

Impact of non-native tree species in Europe on soil properties and biodiversity: a review

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Abstract

In the context of global change, the integration of non-native tree (NNT) species into European forestry is increasingly being discussed. The ecological consequences of increasing use or spread of NNTs in European forests are highly uncertain, as the scientific evidence is either constraint to results from case studies with limited spatial extent, or concerns global assessments that lack focus on European NNTs. For either case, generalisations on European NNTs are challenging to draw. Here we compile data on the impacts of seven important NNTs (*Acacia dealbata*, *Ailanthus altissima*, *Eucalyptus globulus*, *Prunus serotina*, *Pseudotsuga menziesii*, *Quercus rubra*, *Robinia pseudoacacia*) on physical and chemical soil properties and diversity attributes in Europe, and summarise commonalities and differences. From a total of 103 publications considered, studies on diversity attributes were overall more frequent than studies on soil properties. The effects on soil properties varied greatly among tree species and depended on the respective soil property. Overall, increasing (45%) and decreasing (45%) impacts on soil occurred with similar frequency. In contrast, decreasing impacts on biodiversity were much more frequent (66%) than increasing ones (24%). Species phylogenetically distant from European tree species, such as *Acacia dealbata*, *Eucalyptus globulus* and *Ailanthus altissima*, showed the strongest decreasing impacts on biodiversity. Our results suggest that forest managers should be cautious in using NNTs, as a majority of NNT stands host fewer species when compared with native tree species or ecosystems, likely reflected in changes in biotic interactions and ecosystem functions. The high variability of impacts suggests that individual NNTs should be assessed separately, but NNTs that lack European relatives should be used with particular caution.

Keywords

biodiversity, biogeography, forest management, pairwise stand comparisons, soil impacts

Introduction

Many non-native tree (NNT) species were introduced to Europe, particularly after the 16th century (Brundu and Richardson 2016). Some of these species have been deliberately favoured across Europe through cultivation, mostly because of the different goods and services they provide to societies (Castro-Díez et al. 2019; Brundu et al. 2020; Pötzelsberger et al. 2020a; Castro-Díez et al. 2021). After their initial introductions, some of the NNTs have spread without further human intervention, profiting from suitable soil and climate, competitive superiority and/or habitat disturbance, eventually becoming naturalised, or even invasive (Dodet and Collet 2012). NNTs in Europe include species that are planted for timber (e.g. *Eucalyptus globulus*, *Robinia pseudoacacia*, *Pseudotsuga menziesii*, *Picea sitchensis*; Brundu and Richardson 2016; Brus et al. 2019; Spiecker et al. 2019; Øyen and Nygaard 2020) or once were used for ornamental purposes and have spread since (e.g. *Ailanthus altissima* and *Acacia dealbata*). Overall, NNTs

cover an area of approximately 8.54 million ha, of which *R. pseudoacacia* (2.44 million ha) and *E. globulus* (1.46 million ha) are the most abundant (Fig. 1), corresponding to about 4% of the forest cover in Europe (Brus et al. 2019). This overall percentage hides considerable disparities among European regions and countries. For example, the most abundant tree species in Portugal (*E. globulus*), Hungary (*R. pseudoacacia*) and the UK (*P. sitchensis*) are non-native, while in most other European countries NNTs have a minor importance compared to native tree species (Hasenauer et al. 2016).

The pros and cons of economically valuable NNTs is a topic of lively debate because of the possible detrimental impacts on the ecosystems that may result from the expansion of these species (Campagnaro et al. 2018; Castro-Díez et al. 2019; Pötzelsberger et al. 2020b; Wagner et al. 2021; Wohlgemuth et al. 2021). In addition, NNTs are increasingly discussed in the frame of global change (Brundu and Richardson 2016) and the consequences of climate change on biological invasions and adequate management practices (e.g. Walther et al. 2009). Because of this concern, a large and diverse body of legislation has been created in many European countries, aiming at regulating the establishment of NNTs (Pötzelsberger et al. 2020b). One of the most important pieces of legislation is Regulation (EU) No 1143/2014, the core of which is a list of invasive alien species of concern to the EU, including some NNTs (e.g. *A. altissima* and *Acacia saligna*). Among other provisions, the regulation refers the obligation of the different EU Member States to have in place effective management measures for invasive alien species of EU concern that are widespread. In addition, guidelines on the management of NNTs have been proposed by several authors, aiming at minimising their possible detrimental impacts (Brundu and Richardson 2016; Sitzia et al. 2016; Campagnaro et al. 2018; Brundu et al. 2020).

Among the ecological impacts commonly attributed to NNTs, those related to soil and biodiversity are feasible to measure, functionally important and therefore particularly attractive for research (Hulme et al. 2013). The impacts of NNTs on soil properties can have long-term ecological consequences given the importance of soil as a basis for ecosystem functioning. Among the impacts on soil properties and processes most frequently attributed to NNTs are those related to changes in nitrogen content (Castro-Díez et al. 2009) and other nutrients (Medina-Villar et al. 2016), decomposition rate of organic matter (Godoy et al. 2010), pH (Cremer and Priezel 2017) and organic carbon (Jackson et al. 2002; Zerva et al. 2005). Soil changes induced by NNTs may be viewed as either beneficial or detrimental, depending on the perspective. For example, an increase in soil nitrogen originated by a leguminous species may be considered beneficial from a farmer's perspective, but detrimental from a conservationist's perspective. It may be detrimental if it alters ecosystem functions and processes of a site or preventing the survival of species naturally-adapted to nutrient-poor soils such as sand dune species (Huston and Smith 1987). However, it may be beneficial if we consider the improvement of soil fertility, for example when rehabilitating mined areas (Dutta and Agrawal 2003; Vlachodimos et al. 2013; Yuan et al. 2018) or improving the conditions for nitrophilous weed species (Yelenik et al. 2004). As to biodiversity, there is certainly a solid argument for the detrimental impacts of NNTs in situations where they reduce richness and diversity of native taxa, or the abundance of native animal or plant populations. A large body of literature has been produced on the

impacts of European NNT species on biodiversity, ranging from microbes (Krevš and Kučinskienė 2017) to plant communities (Chabrierie et al. 2007), invertebrates (Gossner 2016) or birds (Calviño-Cancela 2013).

A large number of papers on the impacts of NNTs has accumulated steadily during the previous century and more rapidly after the launching of the Millennium Ecosystem Assessment (Hassan et al. 2005). Researchers have been particularly keen in conducting comparisons between ecosystems populated by NNTs and native vegetation (NV; mostly native tree (NT) species or native treeless or open ecosystems (OE)), using similar site and climate conditions, to quantify the impact on specific ecosystem properties. Such studies are highly valuable as they often generate robust results based on sound statistical designs. However, the impact of NNTs can be highly context-dependent (Castro-Díez et al. 2019; Sapsford et al. 2020; Castro-Díez et al. 2021), and may vary, e.g. according to the management history of the studied stands, the soil and climate characteristics of the sites, or to the NV to which it is compared. European-wide or global assessments have so far focused on the impact of NNTs on ecosystem services (Castro-Díez et al. 2019), on the impact of mainly invasive plant species on communities and ecosystems (Pyšek et al. 2012), or on the impact of five major NNTs in Natura 2000 sites in Europe (Campagnaro et al. 2018). Nevertheless, a standardised analysis on the impact of NNTs on soil properties and biodiversity based on the existing literature is lacking.

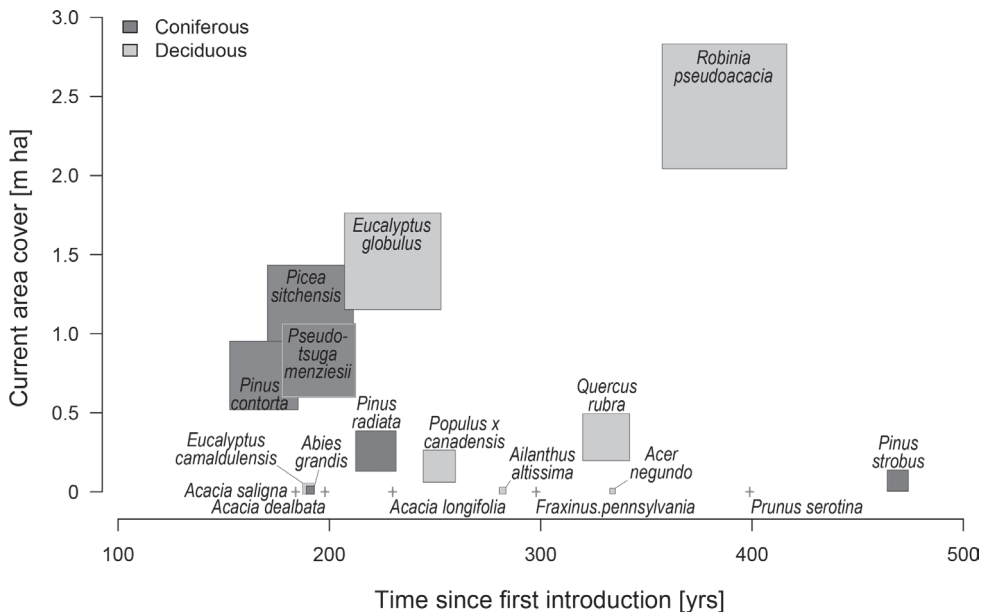


Figure 1. Current forest area cover of 18 selected NNTs in Europe and year since first introduction (based on Sanz-Elorza et al. 2004; Hasenauer et al. 2016; Badalamenti et al. 2018; Brus et al. 2019). The surface of each square is proportional to the surface covered by each NNT in Europe. The coordinates correspond to the centroid of the square. For NNTs with insufficient information, the symbol '+' is used.

To fill this knowledge gap, here we select seven important NNTs and compile data from a large body of literature on their impacts on soil and biodiversity in Europe, to summarise their commonalities and differences. Specifically, in this study we aim to: (a) assess the relative importance of the different NNTs and their impacts based on published papers, dissertations and reports; (b) assess the impacts of NNTs on soil properties and diversity attributes of different taxa in forests of Europe, based on pairwise comparisons against NV; (c) analyse the commonalities and differences in the impacts of selected NNTs; and (d) discuss the factors that may explain similar or contrasting responses based on available information on NNT traits, biogeography and management.

Materials and methods

NNT selection and workflow

This study was initiated in the frame of the COST Action Non-Native Tree Species for European Forests – Experiences, Risks and Opportunities (FP 1403; 2014–18). From the more than 150 NNTs growing in European forests and forestry trials (Brus et al. 2019), we initially selected the 18 most important ones (Table 1), with their importance assessed according to their forest area cover (if available), and the presence in numerous European countries (Europe defined geographically, but excluding Russia and including Turkey), and/or their rapid spread. We assumed that for the species with these three characteristics, there are likely to be more studies and publications on the impacts. A species is defined as being non-native to Europe if its native range is wholly outside of Europe. Thus, tree species native to Europe but planted outside of their regional distributional range, such as *Pinus nigra*, *Larix decidua* or *Picea abies* were not considered as being non-native even when planted outside of their native range.

The workflow was divided into three phases. In the first phase, we searched the Web of Science (WOS) using the name of the NNT species (e.g. *Prunus serotina*; see Table 1; Fig. 2) as search string. The search covered all papers published until August 2021. Publications retrieved from the search were filtered in order to only retain those featuring pairwise comparisons of NNTs vs. NV regarding effects on physical and chemical soil properties and diversity attributes (abundance, species richness, diversity) of different taxonomic groups studied in European countries. We extended the comparisons with NTs to non-forest ecosystems (OE), as long as they represented a reference for naturalness in the study area. In this phase, four species (*Acacia longifolia*, *A. saligna*, *Eucalyptus camaldulensis* and *Populus × canadensis*) were excluded from further examination due to the low number of studies ($n < 20$). To increase the number of studies, we extended the search in the second phase to (i) scientific literature with no restriction on language, and (ii) PhD and MSc theses, or other studies published in non-WOS journals or books. Then, the statistical design of pairwise comparisons (NNTs vs. NV) of the selected studies was checked, and the results were examined for analysis of statistical significance, be

it based on tests, figures with error bars, data tables allowing for calculating, e.g. t-tests, or reporting significance. Because of the great variety of indicators used in different studies for assessing differences in soil properties and diversity attributes, the parameters were aggregated, according to Tables 2, 3. Three other species (*Fraxinus pennsylvanica*, *Abies grandis* and *Pinus contorta* var. *latifolia*) were excluded from the analysis because of the low numbers of soil properties or taxa groups concerning these species.

In the third phase, we focused on NNTs having >150 comparisons (cases), where a comparison of NNTs vs. NV regarding one soil property or one species group is one case. As a result, *Acer negundo* (n = 21), *P. sitchensis* (n = 23), *Pinus radiata* (n = 2) and *Pinus strobus* (n = 8) were excluded, leaving seven species: *A. dealbata*, *R. pseudoacacia*, *Quercus rubra*, *E. globulus*, *P. serotina*, *A. altissima* and *P. menziesii*. For the final seven NNTs selected from the 18 focal ones, a total of 103 scientific publications (Suppl. material 1: table S1, fig. 2) with pairwise comparisons regarding soil properties and diversity attributes were included in the analysis. The number of papers found for the NNTs positively correlates with the area cover, with most studies concerning *R. pseudoacacia* (n = 32), *P. menziesii* (n = 27) and *E. globulus* (n = 22) (Suppl. material 1: fig. S1). For three species the number of publications was too low (*P. sitchensis*, n = 4; *P. radiata*, n = 1; and *P. strobus*, n = 1), even though these species are among the most widely planted NNTs in Europe.

Table 1. Non-native tree species (NNTs) in Europe considered for literature searches (phase 1), the number of European countries where the species is present (Hasenauer et al. 2016; Brus et al. 2019; gbif.org), total area cover (if indicated, otherwise NA), and selection for final comparisons in regard to a sufficient number of pairwise comparisons. Only NNTs that reached the end of phase 3 had a sufficient number of papers on their impacts.

Family	Species	Origin	Presence in European countries		Considered in study phase
			Countries #	Area [ha]	
Broadleaves					
Fabaceae	<i>Acacia dealbata</i>	Australia	5	NA	3
Fabaceae	<i>Acacia longifolia</i>	Australia	5	NA	1
Fabaceae	<i>Acacia saligna</i>	Australia	10	NA	1
Fabaceae	<i>Robinia pseudoacacia</i>	North America	29	2.437.600	3
Fagaceae	<i>Quercus rubra</i>	North America	24	345.333	3
Myrtaceae	<i>Eucalyptus camaldulensis</i>	Australia	4	20.000	1
Myrtaceae	<i>Eucalyptus globulus</i>	Australia	6	1.458.000	3
Oleaceae	<i>Fraxinus pennsylvanica</i>	North America	10	NA	2
Rosaceae	<i>Prunus serotina</i>	N or C America	14	NA	3
Salicaceae	<i>Populus × canadensis</i>		14	162.274	1
Sapindaceae	<i>Acer negundo</i>	N or C America	16	4.724	2
Simaroubaceae	<i>Ailanthus altissima</i>	Asia	18	7.142	3
Conifers					
Pinaceae	<i>Abies grandis</i>	North America	11	10.459	2
Pinaceae	<i>Picea sitchensis</i>	North America	13	1.160.400	2
Pinaceae	<i>Pinus radiata</i>	North America	3	257.000	2
Pinaceae	<i>Pinus contorta</i> var. <i>latifolia</i>	North America	11	736.000	2
Pinaceae	<i>Pinus strobus</i>	North America	19	70.382	2
Pinaceae	<i>Pseudotsuga menziesii</i>	North America	32	830.707	3

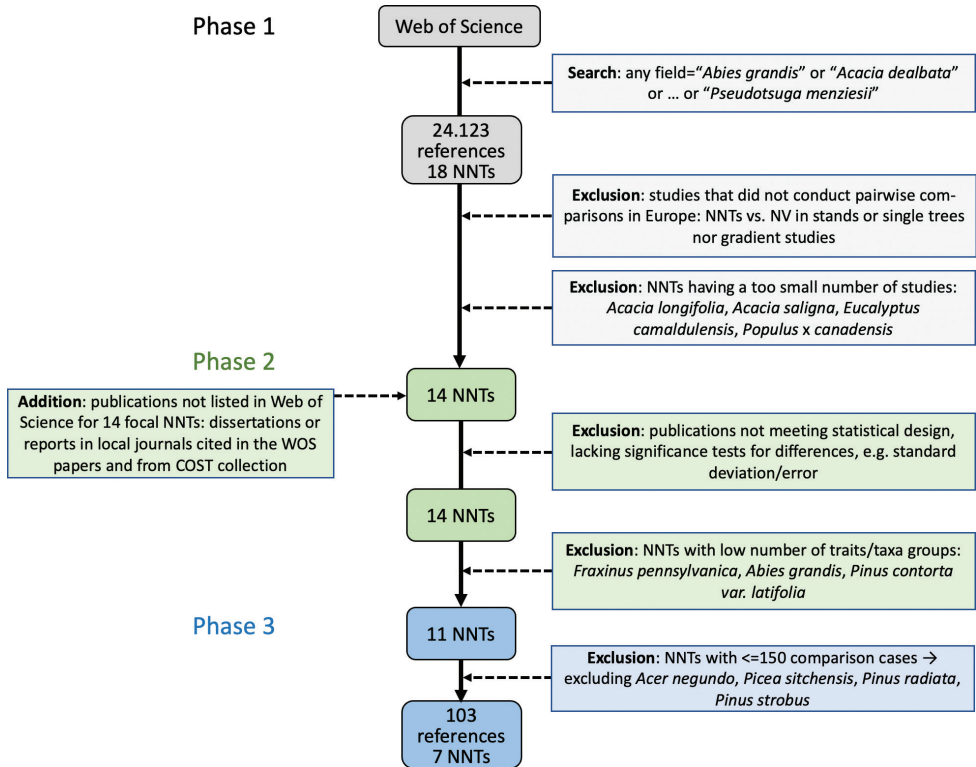


Figure 2. Flowchart of the selection of publications and non-native tree species (NNT). Studies on the effects of NNTs in European forests on soil properties and diversity attributes of different taxonomic groups were considered.

Data analysis

Aggregated soil properties and diversity attributes were counted according to increasing (+1), neutral (0) or decreasing (-1) effects ($p < 0.05$) for the final seven NNTs. The presence of an NNT was considered to have an increasing or decreasing effect if the average values of an attribute reported for NNT stands/individuals were significantly higher or lower when compared with NV stands/individuals. The terms increasing and decreasing relate to the direction of change rather than any judgement about whether the effect on the ecosystem is beneficial/detrimental. While for diversity attributes, increasing effects translate to an increase of abundance- or diversity related attributes, increasing effects with respect to soil properties can be, for some examples, interpreted as having an adverse effect on an ecosystem. For example, an increase in C:N ratio indicates a reduction of N availability, e.g. reduced soil activity.

Due to the great variety of soil properties and diversity attributes used in the studies, comparable traits were aggregated. Cases of increasing, decreasing and neutral effects were counted and used to display differences among NNTs. The numbers then served for transformations to percentages. As these balances reflect all cases found for

Table 2. Most frequently analysed soil properties collected from 103 papers, aggregated and by original description, including number of cases (No); for a complete list of all properties mentioned in the references, see Suppl. material 1: table S1.

Soil properties, aggregated	Soil properties, original	No
N	N, N floor, N foliar, N litter, N mineral, N soil, N stock, N topsoil, N topsoil stock, N total, N total floor, N total topsoil, NH_4^+ , NH_4^+ topsoil, NH_4^+ , NO_2^- , NO_3^- , NO_3^- topsoil, $\text{NO}_3^-/\text{NH}_4^+$	223
pH	pH floor, pH A, pH B, pH H_2O , pH- H_2O floor, pH H_2O topsoil, pH KCl, pH KCl floor, pH KCl litter, pH KCl topsoil, pH L, pH litter, pH soil, pH topsoil	149
C:N	C:N, C:N A, C:N B, C:N floor, C:N foliar, C:N litter, C:N organic, C:N soil, C:N topsoil	93
Ca	Ca+, Ca+ floor, Ca+ litter, Ca+ soil, Ca+ topsoil, Ca_2^+ , Ca_2^+ exchangeable	70
K	K, K available, K floor, K topsoil, K topsoil available, K total floor, K soil, K total topsoil, K+, K+ floor, K_2O	67
Mg	Mg, Mg floor, Mg soil, Mg total floor, Mg total topsoil, Mg_2^+ , Mg_2^+ floor, MgO	60
P	P, P available, P available topsoil, P exchangeable, P foliar, P total, P total floor, P total topsoil, P total, P_2O_2 , P_2O_3 , P_2O_4 , P_2O_5 , P_2O_6 , P_2O_7 , PO_4	60
CEC	Cation exchange capacity: CEC, CEC floor, CEC litter, CEC topsoil	58

soil properties and diversity attributes, irrespective of whether these cases refer to similar soil properties or closely related taxonomic groups in a specific reference, possible nested cases may lead to biased results. Therefore, averages of cases per aggregated soil property and diversity attribute were also calculated reference-wise and balances were re-calculated accordingly. For example, Buchholz et al. (2015) compared different insect taxonomic groups regarding abundance, species richness and beta-diversity in *R. pseudoacacia* and *Betula pendula* stands in the city of Berlin, Germany. From 17 cases, four were significantly decreasing (-1), and in 13 cases no significant differences were found (0). For this reference, the average effect on insects was calculated as -0.24 (-4/17). Three other references reported all decreasing effects of *R. pseudoacacia* on insects (1× in Reif et al. 2016, 1× in Hejda et al. 2017, and 2× in Kadlec et al. 2018). Averaging for all cases affecting insects, the total effect of *R. pseudoacacia* was calculated as -0.38 (-8/21) for this diversity attribute. In contrast, if the average effect on insects was calculated separately for the four references (-0.24, -1, -1, -1), and then the average total effect was calculated, then the total effect was -0.81 (-3.24/4).

To summarise our results of the effects of the final seven NNTs on soil properties and diversity attributes, we used a Principal Components Analysis (PCA). Effect scores for each NNT are based on total averages. Only the effects with data available for all NNTs were considered in this analysis. All analyses and graphs were developed using the statistical software R version 4.1.3 (R Development Core Team, 2022) and the packages dplyr, ggplot2, rgdal and raster.

Data availability

The data underpinning the analysis reported in this paper are deposited at <https://doi.org/10.16904/envidat.350>.

Table 3. Most frequent taxa groups (aggregated) from 103 papers, with original taxa groups, diversity attributes, and number of cases (No).

Coarse taxa group	Taxa groups mentioned in the references	Biodiversity measures	No
Vascular plants	Garden natives, geophytes, hemicryptophytes, nemoral plant species, nitrophilous species, rare plant species, road natives, shrubs, small herbs, tall herbs, therophytes, tree regeneration, trees, vascular plants, wood natives	Abundance, biomass, cover, alpha-, beta-, gamma- diversity	720
Microorganisms	Ammonification, ammonification rate, acid phosphatase (AP) activity, bacteria, beta-glucosidase (BG) activity, decomposition, fungi, enzyme activity, glycine aminopeptidase (GAP) activity, geometric mean of enzymatic activities (GMEA), microbes, mineralisation, mineralisation rate, N mineralisation, nitrification rate, soil species	Abundance, activity rates, alpha-diversity	229
Insects	Blattodea; Coleoptera: <i>taxonomic:</i> Carabidae, Staphylinidae, Scolytidae, <i>functional:</i> phytophagous, xylophagous, zoophagous, aphidophagous, mycetophagous, copro-/sapro-/necrophagous, omniphagous, saproxylic; Dermoptera; Diptera: Brachycera (all, Syrphidae), Nematocera; Hemiptera: Sternorhyncha – Aphidina, Psyllidae; Auchenorrhyncha; Heteroptera; Hymenoptera: Formicidae, others; Lepidoptera (all, moths, Heterocera, larvae); Neuroptera; Psocoptera; Raphidioptera; Thysanoptera; holometabolic larvae; other insects or not further distinguished	Abundance, biomass, alpha-, beta-, gamma-diversity	193
Other arthropods	Arachnida: Acari (Acaridida, Actinedida, Gamasina, Oribatida; Gymnonota, Macropylina, Poronota), Araneae, Opiliones; Collembola (Entomobryomorpha, Poduromorpha, Symphypleona); Myriapoda: Chilopoda, Diplopoda; Isopoda; Entognatha: Protura Functional arthropod groups: aerial, micro-/macro, mycetophagous, polyphagous, saprophagous, soil-dwelling	Abundance, biomass, alpha-, beta-diversity	165
Bryophytes	Bryophytes	Abundance, alpha-, beta-diversity	78
Birds	Bird species	Abundance, alpha-diversity	70
Mammals	Bats, carnivores, mammals	Abundance	24
Lichens	Lichens	Abundance, alpha-diversity	17

Results

The majority of the selected studies were conducted in Central Europe and the Western Mediterranean region, while studies on NNTs in the British Isles, North and East Europe (e.g. *P. sitchensis* or *A. negundo*) were excluded because of the low numbers of cases (Fig. 3). Among the NNTs, *P. menziesii* (n = 615), *R. pseudoacacia* (n = 391) and *A. dealbata* (n = 360) accumulated most cases, followed by *P. serotina* (n = 315), *Q. rubra* (n = 230), *E. globulus* (n = 207) and *A. altissima* (n = 158).

In general, the different NNTs were compared with the NV that was dominant in each study region (Suppl. material 1: table S3). For *A. dealbata* and *E. globulus*, Mediterranean pine (e.g. *Pinus pinaster*) and oak species (e.g. *Quercus ilex* and *Q. suber*) but also Mediterranean shrubland types were used for the comparisons. *Ailanthus altissima* was mostly studied in floodplains characterised by the presence of poplar (*Populus* spp.) species. For *P. serotina* and *Q. rubra*, both growing mostly in Central Europe, *Pinus*

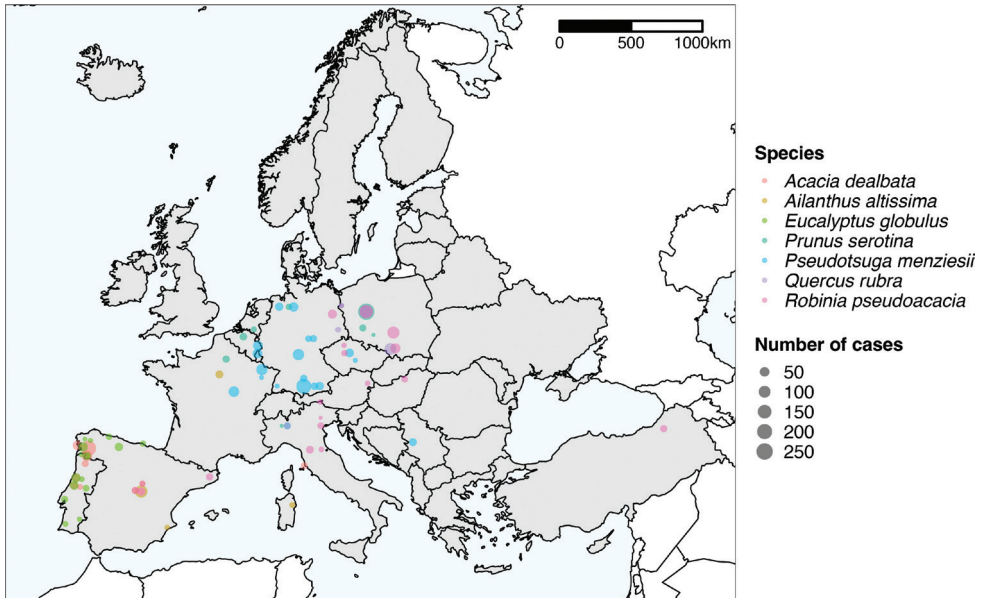


Figure 3. Geographic distribution of studies with pairwise comparisons between tree species non-native to Europe (NNTs; countries considered for this study in grey) and native vegetation (NV), and number of cases for each of the seven NNTs with in total sufficiently high numbers of cases (>150).

sylvestris, oak species (*Quercus* spp.) and *Fagus sylvatica* were mostly the native references. For *P. menziesii*, the native references were mostly *Picea abies* and *F. sylvatica*, and for *R. pseudoacacia* the native references were mostly pine and oak species.

Soil properties

From 780 soil property comparisons collected for the seven NNTs, the aggregated properties N ($n = 223$), pH ($n = 152$), and C:N ($n = 93$) were the most frequently considered properties in the studies (Fig. 4, Suppl. material 1: table S2). Except for cases regarding *P. menziesii*, the other soil properties received little attention, in particular cation exchange capacity (CEC), Mg, K, P and Ca.

The number of cases per species and per soil property was uneven (Fig. 4). Among the NNTs, the most studied was *P. menziesii* with the highest number of overall soil property case studies ($n=364$), followed by *A. dealbata* ($n=135$) and *R. pseudoacacia* ($n=108$). The lowest number of cases was found for *Q. rubra* ($n=32$). Of all soil property cases considered, 16.9% were decreasing, 61.5% neutral, and 21.5% increasing. Out of 56 possible combinations of eight aggregated soil properties for each of the seven NNTs, the literature review retrieved information on 49 combinations. Of these, impacts were decreasing in 19 cases (39%), neutral in eight (16%) and increasing in 22 (45%).

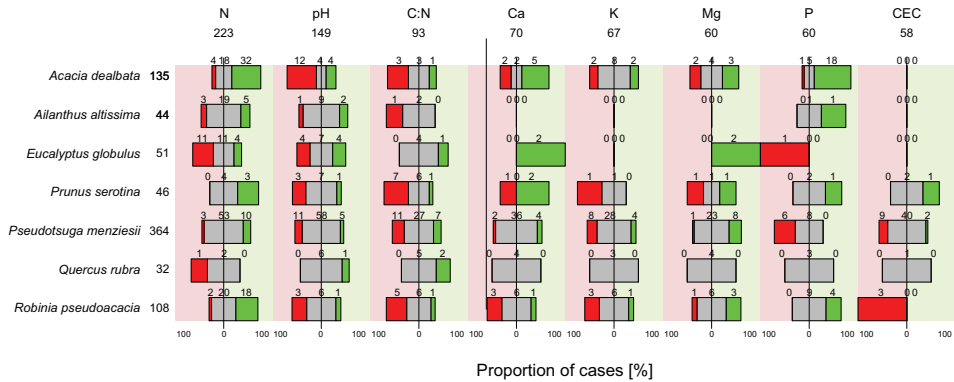


Figure 4. Proportion of cases with significant increasing (green), significant decreasing (red) or neutral (grey; non-significant) effects of the seven tree species non-native to Europe (NNTs) on soil properties (aggregations listed in Table 2) found for each NNT in comparison to stands of native vegetation (NV). Numbers of cases are shown next to the NNTs names, below the soil properties and above the bars. Increasing, decreasing and neutral effects were based on statistical significance ($p < 0.05$).

The following clear trends could be observed: *A. dealbata* increased nitrogen and phosphorus and decreased pH in soils. C:N ratio decreased, e.g. soil activity became higher, in stands of *P. serotina* and *R. pseudoacacia*. In many cases ‘no changes’ was the most common outcome per species and soil property; in particular, this was observed for *A. altissima* for nitrogen and pH, *P. menziesii* for nitrogen, pH, C:N, calcium, potassium, magnesium and CEC, and *R. pseudoacacia* for pH and, to some extent, also for nitrogen.

Diversity attributes

Of all cases considered, the occurrence of NNTs was recorded as having a decreasing effect in 22.4% of cases, a neutral effect in 65.4% of cases, and an increasing effect in 12.1% of cases.

The number of cases per species and per diversity attribute was more even than for soil properties (Fig. 5). The highest numbers of cases were recorded for *R. pseudoacacia* ($n=283$), *P. serotina* ($n=269$) and *P. menziesii* ($n=251$); whereas the lowest numbers of cases were recorded for *E. globulus* ($n=156$) and *A. altissima* ($n=114$). The category vascular plants was the most frequently studied taxonomic group ($n=720$), while several other groups were rarely studied (birds, bryophytes, mammals, lichens). Most decreasing effects were reported for *E. globulus* and – to a considerable extent – also for *A. altissima*. While in a majority of cases, *P. serotina* presented increasing effect balances, *R. pseudoacacia* had one increasing effect out of seven combinations, *P. menziesii* two increasing effects out of five combinations, and *A. dealbata* two increasing effects out of six combinations. In contrast to the reviewed effects on soil properties,

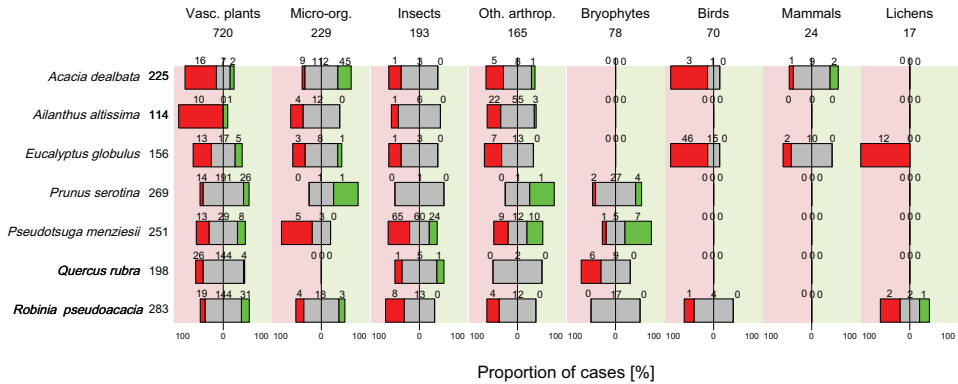


Figure 5. Proportion of cases with increasing (green), decreasing (red) or non-significant (grey) effects of tree species non-native to Europe (NNTs) on diversity attributes (abundance, species richness or diversity) of different taxonomic groups in comparison to native vegetation (NV). Numbers of cases are shown next to the NNTs names, below the diversity attributes and above the bars. Increasing, decreasing and neutral effects were based on statistical significance ($p < 0.05$).

the consistency of the effects on taxa groups was greater. *Acacia dealbata*, *A. altissima*, *E. globulus* and *Q. rubra* had clearly decreasing effect balances on vascular plant species diversity when compared to native counterparts.

Out of 56 possible combinations, the literature review retrieved information on 38. Out of these balances of NNTs occurrences, 25 (65.8%) had a decreasing effect, 9 (23.7%) an increasing effect, and 4 (10.5%) a neutral effect.

Effects of diversity attributes were finally compared between the two approaches of averaging cases (Fig. 6). Averages using only one value for a taxa group per reference (grey bars) corresponded quite well with averages over all diversity attributes, e.g. taxa groups per NNT (black bars). Only in a few cases, such as vascular plants and bryophytes on *P. serotina* and lichens on *R. pseudoacacia*, did the use of subordinate groups contrast with the averages per reference.

Consistently available soil properties and diversity attributes were used to analyse the different effects of NNTs by Principal Components Analysis (PCA). While cases for all NNTs were available for the soil variables N, P, C:N ratio and pH, three taxa groups (insects, other arthropods and vascular plants) served for comparisons of all NNTs (Suppl. material 1: fig. S2). In the soil biplot, *E. globulus* and *Q. rubra* tended to increase C:N ratio, e.g. decreased soil activity, and increased pH in the case of *Q. rubra*. In the opposite direction, *A. dealbata*, *R. pseudoacacia* and *P. serotina* corresponded to increased N- and P-contents as well as decreased C:N ratio, indicating increased soil activity. Equally, the presence of NNTs (except for *Q. rubra* and *A. altissima*) tended to decrease pH. While *P. menziesii* seemed to slightly decrease soil activity (e.g. increase C:N) and slightly deplete N and P, *A. altissima* corresponded to an increased P content in soils.

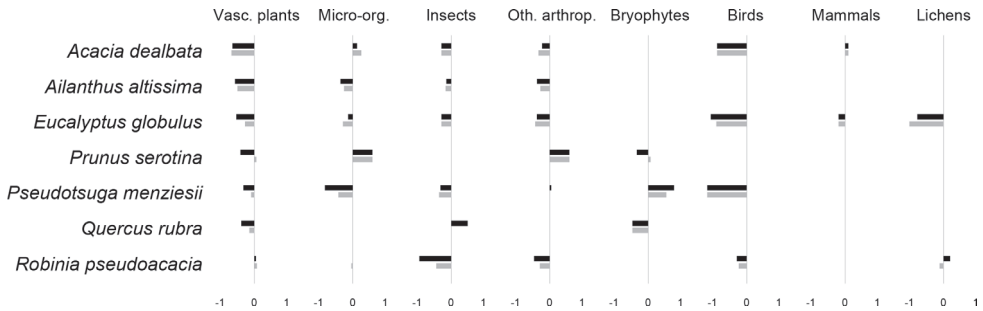


Figure 6. Averaged effects (increasing=1, decreasing=-1, none=0) of tree species non-native to Europe (NNTs) on the most frequently mentioned taxonomic groups. Grey bars indicate averaged effects using all cases (e.g. subordinate groups) found in the references; black bars indicate average values of one value for each reference and taxonomic group (e.g. subordinate groups are averaged per reference).

In contrast to the soil biplot, the biodiversity biplot resulted in complex patterns of taxa groups and NNTs that are mainly driven by the strongest signals of diversity \times species interactions and distorting weaker signals (Suppl. material 1: fig. S2). While *A. altissima* and *A. dealbata* clearly decreased vascular plant diversity, most NNTs decreased both insect and arthropod diversity.

Discussion

Most studied NNTs and most studied impacts

The number of comparisons between tree species non-native to Europe (NNTs) and native vegetation (NV) are an indicator of the effort that has been invested by researchers in the study of different impacts of these NNTs on native ecosystems. This effort may give us information on the importance of each combination of species impact for the scientific community (e.g. Pyšek et al. 2020). Our analyses demonstrate that the most abundant studies found on pairwise comparisons between NNTs and NV matched the widespread NNTs *P. menziesii*, *R. pseudoacacia*, *E. globulus* and *Q. rubra*, but also three NNTs (*A. altissima*, *A. dealbata* and *P. serotina*) with comparatively small area cover. In contrast, although the conifers *P. sitchensis*, *P. strobus* and *P. contorta* var. *latifolia* have been quite widely planted, there were too few studies with pairwise comparisons to be considered in our analyses. Most likely, the reason for the disparity between the area occupied and the number of studies (or comparisons) is the invasive status of *A. altissima*, *A. dealbata* and *P. serotina* in several countries, the spread of these species and their impact on native ecosystems during the last decades. Many papers dealing with these species mention their invasiveness in the respective introduction sections, serving as a justification for the study. On the other hand, for the four most studied species (*P. menziesii*, *R. pseudoacacia*, *E. globulus* and *Q. rubra*) there is no

apparent relationship between the area occupied by each species and the number of cases. For example, *P. menziesii*, which is an economically important species in terms of timber production particularly in France and Germany, is by far the most studied species in our database with 615 cases but it occupies only one third of the area of *R. pseudoacacia* (Brus et al. 2019), with 391 cases.

According to our database, the number of comparisons between NNTs and NV was higher for diversity in taxonomic groups than for soil properties. There may be various reasons for this. Researchers can assess a large number of taxa groups in the same study, sometimes using the same plot, as is the case for plant studies. On the other hand, there is a much larger number of taxa to be studied than soil properties. Within the universe of different soil properties, soil nitrogen, pH and C:N, were the most studied, probably because of their ecophysiological relevance for plants and ecosystems, but also because their assessment is relatively easy affordable. As for taxonomic groups, the variation in the abundance of vascular plants was more studied than the variation of all other groups. Methodological reasons, including high costs for sorting and identifying species-rich groups such as insects can explain this imbalance. In contrast, mammals and lichens were the least studied groups of our selection, with the lowest number of cases and the lowest number of NNTs. The difficulties associated with mammal censuses at the scale most NNTs were planted is probably the main reason for the dearth of studies. As for lichens, only a few available studies point to an underrepresentation in such comparisons of NNTs and NV, a phenomenon that may produce bias in the interpretation of NNT impacts (Hulme et al. 2013).

Impacts of NNTs on soil properties

Our results show inconsistent impacts on soil properties. Most studies show no significant effects on soil properties, indicating that in many conditions, other intrinsic local factors, namely parent bedrock, soil type or topography may be more important than the tree species. However, some soil impacts seem to be strongly related to particular tree species. This is the case of nitrogen, which is increased by the two Fabaceae species (*A. dealbata* and *R. pseudoacacia*). This is in line with the findings by Castro-Díez et al. (2019) who found a strong phylogenetic signal in the effect of NNT on soil fertility mostly because of N-fixing species. However, soil fertility comes at the cost of soil acidification as a direct or indirect consequence of nitrogen fixation (Tang et al. 1999).

We would expect fast-growing species, such as *E. globulus*, to produce an increasing effect on nitrogen content due to increased productivity, which could contribute to increase the organic matter by stronger root growth and increased litter input (Evans 2009). However, this was not the case in the studies assessed here. In fact, the short-rotation silviculture (Tomé et al. 2021), and the slow litter decomposition (e.g. Pozo et al. 1998) in *E. globulus* stands, probably leads to lower soil nitrogen content and a concomitant increase in C:N (Castro-Díez et al. 2012; Mallen-Cooper et al. 2022).

Impacts of NNT on biodiversity attributes

The different taxonomic groups were, in a majority of cases negatively impacted by the studied NNTs when compared with the status of local NV. However, there are remarkable exceptions among the eight taxonomic groups examined and among the seven NNTs. With respect to microorganisms, for instance, there were two times more studies showing an increasing rather than a decreasing biodiversity. Most of these studies refer to *A. dealbata*. The results for this NNT may be linked to the results found for soil. The higher nutrient concentration found in most comparisons translates into a higher microbial activity, as found for example by Souza-Alonso et al. (2014). Bryophytes were also increasingly impacted, particularly by *P. menziesii*. Apparently, in this case the moist environment provided by closed and dense canopies of *P. menziesii* stands are likely to cause an increase of bryophytes, while the less shade-tolerant vascular plants declined (Finch and Szumelda 2007). Furthermore, several NNTs had no effect on biodiversity attributes of different taxonomic groups, e.g. regarding vascular plants under *R. pseudoacacia* (Sitzi et al. 2012; Vítková et al. 2017) and *P. serotina* (Chabrerie et al. 2010).

As for vascular plants, the most studied taxonomic group, different reasons may explain the increasing or decreasing biodiversity responses to NNTs, found in our review. *A. dealbata*, *A. altissima* and *E. globulus* were associated with marked detrimental impacts on plant diversity and abundance. In the case of *A. dealbata*, the reasons for the decrease have been related to light competition (Lorenzo et al. 2012), allelopathic effects (Lorenzo and Rodríguez-Echeverría, 2012), and changes in soil nutrients and microbial composition (Rodríguez-Echeverría et al. 2013). Similar reasons were referred to the decreasing plant diversity in stands of *A. altissima*, namely direct competition and allelopathic effects (Motard et al. 2015). The reasons behind the decreasing biodiversity response to *E. globulus*, may be related to intensive management practices. *Eucalyptus globulus* stands are usually coppiced every 10–12 years along three rotations, and the understory is often removed (Tomé et al. 2021). These frequent disturbances may contribute to the decrease of plant diversity (Lomba et al. 2011; Vaz et al. 2019). Other authors, however, point to intrinsic characteristics of *E. globulus* that may be associated to the impact on plant diversity, including the amount of light that reaches the soil, preventing the establishment of shade-tolerant species or the lack of seed-dispersing birds (Calviño-Cancela 2013). Allelopathy, which inhibits germination and root growth of understory plants, has been referred to by many authors (e.g. Souto et al. 2001; Becerra et al. 2018), while a more recent study did not find evidence of allelopathic effects of *E. globulus* on Californian native species (Nelson et al. 2021). This latter work suggests that other mechanisms, such as changes in osmotic potential and water or light acquisition, may better explain the suppression of understory in *E. globulus* plantations. As for *P. menziesii*, the reasons for lowered plant diversity and abundance are normally related with the dense cover of plantations before thinning, strongly shading the ground (Augusto et al. 2002; Finch and Szumelda 2007). In contrast, according to Budde (2006) and Podrázský et al. (2014), species richness and abundance

can be increased in comparison to native stands of *P. sylvestris*, *P. abies*, *F. sylvatica* and *Quercus* spp., which obviously strongly depends on management intervention applied to *P. menziesii* stands aimed to support continuous growth and equally increase light transmission. Comparisons of *R. pseudoacacia* stands with NV resulted mostly in non-significant effects, i.e. vascular plant diversity did not differ in the paired stands. There were, however, more cases with increasing than decreasing responses of biodiversity, e.g. Buchholz et al. (2015). Examples with reduced biodiversity highlight the dominance of nitrophilous species in *R. pseudoacacia* stands in contrast to herbaceous vegetation in native forests (Benesperi et al. 2012), or the lack of native plant species adapted to low pH and nitrogen levels in favour of exotic and ubiquitous species in *R. pseudoacacia* plantations (Piwczyński et al. 2016). The fact that an increase in nitrogen was observed in only half of the cases for *R. pseudoacacia* vs. NV may explain why this NNT does not seem to have a general cascade effect on vascular plant diversity.

The higher numbers of increasing vs. decreasing biodiversity responses to *P. serotina* are surprising and reflect the context of the studies considered in the analyses. For *P. serotina*, many increasing cases originate from two studies by Dyderski and Jagodziński (2021a, 2021b), in which several diversity attributes are listed. Most of them refer to *P. serotina* growing in *Pinus sylvestris* stands or plantations and were compared mostly with dense and species-poor *Fagus sylvatica* stands. In contrast, the paper-balanced score in Fig. 6 (in black; only one average value per taxonomic group per paper), results in a distinct decreasing response in vascular plant diversity. This corresponds with many studies that report a reduction in light levels caused by the presence of *P. serotina* (e.g. Starfinger et al. 2003; Chabrerie et al. 2010; Dyderski and Jagodziński 2019).

In summary, it is challenging to disentangle the different factors responsible for a certain impact and to ascertain which factors are more important when it comes to cultivated NNTs (Augusto et al. 2002; Tomé et al. 2021). Similarly to *E. globulus*, plantations of other NNTs are often intensively managed in relatively short rotations to maximise timber production, which results in specific disturbance and light availability regimes across the cultivation cycle (Augusto et al. 2002). These disturbance regimes may include pruning, thinning, understorey removal and a clear cut at the end of a rotation. Therefore, cultivation history needs to be considered to better understand the long-term impacts of NNTs on biodiversity (e.g. Carneiro et al. 2008). However, the control for management influence, allowing its separation from the intrinsic species characteristics, is not included in most studies that compared NNTs and NV. The discussion on this topic becomes even more problematic with cultivated NNTs that spread spontaneously and mix with both native and non-native species, such as in the case for *E. globulus* in the Iberian Peninsula (Tomé et al. 2021) and *R. pseudoacacia* in Central Europe (Vítková et al. 2017). More sound conclusions can be drawn from those species that are currently not cultivated and which are considered noxious weeds by national legislations, such as *A. altissima* or *A. dealbata* (Pötzelsberger et al. 2020b). Given their invasive behaviour, there is a strong probability that most stands have been naturally-regenerated and that no management operations have influenced the impacts they cause.

According to our results, the NNTs that cause the strongest impact on biodiversity are those that are phylogenetically distant from European plant species. This is in line with other studies showing the importance of congeneric plant species in the establishment and survival of other living organisms that are part of the ecosystem (Harvey et al. 2012; Spafford et al. 2013). *A. dealbata*, *E. globulus* and *A. altissima* are associated with the lowest biodiversity in comparison to NV. While, as previously stated, the role of management should be taken into account in the case of *E. globulus*, this role is not a significant factor in *A. dealbata* and *A. altissima*. Therefore, one possible explanation is the lack of eco-evolutionary history with local native species, making it more difficult to establish ecological interactions, such as pollination, herbivory, seed dispersal and entire food webs, in particular when the planted area is small and thus interactions with NV are rare. Nonetheless, there are cases of strong ecological integration of NNTs, such as the case reported for the pollination of *E. globulus* in Galicia, Spain (Calviño-Cancela and Neumann 2015). However, this might occur at the expense of reproductive success and maintenance of native plant populations (Arceo-Gómez and Ashman 2016). The development of these NNT-based novel ecosystems should therefore be taken into consideration when assessing and analysing the impact of NNTs on native species (Hobbs et al. 2006). Besides intrinsic factors of NNTs related to the phylogenetic relatedness (e.g. secondary plant compounds) also structural properties (bark, canopy architecture) as well as co-introductions of associated species can be important in some cases as shown for *P. menziesii* (Gossner et al. 2005; Gossner and Ammer 2006; Gossner 2016).

Conclusions

Our review provides an overview of current knowledge of the effects of NNTs on selected soil properties and diversity attributes and thus a general basis for the discussion on planting and favouring of NNTs in Europe in the face of global change. It shows that despite its relevance, information on the ecological impacts of NNTs is still limited for most species. Our results for seven NNTs with sufficient data suggest that overall impacts on soil properties are low, and in some cases NNTs may even increase soil fertility. However, nutrient enrichment that facilitates the spreading of ruderal or expansive species needs to be carefully assessed, especially in naturally nutrient-poor environments that are particularly important for biodiversity conservation. Significant negative impacts on biodiversity—in particular on vascular plants, insects, and other arthropods—are observed more frequently and suggest a cautious use of NNTs, especially for species that have no close relatives in Europe. In addition to these general trends, our results suggest a strong context-dependency of impacts, especially with respect to focal taxa mainly occurring in different regions and structural properties of the managed stands.

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References

- Arceo-Gómez G, Ashman TL (2016) Invasion status and phylogenetic relatedness predict cost of heterospecific pollen receipt: Implications for native biodiversity decline. *Journal of Ecology* 104(4): 1003–1008. <https://doi.org/10.1111/1365-2745.12586>
- Augusto L, Ranger J, Binkley D, Rothe A (2002) Impact of several common tree species of European temperate forests on soil fertility. *Annals of Forest Science* 59(3): 233–253. <https://doi.org/10.1051/forest:2002020>
- Badalamenti E, Cusimano D, La Mantia T, Pasta S, Romano S, Troia A, Iardi V (2018) The ongoing naturalisation of *Eucalyptus* spp. in the Mediterranean Basin: New threats to native species and habitats. *Australian Forestry* 81(4): 239–249. <https://doi.org/10.1080/0049158.2018.1533512>
- Becerra PI, Catford JA, Inderjit Luce McLeod M, Andonian K, Aschehoug ET, Montesinos D, Callaway RM (2018) Inhibitory effects of *Eucalyptus globulus* on understorey plant growth and species richness are greater in non-native regions. *Global Ecology and Biogeography* 27(1): 68–76. <https://doi.org/10.1111/geb.12676>
- Benesperi R, Giuliani C, Zanetti S, Gennai M, Lippi MM, Guidi T, Nascimbene J, Foggi B (2012) Forest plant diversity is threatened by *Robinia pseudoacacia* (black-locust) invasion. *Biodiversity and Conservation* 21(14): 3555–3568. <https://doi.org/10.1007/s10531-012-0380-5>
- Brundu G, Richardson DM (2016) Planted forests and invasive alien trees in Europe: A Code for managing existing and future plantings to mitigate the risk of negative impacts from invasions. *NeoBiota* 30: 5–47. <https://doi.org/10.3897/neobiota.30.7015>
- Brundu G, Pauchard A, Pyšek P, Pergl J, Bindewald AM, Brunori A, Canavan S, Campagnaro T, Celesti-Grapow L, Dechoum MDS, Dufour-Dror J-M, Essl F, Flory SL, Genovesi P, Guarino F, Guangzhe L, Hulme PE, Jäger H, Kettle CJ, Krumm F, Langdon B, Lapin K, Lozano V, Le Roux JJ, Novoa A, Nuñez MA, Porté AJ, Silva JS, Schaffner U, Sitzia T, Tanner R, Tshidada N, Vítková M, Westergren M, Wilson JR, Richardson DM (2020) Global guidelines for the sustainable use of non-native trees to prevent tree invasions and mitigate their negative impacts. *NeoBiota* 61: 65–116. <https://doi.org/10.3897/neobiota.61.58380>
- Brus R, Pötzelsberger E, Lapin K, Brundu G, Orazio C, Straigyte L, Hasenauer H (2019) Extent, distribution and origin of non-native forest tree species in Europe. *Scandinavian Journal of Forest Research* 34(7): 533–544. <https://doi.org/10.1080/02827581.2019.1676464>
- Buchholz S, Tietze H, Kowarik I, Schirmel J (2015) Effects of a major tree invader on urban woodland arthropods. *PLoS ONE* 10(9): e0137723. <https://doi.org/10.1371/journal.pone.0137723>

- Budde S (2006) Auswirkungen des Douglasienanbaus auf die Bodenvegetation im nordwestdeutschen Tiefland. Cuvillier Verlag, Göttingen, 111 pp.
- Calviño-Cancela M (2013) Effectiveness of eucalypt plantations as a surrogate habitat for birds. *Forest Ecology and Management* 310: 692–699. <https://doi.org/10.1016/j.foreco.2013.09.014>
- Calviño-Cancela M, Neumann M (2015) Ecological integration of eucalypts in Europe: Interactions with flower-visiting birds. *Forest Ecology and Management* 358: 174–179. <https://doi.org/10.1016/j.foreco.2015.09.011>
- Campagnaro T, Brundu G, Sitzia T (2018) Five major invasive alien tree species in European Union forest habitat types of the Alpine and Continental biogeographical regions. *Journal for Nature Conservation* 43: 227–238. <https://doi.org/10.1016/j.jnc.2017.07.007>
- Carneiro M, Fabião A, Martins MC, Fabião A, Abrantes Da Silva M, Hilário L, Lousá M, Madeira M (2008) Effects of harrowing and fertilisation on understory vegetation and timber production of a *Eucalyptus globulus* Labill. plantation in Central Portugal. *Forest Ecology and Management* 255(3–4): 591–597. <https://doi.org/10.1016/j.foreco.2007.09.028>
- Castro-Díez P, González-Muñoz N, Alonso A, Gallardo A, Poorter L (2009) Effects of exotic invasive trees on nitrogen cycling: A case study in Central Spain. *Biological Invasions* 11(8): 1973–1986. <https://doi.org/10.1007/s10530-008-9374-3>
- Castro-Díez P, Fierro-Brunnenmeister N, Gonzalez-Munoz N, Gallardo A (2012) Effects of exotic and native tree leaf litter on soil properties of two contrasting sites in the Iberian Peninsula. *Plant and Soil* 350(1–2): 179–191. <https://doi.org/10.1007/s11104-011-0893-9>
- Castro-Díez P, Vaz AS, Silva JS, van Loo M, Alonso Á, Aponte C, Bayón Á, Bellingham PJ, Chiuffo MC, DiManno N, Julian K, Kandert S, La Porta N, Marchante H, Maule HG, Mayfield MM, Metcalfe D, Monteverdi MC, Núñez MA, Ostertag R, Parker IM, Peltzer DA, Potgieter LJ, Raymundo M, Rayome D, Reisman-Berman O, Richardson DM, Roos RE, Saldaña A, Shackleton RT, Torres A, Trudgen M, Urban J, Vicente JR, Vilà M, Ylloja T, Zenni RD, Godoy O (2019) Global effects of non-native tree species on multiple ecosystem services. *Biological Reviews of the Cambridge Philosophical Society* 94(4): 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. *The Science of the Total Environment* 778: 146141. <https://doi.org/10.1016/j.scitotenv.2021.146141>
- Chabrierie O, Hoeblich H, Decocq G (2007) Determinism and ecological consequences of the invasive dynamics of late cherry (*Prunus serotina* Ehrh.) on plant communities in Compiègne forest. *Acta Botanica Gallica* 154: 383–394. <https://doi.org/10.1080/12538078.2007.10516071>
- Chabrierie O, Loinard J, Perrin S, Saguez R, Decocq G (2010) Impact of *Prunus serotina* invasion on understory functional diversity in a European temperate forest. *Biological Invasions* 12(6): 1891–1907. <https://doi.org/10.1007/s10530-009-9599-9>
- Cremer M, Prietzel J (2017) Soil acidity and exchangeable base cation stocks under pure and mixed stands of European beech, Douglas fir and Norway spruce. *Plant and Soil* 415(1–2): 393–405. <https://doi.org/10.1007/s11104-017-3177-1>
- Dodet M, Collet C (2012) When should exotic forest plantation tree species be considered as an invasive threat and how should we treat them? *Biological Invasions* 14(9): 1765–1778. <https://doi.org/10.1007/s10530-012-0202-4>

- Dutta RK, Agrawal M (2003) Restoration of opencast coal mine spoil by planting exotic tree species: A case study in dry tropical region. *Ecological Engineering* 21(2–3): 143–151. <https://doi.org/10.1016/j.ecoleng.2003.10.002>
- Dyderski MK, Jagodziński AM (2019) Context-dependence of urban forest vegetation invasion level and alien species' ecological success. *Forests* 10(1): 26. <https://doi.org/10.3390/f10010026>
- Dyderski MK, Jagodziński AM (2021a) How do invasive trees impact shrub layer diversity and productivity in temperate forests? *Annals of Forest Science* 78(1): 20. <https://doi.org/10.1007/s13595-021-01033-8>
- Dyderski MK, Jagodziński AM (2021b) Impacts of invasive trees on alpha and beta diversity of temperate forest understories. *Biological Invasions* 23(1): 235–252. <https://doi.org/10.1007/s10530-020-02367-6>
- Evans J (2009) The multiple roles of planted forests. In: Evans J (Ed.) *Planted forests: uses, impacts, and sustainability*. CABI, Wallingford, 61–90. <https://doi.org/10.1079/9781845935641.0061>
- Finch O-D, Szumelda A (2007) Introduction of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) into Western Europe: Epigeic arthropods in intermediate-aged pure stands in northwestern Germany. *Forest Ecology and Management* 242(2–3): 260–272. <https://doi.org/10.1016/j.foreco.2007.01.039>
- Godoy O, Castro-Díez P, Van Logtestijn RSP, Cornelissen JHC, Valladares F (2010) Leaf litter traits of invasive species slow down decomposition compared to Spanish natives: A broad phylogenetic comparison. *Oecologia* 162(3): 781–790. <https://doi.org/10.1007/s00442-009-1512-9>
- Gossner MM (2016) Introduced tree species in central Europe – consequences for arthropod communities and species interactions. In: Krumm F, Vítková L (Eds) *Introduced tree species in European forests: Opportunities and challenges*. European Forest Institute, 264–282.
- Gossner M, Ammer U (2006) The effects of Douglas-fir on tree-specific arthropod communities in mixed species stands with European beech and Norway spruce. *European Journal of Forest Research* 125(3): 221–235. <https://doi.org/10.1007/s10342-006-0113-y>
- Gossner M, Gruppe A, Simon U (2005) Aphidophagous insect communities in tree crowns of the neophyte Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] and Norway spruce (*Picea abies* L.). *Journal of Applied Entomology* 129(2): 81–88. <https://doi.org/10.1111/j.1439-0418.2005.00937.x>
- Harvey KJ, Nipperess DA, Britton DR, Hughes L (2012) Australian family ties: Does a lack of relatives help invasive plants escape natural enemies? *Biological Invasions* 14(11): 2423–2434. <https://doi.org/10.1007/s10530-012-0239-4>
- Hasenauer H, Gazda A, Konnert M, Mohren G, Pötzelsberger E, Spiecker H, Van Loo M (Eds) (2016) *Non-native tree species for European forests: Experiences, risks and opportunities*. University of Natural Resources and Life Sciences, Vienna, 427 pp.
- Hassan R, Scholes R, Ash N (2005) *Ecosystems and human well-being: Current state and trends*. Island Press, Washington, 917 pp.

- Hejda M, Hanzelka J, Kadlec T, Štrobl M, Pyšek P, Reif J (2017) Impacts of an invasive tree across trophic levels: Species richness, community composition and resident species' traits. *Diversity & Distributions* 23(9): 997–1007. <https://doi.org/10.1111/ddi.12596>
- Hobbs RJ, Arico S, Aronson J, Baron JS, Bridgewater P, Cramer VA, Epstein PR, Ewel JJ, Klink CA, Lugo AE, Norton D, Ojima D, Richardson DM, Sanderson EW, Valladares F, Vilà M, Zamora R, Zobel M (2006) Novel ecosystems: Theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography* 15(1): 1–7. <https://doi.org/10.1111/j.1466-822X.2006.00212.x>
- Hulme PE, Pyšek P, Jarošík V, Pergl J, Schaffner U, Vilà M (2013) Bias and error in understanding plant invasion impacts. *Trends in Ecology & Evolution* 28(4): 212–218. <https://doi.org/10.1016/j.tree.2012.10.010>
- Huston M, Smith T (1987) Plant succession – Life-history and competition. *American Naturalist* 130(2): 168–198. <https://doi.org/10.1086/284704>
- Jackson RB, Banner JL, Jobbágy EG, Pockman WT, Wall DH (2002) Ecosystem carbon loss with woody plant invasion of grasslands. *Nature* 418(6898): 623–626. <https://doi.org/10.1038/nature00910>
- Kadlec T, Štrobl M, Hanzelka J, Hejda M, Reif J (2018) Differences in the community composition of nocturnal Lepidoptera between native and invaded forests are linked to the habitat structure. *Biodiversity and Conservation* 27(10): 2661–2680. <https://doi.org/10.1007/s10531-018-1560-8>
- Krevš A, Kučinskienė A (2017) Influence of invasive *Acer negundo* leaf litter on benthic microbial abundance and activity in the littoral zone of a temperate river in Lithuania. *Knowledge and Management of Aquatic Ecosystems* 418(418): 26. <https://doi.org/10.1051/kmae/2017015>
- Lomba A, Vicente J, Moreira F, Honrado J (2011) Effects of multiple factors on plant diversity of forest fragments in intensive farmland of Northern Portugal. *Forest Ecology and Management* 262(12): 2219–2228. <https://doi.org/10.1016/j.foreco.2011.08.014>
- Lorenzo P, Rodríguez-Echeverría S (2012) Influence of soil microorganisms, allelopathy and soil origin on the establishment of the invasive *Acacia dealbata*. *Plant Ecology & Diversity* 5(1): 67–73. <https://doi.org/10.1080/17550874.2012.713404>
- Lorenzo P, Pazos-Malvido E, Rubido-Bará M, Reigosa MJ, González L (2012) Invasion by the leguminous tree *Acacia dealbata* (Mimosaceae) reduces the native understorey plant species in different communities. *Australian Journal of Botany* 60(8): 669–675. <https://doi.org/10.1071/BT12036>
- Mallen-Cooper M, Atkinson J, Xirocostas ZA, Wijas B, Chiarenza GM, Dadzie FA, Eldridge DJ (2022) Global synthesis reveals strong multifaceted effects of eucalypts on soils. *Global Ecology and Biogeography* 31(8): 1667–1678. <https://doi.org/10.1111/geb.13522>
- Medina-Villar S, Rodríguez-Echeverría S, Lorenzo P, Alonso A, Pérez-Corona E, Castro-Díez P (2016) Impacts of the alien trees *Ailanthus altissima* (Mill.) Swingle and *Robinia pseudoacacia* L. on soil nutrients and microbial communities. *Soil Biology & Biochemistry* 96: 65–73. <https://doi.org/10.1016/j.soilbio.2016.01.015>
- Motard E, Dusz S, Geslin B, Akpa-Vinceslas M, Hignard C, Babiari O, Clair-Maczulajtyts D, Michel-Salzat A (2015) How invasion by *Ailanthus altissima* transforms soil and litter

- communities in a temperate forest ecosystem. *Biological Invasions* 17(6): 1817–1832. <https://doi.org/10.1007/s10530-014-0838-3>
- Nelson KM, Bisbing S, Grossenbacher DL, Ritter M, Yost JM (2021) Testing an invasion mechanism for *Eucalyptus globulus*: Is there evidence of allelopathy? *American Journal of Botany* 108(4): 607–615. <https://doi.org/10.1002/ajb2.1635>
- Øyen BH, Nygaard PH (2020) Impact of Sitka spruce on biodiversity in NW Europe with a special focus on Norway—evidence, perceptions and regulations. *Scandinavian Journal of Forest Research* 35(3–4): 117–133. <https://doi.org/10.1080/02827581.2020.1748704>
- Piwczyński M, Puchałka R, Ulrich W (2016) Influence of tree plantations on the phylogenetic structure of understorey plant communities. *Forest Ecology and Management* 376: 231–237. <https://doi.org/10.1016/j.foreco.2016.06.011>
- Podrázský V, Martiník A, Matějka K, Viewegh J (2014) Effects of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) on understory layer species diversity in managed forests. *Journal of Forest Science* 60(7): 263–271. <https://doi.org/10.17221/49/2014-JFS>
- Pötzelsberger E, Spiecker H, Neophytou C, Mohren F, Gazda A, Hasenauer H (2020a) Growing non-native trees in European forests brings benefits and opportunities but also has its risks and limits. *Current Forestry Reports* 6(4): 339–353. <https://doi.org/10.1007/s40725-020-00129-0>
- Pötzelsberger E, Lapin K, Brundu G, Adriaens T, Andonovski V, Andrašev S, Bastien J-C, Brus R, Čurović M, Čurović Ž, Cvjetković B, Đodan M, Domingo-Santos JM, Gazda A, Henin J-M, Hernea C, Karlsson B, Keča L, Keren S, Keserű Z, Konstantara T, Kroon J, La Porta N, Lavnyy V, Lazdina D, Lukjanova A, Maaten T, Madsen P, Mandjukovski D, Marín Pageo FJ, Marozas V, Martinik A, Mason WL, Mohren F, Monteverdi MC, Neophytou C, Neville P, Nicolescu V-N, Nygaard PH, Orazio C, Parpan T, Perić S, Petkova K, Popov EB, Power M, Rédei K, Rousi M, Silva JS, Sivacioğlu A, Socratous M, Straigytė L, Urban J, Vandekerckhove K, Waśik R, Westergren M, Wohlgemuth T, Ylioja T, Hasenauer H (2020b) Mapping the patchy legislative landscape of non-native tree species in Europe. *Forestry* 93(4): 567–586. <https://doi.org/10.1093/forestry/cpaa009>
- Pozo J, Basaguren A, Elósegui A, Molinero J, Fabre E, Chauvet E (1998) Afforestation with *Eucalyptus globulus* and leaf litter decomposition in streams of northern Spain. *Hydrobiologia* 373/374: 101–109. <https://doi.org/10.1023/A:1017038701380>
- Pyšek P, Jarosik V, Hulme PE, Pergl J, Hejda M, Schaffner U, Vila 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. *Global Change Biology* 18(5): 1725–1737. <https://doi.org/10.1111/j.1365-2486.2011.02636.x>
- Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM, Carlton JT, Dawson W, Essl F, Foxcroft LC, Genovesi P, Jeschke JM, Kühn I, Liebhold AM, Mandrak NE, Meyerson LA, Pauchard A, Pergl J, Roy HE, Seebens H, van Kleunen M, Vilà M, Wingfield MJ, Richardson DM (2020) Scientists' warning on invasive alien species. *Biological Reviews of the Cambridge Philosophical Society* 95(6): 1511–1534. <https://doi.org/10.1111/brv.12627>
- R Development Core Team (2022) R: A language and environment for statistical computing. Vienna, Austria.
- Reif J, Hanzelka J, Kadlec T, Štrobl M, Hejda M (2016) Conservation implications of cascading effects among groups of organisms: The alien tree *Robinia pseudoacacia* in the Czech

- Republic as a case study. *Biological Conservation* 198: 50–59. <https://doi.org/10.1016/j.biocon.2016.04.003>
- Rodríguez-Echeverría S, Afonso C, Correia M, Lorenzo P, Roiloa SR (2013) The effect of soil legacy on competition and invasion by *Acacia dealbata* Link. *Plant Ecology* 214(9): 1139–1146. <https://doi.org/10.1007/s11258-013-0238-2>
- Sanz-Elorza M, Dana Sánchez ED, Sobrino Vesperinas E (2004) Atlas de las Plantas Alóctonas Invasoras en España, Madrid.
- Sapsford SJ, Brandt AJ, Davis KT, Peralta G, Dickie IA, Gibson RD II, Green JL, Hulme PE, Nuñez MA, Orwin KH, Pauchard A, Wardle DA, Peltzer DA (2020) Towards a framework for understanding the context dependence of impacts of non-native tree species. *Functional Ecology* 34(5): 944–955. <https://doi.org/10.1111/1365-2435.13544>
- Sitzia T, Campagnaro T, Dainese M, Cierjacks A (2012) Plant species diversity in alien black locust stands: A paired comparison with native stands across a north-Mediterranean range expansion. *Forest Ecology and Management* 285: 85–91. <https://doi.org/10.1016/j.foreco.2012.08.016>
- Sitzia T, Campagnaro T, Kowarik I, Trentanovi G (2016) Using forest management to control invasive alien species: Helping implement the new European regulation on invasive alien species. *Biological Invasions* 18(1): 1–7. <https://doi.org/10.1007/s10530-015-0999-8>
- Souto XC, Bolano JC, Gonzalez L, Reigosa MJ (2001) Allelopathic effects of tree species on some soil microbial populations and herbaceous plants. *Biologia Plantarum* 44(2): 269–275. <https://doi.org/10.1023/A:1010259627812>
- Souza-Alonso P, Novoa A, González L (2014) Soil biochemical alterations and microbial community responses under *Acacia dealbata* Link invasion. *Soil Biology & Biochemistry* 79: 100–108. <https://doi.org/10.1016/j.soilbio.2014.09.008>
- Spafford RD, Lortie CJ, Butterfield BJ (2013) A systematic review of arthropod community diversity in association with invasive plants. *NeoBiota* 16: 81–102. <https://doi.org/10.3897/neobiota.16.4190>
- Spiecker H, Lindner M, Schuler J (2019) Douglas-fir – an option for Europe. *What Science Can Tell Us* 9, European Forest Institute, Joensuu, Finland, 1–124.
- Starfinger U, Kowarik I, Rode M, Schepker H (2003) From desirable ornamental plant to pest to accepted addition to the flora? The perception of an alien tree species through the centuries. *Biological Invasions* 5(4): 323–335. <https://doi.org/10.1023/B:BINV.0000005573.14800.07>
- Tang C, Unkovich MJ, Bowden JW (1999) Factors affecting soil acidification under legumes. III. Acid production by N_2 -fixing legumes as influenced by nitrate supply. *The New Phytologist* 143(3): 513–521. <https://doi.org/10.1046/j.1469-8137.1999.00475.x>
- Tomé M, Almeida MH, Barreiro S, Branco MR, Deus E, Pinto G, Silva JS, Soares P, Rodríguez-Soalleiro R (2021) Opportunities and challenges of *Eucalyptus* plantations in Europe: The Iberian Peninsula experience. *European Journal of Forest Research* 140(3): 489–510. <https://doi.org/10.1007/s10342-021-01358-z>
- Vaz AS, Honrado JP, Lomba A (2019) Replacement of pine by eucalypt plantations: Effects on the diversity and structure of tree assemblages under land abandonment and implications for landscape management. *Landscape and Urban Planning* 185: 61–67. <https://doi.org/10.1016/j.landurbplan.2019.01.009>

- Vítková M, Müllerová J, Sádlo J, Pergl J, Pyšek P (2017) Black locust (*Robinia pseudoacacia*) beloved and despised: A story of an invasive tree in Central Europe. *Forest Ecology and Management* 384: 287–302. <https://doi.org/10.1016/j.foreco.2016.10.057>
- Vlachodimos K, Papatheodorou EM, Diamantopoulos J, Monokrousos N (2013) Assessment of *Robinia pseudoacacia* cultivations as a restoration strategy for reclaimed mine spoil heaps. *Environmental Monitoring and Assessment* 185(8): 6921–6932. <https://doi.org/10.1007/s10661-013-3075-9>
- Wagner V, Večeřa M, Jiménez-Alfaro B, Pergl J, Lenoir J, Svenning JC, Pyšek P, Agrillo E, Biurrun I, Campos JA, Ewald J, Fernández-González F, Jandt U, Rašomavičius V, Šilc U, Škvorc Ž, Vassilev K, Wohlgemuth T, Chytrý M (2021) Alien plant invasion hotspots and invasion debt in European woodlands. *Journal of Vegetation Science* 32(2): e13014. <https://doi.org/10.1111/jvs.13014>
- Walther GR, Roques A, Hulme PE, Sykes MT, Pyšek P, Kühn I, Zobel M, Bacher S, Botta-Dukát Z, Bugmann H, Czúcz B, Dauber J, Hickler T, Jarošík V, Kenis M, Klotz S, Minchin D, Moora M, Nentwig W, Ott J, Panov VE, Reineking B, Robinet C, Semchenko V, Solarz W, Thuiller W, Vilà M, Vohland K, Settele J (2009) Alien species in a warmer world: Risks and opportunities. *Trends in Ecology & Evolution* 24(12): 686–693. <https://doi.org/10.1016/j.tree.2009.06.008>
- Wohlgemuth T, Moser B, Pötzelberger E, Rigling A, Gossner MM (2021) Über die Invasivität der Douglasie und ihre Auswirkungen auf Boden und Biodiversität. *Schweizerische Zeitschrift für Forstwesen* 172(2): 118–127. <https://doi.org/10.3188/szf.2021.0118>
- Yelenik S, Stock W, Richardson D (2004) Ecosystem level impacts of invasive *Acacia saligna* in the South African fynbos. *Restoration Ecology* 12(1): 44–51. <https://doi.org/10.1111/j.1061-2971.2004.00289.x>
- Yuan Y, Zhao Z, Niu S, Li X, Wang Y, Bai Z (2018) Reclamation promotes the succession of the soil and vegetation in opencast coal mine: A case study from *Robinia pseudoacacia* reclaimed forests, Pingshuo mine, China. *Catena* 165: 72–79. <https://doi.org/10.1016/j.catena.2018.01.025>
- Zerva A, Ball T, Smith KA, Mencuccini M (2005) Soil carbon dynamics in a Sitka spruce (*Picea sitchensis* (Bong.) Carr.) chronosequence on a peaty gley. *Forest Ecology and Management* 205(1–3): 227–240. <https://doi.org/10.1016/j.foreco.2004.10.035>

Supplementary material I

Supplementary information

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Data type: tables and figures (docx. file)

Explanation note: table S1: references and number of comparisons per NNT used from these references: Ps.me=*Pseudotsuga menziesii*, Ro.ps=*Robinia pseudoacacia*, Ac.de=*Acacia dealbata*, Pr.se=*Prunus serotina*, Eu.gl=*Eucalyptus globulus*, Qu.ru=*Quercus rubra*, Ai.al=*Ailanthus altissima*; table S2: all collected soil traits from 103 papers, aggregated and by original description, including number of cases (No), alphabetically ordered; table S3: non-native tree species (NNTs) and percentage of native trees (NT) or open ecosystems (OS) to which the cases compare; figure S1: area cover of eleven non-native tree species (NNTs; phase 3, see Fig. 2; + indicates that the species are present on a relatively small area, the threshold being set at 500 ha for this analysis) vs. number of papers with pairwise comparisons meeting standards; figure S2: biplots of Principal Components Analysis (PCA) using the mean effect of NNTs on four soil properties (left) and three taxa groups (right). Only those variables with a complete set of values for all NNTs were considered for building the PCA.

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Supplementary material

Tables

Table S1. References and number of comparisons per NNT used from these references: Ps.me=*Pseudotsuga menziesii*, Ro.ps=*Robinia pseudoacacia*, Ac.de=*Acacia dealbata*, Pr.se=*Prunus serotina*, Eu.gl=*Eucalyptus globulus*, Qu.ru=*Quercus rubra*, Ai.al=*Ailanthus altissima*. The full bibliography of the references is appended.

Reference	Ac.de	Ai.al	Eu.gl	Pr.se	Ps.me	Qu.ru	Ro.ps	Total
Abelho and Graça (1996)			1					1
Aerts et al. (2017)				11				11
Afonso (2012)	18							18
Araújo (1995)			4					4
Augusto et al. (2002)					2			2
Augusto et al. (2003)					46			46
Bärlocher and Graca (2002)			6					6
Barrocas et al. (1998)			4					4
Benesperi et al. (2012)							6	6
Blick and Gossner (2006)					1			1
Bongiorno (1982)			32					32
Brunk (2007)						6		6
Buchholz et al. (2015)							32	32
Budde (2006)					48			48
Calviño-Cancela (2013)			18					18
Calviño-Cancela et al. (2012)			18					18
Calviño-Cancela et al. (2013)			12					12
Castro-Díez et al. (2009)		9					9	18
Castro-Díez et al. (2012)	8	6	20					34
Chabrerie et al. (2010)				3				3
Chauvet et al. (1997)			2					2
Chmura (2013)						82		82
Chmura (2020)						4		4
Constán-Nava et al. (2015)		3						3
Cordero-Rivera et al. (2017)			1					1
Cremer and Prietzel (2017)					80			80
Cremer et al. (2016)					54			54
da Gama et al. (1995)			3					3
Silva et al. (2019)	36		36					72
Desie et al. (2020)				4				4
Dyderski and Jagodziński (2019)							6	6
Dyderski and Jagodziński (2020a)				90		45	63	198
Dyderski and Jagodziński (2020b)				30		15	15	60
Dyderski and Jagodziński (2021a)				70		35	35	140
Dyderski and Jagodziński (2021b)				60		30	30	120
Dzwonko and Loster (1997)							34	34
Finch and Szumelda (2007)					32			32
Gentili et al. (2019)				13		13		26

Goded et al. (2019)		3			3
Godefroid et al. (2005)			1		1
González et al (2020)				1	1
González-Muñoz et al. (2012)	18				18
Gossner and Ammer (2006)				69	69
Gossner and Simon (2002)				18	18
Gossner and Utschick (2004)				42	42
Gossner et al. (2005)				4	4
Gossner et al. (2016)				24	24
Gutiérrez-López et al. (2014)	82				82
Halarewicz and Pruchniewicz (2015)			4		4
Halarewicz and Zolnierz (2014)			1		1
Halarewicz et al. (2017)			6		6
Hanzelka and Reif (2016)				2	2
Hejda et al. (2017)				3	3
Kadlec et al. (2018)				2	2
Knoerzer and Reif (1996)				3	3
Kostić et al (2016)				26	26
Lazzaro et al. (2014)	12				12
Lazzaro et al. (2018)				12	12
Lomba et al. (2011)		5			5
Lorenzo et al. (2010)	36				36
Lorenzo et al. (2012a)	4				4
Lorenzo et al. (2012b)	14				14
Lorenzo et al. (2013)	8				8
Luciañez and Silgado (2007)		6			6
Madeira and Ribeiro (1995)		12			12
Malchair and Carnol (2009)				66	66
Mareschal et al. (2010)				44	44
Medina-Villar et al. (2015)	6			6	12
Medina-Villar et al. (2016)	26			26	52
Montecchiari et al. (2020)				1	1
Motard et al. (2015)	12				12
Motard et al. (2011)	7				7
Nascimbene and Marini (2010)				1	1
Nascimbene et al. (2012)				6	6
Nascimbene et al. (2015)				3	3
Pinto et al. (1997)	6	6			12
Piwczyński et al. (2016)				3	6
Poblador et al. (2019)				16	16
Podrázský et al. (2009)				36	36
Podrázský et al. (2011)				3	3
Prietzl and Bachmann (2012)				14	14
Proença et al. (2010)		4			4
Rawlik et al. (2018)				42	42
Reif et al. (2016)				2	2
Rivas-Salvador et al. (2021)				2	2
Rodríguez et al. (2020)	6				6

Serralheiro and Madeira (1990)				4					4
Sitzia et al. (2012)								2	2
Sitzia et al. (2018)								4	4
Slabejová et al. (2019)								9	9
Sousa and Da Gama (1994)				5					5
Sousa et al. (1997)				5					5
Souza-Alonso et al. (2014)	42								42
Souza-Alonso et al. (2015)	152								152
Starfinger et al. (2003)					11				11
Staska et al. (2014)								4	4
Štrobl et al. (2019)								2	2
Trentanovi et al. (2013)								5	5
Vanderhoeven et al. (2005)					8				8
Vegini et al. (2020)					1				1
Verheyen et al. (2007)					2				2
Vilà et al. (2006)				7					7
Yüksek (2012)								7	7
Total	360	158	207	315	615	230	391	2276	

References

- Abelho M, Graça MAS (1996) Effects of eucalyptus afforestation on leaf litter dynamics and macroinvertebrate community structure of streams in Central Portugal. *Hydrobiologia* 324: 195–204.
- Aerts R, Ewald M, Nicolas M, Piat J, Skowronek S, Lenoir J, Hattab T, Garzón-López CX, Feilhauer H, Schmidtlein S (2017) Invasion by the alien tree *Prunus serotina* alters ecosystem functions in a temperate deciduous forest. *Frontiers in Plant Science* 8: 179.
- Afonso C (2012) Plant-soil feedback and invasion by Australian acacias. Master thesis, Universidade de Coimbra, Portugal.
- Araújo MB (1995) The effect of *Eucalyptus globulus* Labill. plantations on biodiversity: A case study in Serra Portel (South Portugal). Master thesis, University College London, London.
- Augusto L, Ranger J, Binkley D, Rothe A (2002) Impact of several common tree species of European temperate forests on soil fertility. *Annals of Forest Science* 59: 233–253.
- Augusto L, Dupouey JL, Ranger J (2003) Effects of tree species on understory vegetation and environmental conditions in temperate forests. *Annals of Forest Science* 60: 823–831.
- Bärlocher F, Graça MAS (2002) Exotic riparian vegetation lowers fungal diversity but not leaf decomposition in Portuguese streams. *Freshwater Biology* 47: 1123–1135.
- Barrocas H, Da Gama M, Sousa J, Ferreria C (1998) Impact of reafforestation with *Eucalyptus globulus* Labill. on the edaphic collembolan fauna of Serra de Monchique (Algarve, Portugal). *Miscellània Zoològica*: 9–23.
- Benesperi R, Giuliani C, Zanetti S, Gennai M, Lippi MM, Guidi T, Nascimbene J, Foggi B (2012) Forest plant diversity is threatened by *Robinia pseudoacacia* (black-locust) invasion. *Biodiversity Conservation* 21: 3555–3568.
- Blick T, Gossner M (2006) Spinnen aus Baumrkonen-Klopfproben (Arachnida: Araneae), mit Anmerkungen zu *Cinetata gradata* (Linyphiidae) und *Theridion boesenbergi* (Theridiidae). *Arachnologische Mitteilungen* 31: 23–39.

- Bongiorno SF (1982) Land use and summer bird populations in northwestern Galicia, Spain. *Ibis* 124: 1–20.
- Brunk I (2007) Diversität und Sukzession von Laufkäferzönosen in gestörten Landschaften Südbrandenburgs. Dissertation Universität Cottbus, Cottbus.
- Buchholz S, Tietze H, Kowarik I, Schirmel J (2015) Effects of a major tree invader on urban woodland arthropods. *PloS ONE* 10: e0137723.
- Budde S (2006) Auswirkungen des Douglasienanbaus auf die Bodenvegetation im nordwestdeutschen Tiefland. Cuvillier Verlag, Göttingen. 111 p.
- Calviño-Cancela M (2013) Effectiveness of eucalypt plantations as a surrogate habitat for birds. *Forest Ecology and Management* 310: 692–699.
- Calviño-Cancela M, Rubido-Bará M, Van Etten EJ (2012) Do eucalypt plantations provide habitat for native forest biodiversity? *Forest Ecology and Management* 270: 153–162.
- Calviño-Cancela M, De Silanes MEL, Rubido-Bará M, Uribarri J (2013) The potential role of tree plantations in providing habitat for lichen epiphytes. *Forest Ecology and Management* 291: 386–395.
- Castro-Díez P, González-Muñoz N, Alonso A, Gallardo A, Poorter L (2009) Effects of exotic invasive trees on nitrogen cycling: A case study in Central Spain. *Biological Invasions* 11: 1973–1986.
- Castro-Díez P, Fierro-Brunnenmeister N, Gonzalez-Munoz N, Gallardo A (2012) Effects of exotic and native tree leaf litter on soil properties of two contrasting sites in the Iberian Peninsula. *Plant and Soil* 350: 179–191.
- Chabrierie O, Loinard J, Perrin S, Saguez R, Decocq G (2010) Impact of *Prunus serotina* invasion on understory functional diversity in a European temperate forest. *Biological Invasions* 12: 1891–1907.
- Chauvet E, Fabre E, Elosegui A, Pozo J (1997) The impact of eucalypt on the leaf-associated aquatic hyphomycetes in Spanish streams. *Canadian Journal of Botany* 75: 880–887.
- Chmura D (2013) Impact of alien tree species *Quercus rubra* L. on understory environment and flora: A study of the Silesian Upland (southern Poland). *Polish Journal of Ecology* 61: 431–442.
- Chmura D (2020) The spread and role of the invasive alien tree *Quercus rubra* (L.) in novel forest ecosystems in Central Europe. *Forests* 11: 586.
- Constán-Nava S, Soliveres S, Torices R, Serra L, Bonet A (2015) Direct and indirect effects of invasion by the alien tree *Ailanthus altissima* on riparian plant communities and ecosystem multifunctionality. *Biological Invasions* 17: 1095–1108.
- Cordero-Rivera A, Álvarez AM, Álvarez M (2017) Eucalypt plantations reduce the diversity of macroinvertebrates in small forested streams. *Animal Biodiversity and Conservation* 40: 87–97.
- Cremer M, Prietzel J (2017) Soil acidity and exchangeable base cation stocks under pure and mixed stands of European beech, Douglas fir and Norway spruce. *Plant and Soil* 415: 393–405.
- Cremer M, Kern NV, Prietzel J (2016) Soil organic carbon and nitrogen stocks under pure and mixed stands of European beech, Douglas fir and Norway spruce. *Forest Ecology and Management* 367: 30–40.
- da Gama MM, Sousa JP, Vasconcelos TM (1995) Comparison of Collembolan populations structure from Portuguese forests of *Pinus pinaster* Aiton and *Eucalyptus globulus* Labill. *Polskie Pismo Entomologiczne* 64: 1–4.
- da Silva LP, Heleno RH, Costa JM, Valente M, Mata VA, Gonçalves SC, Da Silva AA, Alves J, Ramos JA (2019) Natural woodlands hold more diverse, abundant, and unique biota than novel anthropogenic forests: a multi-group assessment. *European Journal of Forest Research* 138: 461–472.

- Desie E, Vancampenhout K, Van Den Berg L, Nyssen B, Weijters M, Den Ouden J, Muys B (2020) Litter share and clay content determine soil restoration effects of rich litter tree species in forests on acidified sandy soils. *Forest Ecology and Management* 474: 118377.
- Dyderski MK, Jagodziński AM (2019) Context-dependence of urban forest vegetation invasion level and alien species' ecological success. *Forests* 10: 26.
- Dyderski MK, Jagodziński AM (2020a) Impact of invasive tree species on natural regeneration species composition, diversity, and density. *Forests* 11: 456.
- Dyderski MK, Jagodziński AM (2020b) Impacts of alien tree species on the abundance and diversity of terricolous bryophytes. *Folia Geobotanica* 55: 351–363.
- Dyderski MK, Jagodziński AM (2021a) How do invasive trees impact shrub layer diversity and productivity in temperate forests? *Annals of Forest Science* 78: 20.
- Dyderski MK, Jagodziński AM (2021b) Impacts of invasive trees on alpha and beta diversity of temperate forest understories. *Biological Invasions*, 23: 235–252.
- Dzwonko Z, Loster S (1997) Effects of dominant trees and anthropogenic disturbances on species richness and floristic composition of secondary communities in southern Poland. *Journal of Applied Ecology* 861–870.
- Finch O-D, Szumelda A (2007) Introduction of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) into Western Europe: Epigeic arthropods in intermediate-aged pure stands in northwestern Germany. *Forest Ecology and Management* 242: 260–272.
- Gentili R, Ferrè C, Cardarelli E, Montagnani C, Bogliani G, Citterio S, Comolli R (2019) Comparing negative impacts of *Prunus serotina*, *Quercus rubra* and *Robinia pseudoacacia* on native forest ecosystems. *Forests* 10: 842.
- Goded S, Ekroos J, Domínguez J, Azcárate JG, Guitián JA, Smith HG (2019) Effects of eucalyptus plantations on avian and herb species richness and composition in North-West Spain. *Global Ecology and Conservation* 19: e00690.
- Godefroid S, Phartyal SS, Weyembergh G, Koedam N (2005) Ecological factors controlling the abundance of non-native invasive black cherry (*Prunus serotina*) in deciduous forest understory in Belgium. *Forest Ecology and Management* 210: 91–105.
- González I, Sixto H, Rodríguez-Soalleiro R, Oliveira N (2020) Nutrient contribution of litterfall in a short rotation plantation of pure or mixed plots of *Populus alba* L. and *Robinia pseudoacacia* L. *Forests* 11: 1133.
- González-Muñoz N, Costa-Tenorio M, Espigares T (2012) Invasion of alien *Acacia dealbata* on Spanish *Quercus robur* forests: Impact on soils and vegetation. *Forest Ecology and Management* 269: 214–221.
- Gossner M, Simon J (2002) Introduced Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) affects community structure of tree-crown dwelling beetles in a managed European forest. *NeoBiota* 1: 167–179.
- Gossner M, Utschick H (2004) Douglas fir stands deprive wintering bird species of food resource. *NeoBiota* 3: 105–122.
- Gossner M, Ammer U (2006) The effects of Douglas-fir on tree-specific arthropod communities in mixed species stands with European beech and Norway spruce. *European Journal of Forest Research* 125: 221–235.
- Gossner M, Gruppe A, Simon U (2005) Aphidophagous insect communities in tree crowns of the neophyte Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] and Norway spruce (*Picea abies* L.). *Journal of Applied Entomology* 129: 81–88.

- Gossner MM, Wende B, Levick S, Schall P, Floren A, Linsenmair KE, Steffan-Dewenter I, Schulze E-D, Weisser WW (2016) Deadwood enrichment in European forests—Which tree species should be used to promote saproxylic beetle diversity? *Biological Conservation* 201: 92–102.
- Gutiérrez-López M, Ranera E, Novo M, Fernández R, Trigo D (2014) Does the invasion of the exotic tree *Ailanthus altissima* affect the soil arthropod community? The case of a riparian forest of the Henares River (Madrid). *European Journal of Soil Biology* 62: 39–48.
- Halarewicz A, Zolnierz L (2014) Changes in the understorey of mixed coniferous forest plant communities dominated by the American black cherry (*Prunus serotina* Ehrh.). *Forest Ecology and Management* 313: 91–97.
- Halarewicz A, Pruchniewicz D (2015) Vegetation and environmental changes in a Scots pine forest invaded by *Prunus serotina*: What is the threat to terricolous bryophytes? *European Journal of Forest Research* 134: 793–801.
- Halarewicz A, Pruchniewicz D, Kawalko D (2017) Soil properties in Scots pine forest invaded by *Prunus serotina* (Ehrh.). *Sylvan* 161: 149–154.
- Hanzelka J, Reif J (2016) Effects of vegetation structure on the diversity of breeding bird communities in forest stands of non-native black pine (*Pinus nigra* A.) and black locust (*Robinia pseudoacacia* L.) in the Czech Republic. *Forest Ecology and Management* 379: 102–113.
- Hejda M, Hanzelka J, Kadlec T, Štrobl M, Pyšek P, Reif J (2017) Impacts of an invasive tree across trophic levels: species richness, community composition and resident species' traits. *Diversity and Distributions* 23: 997–1007.
- Kadlec T, Štrobl M, Hanzelka J, Hejda M, Reif J (2018) Differences in the community composition of nocturnal Lepidoptera between native and invaded forests are linked to the habitat structure. *Biodiversity and Conservation* 27: 2661–2680.
- Knoerzer D, Reif A (1996) Die Naturverjüngung der Douglasie im Bereich des Stadtwaldes von Freiburg. *AFZ-DerWald* 20/1996: 1117–1121.
- Kostić O, Jarić S, Gajić G, Pavlović D, Marković M, Mitrović M, Pavlović P (2016) The effects of Douglas fir monoculture on stand characteristics in a zone of montane beech forest. *Archives of Biological Sciences* 68: 753–766.
- Lazzaro L, Giuliani C, Fabiani A, Agnelli AE, Pastorelli R, Lagomarsino A, Benesperi R, Calamassi R, Foggi B (2014) Soil and plant changing after invasion: The case of *Acacia dealbata* in a Mediterranean ecosystem. *Science of the Total Environment* 497: 491–498.
- Lazzaro L, Mazza G, d'Errico G, Fabiani A, Giuliani C, Inghilesi AF, Lagomarsino A, Landi S, Lastrucci L, Pastorelli R (2018) How ecosystems change following invasion by *Robinia pseudoacacia*: Insights from soil chemical properties and soil microbial, nematode, microarthropod and plant communities. *Science of the Total Environment* 622: 1509–1518.
- Lomba A, Vicente J, Moreira F, Honrado J (2011) Effects of multiple factors on plant diversity of forest fragments in intensive farmland of Northern Portugal. *Forest Ecology and Management* 262: 2219–2228.
- Lorenzo P, Rodríguez-Echeverría S, González L, Freitas H (2010) Effect of invasive *Acacia dealbata* Link on soil microorganisms as determined by PCR-DGGE. *Applied Soil Ecology* 44: 245–251.
- Lorenzo P, Pazos-Malvido E, Rubido-Bara M, Reigosa MJ, González L (2012a) Invasion by the leguminous tree *Acacia dealbata* (Mimosaceae) reduces the native understorey plant species in different communities. *Australian Journal of Botany* 60: 669–675.
- Lorenzo P, Rubido-Bará M, Rodríguez-Echeverría S, González L (2012b) Impacts of the invasive mimosa (*Acacia dealbata*) on above and belowground diversity in different native ecosystems. *NeoBiota*: 180.

- Lorenzo P, Pereira CS, Rodríguez-Echeverría S (2013) Differential impact on soil microbes of allelopathic compounds released by the invasive *Acacia dealbata* Link. *Soil Biology and Biochemistry*. 57: 156–163.
- Luciañez M, Silgado N (2007) Estudio ecológico de las comunidades de Colémbolos en zonas reforestadas con eucalipto y pino en Asturias (noroeste de la Península Ibérica). *Boletín Sociedad Entomológica Aragonesa* 1: 325–332.
- Madeira M, Ribeiro C (1995) Influence of leaf litter type on the chemical evolution of a soil parent material (sandstone). *Biogeochemistry* 29: 43–58.
- Malchair S, Carnol M (2009) Microbial biomass and C and N transformations in forest floors under European beech, sessile oak, Norway spruce and Douglas-fir at four temperate forest sites. *Soil Biology and Biochemistry* 41: 831–839.
- Mareschal L, Bonnaud P, Turpault MP, Ranger J (2010) Impact of common European tree species on the chemical and physicochemical properties of fine earth: An unusual pattern. *European Journal of Soil Science* 61: 14–23.
- Medina-Villar S, Castro-Díez P, Alonso A, Cabra-Rivas I, Parker I, Pérez-Corona E (2015) Do the invasive trees, *Ailanthus altissima* and *Robinia pseudoacacia*, alter litterfall dynamics and soil properties of riparian ecosystems in Central Spain? *Plant and Soil* 396: 311–324.
- Medina-Villar S, Rodríguez-Echeverría S, Lorenzo P, Alonso A, Pérez-Corona E, Castro-Díez P (2016) Impacts of the alien trees *Ailanthus altissima* (Mill.) Swingle and *Robinia pseudoacacia* L. on soil nutrients and microbial communities. *Soil Biology and Biochemistry* 96: 65–73.
- Montecchiari S, Tesi G, Allegrezza M (2020) Effects of *Robinia pseudoacacia* coverage on diversity and environmental conditions of central-northern Italian *Quercus pubescens* sub-mediterranean forests (habitat code 91AA*): A threshold assessment. *Annali di Botanica*: 33–54.
- Motard E, Muratet A, Clair-Maczulajtys D, Machon N (2011) Does the invasive species *Ailanthus altissima* threaten floristic diversity of temperate peri-urban forests? *Comptes Rendus Biologies* 334: 872–879.
- Motard E, Dusz S, Geslin B, Akpa-Vinceslas M, Hignard C, Babiari O, Clair-Maczulajtys D, Michel-Salzat A (2015) How invasion by *Ailanthus altissima* transforms soil and litter communities in a temperate forest ecosystem. *Biological Invasions* 17: 1817–1832.
- Nascimbene J, Marini L (2010) Oak forest exploitation and black-locust invasion caused severe shifts in epiphytic lichen communities in Northern Italy. *Science of the Total Environment* 408: 5506–5512.
- Nascimbene J, Nimis PL, Benesperi R (2012) Mature non-native black-locust (*Robinia pseudoacacia* L.) forest does not regain the lichen diversity of the natural forest. *Science of the Total Environment* 421: 197–202.
- Nascimbene J, Lazzaro L, Benesperi R (2015) Patterns of β -diversity and similarity reveal biotic homogenization of epiphytic lichen communities associated with the spread of black locust forests. *Fungal Ecology* 14: 1–7.
- Pinto C, Sousa JP, Graca MAS, Da Gama MM (1997) Forest soil Collembola. Do tree introductions make a difference? *Pedobiologia* 41: 131–138.
- Piwczyński M, Puchałka R, Ulrich W (2016) Influence of tree plantations on the phylogenetic structure of understorey plant communities. *Forest Ecology and Management* 376: 231–237.
- Poblador S, Lupon A, Martí E, Sabater F, Sabaté S, Bernal S (2019) The influence of the invasive alien nitrogen-fixing *Robinia pseudoacacia* L. on soil nitrogen availability in a mixed Mediterranean riparian forest. *European Journal of Forest Research* 138: 1083–1093.
- Podrázský V, Remeš J, Hart V, Moser WK (2009) Production and humus form development in forest stands established on agricultural lands – Kostelec nad Černými lesy region. *Journal of Forest Science* 55: 299–305.

- Podrázský V, Viewegh J, Matějka K (2011) Effect of Douglas fir on plant communities in forest ecosystems compared to other tree species. *Zprávy Lesnického Výzkumu* 56: 44–51.
- Prietzl J, Bachmann S (2012) Changes in soil organic C and N stocks after forest transformation from Norway spruce and Scots pine into Douglas fir, Douglas fir/spruce, or European beech stands at different sites in Southern Germany. *Forest Ecology and Management* 269: 134–148.
- Proença VM, Pereira HM, Guilherme J, Vicente L (2010) Plant and bird diversity in natural forests and in native and exotic plantations in NW Portugal. *Acta Oecologica* 36: 219–226.
- Rawlik M, Kasprówicz M (2018) Jagodziński, AM; Kazmierowski, C.; Łukowiak, R.; Grzebisz, W. Canopy tree species determine herb layer biomass and species composition on a reclaimed mine spoil heap. *Science of the Total Environment* 635: 1205–1214.
- Reif J, Hanzelka J, Kadlec T, Štrobl M, Hejda M (2016) Conservation implications of cascading effects among groups of organisms: The alien tree *Robinia pseudacacia* in the Czech Republic as a case study. *Biological Conservation* 198: 50–59.
- Rivas-Salvador J, Štrobl M, Kadlec T, Saska P, Reif J (2021) A non-native woody plant compromises conservation benefits of mid-field woodlots for birds in farmland. *Global Ecology and Conservation* 26: e01458.
- Rodríguez J, Cordero-Rivera A, González L (2020) Characterizing arthropod communities and trophic diversity in areas invaded by Australian acacias. *Arthropod–Plant Interactions* 14: 531–545.
- Serralheiro F, Madeira M (1990) Changes in arthropod soil fauna due to afforestation with *Eucalyptus globulus*. *Agrokémia és Talajtan* 39: 602–606.
- Sitzia T, Campagnaro T, Dainese M, Cierjacks A (2012) Plant species diversity in alien black locust stands: A paired comparison with native stands across a north-Mediterranean range expansion. *Forest Ecology and Management* 285: 85–91.
- Sitzia T, Campagnaro T, Kotze DJ, Nardi S, Ertani A (2018) The invasion of abandoned fields by a major alien tree filters understory plant traits in novel forest ecosystems. *Scientific Reports* 8: 1–10.
- Slabejová D, Bacigál T, Hegedúšová K, Májeková J, Medvecká J, Mikulová K, Šibíková M, Škodová I, Zaliberová M, Jarolímek I (2019) Comparison of the understory vegetation of native forests and adjacent *Robinia pseudacacia* plantations in the Carpathian-Pannonian region. *Forest Ecology and Management* 439: 28–40.
- Sousa JP, Da Gama MM (1994) Rupture in a Collembola community structure from a *Quercus rotundifolia* Lam. forest due to the reafforestation with *Eucalyptus globulus* Labill. *European Journal of Soil Biology* 30: 71–78.
- Sousa JP, Vingada JV, Barrocas H, Da Gama MM (1997) Effects of introduced exotic tree species on Collembola communities: the importance of management techniques. *Pedobiologia* 41: 145–153.
- Souza-Alonso P, Novoa A, González L (2014) Soil biochemical alterations and microbial community responses under *Acacia dealbata* Link invasion. *Soil Biology and Biochemistry*. 79: 100–108.
- Souza-Alonso P, Guisande-Collazo A, González L (2015) Gradualism in *Acacia dealbata* Link invasion: Impact on soil chemistry and microbial community over a chronological sequence. *Soil Biology and Biochemistry* 80: 315–323.
- Starfinger U, Kowarik I, Rode M, Schepker H (2003) From desirable ornamental plant to pest to accepted addition to the flora? The perception of an alien tree species through the centuries. *Biological Invasions* 5: 323–335.

- Staska B, Essl F, Samimi C (2014) Density and age of invasive *Robinia pseudoacacia* modulate its impact on floodplain forests. *Basic and Applied Ecology* 15: 551–558.
- Štrobl M, Saska P, Seidl M, Kocian M, Tajovský K, Řezáč M, Skuhrovec J, Marhoul P, Zbuzek B, Jakubec P (2019) Impact of an invasive tree on arthropod assemblages in woodlots isolated within an intensive agricultural landscape. *Diversity and Distributions* 25: 1800–1813.
- Trentanovi G, Von Der Lippe M, Sitzia T, Ziechmann U, Kowarik I, Cierjacks A (2013) Biotic homogenization at the community scale: Disentangling the roles of urbanization and plant invasion. *Diversity and Distributions* 19: 738–748.
- Vanderhoeven S, Dassonville N, Meerts P (2005) Increased topsoil mineral nutrient concentrations under exotic invasive plants in Belgium. *Plant and Soil* 275: 169–179.
- Vegini E, Lastrucci L, Lazzaro L, Cardarelli E, Martignoni M (2020) Impact of *Prunus serotina* Ehrh. invasion on heathland vegetation: a case of study in North-Western Italy. *Biologia* 75: 327–336.
- Verheyen K, Vanhellemont M, Stock T, Hermy M (2007) Predicting patterns of invasion by black cherry (*Prunus serotina* Ehrh.) in Flanders (Belgium) and its impact on the forest understorey community. *Diversity and Distributions* 13: 487–497.
- Vilà M, Tessier M, Suehs CM, Brundu G, Carta L, Galanidis A, Lambdon P, Manca M, Médail F, Moragues E (2006) Local and regional assessments of the impacts of plant invaders on vegetation structure and soil properties of Mediterranean islands. *Journal of Biogeography* 33: 853–861.
- Yüksek T (2012) The restoration effects of black locust (*Robinia pseudoacacia* L) plantation on surface soil properties and carbon sequestration on lower hillslopes in the semi-humid region of Coruh Drainage Basin in Turkey. *Catena* 90: 18–25.

Table S2. All collected soil traits from 103 papers, aggregated and by original description, including number of cases (No), alphabetically ordered.

Soil traits, aggregated	Soil traits, original description	No
Al	Al, Al floor, Al oxides topsoil, Al topsoil, Al ₃	39
allelopathy	allelopathy, allelopathy microbes, allelopathy plants	4
biomass	biomass benthic organic matter, biomass litter	2
base saturation	BS, BS floor, BS topsoil	32
C	C, C foliar, C litter, C soil, C topsoil, C total	37
C:N	C:N, C:N A, C:N B, C:N floor, C:N foliar, C:N litter, C:N organic, C:N soil, C:N topsoil	93
C:P	C:P	6
Ca	Ca ⁺ , Ca ⁺ floor, Ca ⁺ litter, Ca ⁺ soil, Ca ⁺ topsoil, Ca ₂ ⁺ , Ca ₂ ⁺ exchangeable	70
CaCO ₃	CaCO ₃ soil	1
Cd	Cd	6
CEC	CEC, CEC floor, CEC litter, CEC topsoil	58
conductivity	conductivity	4
Cu	Cu	7

discharge	discharge	1
EC	Exchange Capacity (EC) soil	1
EIV light	Ecological Indicator Value (EIV) light, EIV shading	20
EIV moisture	Ecological Indicator Value (EIV) moisture	29
EIV nitrogen	Ecological Indicator Value (EIV) nitrogen	13
EIV reaction	Ecological Indicator Value (EIV) reaction	19
EIV temperature	Ecological Indicator Value (EIV) temperature	10
electrical conductivity	electrical conductivity	1
F-layer	F-layer	6
Fe	Fe, Fe ₂ ⁺ floor	12
field capacity	field capacity	1
H ⁺	H ⁺	1
humus	humus, humus layer	8
hydrophobicity	hydrophobicity	1
K	K, K available, K floor, K topsoil, K topsoil available, K total floor, K total topsoil, K ⁺ , K ⁺ floor, K ₂ O	67
light transmittance	light transmittance	3
litter	litter lignin, lignin/N litter, litter cover, litter moisture	14
litter layer	litter layer	1
litter water	litter water	1
LMA	Ratio of Leaf Mass to Leaf Area (LMA)	8
LML	% Litter Mass Loss (LML)	3
loss of ignition	loss of ignition	3
Mg	Mg, Mg floor, Mg soil, Mg total floor, Mg total topsoil, Mg ₂ ⁺ floor, MgO	60
Mn	Mn, Mn ₂ ⁺ floor	8
moisture	moisture floor, moisture litter, moisture soil	8
N	N, N floor, N foliar, N litter, N mineral, N soil, N stock, N topsoil, N total, N total floor, N total topsoil, NH ₄ ⁺ , NH ₄ ⁺ topsoil, NO ₂ ⁻ , NO ₃ ⁻ , NO ₃ ⁻ topsoil, NO ₃ ⁻ /NH ₄ ⁺	223
N:P	N:P, N:P foliar	7
Na	Na, Na topsoil, Na ⁺	10
OC	Organic Carbon (OC), OC floor, OC soil, OC stock, OC topsoil	16
OF+OH layer	Organic Fermented horizon (OF) and Organic Humic horizon (OH)	1
OM	Organic Matter (OM), OM floor, OM litter, OM min soil, OM mineral, OM organic, OM soil, OM topsoil	35

oxygen	oxygen	1
P	P, P available, P available topsoil, P exchangeable, P foliar, P total floor, PP total topsoil, P total, P ₂ O ₂ , PO ₄	60
particle density	soil particle density	1
Pb	Pb	6
penetration resistance	soil penetration resistance	1
pH	pH, pH A, pH B, pH floor, pH H ₂ O, pH-H ₂ O floor, pH H ₂ O topsoil, pH KCl, pH KCl floor, pH KCl litter, pH KCl topsoil, pH litter, pH soil, pH topsoil	149
phenols	phenols	1
saturated hydraulic conductivity	soil saturated hydraulic conductivity	1
SEB	Exchangeable Base Cations (SEB)	6
SOC	Soil Organic Carbon (SOC), SOC floor, SOC stock, SOC topsoil	49
soil density	soil bulk density, soil density	2
soil humidity	soil humidity	1
soil moisture	soil moisture	10
soil porosity	soil porosity	3
soil temperature	soil temperature	5
soil water	soil water	1
SOM	Soil Organic Matter (SOM)	22
TOC	Total Organic Carbon (TOC)	1
water availability	water availability	1
wilting point	wilting point	1
Zn	Zn, Zn ²⁺ floor	13

Table S3. Non-native tree species (NNTs) and percentage of native vegetation (NV), i.e. native trees (NT) or open ecosystems (OE) to which the cases compare. The number of cases refer to all soil properties and taxonomic groups.

NNT species	# cases	1st (%)	2nd (%)	3rd (%)	4th (%)
<i>Acacia dealbata</i>	412	<i>Pinus</i> spp. 63.4 %	<i>Quercus</i> spp. 19.9 %	Shrubland 8.5 %	<i>Populus nigra</i> 1.9 %
		<i>Pinus pinaster</i> , <i>Pinus</i> spp.	<i>Quercus faginea</i> , <i>Q. ilex</i> , <i>Q. robur</i> , <i>Q. suber</i>		
<i>Ailanthus altissima</i>	186	<i>Populus</i> spp. 64.0 %	<i>Ulmus minor</i> 12.9 %	<i>Quercus robur</i> 9.7 %	<i>Acer pseudoplatanus</i> 4.3 %

Populus alba, *P. nigra*

<i>Eucalyptus globulus</i>	278	<i>Quercus</i> spp. 44.2 % <i>Quercus canariensis</i> , <i>Q. faginea</i> , <i>Q. robur</i> , <i>Q. rotundifolia</i> , <i>Q. suber</i> , <i>Quercus</i> spp.	<i>Pinus pinaster</i> 30.6 %	<i>Castanea sativa</i> 5.4 %	Shrubland 4.3 %
<i>Prunus serotina</i>	343	<i>Pinus</i> spp. 37.3 % <i>Pinus sylvestris</i> , <i>Pinus</i> spp.	<i>Quercus</i> spp. 36.2 % <i>Quercus petraea</i> , <i>Q. robur</i> , <i>Quercus</i> spp.	<i>Fagus sylvatica</i> 15.5 %	Wasteland 4.7 %
<i>Pseudotsuga menziesii</i>	806	<i>Picea abies</i> 42.8 %	<i>Fagus sylvatica</i> 28.2 %	<i>Quercus</i> spp. 13.5 % <i>Q. petraea</i> , <i>Q. robur</i> , <i>Quercus</i> spp.	<i>Pinus</i> spp. 12.3 % <i>P. sylvestris</i> , <i>Pinus</i> spp.
<i>Quercus rubra</i>	244	<i>Pinus sylvestris</i> 60.7 %	<i>Quercus</i> spp. 26.6 % <i>Quercus petraea</i> , <i>Q. robur</i> , <i>Quercus</i> spp.	<i>Fagus sylvatica</i> 10.3 %	Broadleaved 1.6 %
<i>Robinia pseudoacacia</i>	535	<i>Quercus</i> spp. 27.1 % <i>Quercus petraea</i> , <i>Q. pubescens</i> , <i>Quercus</i> spp.	<i>Pinus</i> spp. 25.1 % <i>Pinus nigra</i> , <i>P. sylvestris</i>	<i>Betula pendula</i> 14.8 %	<i>Populus alba</i> 6.5 %

Figures

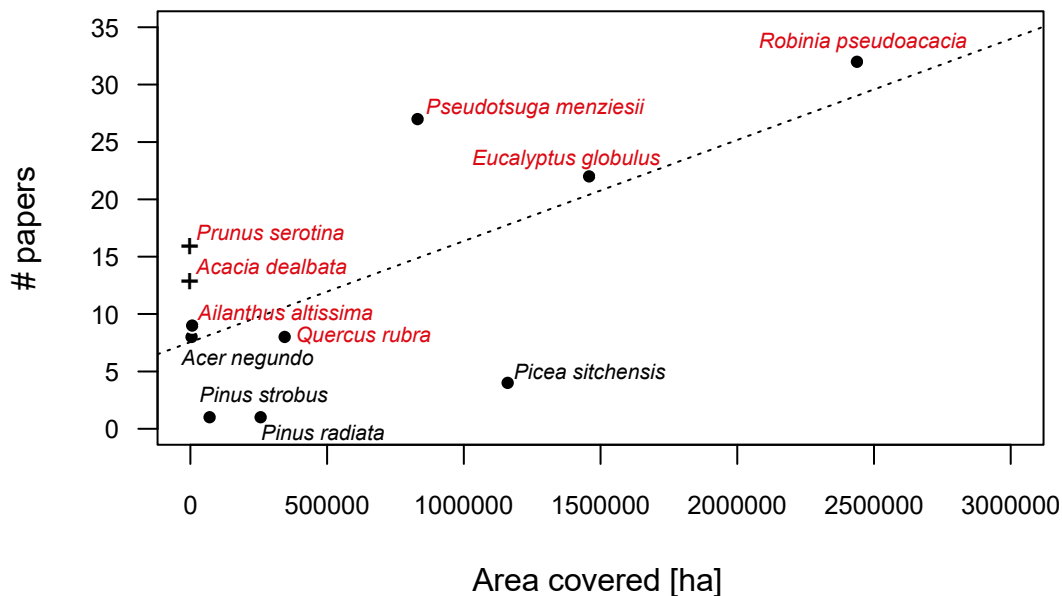


Figure S1. Area cover of eleven non-native tree species (NNTs; phase 3, see Fig. 2; + indicates that the species are present on a relatively small area, the threshold being set at 500 ha for this analysis) vs. number of papers with pairwise comparisons meeting standards. NNTs in red were finally used for all analyses. The number of papers is positively correlated with the area cover of these species in Europe, $p=0.02$, $R^2=0.46$; $y=7.55 + 0.000009 \cdot \text{area}$.

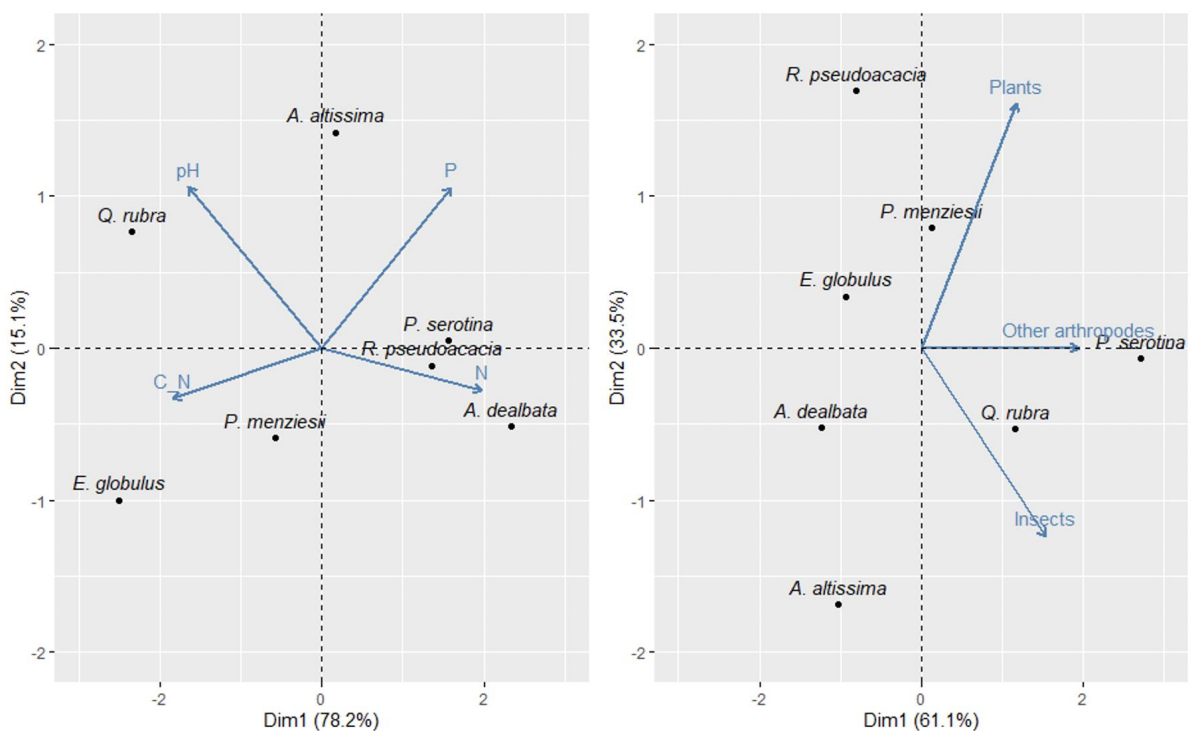


Figure S2. Biplots of Principal Components Analysis (PCA) using the mean effect of NNTs on four soil properties (left) and three taxa groups (right). Only those variables with a complete set of values for all NNTs were considered for building the PCA.