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Established Invasive Tree Species Offer Opportunities for Forest Resilience to Climate Change

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Abstract

Purpose of review A rapidly changing climate is weakening the resilience of forest ecosystems through vitality loss of major native tree species, which reduces the ability of forests to deliver ecosystem services. Established invasive tree species (EITS) may take over the vacant space potentially preventing the regeneration of the preferred native tree species. This paper aims to investigate how expansion of these invasive non-native tree species can be addressed in a context of climate-smart forest management, considering alternatives to costly and often ineffective EITS control measures.

Recent findings We found that forest ecologists increasingly recognize that climate-smart forest management, in particular tree species diversification and close-to-nature forest management, can strengthen the resilience of forests against negative impacts by EITS. In the resulting resilient forest ecosystems, a more closed canopy may deprive EITS of their invasive nature, and EITS may contribute to climate change adaptation.

Summary This review proposes new pathways for forest management transcending the apparent incompatibility between the dominance of EITS and the adaptation capacity of forests and forest management to climate change. Adaptive measures to increase the resilience of forests to climate change may prevent the dominance of EITS. Under such conditions, useful functional traits of these tree species may even contribute to maintenance or enhancement of biodiversity, provisioning of ecosystem services and adaptation to climate change.

Keywords Climate-smart forest management · Non-native species · Invasiveness · Invasibility · Biodiversity · Forest restoration · *Ailanthus altissima* · *Eucalyptus globulus* · *Pinus radiata* · *Prunus serotina* · *Robinia pseudoacacia*

Introduction

Global change, caused by the rapid increase of human activities and the anthropogenic emissions of greenhouse gases, threatens the functioning of forest ecosystems. Climate warming and biological invasions are among the major drivers of ecosystem change, and they are often connected through positive feedback loops [1, 2]. These stressors may affect forest structure and functioning by changing abiotic conditions, vegetation structure and species composition

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[3–8]. Rapid climate warming triggers more frequent and heavier disturbances—including wildfires, windstorms, droughts, insect, and pathogen outbreaks—threatening the ability of forest ecosystems to provide ecosystem services [1, 9–11]. Also, establishing non-native invasive species cause changes in ecosystem structure and functions [12–25].

Tree species have been moved across continents in the past for various reasons (e.g., landscape aesthetics, ecosystem restoration, enrichment of biodiversity or wood production) and in many cases have become part of regional tree species pools worldwide. Some species stand out because of their competitive behaviour and other impacts on ecosystems, and are referred to as 'invasive'. Research on the effects of non-native tree species in forests often focuses on the prevention of new invasions. In this review, we focus on invasive tree species that are already well established and widespread, here called; 'Established Invasive Tree Species'(EITS).

EITS can be harmful to non-forest native ecosystems, like grasslands, rangelands, and savannas [26–28]. As fast-growing tree species with pioneer traits and colonisation potential, they may turn these vegetation types into forests, resulting in potential local extinctions of light-demanding species [28–30]. Covering the impacts of EITS in this context is out of the scope of the paper. Yet, these species may also have significant impacts on forest-related biodiversity, ecosystem processes and related ecosystem services [25, 28, 31–35]. They may directly or indirectly influence the availability of resources for other species by causing drastic changes in the biotic or abiotic environment (e.g., by shading, competition for belowground resources, effects on biogeochemistry through rich litter, N-fixation) [36–38] hampering the regeneration of native tree species [39–42]. In fire-prone regions, EITS can alter fire regimes by increasing fuel availability and flammability [43, 44]. Additionally, EITS may have a high potential for conflict with nature conservation objectives, since they are usually not part of the target forest composition [45, 46]. Yet, some benefits of EITS have also been reported [47–49]. Such benefits may include contributions to species richness [50–52], enhancement of nutrient availability [53–55], provision of ecosystem services [56–58] and genetic conservation of EITS threatened in their native habitat [59].

As forest managers seek a pragmatic way to deal with EITS, the climatic conditions under which they do so are also changing. Global average temperatures have risen rapidly in recent decades, with ensuing droughts and heat waves [60]. The effects of climate change have caused increased tree mortality on all continents [61–63]. Sometimes forests were unable to recover [64], while in other situations, forests reacted by shifts in tree species composition [65]. These observations suggest that persistent and progressive changes in global forests may occur in response to climate change so that the provision of ecosystem services, such as climate regulation, biomass production, food, medicine, water supply and purification, pollination, and habitat provision for forest species, may decline [66–68]. Often EITS are better adapted to these changes, possibly due to higher ecological plasticity and thus broader ecological amplitude of tolerated ecological conditions [57, 69, 70].

The disturbances caused by climate change may also increase the susceptibility of forests to biological invasions due to reduced dispersal, establishment and recruitment of late-successional, long-lived tree species. These conditions favour pioneer trees with high turnover rates, which are attributes of most EITS. Moreover, resources released through mortality, such as light, can locally facilitate the expansion of shade-intolerant EITS. [71–77].

In addition to natural forests with drought-intolerant native trees, forests sensitive to climate change often turn out to be highly disturbed ecosystems with altered abiotic conditions and species composition—such as plantations or forest expansion on abandoned industrial and agricultural sites. Such altered forest ecosystems with abiotic and biotic conditions outside the historical range of variability of a given place are examples of novel ecosystems [50, 51, 78–80]. One expected outcome of climate change is that many of these novel systems will emerge worldwide, with increasing occurrence of EITS as a consequence [81–83].

In research on the resilience of forest ecosystems, the presence of these EITS is commonly perceived as a threat [84–86], whereas some non-invasive, non-native tree species are sometimes expected to contribute to biodiversity, ecosystem services and climate change adaptation [87–90]. In management practice, however, this division between non-invasive and invasive established tree species is not that clear-cut [46], and even EITS can contribute to the provision of ecosystem services [67, 91]. Forest managers and researchers notice that under some circumstances EITS can also contribute to the resilience of forests to the changing climate [57, 92, 93].

One of the main contributions to resilience may be filling vacant niches, so that some aspects of structure and functions recover faster after a disturbance. For instance, some EITS may operate as nurse trees—by regulating the forest microclimate and sometimes promoting litter decomposition – and stimulate forest succession [94–97]. In the scientific literature, these benefits of EITS, based on the same processes that were interpreted previously as signs of invasiveness, have received little research attention so far.

Although human-induced climate change and the presence of invasive species are relatively new phenomena, pressure from stressors is part of any forest ecosystem. The set of mechanisms that jointly ensure the survival and renewal of forest ecosystems under environmental stress will determine their resilience. In forest ecology, various resilience definitions are used that do not all agree [98, 99]. In this paper resilience is understood as the capacity of a forest ecosystem to *absorb* (resist) environmental changes (pressures) and natural and anthropogenic disturbances (pulses) without losing its structure and functions while *adapting* to the changing environmental conditions, the so-called ecological resilience [99–101].

Strictly speaking, forest resilience is often considered to be relative to one specific ecosystem service (e.g., wood production) [98, 102]. However, in most cases forests are expected to provide a wide range of ecosystem services [1, 4, 11, 57, 68, 103]. Thus, the concept of resilience commonly refers to the stability in providing a set of ecosystem services under changing conditions.

In this review we investigate how the presence of EITS can be addressed in the context of climate-smart forest management, aiming to strengthen forest resilience to climate change. We consider the presence of EITS to be no longer avoidable in many regions, already present in forests and often in high density. So, in this context, EITS are not considered as potential or actual threats to forests but as elements that are already present, with a potential contribution to forest resilience against climate change. When we refer to changes in external conditions, we specifically mean the effects of ongoing climate change.

Our research question is twofold:

(1) How can EITS be integrated in forest ecosystems and forest management so that these tree species contribute to forest biodiversity and forest-related ecosystem services?
(2) Can EITS themselves contribute to the climate change adaptation capacity of these forests?

Materials and methods

We carried out a literature review on the role of EITS in forest resilience enhancement to climate change in three steps:

(1) Identification of challenges and benefits of EITS and the possibilities of integrating EITS in forest ecosystems (see section 'EITS challenges and opportunities');
(2) Describing the impact of integrated EITS on biodiversity and ecosystem services, with a focus on timber production (see section 'Contribution of integrated EITS to species diversity and wood production');
(3) Exploring the effects of EITS on climate resilience and their potential to contribute to climate change adaptation (see section 'Contribution of EITS to climate resilience').

We used an informal iterative workflow in which we interpreted data from the literature using expert knowledge and concepts developed by the authors based on years of experience with EITS in forests. We searched for relevant articles in databases such as PubMed, Scopus, and Web of Science. We also consulted experts in the field and discussed the findings with them. Based on the findings, we created a list of key points and synthesised the results of 466 publications, mainly published in the period after the year 2000.

In this review, we restrict ourselves to the impact of tree species on forest ecosystem functioning and the provision of ecosystem services. Therefore, we do not include societal impacts or origin of a species as is often done in assessments of impacts of biological invasions [104–107] but use an ecological definition of invasiveness in which the term describes the competitive advantages that enable a species to proliferate rapidly and conquer new environments [31, 108–112]. Moreover, since EITS are just as permanently present as native tree species in many parts of the world, we separate 'invasive' from 'non-native' [113]. The two dual concepts, invasive vs non-invasive and native vs non-native, yield four possible combinations of these terms. 'Invasive non-native' and 'invasive native' both indicate species that exhibit an invasive character . In this ecological definition of invasiveness, invasive species sustain self-replacing populations over several life cycles, produce reproductive offspring, often in very large numbers, and have the potential to spread over long distances [31, 108–110]. In forests, invasive tree species appear to exhibit typical pioneer behaviour: early seed setting, easy spreading and rapid juvenile growth [35, 92, 114]. These pioneer tree species usually have high light requirements upon establishment [115]. From the extensive lists compiled of invasive tree species [28] we will refer in more detail to five globally widespread EITS, which are each appealing examples in different parts of the world: *Ailanthus altissima* (Mill.) Swingle, *Eucalyptus globulus* Labill., *Pinus radiata* D. Don, *Prunus serotina* Ehrh. and *Robinia pseudoacacia* L. See Table 1 for an overview of their occurrence. A short characterisation of each species, based on this review, is given in separate boxes (see Boxes 1, 2, 3, 4, and 5).

Table 1 EITS with the continent of origin (O), the continent where they are considered invasive (I) [28] and reference to the box with short descriptions of each species

EITS Continent	Africa	North America	South America	Asia	Europe	Oceania	Box
Ailanthus altissima	I	I	I	O/I	I	I	Box 1
Eucalyptus globulus		I	I		I	O/I	Box 2
Pinus radiata	I	O	I	I		I	Box 3
Prunus serotina	I	O			I		Box 4
Robinia pseudoacacia	I	O/I	I		I		Box 5

Invasiveness of EITS appears to vary considerably, from the highly invasive *P. serotina* [116–119]—thanks to efficient dispersal by birds and mammals over short and long distances -, over the moderately invasive *A. altissima* [120–123], *P. radiata* [28, 29, 76] and *R. pseudoacacia* [54, 70, 124]—thanks to efficient wind dispersal -, to the limited invasiveness of *E. globulus* [125–131].

To organise all gathered information and gain insight into the possibilities for enhancing forest resilience to EITS and climate change, we first developed a conceptual framework for forest resilience under climate change (see section 'Forest resilience framework'). This framework was also valuable to address the abundant information on forest adaptation to climate change, resilience against dominance by EITS, and possible contributions of EITS to forest adaptation to climate change. Moreover, it helped us to bridge the apparent contradiction between reducing EITS by strengthening forest resilience, and the possible positive contribution of these EITS to the resilience of the forest ecosystem against climate change. Finally, in the conclusion section, we formulate scenarios and possible solutions for a way forward for EITS integration based on our findings and synthesis.

Forest resilience framework

Following the previous definition, forest resilience has two major components—absorption and adaptation -, both ecosystem reactions to stress grounded in ecosystem processes [132, 133]. Absorption refers to the plasticity of the ecosystem under relatively stable environmental conditions, both at the level of organisms and of the system as a whole. This concept aligns closely with the definition of *engineering resilience*. Under stable conditions the frequency and intensity of disturbances—such as storms, fires, wood harvesting, diseases, and pests – remain within the absorptive capacity of the ecosystem operating under a dynamic equilibrium. This ensures continuity in the composition, structure and functioning of the ecosystem [10, 134]. But when the resilience of a forest ecosystem is weak—e.g., due to extreme herbivore pressure—or the character, intensity or frequency of disturbances fundamentally changes as a result of changing conditions—e.g., climate change and invasive species—then ecosystem processes may not be able to secure the persistence of individuals and recovery of populations. This is where ecosystem adaptation comes into play. Under these changed conditions, the ecosystem develops into one with a different composition, structure and functioning [10, 134]. The interplay of absorption and adaptation, as used in this paper, is also called *ecological resilience* [135, 136].

The dichotomy between absorption and adaptation, as proposed in literature [99, 101, 135] naturally connects to the practical discussion on climate change adaptation. Forest managers try to increase forest resilience for securing ecosystem services by optimising ecosystem processes based on the current vegetation composition, thus, relying on the ecosystem's absorption. When it becomes clear that the current suite of forest tree species face a high risk of losing their vitality due to changing climatic conditions, the forest tree species composition may be adapted in an ongoing and long process by adding new provenances or species, both natives and non-natives [137]. In this way, the absorption capacity is complemented by the adaptation capacity. These two components of resilience, absorption, and adaptation, fit well with the two questions this paper addresses.

(1) First, what effect has absorption of EITS within forest ecosystems on their components – e.g., abiotic conditions, vegetation structure and species composition – on forest biodiversity and ecosystem services?
(2) And secondly can EITS, as an absorbed component of tree diversity and redundancy, contribute to absorption and adaptation of climate change effects?

To clarify the connection between the concepts of absorption and adaptation with the development of forest ecosystems under stress, we developed a forest resilience framework inspired mainly by the unified framework for ecological resilience of Falk et al. 2022 [134] (see Fig. 1).

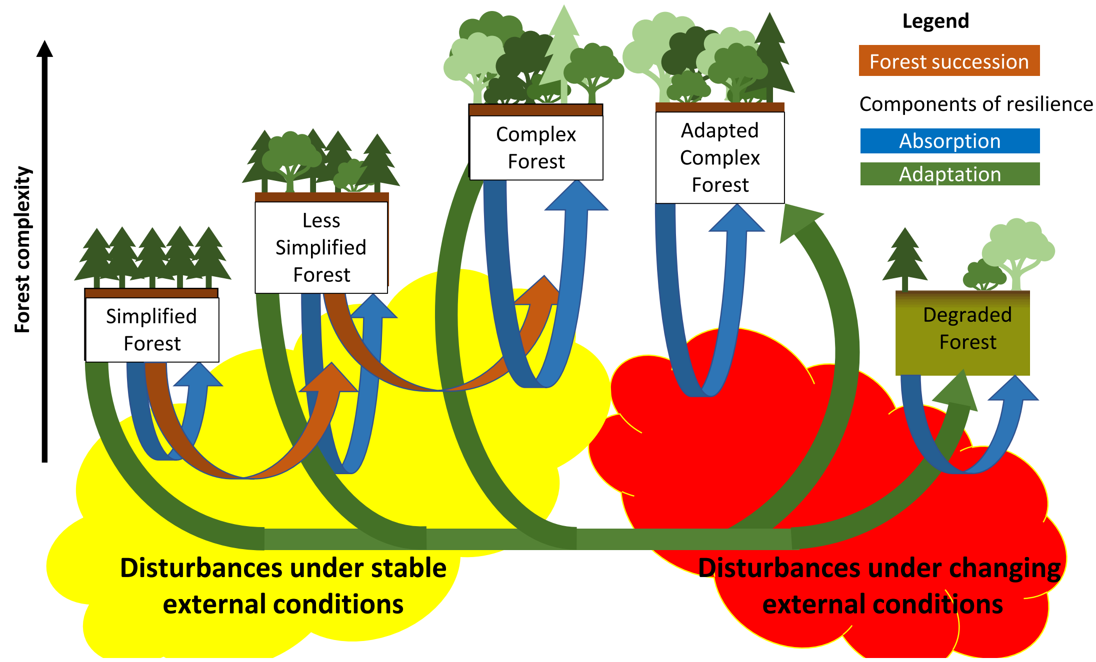


Fig. 1 Framework for forest resilience. Under constant climatic conditions **Complex Forests** will preserve their structure and functions through absorption of stress. **Simplified Forests** under steady state conditions can, through forest succession, develop into **Less Simplified Forest** and when a large tree species pool is present in the landscape, even into **Complex Forests.** When absorption fails, due to changing climatic conditions, adaptation occurs, involving different species or functional groups. Adaptation can lead to an **Adapted Complex Forest** while maintaining structure and function of the pre-disturbance community, or lead to **Degraded forest** as a result of altered structure or function (modified after Falk et al. (2022) [134])

In our framework we make a distinction between simplified and complex forests. Simplified forests occur where past land use has led to limited species diversity, limited redundancy, and simplified structure; these conditions can facilitate dominance of EITS. Complex forests have a more developed structure and are richer in tree species as a result of a lack of management or more extensive management (e.g., close-to-nature forestry). They are less prone to EITS dominance. Through forest succession and disturbances under stable external conditions, simplified forests develop into less simplified forests, which are more structured and richer in tree species – if propagules are present. In the presence of a diverse tree species pool, simplified and less simplified forests can develop into complex forests, characterised by structural and compositional complexity.

Absorption and adaptation are two different resilience components that may occur simultaneously. Under relatively stable climate conditions, absorption of disturbances dominates in complex forests resulting in continuity of ecosystem structure and functioning. Under changing climate conditions, the complex forest ecosystem continues to absorb disturbances. However, when the absorbing capacity is exceeded, adaptation may occur, and the complex forest develops into an adapted complex forest [138].

As long as the joint processes of absorption and adaptation ensure the preservation of structure and function, we speak of resilient forest ecosystems. However due to changing climatic conditions—reinforcing already existing stressors or introducing new ones [82]—forest structure and function may change, in which case forests may become insufficiently resilient [134, 139–141]. According to the FAO Global Forest Resources Assessment, we refer to these resulting forest ecosystems as degraded forests: forests whose structure and functions are negatively affected resulting in systems with lower capacity to supply products and/or services [142]. Simplified and less simplified forests are more at risk of degradation than complex forests due to limited diversity and species redundancy [137].

Resilience is often expressed in terms of a system's insurance by diversity and redundancy [100, 136, 143, 144]. The functional characteristics of tree species influence their performance in terms of growth, survival or reproduction [79]. Greater diversity in tree species with different functional traits is expected to reduce the impact of disturbance or stressors on the forest [60, 80–82, 145] and provide greater adaptability [83] (Fig. 2a). Besides the variation in tree species, it is also important for the resilience of the forest ecosystem that multiple tree species with similar characteristics occur, in

Fig. 2 Illustration of the concepts of functional diversity and redundancy within two stands. **a.** Although the stand in the upper pane consists of only two tree species, it has high functional diversity because they have very different functional properties: for example, one species is a deciduous broadleaf tree, and the other an evergreen conifer. However, because of the large difference in functional properties between these two species, functional redundancy is weak; if one species disappears, several specific functional properties are lost. **b.** The lower stand also has high functional diversity because it consists of six different species, four deciduous broadleaf species and two conifer species with relatively similar characteristics. However, functional redundancy is high in this case because if one species disappears, the variation in functional traits in the stand will be maintained (adapted from Messier et al. 2019 [144])

case one tree species fails due to climate change effects. This is called functional redundancy [82, 84, 85] (Fig. 2b).

EITS challenges and opportunities

Significant negative impacts of EITS on biodiversity, ecosystem processes, and related ecosystem services have been reported [25, 28, 31–35, 146] Conversely, other studies point at the contribution of EITS to species richness, forest resilience, ecosystem services, and climate change adaptation [47, 50, 52, 56, 57, 67, 69, 78, 147, 148]. Either way, EITS may directly or indirectly influence the availability of resources for other species by causing changes in the biotic or abiotic environment [36–38].

EITS, for example, affect nutrient availability and soil fertility, which varies greatly among tree species. Whereas *P. radiata* may acidify the forest soil, most notably on low-fertility sites [149], *P. serotina* [53], *A. altissima* [37] and *R. pseudoacacia* [150] usually increase nutrient availability. *Eucalyptus globulus* litter degrades slowly in monocultures [151], and the high biomass removal in plantation forestry linked to the high productivity of this tree species seems to reduce nutrient availability [152, 153] (See also Table 6). This high productivity also seems to be the main cause of the sometimes observed high water consumption in *E. globulus* plantations [154]. However, even less productive EITS can influence the soil moisture availability for other tree species especially when they have a more efficient water uptake strategy [155].

Light availability can also be affected by the presence of EITS. Under pioneer conditions such as in spontaneous forest development on agricultural land, forest recovery after fire or in plantations consisting of tree species which form a translucent canopy, EITS can form dense shrub layers that alter the light environment that can limit the regeneration of native tree species for several years to decades [28, 156, 157]. Also allelopathic effects have been demonstrated in some EITS—e.g., *A. altissima, P. serotina, R. pseudoacacia, E. globulus*—under laboratory and experimental conditions [157–160], albeit with limited impact on tree species regeneration and survival under field conditions [37, 55, 161–164].

Yet, EITS may also positively influence forest recovery. Due to their invasive trait and frequent shade-intolerant nature, they may rapidly colonize deforested areas and accelerate canopy closure. This may benefit survival of many typical forest plants and animal species as they depend on the microclimate that prevails in forests [26, 88]. Through shading and transpiration, the closed crown canopy causes lower maximum temperatures in summer and higher minima in winter, while maintaining levels of air and soil moisture that can be higher than in the open [86, 87, 165].

Ailanthus altissima has often been planted for ornamental reasons in areas climatically similar to the cool northern side of its native range. Warming of the climate offers expansion potential here, which *A. altissima* uses, piggybacking on road and rail transport. Despite its expansive character, the review shows that where *A. altissima* forms mature forests in the presence of native tree species, the latter rejuvenate easily under its canopy.

TRAITS:

- Deciduous broadleaf pioneer tree, 20 – 30 m high
- More climate resilient than competitors
- Positive impact on nutrient availability
- High quality wood, comparable to *Fraxinus* spp.

NATIVE RANGE:

- Eastern China

INTRODUCTION PATHWAYS:

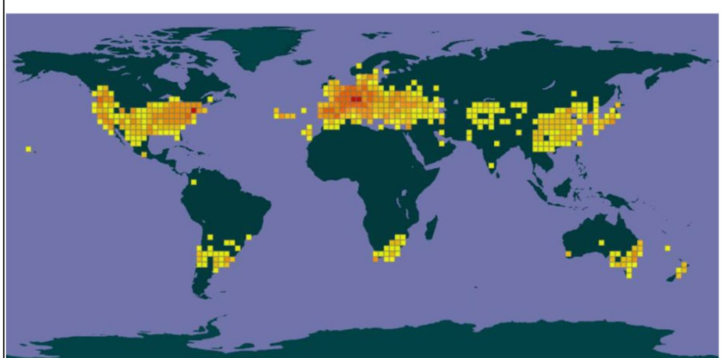
- Horticulture
- Silviculture

INVASION HABITAT:

- Pioneer species in forest margins and open forests, outside forests in urban and rural landscapes, heathlands, dry grasslands, and dunes.

STATUS:

- Naturalized in all continents but Antarctica. Widespread and common in its native Chinese range, Europe, North America, and Australia.



Ailanthus altissima distribution map; colors indicate gradients of occurrence from limited (yellow) to intensive (red) presence (source: https://www.gbif.org/species/3190653).

PICTURE: Native forest development under mature *Ailanthus altissima* forest in the Parcul National Portile de Fier, Romania (with *Acer campestre, Acer monspessulanum, Acer platanoides, Acer pseudoplatanus, Alnus glutinosa, Carpinus betulus, Cornus sanguinea, Corylus avellana, Crataegus monogyna , Euonymus europaeus, Fagus orientalis, Fagus sylvatica, Fraxinus excelsior, Fraxinus ornus, Juglans regia, Lonicera periclymenum, Prunus avium, Prunus spinosa, Quercus cerris, Quercus robur, Sambucus nigra, Tilia cordata, Tilia platyphyllos, Tilia tomentosa, Ulmus glabra and Ulmus minor*) (Photo Bart Nyssen)

Box. 1 *Ailanthus altissima*. Effective nurse tree with rapid spread facilitated by climate change

Through their influence on resources, EITS also influence forest regeneration [39, 40]. Especially when they grow densely, they can reduce the amount of light reaching the soil surface. Thus, they may often promote late successional tree species at the expense of pioneer tree species, thereby accelerating forest succession. Also, when EITS form the tree canopy, the influence of their litter on soil development may play a decisive role. EITS with nutrient-rich leaves may increase the nutrient availability in the topsoil, thereby facilitating the establishment of pioneer and late successional tree species [134, 166]. This positive effect can, in fact, compensate for allelopathic effects [55, 165].

Changes due to the presence of EITS in the light environment and in nutrient and moisture availability in the topsoil also influences the herb layer. Research into the effect of EITS on the herb layer also shows conflicting results. EITS can reduce the biodiversity of the herb layer by promoting a higher abundance of generalist species [167]. But the main effects here are a shift from light-demanding to more shade-tolerant tree species and, in the case of EITS with nutrient-rich litter, to species bound to a richer forest floor. These tree species usually promote development towards specialist forest species [168]. To a greater or lesser extent EITS are host tree species for other organisms [54, 87, 169–173]. Co-evolution of species with their host plants has influence on the species richness associated with tree species. Therefore, with longer presence of EITS, their role as host plants increases [169], especially if they are widespread and congeneric native trees are present [171–174].

These impacts of EITS on the availability of resources and species composition can have an impact on ecosystem services and forest biodiversity. Thus, the presence of EITS may have a high potential for conflict with local nature conservation objectives, from which they are mostly excluded [45, 46]. This is especially the case when these nature conservation objectives are derived from strongly human influenced ecosystems, for instance intensively grazed systems or when tree species composition has been reduced to species that form a translucent canopy. In fire-prone regions, EITS can alter fire regimes by increasing fuel availability and flammability [43, 44]. In general, flammability varies strongly between tree species[175]. Some EITS plantations, such as *E. globulus and P. radiata, are highly flammable*. But broadleaf EITS mostly limit the fire risk of the—usually coniferous—forests in which they are established. A well-known broadleaved exception to this is *E. globulus*, which increases the fire hazard. If grown under a short-rotation, fire risk of *Eucalyptus* spp. is no different from *Pinus* spp. Older trees develop stringy bark that increases the risk of fires spreading because of a tendency to disperse embers from its bark [176].

Integration of EITS into forest ecosystems

The reason for large-scale planting of many EITS, such as *R. pseudoacacia* [54], *E. globulus* [95, 150] and *P. radiata* [177] was wood provisioning in short to medium rotation plantations. Other EITS, such as *P. serotina* and *A. altissima* have been planted for other reasons. For instance *P. serotina* was mainly planted in Europe as a companion tree species in reforestation, mostly with *Pinus sylvestris*, besides some planting for wood production in the nineteenth century [178]. *Ailanthus altissima* was and is a popular ornamental tree [157] and, outside China, its country of origin, only small-scale planting for wood production took place in Austria, Hungary, Argentina, Uruguay, India and New Zealand [179–182].

All these EITS are known for their ability to become invasive [58, 183, 184]. The ability of non-native species to invade new communities depends on their traits and the vulnerability (invasibility) of the community [185]. They usually present pioneer traits associated with plants occurring in early successional stages of forests—high seed production at a young age, fast growth, and short juvenile period—enabling them to rapidly colonise open spaces inside and outside the forest [186–189]. EITS usually combine these pioneer traits with a strong light requirement and high light transparency. However, there are exceptions. Some EITS combine pioneer traits—e.g., early seed setting, efficient propagule spreading and rapid juvenile growth—with late successional species traits—e.g., shade-tolerant, shade-casting, and long-lived. The more shade-tolerant and shade-casting a tree species is, the longer it can dominate forest succession. *Acer platanoides* (which is native to Europe and invasive in other temperate regions) typically is such a tree species, combining traits associated with early successional stages [190, 191], with shade tolerance [191, 192], hence the problems with it in North American forests [190, 191].

Evidence from several studies indicates that very few non-native species invade successionally advanced plant communities [185, 189, 193–196]. Non-native species are completely missing from undisturbed late successional forests [189, 197, 198], and the high diversity of native tree species limits forest invasion by EITS [199]. Ecosystem invasibility is the result of several factors, including physical environmental characteristics, the competitive ability of resident species, and the disturbance regime of the habitat [185, 193, 200, 201]. However, the availability of resources such as light, nutrients and water facilitates the establishment of EITS [71, 202, 203]. For instance, many EITS have low moisture and nutrient requirements and thus may outcompete many native species on sites with reduced nutrient and moisture availability [15, 58, 94, 204–206]. Ecosystem invasibility often results from anthropogenic or natural degradation of forest ecosystems [207]. Thus, the dominance by EITS is usually a symptom, rather than the cause, of limited forest resilience. Due to climate change, the level of degradation of forest ecosystems is generally expected to increase, and with it, their invasibility [75, 132, 208].

Eucalyptus globulus only regenerates in the immediate vicinity of the mother tree. *E. globulus* owes its reputation as an invasive tree species to massive planting in short rotation plantations impeding opportunities for natural regeneration of other species. But simply increasing rotation length to beyond 10 to 20 years creates opportunities for establishment of native species regeneration.

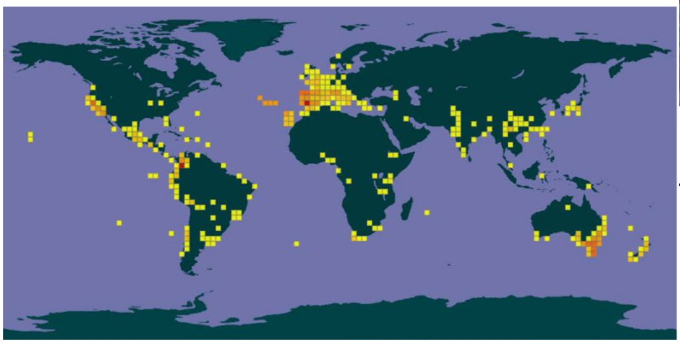
TRAITS:
- Evergreen broadleaf pioneer tree, growing up to 70 m high
- More climate resilient than most competitors
- Wood: mostly used for pulp and paper, but also high-quality timber applications

NATIVE RANGE:
- Australia

INTRODUCTION PATHWAYS:
- Silviculture.

INVASION HABITAT:.
- Low invasion capacity, even in open forests.

STATUS:
- Major occurrence areas globally: Australia (host), Spain, Portugal, California, South Africa and South America. Occurs locally elsewhere in the temperate climatic zone.



Eucalyptus globulus distribution map; colors indicate gradients of occurrence from limited (yellow) to intensive (red) presence (source: https://www.gbif.org/species/3176787).

PICTURE: Native oak and sweet chestnut forest succession under 140 years old 70m high *Eucalyptus globulus* plantation. Souto da Retorta, Galicia, Spain (Photo Bart Nyssen)

Box. 2 *Eucalyptus globulus*. Bad reputation due to short rotation plantation forestry

This degradation can be countered by diversifying the tree species composition. Higher species richness results in higher functional diversity as long as the species in the community present different functional traits and therefore different strategies to acquire resources [209]. Higher functional diversity would reduce susceptibility to invasion through the pre-emption of available resources [210–214]. Additionally, functional trait similarities between resident species and introduced species result in overlapping resource requirements and, as a consequence, in competition among species [209, 214, 215]. As resource requirements overlap increases, competition is intense, and no more species can establish [216–218].

Thus, forest invasibility is a dynamic attribute that can be modulated by resource supply, disturbance regimes, and tree species composition of recipient forest ecosystems [71]. These factors acting in synergy, determine a complex scenario to predict the invasibility of forest ecosystems [76]. Nevertheless, the knowledge of the latter can be used as a management tool to prevent or control EITS in forests [77, 219]. Due to the shade-intolerant nature of the set of EITS addressed here, they are unable to establish in complex forests. Yet, when they are dominant, their translucent crowns enable establishment of late successional species, which eventually makes them disappear from complex forests. However, if the possibility of competition is limited—by lack of seed trees or intensive foraging by a high density of herbivores—resources can be utilized by EITS, thus maintaining their presence [71].

According to this, the possibility of EITS becoming dominant can be reduced by adjusting the abiotic conditions that promote their establishment, such as soil nutrients, soil moisture, or light in the understory by strengthening the vertical forest structure; an approach that fits seamlessly with close-to-nature forest management [220]. At the same time, it is important to strengthen competition from other tree species by promoting the diversity of both pioneer species that can compete in the early stages of succession, and of late-successional species to stimulate forest succession [15, 58, 94, 116, 204–206] (See Table 2).

Table 2 Possibility of reducing EITS dominance in forest ecosystems

Species	Studies on reducing EITS dominance in forest ecosystems
Ailanthus altissima	[55, 121, 221–223]
Eucalyptus globulus	[95, 130, 224–230]
Pinus radiata	[96, 97, 231–242]
Prunus serotina	[94, 164, 165, 205, 243–258]
Robinia pseudoacacia	[54, 70, 124, 259–264]

Table 3 Examples of high-value applications of EITS wood

Species	Saw logs for construction, furniture, or veneer
Ailanthus altissima	[121, 157, 223, 273–282]
Eucalyptus globulus	[153, 283–289]
Pinus radiata	[290–294]
Prunus serotina	[248, 258, 295–300]
Robinia pseudoacacia	[54, 70, 124, 261, 262, 301–307]

Contribution of integrated EITS to species diversity and wood production

Adding a tree species—with its species-specific traits—to an existing forest ecosystem will change its biological diversity. This applies equally to native tree species as to EITS [265]. These effects of EITS on species diversity depend very much on EITS abundance [97]. When EITS density is high, these effects, negative or positive, are greater than when EITS occur in lower density [266]. In cultivated forests (i.e., planted or plantation forests), EITS are often intensively managed in short-rotation monoculture plantations. This short forest development period usually prevents the natural regeneration of native woody species comparable to dense, young stands of native trees [267–269]. However, less intensively managed EITS plantations on longer rotations and abandoned EITS plantations in many regions host a high diversity of plants and birds. This phenomenon is well known for pine and eucalypt plantations [95, 97, 230, 237, 270–272].

In forest ecosystems resilient against EITS dominance, both the negative and positive impacts of EITS on the species composition of the forest ecosystems decrease [96, 225, 265]. The negative effects of the presence of EITS, when dominant, can, in resilient forests, turn into positive diversity effects due to increasing diversity of habitats [265]. Meanwhile, a gradual adaptation takes place between species that are already present and EITS [169, 170].

As explained above, due to the pioneer traits of most EITS, their effects on biodiversity, viewed at the time scale of forest development, can be a transitional pioneer phase, and these EITS are likely to decline eventually if sufficient seed sources of successor species are present [94–96]. Due to this process, in complex forests, EITS are expected to be found only locally and temporarily, as they are part of the pioneer stage after disturbance. Also, they can profit from pioneer conditions at forest edges. But, generally speaking, large-scale negative or positive effects of EITS can dissolve over time in forest succession while small-scale pockets of EITS may remain. Therefore, strengthening resilience against dominance by EITS is likely to ensure that potential effects are limited and will not persist for long.

For some EITS, timber production in plantations is an important reason for planting (e.g., *P. radiata, E. globulus* and *R. pseudoacacia*). The question arises whether these EITS and those whose invasive nature prevents forest managers from using them for timber production outside their area of origin (e.g., *P. serotina* and *A. altissima*) can contribute to wood provisioning in complex forests.

Although in plantation forestry wood production with EITS may be aimed at low-value applications such as firewood, pulp, and paper, EITS are also used to supply wood for high-value applications such as construction framing, furniture, and veneer (see Table 3). However, management of complex forests is characterised by small-scale interventions that limit the amount of light on the forest floor, and the additional growth will be concentrated on a limited number of high-quality trees. Thus, here too, the density of pioneer tree species – and thus of EITS – decreases in favour of late successional species.

The preferred high-end application for the hardwood species *A. altissima*, *E. globulus*, *P. serotina* and *R. pseudoacacia* is in flooring, furniture, and veneer while the softwood *P. radiata* mainly finds valuable applications as structural timber but also for furniture. Experience with silviculture aimed at high-quality wood applications is published for all example EITS (see Table 4). Sometimes, more publications on silviculture for quality wood are available from the area of origin (e.g., *E. globulus* and *P. serotina*) and sometimes from the area of introduction (e.g., *A. altissima*, *P. radiata* and *R. pseudoacacia*). Given the pioneer nature and rapid growth of these EITS, the emphasis in quality wood production is on striving for a large crown with low crown base and, in some cases, timely pruning.

Table 4 Wood production with EITS in complex forest for high-quality wood applications

Species	Experience in area of origin	Experience in introduction area
Ailanthus altissima	[223, 274, 308]	[180, 275–277, 309]
Eucalyptus globulus	[283, 284, 288, 289]	[310]
Pinus radiata	[294]	[293, 294, 311, 312]
Prunus serotina	[295–300, 313–320]	[244, 248–250, 257, 258, 321]
Robinia pseudoacacia	[322]	[54, 70, 261, 262, 302, 304, 306, 323]

Thanks to the wind dispersal of its seeds and its ability to germinate and grow under a range of site conditions, *Pinus radiata* is an efficient pioneer and, according to invasion ecology, an invasive tree species. However, due to its high requirements for light, its invasiveness is usually limited to short vegetation types with potential for forest development. Once established, *P. radiata* becomes like most pine species an efficient nurse tree for native trees, either spontaneous regeneration or enrichment planting.

TRAITS:

- Evergreen coniferous pioneer tree, 15–30 m high
- More climate change tolerant than most competitors
- Negative impact on nutrient availability
- Wood: mostly used for construction timber, pulp and paper.

NATIVE RANGE:

- Endemic to the Californian Monterey Peninsula and several islands off the coast of Baja California (Mexico).

INTRODUCTION PATHWAYS:

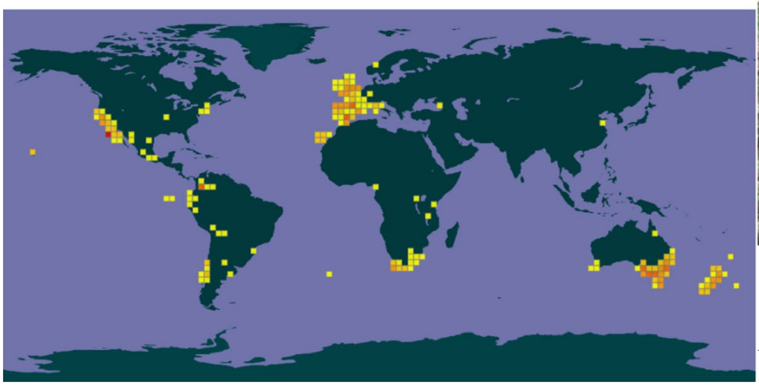
- Silviculture.

INVASION HABITAT:

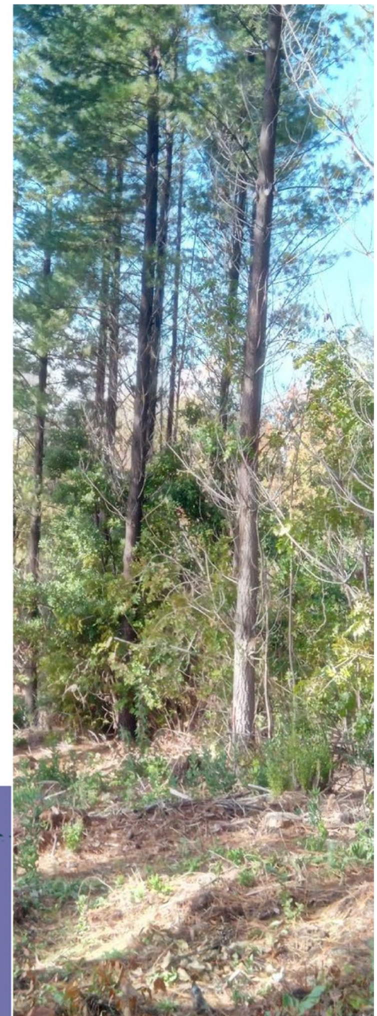
- Pioneer species outside forests in open landscapes, heathlands, dry grassland and dunes.

STATUS:

- Plantation forests mainly along the California coast into southern coastal Oregon, New Zealand (where it is the most common non-native tree), Australia, Chile, SW Europe and South Africa.
- Occurs locally elsewhere in the temperate climatic zone.



Pinus radiata distribution map; colors indicate gradients of occurrence from alimited (yell ow) to intensive (red) presence (source: https://www.gbif.org/species/5285727).



PICTURE: *Pinus radiata* plantation stand, with underplanted seedlings of shade-intolerant (*Nothofagus dombeyi, Nothofagus obliqua*), semi-tolerant (*Nothofagus alpina, Laurelia sempervirens*) and shade tolerant native tree species (*Aextoxicon punctatum; Cryptocarya alba*). South-Central Chile (Photo Klaus Kremer)

Box. 3 *Pinus radiata*. Invasive conifer and nurse tree

Contribution of EITS to climate resilience

The effects of climate change on forests can be wide-ranging and complex [324–326]. Warmer temperatures can increase the frequency and intensity of fires, droughts, and insect outbreaks, while changes in precipitation can lead to flooding, soil erosion, and changes in soil moisture. These changes can cause trees to become stressed and more susceptible to disease, pests, and wildfire. Due to the complexity of the mutually interacting effects of climate change, it is still largely unclear which tree species will face difficulties, leading to changes in tree species diversity, forest composition and vegetation structure, as well which will be favoured [60, 327, 328].

Climate change mainly impacts forests with weak moisture or nutrient supply, or with simplified vegetation structure and restricted tree species diversity and redundancy. These simplified forests often originated from historical and current forest use [134, 137, 329]. If EITS propagules are present, they will often fill the vacant space associated with

Table 5 EITS resilience to climate change: Climatic amplitude, drought, and heat tolerance relative to tree species present in introduction area

Species	Large climatic amplitude	Drought resilience	Heat resilience
Ailanthus altissima	[157, 281, 331]	[157, 281, 332–335]	[157, 332, 333, 335]
Eucalyptus globulus	[150, 154, 336–338]	[283, 338–342]	[336–338]
Pinus radiata	[234, 294, 343–345]	[294, 344, 346, 347]	[294, 344, 346, 347]
Prunus serotina	[244, 348–353]	[244, 335, 349–352, 354]	[244, 335, 349–352]
Robinia pseudoacacia	[54, 70, 322, 355–357]	[54, 159, 335, 356, 358–362]	[54, 262, 335]

the associated disturbances. Given the complexity of climate change effects—changing disease and pest pressures in addition to changing abiotic conditions – it is difficult to predict whether EITS can cope with climate change and contribute to forest climate resilience in a given region. In general, however, it can be stated that most EITS will suffer less from climate change than most competing native tree species due to their often wider climate amplitude, and drought and heat tolerance. This also applies to our sample EITS, including *P. radiata* which has a very small area of origin, mainly on the Monterey Peninsula in California, but an extensive introduced area [330] (see Table 5).

Prunus serotina is a gap tree species capable of quickly restoring the forest climate after disturbances. Native tree species, with the exception of highly light-demanding pioneer tree species, regenerate without any problem under *P. serotina*, whose nurse tree character is enhanced by its fast-decomposing litter.

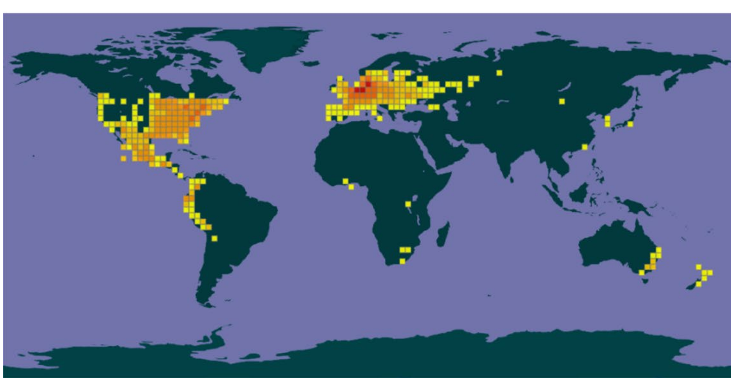
TRAITS:
- Deciduous broadleaf pioneer tree, 20 – 30 m high
- More climate resilient than most competitors
- Positive impact on nutrient availability
- High quality furniture wood

NATIVE RANGE:
- Eastern North America

INTRODUCTION PATHWAYS:
- Horticulture
- Silviculture

INVASION HABITAT:
- Pioneer species in forest margins and open forests, outside forests in open landscapes, heathlands, dry grasslands, and dunes.

STATUS:
- Widespread and common in its native range and on the North European sand belt, from northern France to Poland, where it was extensively planted in the past.
- Occurs locally elsewhere in the temperate climatic zone



Prunus serotina distribution map; colors indicate gradients of occurrence from limited (yellow) to intensive (red) presence (source https://www.gbif.org/species/3021850*)*

PICTURE: Native forest succession (*Acer pseudoplatanus, Acer platanoides, Castanea sativa, Fagus sylvatica, Quercus robur, Carpinus betulus, Sorbus aucuparia, Rhamnus frangula, Ilex aquifolium, Taxus baccata*) in *Prunus serotina* forest. Waasmunster, Belgium (Photo Bart Nyssen)

Box. 4 *Prunus serotina*. From herbicide-treated invasive to accelerator of forest succession

We now delve into the impact of EITS on the ecosystem components relevant for forest resilience to climate change effects: abiotic conditions, vegetation structure, and species composition.

A continuous cycle of nutrients in an ecosystem is a prerequisite for sustainable provision of ecosystem services [363]. In forests, nutrient uptake and litter fall by trees strongly influence nutrient availability {Lavelle, 2005 #3921}{Lavelle, 2005 #3921}{Lavelle, 2005 #3921}{Lavelle, 2005 #3921}{Lavelle, 2005 #3921}{Lavelle, 2005 #3921}{Lavelle, 2005 #3921}[364]. Reduced nutrient availability, caused by soil acidification and the loss of basic cations (e.g., Ca, Mg, K), may threaten the provisioning of ecosystem services [365–368]. Soil acidification is a natural phenomenon in forests (except on limestone), but has been enhanced by centuries of soil-degrading land use and, in industrialised regions, by atmospheric deposition of SOx and NOx [369]. The tree species composition can counteract this acidification. Trees with litter rich in base cations prevent litter accumulation, accelerate nutrient cycling, promote a more diverse soil fauna, and increase nutrient availability in the topsoil [370–372]. Previous studies have identified such rich litter tree species (e.g., *Tilia* sp., *Acer* sp., *Fraxinus* sp., *Prunus* sp.) and demonstrated their soil enrichment capacity [53, 373, 374]. Some of the EITS (e.g., *A. altissima, P. serotina, R. pseudoacacia*) can be categorised as rich litter tree species (See Table 6).

Also the influence of EITS on the moisture supply has only been investigated for some EITS [388, 407]. For example, the highly productive *E. globulus* has been found to lead to large water consumption [154]. However EITS with rich litter (e.g., *A. altissima*, *P. serotina*, *R. pseudoacacia*) are believed to increase the moisture retention capacity of the topsoil through addition of organic matter in the mineral soil. In addition, some EITS can influence the moisture availability of other tree species when they have a moisture absorption strategy that is better adapted to the circumstances [155].

Temperature extremes are strongly buffered in forests compared to open habitats, with lower below-canopy maximum temperatures, higher minimum temperatures, and lower seasonal and interannual variability [408–413]. Ameliorating the forest climate buffers understorey flora and fauna from heat and potentially also from drought (depending on the environmental circumstances) and improves survival and growth in seedlings [134, 414–416]. The microclimate buffering capacity of forests may provide climatic refugia during climate warming [408, 409, 417, 418], reducing the pressure on individuals, populations, species and communities that follows rapid anthropogenic climate change [417, 419–422]. Vertical complexity and structural heterogeneity with a closed canopy and the presence of a subcanopy and of a shrub layer are the most important stand characteristics for climate buffering capacity [134, 409, 413, 415, 416, 423–427]. Most EITS contribute to these forest structure traits, which enhance buffering against climatic extremes (See Table 7).

Table 6 Impact of EITS on Nutrient availability

Species	Positive impact	Negative impact
Ailanthus altissima	[37, 55, 150, 157, 161, 375–378]	
Eucalyptus globulus	[379–387]	[150, 154, 161]*
Pinus radiata		[149, 388–390]**
Prunus serotina	[53, 156, 165, 250, 374, 391–402]	[403]***
Robinia pseudoacacia	[32, 37, 39, 54, 150, 197, 264, 404, 405]****	

* Observed negative effects of *E. globulus* litter on nutrient availability may be explained by short rotation plantations where large quantities of biomass are removed [152, 154, 337, 382]

**Some studies suggest that soil biological processes are not necessarily negatively affected by the presence of *P. radiata* [406]

*** The higher soil acidity in stands with *P. serotina* observed in this study may reflect the initial high soil acidity of the stands prior to invasion, which therefore may have been easier to invade [403]

****In areas with high atmospheric nitrogen pollution, increased N-availability is considered a negative impact, though

Table 7 EITS and forest climate recovery

Species	Fast canopy recovery	Subcanopy and shrub layer
Ailanthus altissima	[121, 157, 281, 428–430]	[121, 281, 428–432]
Eucalyptus globulus	*	*
Pinus radiata	[73, 76, 236, 343]	**
Prunus serotina	[156, 205, 256, 257, 433–442]	[94, 156, 165, 243, 401, 403, 436–448]
Robinia pseudoacacia ***	[54, 70, 124, 150, 163, 264, 335, 449–455]	[54, 70, 150, 163, 456, 457]

* A contribution of *E. globulus* to forest recovery or the formation of a subcanopy or shrub layer is not mentioned. Probably this tree species is limited in this by its high light requirement and low invasive nature

** For *P. radiata*, only a contribution to forest recovery is mentioned, not the formation of a subcanopy or shrub layer of P. radiata. Probably this tree species is limited in this by its high light requirement

*** *R. pseudoacacia* also has a high light requirement and a low invasive character. Its ability to form root sprouts means that this EITS does contribute locally to forest recovery and the formation of a subcanopy or shrub layer, although this is limited to open forests such as pine and oak forests

Table 8 Nurse tree effect and regeneration of late successional species under EITS

EITS species	Nurse tree effect and regeneration of native tree species
Ailanthus altissima	[55, 221, 222]
Eucalyptus globulus	[95, 224–230, 462]
Pinus radiata	[96, 97, 231–237, 462]
Prunus serotina	[94, 164, 165, 243–245, 258]
Robinia pseudoacacia	[70, 124, 259, 260]

Especially in forest restoration, nurse tree effects are important to initiate forest succession [78, 96, 97, 227, 231, 458–461]. EITS may contribute to the rapid build-up of a forest canopy, followed by the below-canopy establishment of late successional species (see Table 8).

Conclusions

EITS integrated into forest ecosystems can contribute to climate change adaptation.

Because of the pioneer character of most EITS, spontaneous forest succession limits their dominance in time and space in most situations. EITS may be temporarily and locally dominant in pioneer situations. However, establishment of mid- and late-successional tree species under their translucent canopy should gradually replace them, over several decades, as long as propagules of these species are present [268, 462].

This integration of EITS in the forest ecosystem can be enhanced by measures aiming at strengthening resilience to climate change. In fact, if climate-adaptive forest management is implemented consistently—optimising abiotic conditions, enhancing structural diversity of the canopy, and increasing tree species diversity—the (dominant) occurrence of EITS in these forests may be reduced and eventually EITS may become regular trees among the other tree species. This may contribute to forest functional diversity and functional redundancy, which helps to secure the continuous provisioning of ecosystem services. For example, *P. radiata* may be able to fulfil functions of native coniferous tree species that are affected by severe pests or disturbances. Likewise, *R. pseudoacacia, P. serotina, A. altissima* and *E. globulus* can act as alternative fast-growing pioneer deciduous trees if certain native species were to decline.

However, this is only true in regions where climate adaptation is served by a structurally rich forest with high functional diversity and functional redundancy. In (semi)-arid regions where forest resilience to climate change is enhanced by giving trees a large growth space in an open forest [463], the proportion of pioneer tree species, and thus EITS, is likely to increase.

Increased resilience through enhanced tree species functional diversity and functional redundancy will not only reduce dominance by EITS but also reduces the likelihood of any new invasive non-native tree and shrub species to establish in the forest. Reducing forest invasibility is most effective for tree species with high light requirements and light transmission. Reducing forest invasibility is most effective for the majority of EITS (e.g., *P. serotina, R. pseudoacacia, A. altissima, E. globulus* or *P. radiata)*, which are light-demanding pioneers. Reducing abundance by forest succession is less effective for the exceptional EITS combining pioneer traits—e.g., early seed setting, efficient propagule spreading, and rapid juvenile growth—with late successional species traits—e.g., shade-tolerant, shade-casting, and long-lived. The higher the shade-tolerance or the shade-casting capacity of EITS, the more difficult their integration into the forest ecosystem without them becoming dominant tree species. Members of the genus *Acer,* and more specifically *Acer platanoides,* are in this category [190, 191].

In resilient forest ecosystems EITS may contribute to further climate change adaptation due to their often higher drought and heat tolerance, and their pioneer character, translating into rapid restoration of a forest microclimate after a stand-replacing disturbance, and a capacity to fulfil the role of nurse tree for establishment of native late-successional species [461]. EITS may further enhance multiple elements of forest structure: abiotic conditions, vegetation structure, and species composition.

The extent and manner in which EITS contribute to climate change adaptation vary depending on the tree species. Nevertheless, EITS are often approached as a homogeneous group in studies of their effects on forest ecosystems [30, 362, 464]. Since the differences between EITS are similar to the differences among native pioneer tree species, information important for evaluating such effects is then insufficiently considered. Given the significant variations among EITS, it is essential to impartially assess their specific contributions to climate change adaptation, biodiversity, and ecosystem services, without bias towards their origin. There is a great need for further forest research on the autecology, synecology, contribution to associated biodiversity, ecosystem processes, and ecosystem services of the different EITS in specific contexts, just as it has been done in the past for native tree species. EITS have become part of the regional tree species pools of many areas worldwide [465]. They therefore deserve intensified fundamental and applied research into their ecosystem functioning.

Of all example trees in this review, *Robinia pseudoacacia* is probably one of the most heat and drought tolerant temperate deciduous tree species and one of the least invasive. Planted widely over an estimated area of over 30,000 km^2, in North America, Europe, temperate Asia, temperate South America, northern and southern Africa, Australia, and New Zealand.

TRAITS:

- Deciduous broad-leaved pioneer tree, 20-25 m high
- More climate resilient than competitors
- Nitrogen fixer, positive impact on soil fertility
- Wood: biomass, poles, and quality timber for outdoor use

NATIVE RANGE:

- Eastern North America

PATHWAYS:

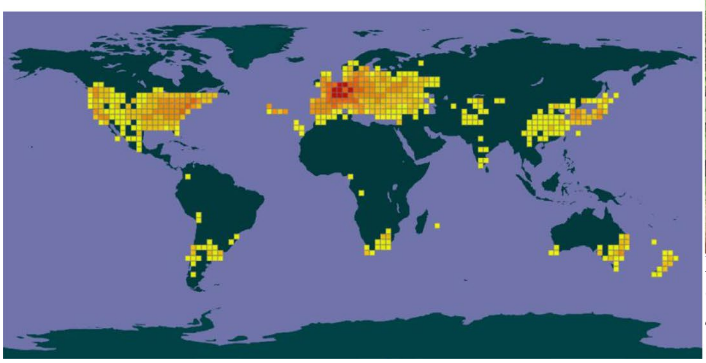
- Horticulture
- Erosion control on dikes, embankments
- Silviculture

INVASION HABITAT:

- Pioneer species in forest margins and open forests, outside forests in open landscape, heathlands, dry grassland, and dunes.

STATUS:

- Widespread and common in North America and Europe, but also in South America, South Africa, and China.
- Occurs locally elsewhere in the temperate climatic zone.



Robinia pseudoacacia distribution map; colors indicate gradients of occurrence from limited (yellow) to intensive (red) presence (source https://www.gbif.org/species/5352251).

PICTURE: Massive native forest regeneration (*Acer pseudoplatanus, Acer platanoides, Tilia cordata, Fagus sylvatica, Quercus robur, Carpinus betulus, Sorbus aucuparia, Rhamnus frangula, Ilex aquifolium, Taxus baccata*) in adult *Robinia pseudoacacia* forest. Waasmunster, Belgium (Photo Bart Nyssen)

Box. 5 *Robinia pseudoacacia*. A heat and drought tolerant pioneer widely cultivated for wood production

Integration of EITS is promising for forest managers

Preventing dominance of EITS and enhancing forest resilience under changing climatic conditions are mostly seen as separate tasks by forest managers. However, this review shows that these two processes are actually related. Forest management strategies can target increased ecosystem resilience to multiple disturbances [144]. Silvicultural measures aimed at increasing resilience to a changing climate, can simultaneously contribute to increasing resilience to dominance by EITS, especially if such measures restore complex forest structure and tree species diversity [1, 8]. Such an approach also underpins close-to-nature forest management [433].

The contribution that EITS can make to climate change adaptation in forests is promising for forest managers: the large budgets previously reserved for control can be better used to further increase resilience of forests to disturbances exacerbated by global changes. Also, by integrating EITS, forest managers have additional tree species at their disposal to achieve their management objectives.

Here it is essential to emphasise that the integration potential of EITS depends on physical site characteristics, the local forest composition and structure, and on the forest objectives pursued. Strengthening resilience to EITS dominance in conjunction with reinforced resilience to the effects of global warming is not suitable for forests with a natural open canopy structure or where an open canopy structure is aimed for (e.g., to achieve established nature conservation goals or to enhance drought adaptation). Nor is this approach suitable for mono-specific plantation forests, except when these should be changed into mixed structured forests. Resilience – absorption, in this case—towards EITS may be high in plantations of shade-casting tree species but the pursued even-aged monoculture has too little vegetation structure and diversity of tree species to absorb and adapt to climate change impacts.

Yet, notwithstanding all the differences in how the presence of distinct EITS works out in diverse forest ecosystems, society has much to gain from a non-biased approach to these 'new' tree species [466]. The sustainable delivery of forest ecosystem services under rapidly changing climatic conditions may partly depend on EITS.

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  This 2011 comment in Nature by renowned ecologists is an early manifestation of a paradigm shift among biological invasion researchers. Replacing a biased anti-exotic stance with a neutral approach to these new species in both research design and implementation as a prerequisite for advancing the understanding how to deal with newcomers in ecosystems.

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  This letter notes the current trend in forest vitality loss that demonstrates the urgent need for forest adaptation. Authors note that measures are insufficiently adopted by foresters in the field and question the reasons for this inaction that cripples climate-smart forest management. A way forward is proposed, using a diversity-based no-regret approach consistent with available knowledge.

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  Using the functional network approach, this paper provides forest practitioners with a well-researched yet easy-to-use tool to evaluate functional diversity, vulnerability and functional connectivity at the landscape level. This tool can be used to inform plans for improving ecosystem adaptability to changing environmental conditions and societal demands.

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  This article presents results of experimental studies on the effects of using non-native eucalyptus (*Eucalyptus*

spp.) as a transitional phase in tropical forest restoration on above-ground biomass accumulation, regeneration of native woody species and financial viability. Many of the negative effects attributed to eucalypts on the growth and natural regeneration of native trees depend on characteristics of the production system, landscape structure, soil and climate in which they are grown, rather than on the presence of eucalypts per se.

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  This report, prepared for Te Uru Rākau - New Zealand Forestry Service - lays the foundation for national policy in dealing with EITS. It summarises current knowledge on how exotic forest - in New Zealand consisting mainly of radiata pine (*Pinus radiata* D. Don) - can best be converted to native forest.

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  This review provides a broad overview of the ecology, adaptability to climate change and contribution to ecosystem services of black locust (*Robinia pseudoacacia* L.), a tree species, due to its pioneer traits, regarded as invasive in large parts of the world where its range is expected to expand underpredicted climate changes

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  This article presents a solid example of unbiased research on ecological incorporation of an EITS, black cherry (*Prunus serotina* Ehrh.) into native food webs. The authors conclude that evolutionary processes can lead to a specialised herbivorous community on an EITS, reducing invasiveness over time.

- Annighöfer P, Kawaletz H, Terwei A, Mölder I, Zerbe S, Ammer C. Managing an invasive tree species—silvicultural recommendations for black cherry (Prunus serotina Ehrh). Forstarchiv. 2015;86(5):139-52. doi: https://doi.org/10.4432/0300411286139.

  This paper analyses different management options to derive recommendations for the future management of black cherry (*Prunus serotina* Ehrh). The options were evaluated in terms of economic profitability and ecological compatibility. The results show that there are promising strategies to integrate these EITS into the forest ecosystem, which are effective in reducing its density and can result in positive income for landowners.

- Brandner R, Schickhofer G. Tree-of-Heaven (Ailanthus altissima): enormous and wide potential neglected by the western civilisation. Proceedings of the 11th World Conference on Timber Engineering Riva del Garda, Italy2010. p. 1-7.

  This article is an early call for an objective approach to ecosystem services by EITS, in this case Tree of Heaven (*Ailanthus altissima* (Mill.) Swingle). Authors make recommendations regarding the usefulness of the wood and point out its wide application range for furniture and construction purposes, reflecting its huge and wide potential.

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Data Availability No datasets were generated or analysed during the current study.

Declarations

Conflict of Interest The authors declare no competing interests.

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