; Lázaro-Lobo *et al.*, 2023*a*). The superiority of NNTs over NTs in terms of carbon storage and sequestration at the seedling and juvenile stages could also be linked to bias in the variables measured at these early life stages, which mainly were tree growth, height, and aboveground biomass. Thus, further research should evaluate other components of the carbon cycle in young forests (e.g. soil organic carbon and decomposition rate).

(6) Stand type affects differences in carbon cycle between NT and NNT forests

NNT forests had greater carbon stocks and fluxes than NT forests when both were natural/naturalised or planted. However, NT natural forests had greater values for the carbon cycle-related variables than plantations of NNTs. This result could be due to carbon losses from soil and biomass associated with tree plantations and management (Jandl *et al.*, 2007; Liao *et al.*, 2010; Hua *et al.*, 2022). Soil management in NNT plantations may alter belowground processes, decreasing the ability of soil to sequester and store carbon (Liao *et al.*, 2010). For example, intensive site preparation may enhance soil respiration due to increased soil aeration and illumination; it may additionally promote soil compaction when heavy machinery is used, which in turn may promote mortality of soil fauna (Jandl *et al.*, 2007; Liao *et al.*, 2010). Thus, the contribution of NNT tree plantations to carbon sequestration can be enhanced by forest managers through sustainable forest management (e.g. promoting less-intensive forest practices, minimising disturbance to the stand structure and soil, and implementing selective harvesting instead of clear-cutting) (Jandl *et al.*, 2007; Ruiz-Peinado *et al.*, 2017; Ameray *et al.*, 2021).

V. CONCLUSIONS

(1) Our results provide a broad insight into the effect of NNTs on the carbon cycle, which may be used to inform forestry policies. Aboveground carbon stocks were considerably greater in NNT forests, but belowground carbon stocks, particularly soil organic carbon, were greater in NT forests. Given that forest soil is a major component of the carbon cycle and the main terrestrial sink of carbon, forestry policies aimed at improving long-term carbon sequestration and storage should promote NT forests.

(2) Among fluxes, carbon uptake rate was higher in NNT forests, while carbon loss rate did not differ between NT and NNT forests. We also found that plantations of NNTs had lower values for the carbon cycle-related variables than NT natural forests. Policymakers should ensure the application of sustainable silvicultural activities to increase the capacity of plantations to store and sequester carbon in the long term.

(3) Promoting NNT plantations as a tool to enhance forest carbon sinks may have beneficial effects in the short term. However, these carbon stocks, mostly in aboveground biomass, are more easily lost by disturbances than belowground carbon stocks, which are greater in NT forests. Additionally, it must be considered that some NNTs may become invasive and their positive effects on carbon sequestration can be offset by negative impacts they cause to biodiversity and to other ecosystem services, including provisioning, regulating, and cultural services.

(4) Most studies were conducted in developed countries with warm temperate climates, and a few species that show invasive behaviour were over-represented. This suggests that future research on carbon storage and sequestration should focus on a wider range of species and climate types. Overcoming these biases would greatly increase our understanding of the impacts of NNT on the carbon cycle.

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VII. AUTHOR CONTRIBUTIONS

A. L.-L. and P. C.-D. conceived the idea; A. L.-L. performed the literature search; all authors collected data, P. C.-D. performed the meta-analysis, A. L.-L. wrote the first draft of the manuscript, all authors contributed substantially to revisions, and A. L.-L. and P. C.-D. addressed the Editor's and reviewers' comments.

VIII. DATA AVAILABILITY STATEMENT

Appendix S1 is also available at: Mendeley Data, V1, doi: 10.17632/vzsnr3xxmx.1.

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X. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Data extracted from selected studies.

Appendix S2. Full list of the reviewed articles.

Appendix S3. R code used for data analysis.

Appendix S4. The Preferred Reporting Items for Systematic reviews and Meta-Analyses (PRISMA) statement for this meta-analysis (O'Dea *et al.*, 2021).

Table S1. Summary results of multi-level meta-analyses (MLMAs) performed with different moderators.

Table S2. Summary results of the structured multi-level meta-analysis (MLMA) assessing the effects of non-native trees (NNT) on several categories of carbon cycle variables [C fluxes, aboveground (AG) C stock, and belowground (BG) C stock] using the full data set, with study type included as a fixed factor.

Table S3. Summary results of the structured multi-level meta-analyses (MLMA) assessing the effects of non-native trees (NNT) on several categories of carbon cycle variables [C fluxes, aboveground (AG) C stock, and belowground (BG) C stock] using the full data set, with tree age included as a fixed factor.

Table S4. Summary results of the structured multi-level meta-analyses (MLMA) assessing the effects of non-native trees (NNT) on several categories of carbon cycle variables [C fluxes, aboveground (AG) C stock, and belowground (BG) C stock] using the full data set, with stand type included as a fixed factor.

Table S5. Tests of publication bias in the structured multi-level meta-analyses (MLMAs) assessing the effects of non-native trees (NNT) on the carbon cycle.

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