Searching for predictors of the variability of impacts caused by non-native trees on regulating ecosystem services worldwide

Alberto Romero-Blanco [a,*], Pilar Castro-Díez [a], Adrián Lázaro-Lobo [a], Rafael Molina-Venegas [b,c], Paula Cruces [a], Petr Pyšek [d,e]

[a] Universidad de Alcalá, Facultad de Ciencias, Department of Life Sciences, Unidad de Ecología, Biological Invasions Research Group, Plaza de San Diego S/N, Alcalá de Henares, 28805 Madrid, Spain
[b] Departamento de Ecología, Facultad de Ciencias, Universidad Autónoma de Madrid, Madrid, Spain
[c] Universidad de Alcalá, Facultad de Ciencias, Department of Life Sciences, Unidad de Ecología, Global Change Ecology and Evolution Group, Plaza de San Diego S/N, Alcalá de Henares, 28805 Madrid, Spain
[d] Czech Academy of Sciences, Institute of Botany, Department of Invasion Ecology, CZ-252 43 Průhonice, Czech Republic
[e] Department of Ecology, Faculty of Science, Charles University, Viničná 7, CZ-128 44 Prague, Czech Republic

HIGHLIGHTS

- The impacts of exotic trees on regulating ecosystem services are modulated by climate.
- Wetter and warmer climates promote positive impacts of exotic trees.
- Human population density is also an important impact modulator.
- Exotic tree impacts are greater in more densely populated areas.
- Climate should be considered when deciding on the introduction of new exotic trees.

GRAPHICAL ABSTRACT
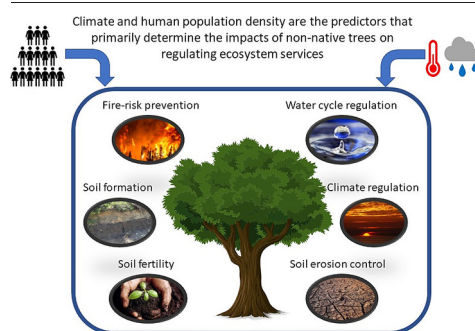
ARTICLE INFO

ABSTRACT

Humans have introduced non-native trees (NNT) all over the world to take advantage of the plethora of benefits they provide. However, depending on the context, NNT may present a diverse range of effects on ecosystem services (ES), from benefits to drawbacks, which may hinder the development of policies for these species. Unfortunately, the attempts so far to understand the impacts of NNT on ES only explained a low proportion of their variation. Here we analyze the variation in impacts of NNT on regulating ecosystem services (RES) by using a global database, which covers the effect size of multiple NNT species on six RES (climate regulation, soil erosion regulation, soil fertility, soil formation, hydrological cycle regulation, and fire protection). We used a wide range of predictors to account for the context-dependency of impacts distributed in five groups: the RES type, functional traits of both the NNT and the dominant NT of the recipient ecosystem, phylogenetic and functional distances between NNT and NT, climatic context, and human population characteristics. Using boosted regression trees and regression trees, we found that the most influential predictors of NNT impacts on RES were annual mean temperatures and precipitation seasonality, followed by the type of RES, human population density, and NNT height. In regions with warm temperatures and low seasonality, NNT tended to increase RES. NNT impacts were greater in densely populated regions. Smaller NNT exerted greater positive impacts on climate regulation and soil erosion regulation in tropical regions than in other climates. We highlight that benign climates and high population density exacerbate the effects of NNT on RES, and that soil fertility is the most consistently affected RES. Knowledge of the factors that modulate NNT impacts can help to predict their potential effects on RES in different parts of the world and at various environmental settings.

1. Introduction

Trees have always attracted great interest for the multitude of ecosystem services (ES) they provide, which are defined as the benefits that humans obtain from ecosystems (Chaudhary et al., 2015; MEA, 2005). From trees we obtain raw materials for livelihood support (provisioning ES), or educational, scientific, spiritual, and recreational benefits (cultural ES) (Haines-Young & Potschin, 2018; MEA, 2005; Vaz et al., 2018). Trees also contribute greatly to ecosystem functions, i.e., the ecological processes that control the fluxes of energy and resources through an environment. As such, trees play a pivotal role as regulators of soil erosion, climate, pollination, and water and air quality (i.e. regulating ES, RES; (Dickie et al., 2014; Haines-Young & Potschin, 2018; Pejchar & Mooney, 2009)). Humans have extensively planted trees beyond their native ranges to meet the growing demand of benefits they provide (MacDicken et al., 2015), which may in turn enhance ecosystem functioning. For example, a global-scale meta-analysis conducted by Castro-Díez et al. (Castro-Díez et al., 2019) showed that non-native trees (NNT) tended to enhance many of the RES considered in the study (climate regulation, soil erosion control, soil fertility, and soil formation). However, Castro-Díez et al. (Castro-Díez et al., 2019) also revealed a wide variety of impacts of NNT on the same ES type, highlighting the context-dependency of the impacts.

Previous research suggests an array of factors that may explain the variation in impacts of NNT on ES (Castro-Díez et al., 2021; Pyšek et al., 2012; Vilà et al., 2011). Firstly, the intrinsic properties of non-native species are a relevant source of impact variability (e.g., (Castro-Díez et al., 2019; Castro-Díez et al., 2021; Vilà et al., 2011; Xu et al., 2022; Zhou & Staver, 2019)). For example, nitrogen (N)-fixing NNT tend to produce greater impacts on the N cycle than non-N-fixing NNT (Castro-Díez et al., 2014; Liao et al., 2008; Vilà et al., 2011). The functional structure of the recipient community may also explain differences of NNT effects on ES, as NNT with novel traits in the recipient communities may produce greater impacts than NNT with redundant traits. For instance, N-fixing NNT have greater impacts on N cycles in ecosystem lacking native N-fixers (Castro-Díez et al., 2014; Liao et al., 2008; Vilà et al., 2011), or impacts of NNT are greater in treeless communities (Mack, 2003). Indeed, Castro-Díez et al. (Castro-Díez et al., 2014) found that the functional distance between non-native naturalized plants and dominant native plants partially explained the variation in impacts of non-native plants on the N cycle. The phylogenetic relatedness may be another explanatory factor if traits (or trait values) that determine the impacts show some degree of phylogenetic signal (Castro-Díez et al., 2011; Castro-Díez et al., 2014; Rejmanek & Richardson, 1996). The climatic conditions and the vertical structure of recipient communities may additionally explain the variation in impacts of NNT (Xu et al., 2022). For instance, Castro-Díez et al. (Castro-Díez et al., 2014) found greater impacts of non-native plants on the N cycle in areas with warmer and wetter climates. Castro-Díez et al. (Castro-Díez et al., 2021) showed that non-native eucalypts had more negative impacts on soil fertility in temperate than in tropical forests, and that non-native pines decreased soil formation in forests but not in grasslands. Likewise, the impacts of non-native woody species with high water requirements can be critical on water cycles, especially in regions with water-limited climates (Caldeira et al., 2015). Finally, the richness and abundance of non-native species can increase with human population densities, thus amplifying their impacts on ES (McKinney, 2001; McKinney, 2002; Pyšek et al., 2002; Spear et al., 2013). Additionally, the degree of environmental degradation caused by human activities was shown to increase the probability that ES are altered by NNT (Castro-Díez et al., 2011; Catford et al., 2011; Edward et al., 2009). Moreover, all the potential predictors described above may interact in complex ways to explain NNT impacts on ES, and few studies have attempted to analyze such a variety of predictors and their interactions at a global scale (Castro-Díez et al., 2019; Castro-Díez et al., 2021; Pyšek et al., 2012). This lack of appropriate design could be a reason why previous studies addressing the impacts of NNT on ES only explained a low proportion of observed variance.

The novelty of our study lies in 1) the identification of new or underexplored sources of variation in impacts and 2) the simultaneous analysis of different groups of potential predictors of variation in a global database. We aimed to understand how different predictors may interact to explain the variety of NNT impacts on six RES in forest communities worldwide, including climate regulation, soil erosion regulation, soil fertility, soil formation, fire protection, and hydrological cycle regulation. We focused on forests because of the wide range of ES they provide, as explained above. We simultaneously assessed the role of five groups of predictors: (1) RES type, (2) functional traits of NNT and NT, (3) the phylogenetic and functional relatedness between NNT and the dominant NT in the recipient communities, (4) climate, and (5) human population density. We hypothesized that (1) functional traits play an important role in explaining the variation in impacts of NNT on RES, 2) NNT that are more phylogenetically and functionally distant from the dominant NTs of the recipient community have greater impacts than those that are more closely related, (3) the impacts caused by NNT vary depending on climatic conditions of the recipient region, (4) human influence, here expressed as the human population density, will exacerbate the impacts of NNT.

2. Material and methods

2.1. The data set

Our data were obtained from the global database compiled by Castro-Díez et al. (Castro-Díez et al., 2019) (available at *Repositorio Madroño*, doi: 10.21950/EGM8SE), that includes information extracted from 1683 case studies conducted all over the world. The names of some RES categories employed by Castro-Díez et al. (Castro-Díez et al., 2019) were slightly modified to adjust them to the RES categories proposed by the Common International Classification of Ecosystem Services (CICES) V5.1 (Haines-Young & Potschin, 2018) (see Table S1 in the Supplementary Material for terminology correspondences of RES categories). Each case study (i.e. rows of the data set) consisted of a comparison between a site dominated by a NNT with a nearby site with similar environmental conditions dominated by a NT that served as a control (see Supplementary Material S1 for details on building the database and its structure). The magnitude of the difference was assessed by calculating the effect size as Hedges' *d* (Supplementary Material S2). The effect size is a unitless metric used in meta-analyses that captures the magnitude of change of a variable in a comparison. The Hedges' *d* values may range from $-\infty$ to $+\infty$, estimating the size and direction of effects. Positive values indicate that the NNT species increases the ES and vice versa (Rosenberg et al., 2000). The summary effect resulting from aggregating all case studies was presented in Castro-Díez et al. (Castro-Díez et al., 2019). Here, we aim at explaining the variation in impacts across case studies using the effect size as dependent variable. We removed original case studies with insufficient or ambiguous information on NNT or NT identities (i.e. the name of the species was not specified), those of non-forest ecosystems (deserts, grasslands and shrublands) or non-tree or shrub NT species (e.g. herbaceous, ferns), and those performed under experimental conditions. Finally, we retained 773 case studies derived from 64 publications, encompassing 76 NNT species and six RES: climate regulation, soil erosion regulation, soil fertility, soil formation, fire protection, and hydrological cycle regulation. The data set is publicly available in the FigShare repository ((Romero-Blanco et al., 2022); https://doi.org/10.6084/m9.figshare.20141483.v3).

2.2. Predictors of variation in impacts of NNT

We initially selected a set of 28 predictors with potential to explain the variation in NNT impacts on RES, classified in the following categories: RES type; functional traits; relationship between NNT and NT; climatic predictors; and anthropogenic factors. However, we excluded seven predictors that did not meet the quality standards that we set for our research (see Supplementary Material Table S2 for an extended description), thus retaining 21 out of the 28 originally considered (see Table 1).

Table 1
Final set of predictors selected to explain the variation in impacts of NNT on RES.

Predictor group	Variable name and type[a]	Categories of QL variables
RES type	RES type (QL)	Climate regulation; soil erosion regulation; soil fertility; soil formation; fire protection; hydrological cycle regulation
Functional traits	Leaf nitrogen content (QT)	–
	Plant height (QT)	–
	Specific leaf area (QT)	–
	Wood density (QT)	–
	Leaf compoundness (QL)	Simple; compound
	Leaf habit (QL)	Deciduous; evergreen; deciduous/evergreen
	Nitrogen fixing capacity (QL)	Yes, no
	Resprouting capacity (QL)	Yes, no
Relationship between NNT and NT	Functional distance (QT)	–
	Phylogenetic distance (QT)	–
Climatic	Annual mean temperature (QT)	–
	Temperature seasonality (QT)	–
	Precipitation of the driest month (QT)	–
	Precipitation seasonality (QT)	–
Anthropogenic factors	Human population density (QT)	–

[a] QT: quantitative, QL: qualitative.

2.2.1. Functional traits

We compiled a set of functional traits for all the species (NNT and NT) in our database. The selected traits pertain to the economy of water, light, nutrients, and life history of species. Data were initially collected from the TRY database (Kattge et al., 2011) and then completed with other online resources (Table S3; Supplementary Material). Missing values were imputed using trait correlation structure. We only considered imputed information in subsequent analyses if the estimated prediction error was <0.5 in the cross-validation trials (see Supplementary Material S3 for a detailed description). Traits with ≥60 % of missing values were directly discarded (see Table 2 for a description of the traits used in the study).

2.2.2. Phylogenetic distances

We obtained a set of time-calibrated phylogenies for the species analysed in the study using the R package *V.PhyloMaker* (Jin & Qian, 2019). *V.PhyloMaker* uses the largest species-level mega-phylogeny of vascular plants published to date (GBOTB.extended; see (Jin & Qian, 2019)) to generate a subtree from a given species list (that was standardized to the nomenclatural and spelling criteria of The Plant List (The Plant List, 2013)), following a three-steps procedure that can be consulted in Supplementary Material S4. To account for phylogenetic uncertainty (i.e., random binding of PUTs), we repeated this procedure iteratively until we obtained 1000 different trees. Pairwise phylogenetic distance matrices were derived from the trees using the R function *cophenetic* (R Core Team, 2021), and all subsequent analyses were replicated and results averaged over the 1000 matrices (Rangel et al., 2015).

2.2.3. Functional distances

We used those functional traits selected in the previous step (see Table 2) to calculate the functional distances between NNT and the

dominant NT in the recipient communities. First, we explored the correlation structure among the selected traits using different methods (see Supplementary Material S5). Subsequently, we computed a multi-trait dissimilarity matrix with the *gawdis* R package, which ensures an equitable contribution of the different traits in the computation of multi-trait dissimilarity (De Bello et al., 2020). Some traits showed a moderate correlation (0.5–0.7) (Table S4), which suggests that they may have a strong influence in the computation of multi-trait dissimilarities. Thus, we adopted two approaches: (1) we grouped correlated traits to ensure a similar contribution of groups to the dissimilarity matrix (De Bello et al., 2020) and (2) we removed correlated traits (leaf compoundness and leaf nitrogen content) and computed the dissimilarity matrix with the remaining traits (not grouped). The resultant values from each approach were scaled between 0 (species functionally identical) and 1 (species completely different) (De Bello et al., 2020). Given that distance values from both approaches were strongly correlated (Pearson's $r = 0.94$), we used the mean distance values from the two approaches as the final predictor for the analyses.

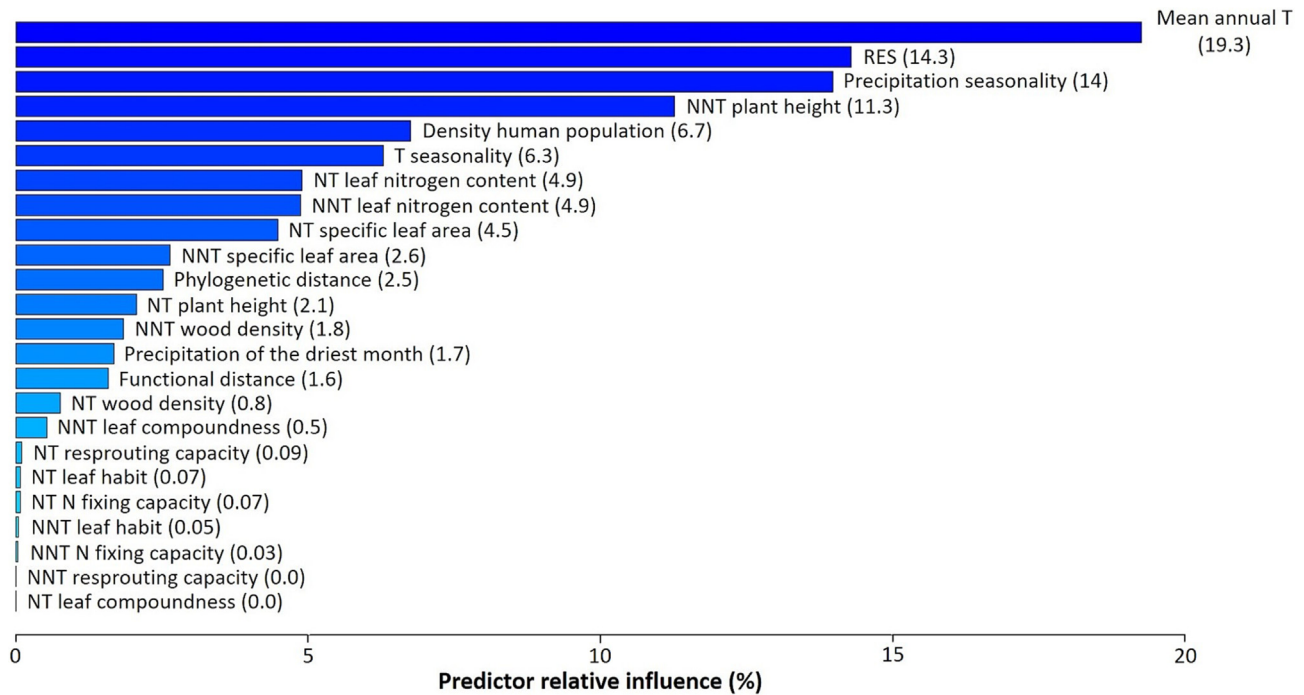### 2.2.4. Climatic predictors

For each case study, the geographical coordinates of the sites were extracted from the source papers or inferred from a georeferenced map if not provided in the paper. If multiple sites were included in the same case study, we selected the coordinates of the centroid of the minimum convex polygon connecting them. Climatic variables were obtained from WorldClim version 2 (Fick & Hijmans, 2017), and included 19 descriptors with a resolution of 10 arc-minutes ($\sim$ 340 km^2) for the period 1970–2000. We selected a subset of variables accounting for seasonality (variation in temperature and precipitation along the year), annual means of temperature and precipitation, and climate extremes (precipitation of the driest month and temperature of the coldest month) (Table 1 and Supplementary Material Table S2). Subsequently, we assessed the collinearity between selected variables and those with strong correlations were discarded (Pearson's $r \geq 0.7$; Supplementary Material Table S2) (Dormann et al., 2013). The final set of climate predictors used for the analyses is shown in Table 1.

2.2.5. Anthropogenic predictor

The anthropogenic context was characterized as the human population density, a widely used proxy for assessing human footprint in macroecological studies (Pyšek et al., 2010; Sanderson et al., 2002). Using the coordinates of each case study, we obtained the human population density for the year 2020 with a resolution of 15 arc-minutes ($\sim$30 km) from the Center for International Earth Science Information Network - CIESIN - Columbia University (Center for International Earth Science Information Network - CIESIN - Columbia University, 2018).

2.3. Data analysis

To assess the explanatory power of our predictors on the impacts of NNT on RES, we combined Boosted Regression Trees (BRT) and regression trees. Regression trees can handle qualitative and quantitative predictors, non-linear variables, and do not need prior transformation or outlier elimination (Elith et al., 2008; Feld et al., 2015), which represent clear advantages over more classic regression models. Briefly, regression trees split the response

Table 2
Final set of traits used to explain the variation in impacts of NNT on RES, and their functional roles.

Trait	Type	Measurement units	Functional role
Leaf nitrogen content	Quantitative	mg/g	Light acquisition, photosynthetic capacity
Plant height	Quantitative	m	Light acquisition, dispersal distance, above-ground competition
Specific leaf area	Quantitative	mm^2/mg	Light acquisition, photosynthetic capacity, growth rate
Wood density	Quantitative	g/cm^3	Water storage and dynamics, hydraulic capacity, tree longevity
Leaf compoundness	Qualitative	Simple, compound	Control of water loss, light acquisition, water regulation
Leaf habit	Qualitative	Deciduous, evergreen or deciduous/evergreen	Light acquisition, photosynthetic capacity, nutrient use efficiency
Nitrogen fixation capacity	Qualitative	Yes, no	Growth rate, nutrient acquisition
Resprouting capacity	Qualitative	Yes, no	Recovery after disturbances

Fig. 1. Relative contribution of predictors to the explained variance (%), based on Boosted Regression Tree analysis. Numbers in brackets indicate the precise contribution of each predictor.

variable into homogenous groups recursively (De'ath & Fabricius, 2000), and the predictor that explains the greatest deviance in the response variable is selected at each splitting node to fit a prediction model (Loh, 2011).

We performed the analyses following a three-step procedure. First, we checked the collinearity between predictors following the methods described in Supplementary Material S5 and removed those with strong correlations (≥ 0.7; Supplementary Material Table S2) (Dormann et al., 2013). Second, we performed a BRT analysis to assess relative importance of predictors (i.e., the proportion of the variance explained by each predictor) (see Supplementary Material S6 for further details). Third, to disentangle the combined effects of predictors, we performed a Generalized Linear Mixed Model tree (GLMM tree) using those predictors that explained ≥ 5 % of the variance in the previous BRT. The GLMM was performed using the "glmertree" function of the *glmertree* package (Fokkema et al., 2018). Missing values were excluded from the analysis. We used a GLMM tree to account for possible non-independence among case studies, which is a common problem in meta-analyses on environmental information (Castro-Díez et al., 2019; Nakagawa & Santos, 2012). Non-independence derives from the fact that the same study may provide several case studies, which are more closely related with each other than with other cases coming from different studies. We identified three sources of pseudo-replication in our data set: 1) multiple controls: when the same NNT was compared with several NTs in the same study; 2) multiple sites: the same variable was assessed in the same study at several sites, and each site was considered as a case study; 3) multiple outputs: the same study provided measures of different variables in the same sampling. The three issues were addressed by including the source paper (identified by "reference") as a random factor and case study was nested within reference.

3. Results

3.1. Data set exploration

Most publications came from North America and Europe (Fig. S2; Supplementary Material). Case studies were unevenly distributed across species, with *Acacia mangium* and *Tectona grandis* accounting for the largest number of cases (84 each) (Table S5; Supplementary Material). NNT

populations were mainly on plantations (74 % of case studies). The RES with the largest number of case studies was soil formation (313), followed by climate regulation (210), soil fertility (130), soil erosion regulation (52), hydrological cycle regulation (36), and fire protection (32). All continents except Antarctica were represented in our data set, although case studies were unevenly distributed across world regions with Central and South America showing the highest number of case studies (Fig. S3; Supplementary Material). Some RES (climate regulation, soil formation and fertility) were also over-represented within regions (Fig. S3; Supplementary Material).

3.2. Assessing the relative importance of predictors

Our predictors explained 16 % of the variance in effect sizes of NNT on RES according to the BRT (see Fig. 1 for the relative contribution of each predictor to the explained variance). Predictors that contributed to explain ≥ 5 % of the observed variance included climate variables (mean annual temperature and precipitation and temperature seasonality), human population density, type of RES, and NNT height (Fig. 1). Retained predictors for the regression tree accounted for 71.9 % of the explained variance.

3.3. Disentangling the combined effects of predictors

Two climatic variables (mean annual temperature and precipitation seasonality) appeared in the first splits of the tree (Fig. 2). Negative effect sizes of NNT on RES were found only in the coldest regions (mean annual temperatures ≤ 12.8 °C; terminal nodes 2 and 3 of Fig. 2). The greatest negative effect sizes corresponded to regions with ≤ 8.4 °C of mean annual temperature and high precipitation seasonality (>61.9, terminal node 2 of Fig. 2). In contrast, the mean effect size was positive in cold regions with more regular precipitation (≤ 61.9) (Fig. 2; terminal node 1). On the other hand, in warmer regions (>12.8 °C) with regular rainfalls (precipitation seasonality ≤ 30.4), the mean effect size was great and positive (Fig. 2; terminal node 4).

In the next splitting node, soil fertility was separated from the rest of RES. In temperate to warm regions (over 12.8 °C of annual mean temperature) with irregular precipitation (seasonality >30.4), NNT had positive

Fig. 2. Regression tree showing the predictors with the greatest influence on the impacts of NNT on RES. Values in blue are the splitting criteria for each splitting predictor and *p*-values (in red) report the best suitable predictor at a given splitting point (α = 0.05). Numbers outside parentheses at terminal nodes indicate the mean of the effect size and those inside the parenthesis are the numbers of case studies. The average effect size (number outside the parenthesis) for all case studies (number inside the parenthesis) is shown at the top of the tree.

effects on soil fertility (terminal node 5), and the remaining RES were in turn split. The effects of NNT on fire protection, hydrological cycle regulation and soil formation were determined by the temperature seasonality. NNT showed greater positive effects in regions with lower annual oscillations in temperature than in those where temperatures are less regular (Fig. 2; terminal nodes 11 and 12).

Human population density determined the effects of NNT on climate regulation and soil erosion regulation, which were greater and positive in densely populated regions (Fig. 2; terminal node 10). In less densely populated areas, the mean annual temperature played an important role again. In moderately warm areas (temperatures between 12.8 and 26 °C), NNT contributed positively to climate regulation and soil erosion regulation. However, those contributions were slightly higher in environments with high precipitation seasonality (>52.7) (Fig. 2; terminal nodes 6 and 7). The height of NNT influenced their effects only in regions where annual mean temperatures exceed 26 °C (tropical climates), so that taller trees showed fewer positive effects on climate regulation and soil erosion regulation (Fig. 2; terminal nodes 8 and 9).

4. Discussion

4.1. The data set

We obtained a heterogeneous distribution of case studies across RES and world regions. Although the highest number of publications came from North America and Europe, Central and South America accounted for the largest number of case studies due to a higher number of cases per publication. Only 12 species covered half of the case studies in our database, which suggests that researchers often tend to focus on the same NNT species, usually those that are more invasive and with greater

socio-ecological impacts (Hulme et al., 2013; Pyšek et al., 2009). Also, most case studies corresponded to planted NNT, perhaps because plantations are of a greater economic interest than naturalized populations and, subsequently, are the subject of more studies. This may have determined the predominance of certain species or genera in our database, such as *Acacia* sp., *Tectona grandis*, *Eucalyptus* sp., or *Pinus* sp., as they are preponderantly selected for plantations (Richardson, 1998; Zobel et al., 1987).

4.2. Relative importance of predictors

High variation is inherent to ecological studies, mostly if they integrate data from multiple studies, as effect sizes come from different species and contexts worldwide (Senior et al., 2016). In this study, all the selected predictors explained 16 % of the variation in effects of NNT on RES. We were able to explain a high proportion of this variation compared to what is usually reported in ecological meta-analyses (Senior et al., 2016). Indeed, previous studies assessing the variation in impacts of NNT used a limited set of predictors (e.g., N-fixing ability, life form, biome, type of ecosystem) (Castro-Díez et al., 2019; Castro-Díez et al., 2021; Pyšek et al., 2012; Vilà et al., 2011).

The best predictors of NNT impacts pertained to climate, anthropogenic factors, type of RES, and NNT height. Climatic filters can limit the success of NNT establishment and performance, and thus their capacity to alter ecosystem processes and services (Castro-Díez et al., 2014; Castro-Díez et al., 2019; Castro-Díez et al., 2021). A novel result is the importance of human population density in determining the impacts of NNT on RES. Vaz et al. (Vaz et al., 2018) already used a similar predictor, the global human influence index, to explain the effects of NNT on cultural ES. Human population density is related to the level of ecosystem disturbance and the introduction of NNT to meet the demands of human populations for resources; these

factors modulate the establishment and spread of NNT and, consequently, their effects on RES (Catford et al., 2011; Edward et al., 2009; Spear et al., 2013). The type of RES appeared as one of the important predictors of NNT impact, suggesting that the sign and magnitude of NNT impacts differ among individual RES. In fact, Castro-Díez et al. (Castro-Díez et al., 2019), that addressed NNT impacts on each RES separately, found that the impacts on most RES were positively correlated with each other, except for fire-risk prevention, which was negatively correlated with water regulation and soil erosion control. This means that NNT can enhance some RES while impairing others. For example, NNT with high biomass productivity can increase soil formation and erosion regulation (Castro-Díez et al., 2019). However, biomass accumulation implies more fuel in the system and a reduction in the capacity of ecosystems to protect against fires (Castro-Díez et al., 2019). The significant effect of the NNT height is consistent with our expectation that some functional traits would appear among the predictors with the greatest explanatory power since they ultimately determine the ability of species to use resources and modify their environments (Ehrenfeld, 2010). Plant height was also identified as a trait supporting the impacts of non-native plants on species richness of invaded communities (Pyšek et al., 2012).

Surprisingly, some predictors that have been previously reported as major determinants of the impacts of NNT on RES, contributed little to the explained variance in our study. The relative importance of these predictors, such as the ability of NNT to fix N, may have been obscured by the great weight of climate and other predictors when analyzing all RES as a whole. For instance, Castro-Díez et al. (Castro-Díez et al., 2019) considered RES separately and did find a remarkable effect of N-fixing NNT on soil fertility and formation, soil erosion control, and water regulation. Likewise, we found a small influence of leaf habit on the variation in impacts of NNT on RES, even though previous research highlights the importance of this predictor, as deciduous and evergreen NNT produce litter with different decomposition rates (Aerts, 1995; Aerts & Chapin, 1999; Berendse & Scheffer, 2009). Nevertheless, the results obtained for other predictors, such as the small contribution of phylogenetic distances, are similar to those reported in previous studies (Castro-Díez et al., 2014), supporting the idea that closely and distantly related species can exert similar impacts on RES. In this global-scale analysis, climate played a major role and overshadowed the influence of other predictors. However, the explanatory power of these factors may emerge at more local scales.

4.3. Combined effects of predictors

The regression tree allowed us to detect the main patterns and their underlying variables. Predictors in the upper part of the tree determined more pronounced differences in the variation in impacts of NNT on RES between nodes than predictors lower down the tree. Climatic variables dominated the top of the tree, which highlights the pivotal role of climate on determining NNT impacts on RES. The type of RES and human population density also had an influential position in the tree, while NNT height appeared at the bottom, indicating the relatively minor role of this trait.

Previously, Castro-Díez et al. (Castro-Díez et al., 2019; Castro-Díez et al., 2021) observed that climate (captured by biome type) explained an important part of the variation in impacts of NNT on RES. Other studies also noted the context-dependency of the impacts of NNT (Castro-Díez & Alonso, 2017; Castro-Díez et al., 2014; Xu et al., 2022). Here, we aimed to get a more detailed understanding of the influence of climate on the impacts of NNT by using more specific climatic variables. Low temperatures and high seasonality (both in temperature and precipitation) limited the capacity of NNT to increase RES, or even promoted negative impacts. Stressful climatic conditions in terms of temperature and water availability act as abiotic filters that restrict the chances of establishment and propagation of non-native species in the recipient environments (Alpert et al., 2000), a circumstance that can lead to low impacts of NNT on ecosystem functions and services. These conditions can also limit the NNT productivity, which may ultimately lead to small or negative impacts on RES that are strongly dependent on the rate of biomass production (Castro-Díez et al., 2019;

Castro-Díez et al., 2021). In contrast, under benign climatic conditions, NNT may achieve a high productivity and thus contribute positively to climate regulation (through carbon sequestration) and soil fertility, formation and erosion regulation and hydrological cycle regulation (through an increased supply of organic matter to the soil and root formation) (Castro-Díez et al., 2019; Evans, 2009; Lal, 2020; Libohova et al., 2018; Silva & Tomé, 2016). However, these trends may be altered by climate change. In fact, non-native species can exacerbate the negative impacts of climate change on ES by acting synergistically with it (Caldeira et al., 2015; López et al., 2022; Vilà et al., 2021). For example, non-native woody species with high water use rates can aggravate the impacts of extreme drought events on the regulation of hydrological cycles and other water-related ES (Caldeira et al., 2015; Diez et al., 2012; Rascher et al., 2011).

NNT showed greater positive effects on climate regulation and soil erosion regulation in more densely populated regions (China and Turkey). Denser human populations exert stronger demands for natural resources (food, raw materials), which can result in stronger disturbances of natural forests and greater demand for the introduction and spread of NNT (Allen & Barnes, 1985; Mather, 1993; Myers & Bazely, 2003; Pyšek et al., 2010; Williams, 1994). Humans select NNT for introduction based on their higher productivity relative to native species (Richardson, 1998; Woziwoda et al., 2014), which would explain the positive impacts on climate regulation and soil erosion regulation that we found.

Smaller NNT showed a larger positive effect size on climate regulation and soil erosion regulation than taller trees in tropical regions where annual mean temperatures exceed 26 °C. This was unexpected, as previous findings suggest a greater impact towards taller non-native species (Martin et al., 2017; Ni et al., 2021). Further research will be required to elucidate the underlying mechanisms that may explain this pattern.

Our study is based on data collected from numerous publications available in the literature, which may contain different biases. As our exploration showed, most of the studies come from Europe and North America, only a few NNT species are repeatedly studied, and some RES are analysed more frequently than others. These issues should be considered when interpreting our results. Also, our data set may become outdated as new results and studies are published. Thus, future updates would be necessary, an effort that could also reduce the aforementioned biases.

Our results suggest that policymakers should take the role of the context as a modulator of the impacts of NNT on RES into consideration when deciding about the introduction of new NNT. However, we also call for caution, as NNT may have simultaneous impacts in many ecosystem levels and, sometimes, NNT can promote some RES while impairing other services, ecosystem functions, or even native communities (Castro-Díez et al., 2019; Potgieter et al., 2017).

5. Conclusions

Our global-scale analysis suggests that climate is the main predictor of the impacts of NNT on RES. Highly productive regions, i.e., with constant warm temperatures and sustained rainfalls, promote positive impacts, possibly because NNT can reach their maximum productivity potential there. This close dependence on the climatic characteristics of the recipient communities may lead to the modification of the magnitude and sign of the effects of NNT on RES under future climate change scenarios. The impacts of NNT on soil fertility were more consistent than on other RES. A novel result is the remarkable influence of human population density, a predictor that has been little explored so far. Our findings can be useful to inform decision making for introducing NNT species that may enhance ecosystem functions and fulfil an increasing demand of ES, although policymakers should also focus on the potential trade-offs between ES that may arise.

CRediT authorship contribution statement

AR-B: Conceptualization, formal analysis, investigation, methodology, writing. **PC-D**: Conceptualization, manuscript review, writing, supervision, project administration, funding acquisition. **AL-L**: Formal analysis,

methodology, manuscript review. **RM-V**: Methodology, manuscript review.
PC: Methodology. **PP**: Manuscript review.

Data availability

The link to the raw data is shared in the Manuscript file

Declaration of competing interest

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.162961.

References

Aerts, R., 1995. The advantages of being evergreen. Trends Ecol. Evol. 10, 402–407. https://doi.org/10.1016/s0169-5347(00)89156-9.

Aerts, R., Chapin III, F.S., 1999. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Adv. Ecol. Res. 30, 1–67. https://doi.org/10.1016/S0065-2504(08)60016-1.

Allen, J.C., Barnes, D.F., 1985. The causes of deforestation in developing countries. Ann. Assoc. Am. Geogr. 75, 163–184.

Alpert, P., Bone, E., Holzapfel, C., 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspect. Plant Ecol. Evol. Syst. 3, 52–66. https://doi.org/10.1078/1433-8319-00004.

Berendse, F., Scheffer, M., 2009. The angiosperm radiation revisited, an ecological explanation for Darwin's 'abominable mystery'. Ecol. Lett. 12, 865–872. https://doi.org/10.1111/j.1461-0248.2009.01342.x.

Caldeira, M.C., Lecomte, X., David, T.S., Pinto, J.G., Bugalho, M.N., Werner, C., 2015. Synergy of extreme drought and shrub invasion reduce ecosystem functioning and resilience in water-limited climates. Sci. Rep. 5, 15110. https://doi.org/10.1038/srep15110.

Castro-Díez, P., Alonso, A., 2017. Alteration of nitrogen cycling as a result of invasion. In: Vilà, M., Hulme, P.E. (Eds.), Impact of Biological Invasions on Ecosystem Services. Springer International Publishing, Cham, pp. 49–62.

Castro-Díez, P., Godoy, O., Saldaña, A., Richardson, D.M., 2011. Predicting invasiveness of Australian acacias on the basis of their native climatic affinities, life history traits and human use: predicting invasiveness of Australian acacia spp. Divers. Distrib. 17, 934–945. https://doi.org/10.1111/j.1472-4642.2011.00778.x.

Castro-Díez, P., Godoy, O., Alonso, A., Gallardo, A., Saldaña, A., 2014. What explains variation in the impacts of exotic plant invasions on the nitrogen cycle? A meta-analysis. Ecol. Lett. 17, 1–12. https://doi.org/10.1111/ele.12197.

Castro-Díez, P., Vaz, S.A., Silva, J.S., van Loo, M., Alonso, A., Aponte, C., et al., 2019. Global effects of non-native tree species on multiple ecosystem services. Biol. Rev. 94, 1477–1501. https://doi.org/10.1111/brv.12511.

Castro-Díez, P., Alonso, Á., Saldaña-López, A., Granda, E., 2021. Effects of widespread non-native trees on regulating ecosystem services. Sci. Total Environ. 778, 146141. https://doi.org/10.1016/j.scitotenv.2021.146141.

Catford, J.A., Vesk, P.A., White, M.D., Wintle, B.A., 2011. Hotspots of plant invasion predicted by propagule pressure and ecosystem characteristics. Divers. Distrib. 17, 1099–1110. https://doi.org/10.1111/j.1472-4642.2011.00794.x.

Center for International Earth Science Information Network - CIESIN - Columbia University, 2018. Gridded Population of the World, Version 4 (GPWv4): Population Density, Revision 11. NASA Socioeconomic Data and Applications Center (SEDAC), Palisades, NY https://doi.org/10.7927/H49C6VHW.

Chaudhary, S., McGregor, A., Houston, D., Chettri, N., 2015. The evolution of ecosystem services: a time series and discourse-centered analysis. Environ. Sci. Policy 54, 25–34. https://doi.org/10.1016/j.envsci.2015.04.025.

De Bello, F., Botta-Dukát, Z., Lepš, J., Fibich, P., 2020. Towards a more balanced combination of multiple traits when computing functional differences between species. Methods Ecol. Evol. 12, 443–448. https://doi.org/10.1111/2041-210X.13537.

De'ath, G., Fabricius, K.E., 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81, 3178–3192. https://doi.org/10.1890/0012-9658(2000)081[3178:CARTAP]2.0.CO;2.

Dickie, I.A., Bennett, B.M., Burrows, L.E., Nunez, M.A., Peltzer, D.A., Porte, A., et al., 2014. Conflicting values: ecosystem services and invasive tree management. Biol. Invasions 16, 705–719.

Diez, J.M., D'Antonio, C.M., Dukes, J.S., Grosholz, E.D., Olden, J.D., Sorte, C.J.B., et al., 2012. Will extreme climatic events facilitate biological invasions? Front. Ecol. Environ. 10, 249–257. https://doi.org/10.1890/110137.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., et al., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x.

Edward, E., Munishi, P.K., Hulme, P.E., 2009. Relative roles of disturbance and propagule pressure on the invasion of humid tropical forest by Cordia alliodora (Boraginaceae) in Tanzania. Biotropica 41, 171–178. https://doi.org/10.1111/j.1744-7429.2008.00474.x.

Ehrenfeld, J.G., 2010. Ecosystem consequences of biological invasions. Annu. Rev. Ecol. Evol. Syst. 41, 59–80. https://doi.org/10.1146/annurev-ecolsys-102209-144650.

Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. J. Anim. Ecol. 77, 802–813. https://doi.org/10.1111/j.1365-2656.2008.01390.x.

Evans, J., 2009. The multiple roles of planted forests. In: Evans, J. (Ed.), Planted Forests: Uses, Impacts, And Sustainability. CAB International and FAO, pp. 61–90.

Feld, C.K., Segurado, P., Gutiérrez-Cánovas, C., 2015. Analysing the impact of multiple stressors in aquatic biomonitoring data: A 'cookbook' with applications in R. Sci. Total Environ. 15, 1320–1339. https://doi.org/10.1016/j.scitotenv.2016.06.243.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302–4315. https://doi.org/10.1002/joc.5086.

Fokkema, M., Smits, N., Zeileis, A., Hothorn, T., Kelderman, H., 2018. Detecting treatment-subgroup interactions in clustered data with generalized linear mixed-effects model trees. Behav. Res. Methods 50, 2016–2034. https://doi.org/10.3758/s13428-017-0971-x.

Haines-Young, R., Potschin, M., 2018. Common International Classification of Ecosystem Services (CICES) V5.1 And Guidance on the Application of the Revised Structure. European Environment Agency.

Hulme, P.E., Pyšek, P., Jarošík, V., Pergl, J., Schaffner, U., Vilà, M., 2013. Bias and error in understanding plant invasion impacts. Trends Ecol. Evol. 28, 212–218. https://doi.org/10.1016/j.tree.2012.10.010.

Jin, Y., Qian, H., 2019. V.PhyloMaker: an R package that can generate very large phylogenies for vascular plants. Ecography 42, 1353–1359. https://doi.org/10.1111/ecog.04434.

Kattge, J., Diaz, S., Lavorel, S., Prentice, C., Leadley, P., Boenisch, G., et al., 2011. TRY - a global database of plant traits. Glob. Chang. Biol. 17, 2905–2935.

Lal, R., 2020. Soil organic matter and water retention. Agron. J. 11, 3265–3277. https://doi.org/10.1002/agj2.20282.

Liao, C.Z., Peng, R.H., Luo, Y.Q., Zhou, X.H., Wu, X.W., Fang, C.M., et al., 2008. Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. New Phytol. 177, 706–714. https://doi.org/10.1111/j.1469-8137.2007.02290.x.

Libohova, Z., Seybold, C., Wysocki, D., Wills, S., Schoeneberger, P., Williams, C., et al., 2018. Reevaluating the effects of soil organic matter and other properties on available water-holding capacity using the National Cooperative Soil Survey Characterization Database. J. Soil Water Conserv. 73, 411–421. https://doi.org/10.2489/jswc.73.4.411.

Loh, W.Y., 2011. Classification and regression trees. WIRES Data Min. Knowl. 1, 14–23.

López, B.E., Allen, J.M., Dukes, J.S., Lenoir, J., Vilà, M., Blumenthal, D.M., et al., 2022. Global environmental changes more frequently offset than intensify detrimental effects of biological invasions. PNAS 119, e2117389119. https://doi.org/10.1073/pnas.2117389119.

MacDicken, K., Jonsson, O., Piña, L., Maulo, S., Adikari, Y., Garzuglia, M., et al., 2015. Global Forest Resources Assessment 2015: How Have the World's Forests Changed? FAO, Rome

Mack, R.N., 2003. Phylogenetic constraint, absent life forms, and preadapted alien plants: a prescription for biological invasions. Int. J. Plant Sci. 164, S183–S196. https://doi.org/10.1086/368399.

Martin, P.A., Newton, A.C., Bullock, J.M., 2017. Impacts of invasive plant son carbon pools depend on both species' traits and local climate. Ecology 98, 1026–1035. https://doi.org/10.1002/ecy.1711.

Mather, A., 1993. Afforestation. Policies, Planning And Progress. Belhaven Press, London.

McKinney, M.L., 2001. Effects of human population, area, and time on non-native plant and fish diversity in the United States. Biol. Conserv. 100, 243–252. https://doi.org/10.1016/S0006-3207(01)00027-1.

McKinney, M.L., 2002. Influence of settlement time, human population, park shape and age, visitation and roads on the number of alien plant species in protected areas in the USA. Divers. Distrib. 8, 311–318. https://doi.org/10.1046/J.1472-4642.2002.00153.X https://translate.google.com/website?sl=en&tl=es&prev=search&u=.

MEA, 2005. Ecosystem And Human Well-being: A Synthesis. Island Press, Washington, DC.

Myers, J., Bazely, D., 2003. Ecology And Control of Introduced Plants. Cambridge University Press, Cambridge.

Nakagawa, S., Santos, E.S.A., 2012. Methodological issues and advances in biological meta-analysis. Evol. Ecol. 26, 1253–1274. https://doi.org/10.1007/s10682-012-9555-5.

Ni, M., Deane, D.C., Li, S., Wu, Y., Sui, X., Zu, H., et al., 2021. Invasion success and impacts depend on different characteristics in non-native plants. Divers. Distrib. 27, 1194–1207. https://doi.org/10.1111/ddi.13267.

Pejchar, L., Mooney, H.A., 2009. Invasive species, ecosystem services and human wellbeing. Trends Ecol. Evol. 24, 497–504.

Potgieter, L.J., Gaertner, M., Kueffer, C., Larson, B.M.H., Livingstone, S.W., O'Farrell, P.J., Richardson, D.M., 2017. Alien plants as mediators of ecosystem services and disservices in urban systems: a global review. Biol. Invasion 19, 3571–3588. https://doi.org/10.1007/s10530-017-1589-8.

Pyšek, P., Vojtech, J., Tomáš, K., 2002. Patters of invasion in temperate nature reserves. Biol. Conserv. 104, 13–24. https://doi.org/10.1016/S0006-3207%2801%2900150-1.

Pyšek, P., Jarošík, V., Pergl, J., Randall, R., Chytrý, M., Kühn, I., et al., 2009. The global invasion success of Central European plants is related to distribution characteristics in their native range and species traits. Divers. Distrib. 15, 891–903. https://doi.org/10.1111/j.1472-4642.2009.00602.x.

Pyšek, P., Jarošík, V., Hulme, P.E., Kühn, I., Wild, J., Arianoutsou, M., et al., 2010. Disentangling the role of environmental and human pressures on biological invasions across Europe. PNAS 107, 12157–12162. https://doi.org/10.1073/pnas.1002314107.

Pyšek, P., Jarošík, V., Hulme, P.E., Pergl, J., Hejda, M., Schaffner, U., Vilà, M., 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. Glob. Chang. Biol. 18, 1725–1737. https://doi.org/10.1111/j.1365-2486.2011.02636.x.

R Core Team, 2021. R: A Language And Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Rangel, T.F., Colwell, R.K., Graves, G.R., Fučíková, K., Rahbek, C., Diniz-Filho, J.A.F., 2015. Phylogenetic uncertainty revisited: implications for ecological analyses. Evolution 69, 1301–1312. https://doi.org/10.1111/evo.12644.

Rascher, K.G., Große-Stoltenberg, A., Máguas, C., Werner, C., 2011. Understory invasion by Acacia longifolia alters the water balance and carbon gain of a Mediterranean pine forest. Ecosystems 14, 904–919. https://doi.org/10.1007/s10021-011-9453-7.

Rejmanek, M., Richardson, D.M., 1996. What attributes make some plant species more invasive? Ecology 77, 1655–1661. https://doi.org/10.2307/2265768.

Richardson, D.M., 1998. Forestry trees as invasive aliens. Conserv. Biol. 12, 18–26.

[FigShare]Romero-Blanco, A., Castro-Díez, P., Lázaro-Lobo, A., Molina-Venegas, R., Cruces, P., Pyšek, P., 2022. Global database with the effect size of many non-native tree species on regulating ecosystem services. Dataset (v3). https://doi.org/10.6084/m9.figshare.20141483.v3.

Rosenberg, M.S., Adams, D.C., Gurevitch, J., 2000. MetaWin: Statistical Software for Meta-analysis. Version 2.0. Sinauer Associates, Sunderland, MA, USA.

Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V., Woolmer, G., 2002. The human footprint and the last of the wild. Bioscience 52, 891–904. https://doi.org/10.1641/0006-3568(2002)052[0891:THFATL]2.0.CO;2.

Senior, A.M., Grueber, C.E., Kamiya, T., Lagisz, M., O'Dwyer, K., Santos, E.S.A., Nakagawa, S., 2016. Heterogeneity in ecological and evolutionary meta-analyses: its magnitude and implications. Ecology 97, 3293–3299. https://doi.org/10.1002/ecy.1591.

Silva, J.S., Tomé, M., 2016. Tasmanian blue gum in Portugal – opportunities and risks of a widely cultivated species. In: Krumm, F., Vítková, L. (Eds.), Introduced Tree Species in European Forests: Opportunities And Challenges. European Forest Institute, Freiburg, pp. 352–361.

Spear, D., Foxcroft, L.C., Bezuidenhout, H., McGeoch, M.A., 2013. Human population density explains alien species richness in protected areas. Biol. Conserv. 159, 137–147. https://doi.org/10.1016/j.biocon.2012.11.022.

The Plant List, 2013. Version 1.1. Published on the Internet.Available online at http://www.theplantlist.org/ accessed on March, 2021.

Vaz, A.S., Castro-Díez, P., Godoy, O., Alonso, A., Vilà, M., Saldaña, A., et al., 2018. An indicator-based approach to analyse the effects of non-native tree species on multiple cultural ecosystem services. Ecol. Indic. 85, 48–56. https://doi.org/10.1016/j.ecolind.2017.10.009.

Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarosik, V., Maron, J.L., et al., 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecol. Lett. 14, 702–708. https://doi.org/10.1111/j.1461-0248.2011.01628.x.

Vilà, M., Beaury, E.M., Blumenthal, D.M., Bradley, B.A., Early, R., Laginhas, B.B., et al., 2021. Understanding the combined impacts of weeds and climate change on crops. Environ. Res. Lett. 16, 034043. https://doi.org/10.1088/1748-9326/abe14b.

Williams, M., 1994. Forests and tree cover. In: Meyer, W.B., Turner II, B.L. (Eds.), Changes in Land Use And Land Cover: A Global Perspective. Cambridge University Press, Cambridge, pp. 97–124.

Woziwoda, B., Kopec, D., Witkowski, J., 2014. The negative impact of intentionally introduced Quercus rubra L. on a forest community. Acta Soc. Bot. Pol. 83, 39–49. https://doi.org/10.5586/asbp.2013.035.

Xu, H., Liu, Q., Wang, S., Yang, G., Xue, S., 2022. A global meta-analysis of the impacts of exotic plant species invasion on plant diversity and soil properties. Sci. Total Environ. 810, 152286. https://doi.org/10.1016/j.scitotenv.2021.152286.

Zhou, Y., Staver, A.C., 2019. Enhanced activity of soil nutrient-releasing enzymes after plant invasion: a meta-analysis. Ecology 100, e02830. https://doi.org/10.1002/ecy.2830.

Zobel, B.J., van Wyk, G., Stahl, P., 1987. Growing Exotic Forests. John Wiley & Sons, New York.