Biodiversity and ecosystem service contributions of trees

A review for environmental risk assessments of non-native plant pests in Sweden

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Abstract

Plant pests, particularly non-native species, can have a profound impact on their host plants. Trees are the foundation of forest ecosystems and serve as important structures in agricultural landscapes and urban areas. In Sweden, forests cover around 70 % of Sweden's land area and serve as an important national resource for the economy and for biodiversity. Consequently, introductions of non-native tree pests can cause significant economic and environmental damage.

Pest risk analysis (PRA) provides the foundation and scientific evidence to inform decisions to mitigate and manage the introduction of non-native plant pests into new areas. PRA involves structured and standardized procedures to assess the risks posed by non-native pests to a country or territory. There are general guidelines on the assessment of impact, including economic, environmental, and social aspects, as well as both direct and indirect effects.

Regarding environmental impacts, two major constituents of a natural ecosystem are highlighted in environmental impact assessments of plant pest invasions; biodiversity and ecosystem services. However, there is no consensus of how environmental assessments in PRAs should be performed, and different methods are used in different assessments schemes. Overall, within pest risk assessments, there is a need for a more comprehensive understanding of the environmental consequences of plant pest invasions.

The aim of this review is to summarize the main values provided by trees and compile the available information on the biodiversity and the ecosystem services to which trees contribute. All major tree species and genera found across various landscapes in Sweden were included in the report, including forests, agricultural land, and urban environments.

In terms of biodiversity, we define values at risk based on the number of native species associated with individual tree species. We also identify valuable habitats where trees play an important structural role, such as old-growth forests, protected forest areas, and habitat types as defined in the Habitat Directive. Concerning ecosystem services, we summarize the contributions of trees within ecosystems identified as important for providing these services. These ecosystem services primarily cover provisioning, regulating, and cultural services. The contribution of trees for these services are described across various ecosystems, including forests, agro-ecosystems, semi-natural grasslands and urban areas. When possible, we present case studies that investigate the effects and magnitude of impacts that tree pests and pathogens have on biodiversity and the provisioning of ecosystem services. These examples, along with the reviews of the main ecosystem services provided by trees, aims to provide guidance for estimating risks in the context of pest risk assessments.

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1. Introduction

Plant pests[1], especially non-native species, can have a large impact on plants, which they use as hosts. The extent of the impact depends on the type of damage caused and the particular plant species being affected as well as the functions and processes to which these plant species contribute. Non-native plant pests may thereby have a detrimental effect not only on the socioeconomic values linked to the production of resources such as food and raw material but also on the associated environmental values of the affected plants.

Trees are not only fundamental structures of forests, but also integral features of urban areas and agricultural landscapes. In Sweden, forests cover approximately 70 % of the land area and serve as an important national resource for the economy (KSLA 2015, Skogsdata 2022). Trees also contribute both directly and indirectly to biodiversity and the ecosystems' many processes and functions (e.g., Boyd et al. 2013, Mitchell et al. 2014). These processes and functions, in turn, provide a range of ecosystem services that benefit human well-being (e.g., Costanza et al. 1997).

Pest risk analysis (PRA) provides the foundation and scientific evidence to inform decisions to mitigate and manage the introduction of non-native plant pests into new areas. A PRA is a structured and standardized procedure used to assess the risks non-native pests constitute to a country or territory. The IPPC defines a PRA as: "The process of evaluating biological or other scientific and economic evidence to determine whether an organism is a **pest**, whether it should be regulated, and the strength of any **phytosanitary measures** to be taken against it" (ISPM 5 (FAO 2023)).

Assessing the potential impact of a pest is an important part of risk assessments, helping to determine which non-native plant pests should be classified as quarantine pests. According to the International Plant Protection Convention (IPPC), which Sweden and 184 other countries have signed, a quarantine pest is "a pest of potential economic importance […]" where the term "economic importance" also includes social, cultural, and other impacts such as ecosystem services and aesthetic values (FAO 2021, IPPC 2023). Information on the environmental values associated with affected plants is thus necessary for conducting pest risk assessments (Gilioli et al.

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[1] Plant pests are defined as "Any species, strain or biotype of plant, animal or pathogenic agent injurious to plants or plant products. Note: In the IPPC, "plant pest" is sometimes used for the term "pest" [FAO, 1990; revised ISPM 2, 1995; IPPC, 1997; CPM, 2012]" (FAO 2023)

2014, Mitchell et al. 2014). Unfortunately, pest risk assessments tend to focus on the monetary impact on provisioning services, while other types of services are often overlooked (Boyd et al. 2013).

This review aims to support the evaluation of environmental impacts caused by pests of woody plants in pest risk assessments, by summarizing the current data and information on biodiversity and ecosystem services associated with various tree species in Sweden. By describing the values at risk, it serves as a foundation for environmental risk assessments of new plant pests affecting trees in Sweden and will facilitate the assessment of potential impacts in future PRAs.

2. Background

2.1 Considerations of environmental impact in pest risk assessments

The requirements of conducting a PRA are described in International Standards on Phytosanitary Measures (ISPMs) provided by the IPPC governing body. As part of a PRA, the probability of pest entry, establishment and spread, together with the potential consequences, are assessed, as outlined especially in ISPM 11 (FAO 2021). General guidelines are provided on the assessment of impact, which includes economic, environmental, and social impacts, as well as both direct and indirect effects (FAO 2021 and further information in FAO 2023). Athough ISPM 11 serves as a guideline, various PRA schemes employ different approaches to assess environmental impact. The PRA standards developed by the European and Mediterranean Plant Protection Organization (EPPO) and the European Food Safety Authority (EFSA) represent two slightly different approaches. Below is a brief description of how environmental impact is assessed in the two risk assessment schemes.

The decision-support scheme for quarantine pests, developed by EPPO (2011), provides a qualitative assessment of the pest risk. The ‘environmental impact’ is assessed using a number of questions with rating guidance, together with a matrix model to combine the ratings (Kenis et al. 2012).

Both the effects on biodiversity and alterations of ecosystem processes and patterns are assessed separately in the estimate of ‘environmental impact’ (EPPO 2011). However, the questions are not organized or explicitly assessed as different ecosystem services (Kenis et al. 2012). The given reason is that many ecosystem services are covered by other questions on social and economic impacts in the PRA scheme, but also because there is frequently limited data available. EPPO also provides a simplified PRA scheme, which enables a more rapid risk assessment (EPPO 2012). The assessments in this scheme should be based on the same information used for a detailed PRA, but, for example, an overall assessment of the magnitude of impact in the area of potential establishment is performed instead of assessing several sub-questions related to the magnitude of impact (EPPO 2022).

The European Food Safety Authority (EFSA) has developed specific guidance on the environmental risk assessment of plant pests as an extension of their pest risk assessment framework (EFSA Panel on Plant Health 2011, Gilioli et al. 2014). This scheme includes a methodology to assess the impact on both biodiversity and ecosystem services in order to capture both the structural and the functional aspects of the environment (EFSA Panel on Plant Health 2011). The impact on biodiversity is assessed from the level of genes, individuals, populations, and communities, up to the level of ecosystems. The EFSA scheme follows the ecosystem service categorization as outlined in the Millennium Ecosystem Assessment (2005b), but categorizes regulating and supporting services together and considers the provisioning services in relation to other aspects of the impact assessment (e.g., economic impact) to avoid accounting for the same impact twice. The cultural ecosystem services are not included as they fall outside EFSA's area of responsibility (EFSA Panel on Plant Health 2011). The impact assessment is based on estimating the proportional reduction of provisioning of the different ecosystem services. In short, the impact is analysed given an assumed scenario (e.g., the characteristics of the invasion process of a particular plant pest), by identifying the 'service-providing units' being affected (e.g., the potential host plants) and assessing the influence on the functional traits (of the service-providing unit) and the associated change in the provided ecosystem services (EFSA Panel on Plant Health 2011, Gilioli et al. 2014). A quantitative pest risk assessment-guidance was published by EFSA in 2018 replacing the earlier more qualitatively focused PRA scheme (EFSA Panel on Plant Health 2018). Although the guidance on environmental risk assessment (EFSA Panel on Plant Health 2011) remains valid, the key components are incorporated in the new quantitative risk assessment scheme and the impact can then be assessed in terms of continuous uncertainty distributions.

Quick assessments of the environmental impact are also conducted for pests included in risk ranking models, such as FinnPRIO (Heikkilä et al. 2016), as well as for pests assessed during Pest Categorizations by the EFSA Panel on Plant Health (EFSA Panel on Plant Health 2024). Pest categorizations are the first phase of a risk assessment where a potential new plant pest is identified and evaluated with regard to whether it has the characteristics of a quarantine pest or a regulated non-quarantine pest based on its biology, distribution, host range, potential consequences, and available mitigation measures (EFSA Panel on Plant Health 2018).

2.2 Defining the concepts of biodiversity and ecosystem services in the context of pest risk assessment

Two major constituents of a natural ecosystem are highlighted in environmental impact assessments of biological invasions; biodiversity and ecosystem services (Vilà et al. 2010, Simberloff et al. 2013, Gilioli et al. 2014). Biodiversity refers to the variation of life at different spatial scales (from genes via species to ecosystems) and the ecological processes that sustains it, while ecosystem services are the benefits that people get from the environment (Mace et al. 2012, Schröter et al. 2014).

2.2.1 Biodiversity

Biodiversity, or "biological diversity" is defined as “variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems” (Convention on Biological Diversity 2024). There are many different indicators and measures used to describe biodiversity. For example, species richness, community composition, ranges of species populations, and genetic composition are among the variables used for biodiversity assessments (IPBES 2019).

On a national level, to assess the environmental impact of a new plant pest, information about the associated biodiversity of the affected tree hosts (e.g., number of associated species) may serve as a useful metric for evaluation (e.g., Sundberg et al. 2019). Furthermore, the distribution of natural habitats that include these host species may be important, since these habitats may be rare. Consequently, pest impacts could affect the connectivity between these habitat patches.

2.2.2 Ecosystem services

The concept of ecosystem services describes the benefits humans obtain from an ecosystem’s many processes and functions (Millennium Ecosystem Assessment 2005b). Following the Millennium Ecosystem Assessment (2005b), ecosystem services are divided into the following four categories; *provisioning services* such as food and fibre, *regulating services* like pest regulation and climate regulation, *supporting services* such as nutrient cycling, and *cultural services* such as recreation. Furthermore, biodiversity is closely linked to the provision of ecosystem services, and changes in biodiversity can affect the supply of these services (Millennium Ecosystem Assessment 2005b, Mace et al. 2012, Brickhill 2015).

The definition and classification of ecosystem services has been widely debated, especially when using the concept as an operational framework (Boyd and Banzhaf

2007, Brauman et al. 2007, Wallace 2007, Fisher et al. 2009). Some argue that ecosystem services should be limited to final products provided by ecosystems to make the concept more useable in welfare accounting (Boyd and Banzhaf 2007). On the other hand, the proponents of the broader use of the concept argue that recognizing ecosystem processes is fundamental for managing and maintaining the provisioning of the final ecosystem products (Brauman et al. 2007). It has been proposed that functions and processes can be regarded as services if they return human benefit (Gilioli et al. 2014).

The ecosystem services concept, despite debates over its definition and classification, can serve as a valuable tool to connect society to ecosystems and facilitate communication among diverse societal actors, such as scientists and practitioners (see e.g., review by Schröter et al. 2014). In the context of pest risk assessment, evaluating functional traits and natural processes related to ecosystem service provisioning can lead to a more comprehensive understanding of a pest's environmental impact, ultimately resulting in more informed decisions and measures taken to mitigate the impact on final services that benefit humans.

2.2.3 Invasion characteristics of plant pests and their environmental consequences

Factors influencing plant pest invasions and impact

The impact of a plant pest invasion depends on both the characteristics of the invasion process and the properties of the area being invaded. It is therefore important to consider various factors when making assumptions and developing scenarios for plant pest invasions. Such factors include the pest's host range, properties of the tree species, and the environment in which they grow. The magnitude of the environmental consequences will also depend on the temporal and spatial scales of the invasion, as well as the reversibility of the damage. In almost all cases, the impact of a non-native plant pest results in some degree of damage or mortality rather than a complete eradication of host trees. In some cases, the main impact may be a reduction in the aesthetic value of the trees.

Assessment of temporal and spatial scales

The assessment's temporal scale can be considered from various perspectives, such as the speed at which a pest spreads and the rate at which the impact will appear (Gilioli et al. 2014). Temporal scale considerations are used in several current impact assessment schemes e.g., Heikkilä et al. (2016) and EPPO (2022). Detailed information on a pest's spread rate and mortality patterns over time, is therefore highly relevant to many management decisions (e.g., Sharov and Liebhold 1998, Eschtruth et al. 2013).

The spatial scale of an assessment, i.e., the PRA area (FAO 2023), is usually larger than the area of potential establishment. However, in a PRA the "endangered area" (FAO 2023) is also specified, which refers to the part of the area of potential establishment where the presence of the pest is expected to cause economically important losses. To define the endangered area, and the potential impact within it, it is necessary to take into account that biodiversity and ecosystem services provided by different tree individuals may differ depending on the environment in which they are situated. For example, an oak tree in a park may provide different ecosystem services than an oak tree in a forest, and the provision of different services may depend on individual tree age as well (see also Vanneste et al. 2024).

Ecosystem recovery

Following an extreme outbreak of a pest, almost all host trees may be killed and the ecosystem may "recover" either by the regrowth of the affected species or through a change into a new state where the affected tree species is replaced by another (tree) species (see e.g., Boyd et al. 2013, Bjelke et al. 2016, Brunet et al. 2023). The resulting effect on ecosystem services and biodiversity will depend on whether the tree species will be replaced by a species with similar properties or whether some properties will be lost or gained. Thus, there are some general ecosystem services connected to general tree traits (e.g., Hansen et al. 2014) that may decrease directly following a pest outbreak, but these general services may be regained after a certain time period if the trees recover or if killed trees are replaced by new trees. If the affected trees do not recover and no tree regeneration occurs (i.e., a loss of general tree traits), this could lead to a decrease in the provision of certain ecosystem services, such as carbon regulation and soil erosion control. There are also unique ecosystem services connected to particular tree species (e.g., Bjelke et al. 2016, Felton et al. 2020) that may disappear should the species not recover and be replaced by another tree species (i.e., the particular tree species traits are different). The loss of biodiversity and ecosystem services may thus be short-term, long-term, or permanent depending on the succession of the vegetation after an outbreak.

2.3 Aims of the review

The aim of this review is to summarize the main values provided by trees and compile the available information on the biodiversity and the primary ecosystem services to which trees contribute. By describing the values at risk, this review can serve as a foundation for environmental risk assessments of new plant pests affecting trees in Sweden and facilitate the assessment of potential impacts in future PRAs.

3. Methods

3.1 Content and scope

All major tree species and genera found across various landscapes, including forests, agricultural land and urban environments in Sweden following the classification of San-Miguel-Ayanz et al. (2016), were included in the project (Table 1). Furthermore, several common shrubs were also included in the list, but for simplicity, they are referred to as “trees” throughout this report. Two introduced tree species with identified importance and wide distribution were also included (i.e., *Pinus contorta* and *Acer pseudoplatanus*).

In short, the biodiversity associated with different tree species was evaluated at two levels: the species level and the habitat level. At the tree species level, biodiversity was evaluated based on the number of tree-associated species from various organism groups. At the habitat level, we provide an overview of specific habitats valuable for biodiversity in Sweden where trees are key species, i.e., predominantly in forest ecosystems, and additionally, in other habitats outside forests. Furthermore, we provide an overview of trees of conservation value across various landscape types.

The tree-related ecosystem services were evaluated following the categories of ecosystem services in the Millennium Ecosystem Assessment (2005b). Our aim was to identify the main landscape types that contribute to the provisioning of specific ecosystem services, as categorized by Harrison et al. (2010), and to describe the contribution of trees to these services within these landscape types. We also considered the contributions of trees to several important ecosystem services identified in urban areas (Bolund and Hunhammar 1999, Deak Sjöman and Östberg 2020).

We compiled information on both general tree properties and, where available, specific properties of individual tree species. Consequently, our aim was to provide a general overview of the values at risk, as well to highlight how different species may contribute to the provisioning of these services.

Additionally, we provide information about potential impact of non-native plant pests on tree-associated biodiversity and ecosystem services. While no specific plant pest scenario-descriptions are provided here, we summarized various documented examples to illustrate the range of ways in which plant pests can alter processes related to biodiversity and ecosystem services.

3.2 Literature review and data sources

The information used in this report was obtained from the scientific literature, environmental monitoring programs, and various reports. The primary source of information on the distribution and occurrence of tree species in different landscape types was based on several national and regional environmental monitoring programs, including the National Forest Inventory (NFI; Skogsdata 2022), the National survey of semi-natural pastures and meadows (Swedish Board of Agriculture 2023) and regional surveys of grasslands and other biotopes in agricultural land (Glimskär et al. 2016).

Information on biodiversity associated with different tree species was mainly based on a report by Sundberg et al. (2019), and the underlying data was kindly provided by Jonas Sandström at the SLU Swedish Species Information Centre. Some additional data on tree-associated species were downloaded from the species database “Artfakta” maintained by the Swedish Species Information Centre (SLU Artdatabanken 2018). Regarding habitat provision, we present an overview of various indicators for forest and tree-associated biodiversity. These include the extent of old forests and protected areas, as well as occurrence of large, old trees. This overview is based on data from the National Forest Inventory, official statistics on protected areas in Sweden, and additional sources (Höjer and Hultengren 2004, Skogsdata 2014, Glimskär et al. 2016, Jansson et al. 2017, SCB 2022, Skogsdata 2022). Furthermore, we present an overview of tree-bearing habitat types as listed in the Habitats Directive (European Council 1992), with relevant information for Sweden compiled by Westling et al. (2020a).

The literature search on tree-associated ecosystem services was performed using Web of Science, and initially included broad keywords such as ”forest*”, “woodland*”, “tree*”, and “shrub*” in combination with “ecosystem service*” to retrieve general information about trees’ contribution to ecosystem services. As the scope of ecosystem services is very broad, the search was subsequently narrowed down to include a list of specific tree species (listed in Table 1) combined with specific ecosystem services or functions such as “pollination*”, “pest control”, “carbon storage” etc. Within this search, we primarily focused on identifying relevant reviews and comparative studies that estimate the effects of trees in general and the effects of specific tree species on particular ecosystem services and functions. In some cases, data from national inventories were also included. Furthermore, we searched for literature aiming at estimating the effects of non-native tree pests and pathogens on the provisioning of different ecosystem services. We used a list of approximately 180 tree pests and pathogens based on data from

Kenis and Branco (2010) and Santini et al. (2013) including pests on trees that are regulated at the species level in the EU Council Directive 2000/29/EC (European Council 2000)[2] (See Supplementary table 1). The search was done by combining the list of pests with keywords representing specific ecosystem services and functions. The environmental impacts of native pest species with expanding geographic ranges were also considered.

Table 1. Summary of major tree and shrub species in Sweden included in this review. Species are categorized as large/mid-sized trees (T), small trees (t), or shrubs (s), following the classifications of San-Miguel-Ayanz et al. (2016) and the Swedish Museum of Natural History (2018). The most common growth form is listed first if a species falls into two or more categories.

Genera	**Scientific name**	**Common growth form**	**English name**	**Swedish name**
Acer	_A. platanoides_	T	Norway maple	skogslönn
	_A. pseudoplatanus_*	T	Sycamore maple	tysklönn
Alnus	_A. glutinosa_	T	Black alder	klibbal
	A. incana	t, s	Grey alder	gråal
Betula	_B. pendula_	T	Silver birch	vårtbjörk
	B. pubescens	T	Downy birch	glasbjörk
	B. nana	s	Dwarf birch	dvärgbjörk
Carpinus	_C. betulus_	t	Hornbeam	avenbok
Corylus	_C. avellana_	s	Hazel	hassel
Crataegus	_Crataegus_ spp.	s, t	Hawthorn	hagtorn
Euonymus	_E. europaeus_	s, t	Spindle tree	benved
Fagus	_F. sylvatica_	T	Beech	bok
Frangula	_F. alnus_	s, t	Glossy buckthorn	brakved
Fraxinus	_F. excelsior_	T	Ash	ask
Hippophaë	_H. rhamnoides_	s, t	Sea buckthorn	havtorn
Juniperus	_J. communis_	s, t	Common juniper	en
Larix	_L. sibirica_	T	Siberian larch	sibirisk lärk
Malus	_M. sylvestris_	T	Wild apple	vildapel
Picea	_P. abies_	T	Norway spruce	gran
Pinus	_P. sylvestris_	T	Scots pine	tall
	_P. contorta_*	T, t	Lodgepole pine	contortatall
Populus	_P. tremula_	T	Aspen	asp
Prunus	_P. avium_	T, s	Wild cherry	sötkörsbär
	P. padus	t, s	Bird cherry	hägg
	P. spinosa	t	Blackthorn	slån
Quercus	_Q. robur_	T	English oak	skogsek
	Q. petraea	T, t	Sessile oak	bergek
Rhamnus	_R. cathartica_	s, t	Common buckthorn	getapel
Salix	_S. caprea_	T, t, s	Goat willow	sälg
Sambucus	_S. nigra_	s, t	Elder	fläder
Sorbus	_S. aucuparia_	t	Rowan	rönn
	S. intermedia	t, T	Hybrid rowan	oxel
Taxus	_T. baccata_	s, t	Yew	idegran
Tilia	_T. cordata_	T	Small-leaved lime	skogslind
	T. platyphyllos	T	Large-leaved lime	bohuslind
Ulmus	_U. glabra_	T	Wych elm	skogsalm
	U. laevis	t	European white elm	vresalm
	U. minor	T	Field elm	lundalm
Viburnum	_V. opulus_	s	Guelder rose	olvon

* Not native to Sweden.

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[2] Note that a new regulation (EU) 2016/2031 has replaced the previous directive after the literature searches were conducted.

4. Results

In the following sections, we identify and describe the tree-related values at risk due to potential impacts of non-native plant pests on trees, specifically in terms of biodiversity and habitat provisioning, as well as the provisioning of ecosystem services.

In terms of biodiversity, we define the values at risk based on the number of native species associated with individual tree species. In relation to habitat provision, we provide an overview of valuable habitats for biodiversity where trees are important structural components. This overview includes e.g., current estimates of the extent of old-growth forests, habitat types as defined in the Habitats Directive, and the extent of protected forest areas.

Regarding ecosystem services, we follow the framework provided by Harrison et al. (2010) to outline the contribution of trees within ecosystems that have been identified as important for providing these services. The ecosystem services primarily cover provisioning, regulating, and cultural services, and trees' contribution are described across various ecosystems, including forests, agro-ecosystems, semi-natural grasslands, and others.

Provisioning services include the supply of timber and non-timber products, as well as drinking water. Regulating services cover climate regulation, pest regulation, pollination, soil erosion regulation, natural hazard regulation, regulation of peak water flows, and air quality regulation. We also include selected ecosystem services provided by trees in urban environments. Furthermore, we list several relevant roles of trees and forests in providing cultural services. The results concerning specific tree species and genera are summarized in Table 2.

Finally, at the end of each section, when possible, we present known case studies of impacts from tree pests and pathogens, and their magnitudes, on biodiversity or the provisioning of ecosystem services. These examples may be particularly informative for the estimation of risks in the context of pest risk assessment.

Table 2. Overview of review findings on tree species/genera in relation to biodiversity, habitat provision, and ecosystem services. This table consolidates findings from the review, presenting both species-specific (indicated by "x") and genus-level (indicated by "o") information. For detailed information on a particular tree species, refer to the corresponding sections.

	Occurence				Biodiversity		Ecosystem services										
Latin name	Forest land	Agricultural field margins	Pastures and meadows	Urban environments	Species associations	Habitat types	Timber products	Non-timber products	Provision of drinking water	Climate regulation	Pest regulation	Pollination	Soil erosion regulation	Natural hazard regulation	Reduction of peak water flows	Air quality regulation	Cultural services
Acer platanoides	x		o	o	o	x		x		o	o	xo	x	x		o	
Acer pseudoplatanus			o	o	o					o	x					o	
Alnus glutinosa	o		o	o	o	x					o	o	x				
Alnus incana	o		o	o	o	x					o	o	x				
Betula nana					o	x					o						
Betula pendula	o		o	o	o	x	x	o		xo	o	o	x	xo		o	
Betula pubescens	o		o	o	o	x		o		o	o	o	x	xo		o	
Carpinus betulus	x			o		x					o	x	x	x		x	
Corylus avellana		x	x	o	x	x					o	x	x			x	
Crataegus spp.			o	o		x					o	x	x			o	
Euonymus europaeus											x	x	x				
Fagus sylvatica	x		x	o	x	x		x		o	o	x	x	x		o	x
Frangula alnus				o		x						x	x				
Fraxinus excelsior	x		x	o	x	x				o	o	x	x	x		o	x
Hippophae rhamnoides						x						x	x				
Juniperus communis			x	o	x	x					o	x	x				o
Larix sibirica	o			o							o	o	o				
Malus sylvestris			x	o		x					o	x				o	
Picea abies	x		x	o	x	x	x	x		xo	o	x	x			x	x
Pinus contorta	x			o							o		x	x			
Pinus sylvestris	x		x	x	x	x	x	o		xo	o	x	x	x		o	x
Populus tremula	x		x		o	x				o		x	x	x		o	
Prunus avium	x	o	o	o								xo	x	x		o	
Prunus padus		x	x	o		x					x	xo	x			o	
Prunus spinosa		o	x	o		x					x	xo	x			o	
Quercus petraea	o		o	o	o	x				o	o	o	x	x		o	o
Quercus robur	o		o	o	o	x				o	o	o	x	x		o	o
Rhamnus cathartica				o								x	x				
Salix caprea	x	x	x	o	o	x		o			o	x	x			o	
Sambucus nigra				o								x	x				
Sorbus aucuparia	x	x	x	o	o	x						o	x			o	
Sorbus intermedia			o	o	o	x						o				o	
Taxus baccata				o								x	x			o	o
Tilia cordata	x		o	o	o	x				o	o	xo	x	x		o	o
Tilia platyphyllos			o	o	o					o	o		x			o	o
Ulmus glabra	x		o	o	o	x					o	o	x				o
Ulmus leavis			o	o	o						o	o					o
Ulmus minor			o	o	o	x					o	o	x			o	o
Viburnum opulus				o								x					

4.1 Occurrence of tree species in Sweden's different landscape types

In this section, we provide a brief overview of tree inventories in Sweden, encompassing both forested and non-forested areas. We summarize the available information on the diversity and distribution of various tree species within Sweden's landscape types.

Sweden is a country characterized by a predominance of forests. In total, forest land[3] covers 27.9 million hectares or approximately 69 % of the total land area (Skogsdata 2022, 2023). The forest land is classified into productive forest land, which is suitable for timber production, and unproductive forest land, such as subalpine birch forests or tree-covered mires, which have limited potential for timber production[4]. Productive forest land covers about 23.4 million hectares or 58 % of the total land area. Unproductive forest land covers approximately 4.4 million hectares or 11 % of the total land area. Additionally, other wooded land[5] covers 2.3 million hectares, or 6 % of the country's area.

The vast majority of trees in Sweden (98.6 % of the total growing stock according to NFIs data) is found in forest land (Table 3). *Picea abies*, *Pinus sylvestris* and species of *Betula* (mainly *B. pendula* and *B. pubescens*) are the most common tree species, representing 40 %, 40 % and 13 % of the total growing stock, respectively (Table 3) (Skogsdata 2022). In terms of the number of trees, however, *Betula* is the most common tree species (Skogsdata 2023). The proportion of other tree species in forest land is much lower. Among these species, *Populus tremula*, *Alnus* and *Quercus* are relatively more common, each represented by approx. 1.5 % of the total growing stock. The distribution of tree species also depends on the vegetational zone. In the alpine region, in northernmost Sweden, mountain birch forests (*B. pubescens* ssp. *czerepanovii*) are prevalent. Coniferous-dominated forests are characteristic of the boreal region, which covers most of Sweden's land area. In southern Sweden, in the hemi-boreal and nemoral regions, many deciduous species such as *Carpinus*, *Fagus*, *Fraxinus*, *Quercus*, *Tilia and Ulmus* have their main distribution (see e.g., Ahti et al. 1968, Sjörs 1999, Skogsdata 2014).

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[3] Forest land (international definition) - Land spanning more than 0.5 hectares with trees taller than 5 metres and a canopy cover of more than 10 percent, or trees able to reach these thresholds in situ. It does not include land that is predominantly under agricultural or urban land use (FAO 2020).

[4] Under the Forestry Act, productive forest land is defined as forest land that, according to generally accepted criteria, can produce on average at least one cubic metre of wood per hectare and year. Unproductive forest land does not meet the requirements for productive forest land (Skogsdata 2022, Skogsstyrelsen 2023).

[5] Other wooded land (international definition) - Land not classified as "Forest", spanning more than 0.5 hectares; with trees taller than 5 metres and a canopy cover of 5–10 percent, or trees able to reach these thresholds in situ; or with a combined cover of shrubs, bushes and trees of more than 10 percent. It does not include land that is predominantly under agricultural or urban land use (FAO 2020).

Table 3. Growing stock of different tree species (in million m^3 standing volume) in all land areas, forest land and productive forest land. The data is presented as a five-year average (2017–2021), based on the data from the National Forest Inventory (Skogsdata 2022, Riksskogstaxeringen 2023). For detailed information about regional differences, refer to the original publications.

Tree species	**All land areas***		**Forest land***		**Productive forest land**	
	Volume	Proportion (%)	Volume	Proportion (%)	Volume	Proportion (%)
Acer platanoides	3.1	0.1	2.6	0.1	2.6	0.1
Alnus	60.8	1.7	58.7	1.7	57.2	1.7
Betula	465.7	13	452	12.8	401.9	12.1
Carpinus betulus	0.9	0	0.9	0	0.8	0
Fagus sylvatica	23	0.6	22.7	0.6	22.6	0.7
Fraxinus excelsior	5.9	0.2	5	0.1	4.8	0.1
Larix	2.6	0.1	2.6	0.1	2.6	0.1
Picea abies	1 410.6	39.4	1 404.1	39.8	1 353.3	40.6
Pinus contorta	49.3	1.4	49.3	1.4	49.3	1.5
Pinus sylvestris	1 412.2	39.4	1 396.1	39.5	1 304.7	39.1
Populus tremula	63.6	1.8	60.8	1.7	60	1.8
Prunus avium	1.4	0	1	0	1	0
Quercus	49.4	1.4	44.2	1.3	42.9	1.3
Salix caprea	18.5	0.5	17.4	0.5	17	0.5
Sorbus aucuparia	7.3	0.2	6.8	0.2	6.4	0.2
Tilia cordata	1.3	0	1.2	0	1.2	0
Ulmus glabra	1.6	0	1.5	0	1.5	0
Other deciduous tree sp.	5.5	0.2	4.7	0.1	4.6	0.1
Total	**3 582.6**		**3 531.5**		**3 334.5**	

** Including alpine areas (inventoried since 2018)*

Trees that grow outside forest land account for only ca. 1.4 % of the total growing stock in Sweden according to data of the NFI (Riksskogstaxeringen 2023) (Table 3). Similar results have been obtained from a recent study using remote imagery techniques, which estimated that the total canopy cover of trees outside of forests in Sweden is 1.9 %, with urban areas and cropland accounting for 0.4 % and 0.1 %, respectively (Liu et al. 2023). However, while there is currently no comprehensive inventory of trees outside forests in Sweden, some statistics are available regarding the occurrence of trees in agricultural and urban areas.

In agricultural land, two different inventories provide some quantitative information on tree composition. First, the regional inventory of habitats alongside agricultural field margins in southern and middle Sweden measured the cover of fruit-bearing trees and shrubs[6]. On average, the occurence of fruit-bearing trees and bushes is around 40 metres per kilometre (Glimskär et al. 2016). The most common tree species identified in the survey were *Prunus spinosa* and *Salix caprea*, each with a canopy cover of around 8–9 meters per kilometre, followed by *Corylus avellana*, *Sorbus aucuparia*, and *Prunus padus*/*Prunus* sp., each with a canopy cover ranging between 5–7 meters per kilometre. Second, the National survey of semi-natural pastures and meadows inventoried occurrence of trees and shrubs in a total of 87 906 sites (covering in total 350 853 hectares) (Swedish Board of

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[6] Fruit-bearing trees and bushes are species that are recommended to be preserved alongside field margins to benefit pollinators and natural enemies of crop pests (e.g., Swedish Board of Agriculture 2013). The estimates for each individual species are based on the length of the mapped linear object.

Agriculture 2023). The occurrence of trees was categorized into three groups: trees covering less than 10 % of the site area, between 10 % and 30 %, and more than 30 %. In most cases, the presence of specific tree species was estimated to cover less than 10 % of the site area. *Betula* was the most common tree species, present at 53 % of all sites, followed by *Juniperus communis* at 48 %. Other species, including *Quercus*, *S. aucuparia*, *P. sylvestris*, *P. abies*, and *P. tremula*, were present in approximately 30 % to 35 % of the sites. Occurrences of other tree species and genera are summarized in Supplementary table 2.

In urban environments, trees can be found in both urban forest areas and as park and street trees. Among park and street trees, a diverse range of tree species is often encountered. The results from inventories of urban trees in large Scandinavian cities, i.e., Göteborg, Malmö and Stockholm, showed that *Tilia*, *A. platanoides* and *Sorbus intermedia* were the most common tree genera/species. For a detailed summary of street tree species refer to Sjöman et al. (2012) and (2019). Urban forests in larger Swedish cities (i.e., defined as those with more than 10 000 inhabitants) typically cover around 20 % of the urban area. This figure increases to approximately 50 % within a 5 km radius outside urban boundaries. In contrast, in cities situated in agricultural regions, these percentages are generally lower, with urban forest coverage of about 10 % within urban areas and 15 % outside urban boundaries (Nielsen et al. 2017).

The most recent inventory of urban tree species was conducted by the i-Tree Sweden project, which surveyed urban trees in nine larger cities across Sweden (Deak Sjöman and Östberg 2020). *Betula*, *Pinus*, *Quercus* and *Picea* were among the most common tree genera in terms of abundance at the city scale (Table 4). The composition of urban tree species varied based on factors such as latitude and the proportion of forests within urban areas. Additionally, city areas with a higher proportion of urban forests also tended to have a greater number of tree species per area (Deak Sjöman and Östberg 2020).

Additionally, the inventory of urban forests[7] in the NFI showed that several deciduous tree species were more common in urban compared to non-urban forests (Skogsdata 2009). The proportion of the growing stock for these deciduous species was 1–5 % higher in urban, compared to non-urban forests, depending on the region. For instance, several less common tree species, such as *P. tremula* in the northern parts of Sweden and *Quercus* in southern parts of the country, have a much higher representation in urban forests compared to non-urban forests (See Skogsdata 2009 for more details).

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[7] According to Swedish National Forest Inventory (NFI), urban forests are defined as forests located on productive forest land in or near urban areas, with distances ranging from 200 to 7500 meters from urban boundaries depending on population size. Urban forests comprise approximately 2 % of the total forest land (Skogsdata 2009).

Table 4. The proportion of tree genera (in percent) in nine different urban areas according to i-Tree Sweden (Deak Sjöman and Östberg 2020). Note that several non-native tree genera were omitted from this table. For detailed information about specific tree species, refer to the original publication.

	Umeå	**Stockholm**	**Borås**	**Göteborg**	**Hässleholm**	**Helsingborg**	**Malmö**	**Luleå***	**Kristianstad***
Acer	0.1	6.1	6.4	0.9	2.0	8.5	8.5	0.4	4.4
Alnus	0.2	1.0	7.2	3.5	8.6	1.8	2.8	0.8	0.6
Betula	18.0	9.0	21.7	23.7	24.5	6.3	0.0	41.4	34.8
Carpinus	0.0	0.0	1.4	0.0	0.2	10.1	0.0	0.0	0.3
Cornus	0.0	0.0	0.3	0.0	0.0	0.3	0.0	0.0	0.0
Corylus	0.0	0.2	1.0	1.4	1.1	1.5	0.0	0.0	0.9
Crataegus	0.0	0.2	0.2	0.1	0.0	2.8	2.8	0.0	0.6
Fagus	0.0	0.0	1.6	2.1	2.4	8.5	3.8	0.0	0.3
Frangula	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0
Fraxinus	0.0	1.0	0.3	0.9	0.2	2.8	0.9	0.0	2.2
Juniperus	0.0	0.0	0.1	2.3	0.0	0.0	0.0	0.0	0.0
Larix	0.0	0.0	0.0	0.0	0.0	1.8	0.0	0.8	0.0
Malus	0.1	4.2	1.7	0.6	0.8	6.3	4.7	0.0	3.1
Picea	40.1	12.2	9.2	9.5	0.0	0.3	0.0	6.8	10.7
Pinus	28.3	30.9	6.3	27.4	9.9	1.0	0.0	25.1	3.1
Prunus	3.1	2.3	6.8	1.4	3.3	12.6	16.0	2.0	8.5
Pyrus	0.0	0.0	0.3	0.0	0.3	0.0	2.8	0.0	3.1
Quercus	0.0	13.1	10.7	10.4	38.5	14.1	7.5	0.0	1.9
Rhamnus	0.0	0.0	0.0	0.1	0.0	0.3	0.0	0.0	0.0
Salix	1.2	1.3	6.7	3.3	1.2	5.3	6.6	3.2	1.6
Sambucus	0.0	0.0	0.3	0.0	0.3	0.0	0.0	0.0	0.6
Sorbus	5.4	1.3	6.3	5.3	4.4	3.0	7.5	10.0	6.3
Taxus	0.0	0.0	0.0	0.0	0.0	2.3	0.0	0.0	0.0
Tilia	0.1	3.4	1.6	0.2	0.3	4.0	8.5	2.0	6.0
Ulmus	0.0	3.6	1.5	0.6	0.0	0.0	1.9	0.0	0.0
Viburnum	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total	96.7	89.9	91.8	94.3	98.0	93.2	74.5	92.4	89.0
Estimated total number of trees	1 398 186	969 464	271 011	10 230 045	524 576	319 370	185 535	7 598	17 269
Number of trees per hectare	228	47	109	228	126	50	22	31	41
Proportion of canopy cover (%)	28	21	24	40	33	14	19	14	14
Inventory area (ha)	6 408	20 700	2 498	44 784	4 150	6 446	8 500	245	417

* In Luleå and Kristianstad only trees in the city centre were inventoried.

4.2 Biodiversity and habitat provisioning

In this section, we outline the values at risk in terms of biodiversity and habitat provisioning due to potential impact of non-native pest species on tree ecosystems. We describe the biodiversity associated with various tree species as the number of tree-associated species from different organism groups. Additionally, we provide an overview of the extent of old forests, and protected areas, as well as specific habitats where trees are key components for the associated biodiversity. Finally, we provide several examples showing how tree pests and pathogens can affect biodiversity of tree-associated species.

4.2.1 Biodiversity associated with different tree species

Data on species diversity associated with trees in Sweden has been compiled in a report by Sundberg et al. (2019)[8]. Tree-associated species were categorised as (1) host-dependent species with a strong association to a specific tree species or genus[9], (2) specialist species, characterized by their association with one tree species or genus[10], (3) red listed specialist species and (4) dead-wood dependent specialists, which rely on dead wood of a specific tree species for their survival.

Overall, tree-associated species richness was highest on common, long-lived and geographically widespread tree species. *Picea abies*, *P. sylvestris*, *Quercus* and *Betula* had the highest number of host-dependent species (800–1100 species), followed by *Salix*, *F. sylvatica and Populus* (each with ca 600 species) (Table 5). Insects, fungi, and lichens were the most common species groups strongly associated with the trees, followed by bryophytes, arachnids and birds, while few vascular plants and mammals showed strong association with specific tree species.

For the purpose of this overview, the number of specialist species may be a useful metric for pest risk assessment, as species with high host specificity are more prone to co-extinction risks, i.e., where the loss of one species occurs due to the extinction, or even significant decline, of a species it depends on (Dunn et al. 2009, Jönsson and Thor 2012). Thus, even limited impacts on host species could pose threats to species with limited dispersal abilities or those with small populations.

Specialist species, which depend on a specific tree species for their life cycle, represent 18–65 % (depending on the tree species) of the strongly tree-associated species (Sundberg et al. 2019) (Table 5). In general, specialist species are found mostly among species utilizing soft tissue (leaves, flowers etc), followed by species associated with bark and wood of living trees and, finally, species in dead wood. Among the different organism groups, Lepidoptera and Hemiptera have the largest number of specialist species, followed by fungi, beetles, lichens, and bryophytes. The highest specialist species richness is found on *Quercus*, *P. abies*, *P. sylvestris*, and *F. sylvatica* (250–350 species), followed by *Populus, Betula*, *Ulmus* and *F. excelsior* (100–200 species).

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[8] Data on tree-associated species is also accessible through the database managed by the Species Information Centre at Swedish University of Agricultural Sciences. (http://www.artfakta.se)

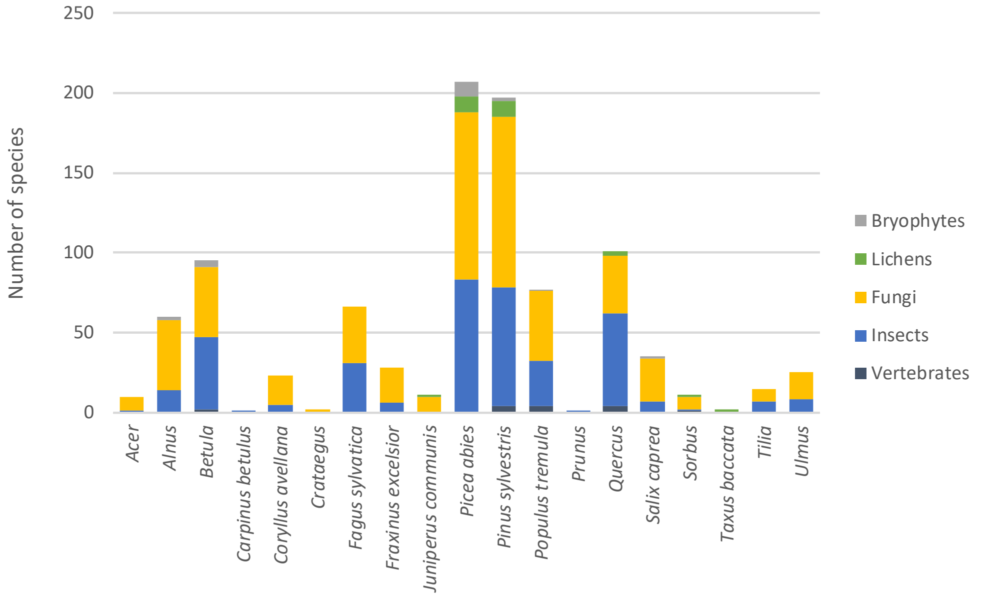
[9] Strongly associated species are defined as species for which the tree taxon is required for >25 % of the species population.

[10] Specialist species are defined as species with a strong association with only one tree taxon and not even having a weak association with other tree taxa

Table 5. Total number of species in different organism groups with a strong association to a specific tree species or genus. Among the species with strong association, some are further categorized as specialist species, red listed specialists and dead wood specialists. Data according to Sundberg et al. (2019).

	Total				**Arachnida**				**Birds**				**Bryophytes**				**Fungi**				**Insects**				**Lichens**				**Other***	
		Specialists				Specialists				Specialists				Specialists				Specialists				Specialists				Specialists				
Tree species	**Strong association**	All specialists	Red-listed	Dead wood	**Strong association**	All specialists	Red-listed	Dead wood	**Strong association**	All specialists	Red-listed	Dead wood	**Strong association**	All specialists	Red-listed	Dead wood	**Strong association**	All specialists	Red-listed	Dead wood	**Strong association**	All specialists	Red-listed	Dead wood	**Strong association**	All specialists	Red-listed	Dead wood	**Strong association**	All specialists
Acer	**139**	56	1	0	**9**	9							**32**				**20**	7			**59**	40	1		**18**				**1**	
Alnus	**356**	110	6	2	**5**	5			**3**				**24**	2	2	1	**156**	45	3	1	**139**	54			**27**	3	1		**2**	1
Betula	**809**	252	15	14	**6**	6			**5**	1			**11**				**306**	84	1	2	**456**	155	14	12	**25**	6				
Corylus avellana	**259**	50	14	3	**2**	2			**1**				**9**				**164**	28	11	2	**75**	18	1	1	**6**	2	2		**2**	
Fagus sylvatica	**641**	136	56	11	**4**	4			**3**	1			**15**				**356**	98	42	7	**229**	30	12	4	**33**	3	2		**1**	
Fraxinus excelsior	**201**	43	15	4	**3**	3							**32**				**56**	8	3	1	**48**	28	10	3	**62**	4	2			
Juniperus communis	**66**	38	1	0	**3**	2			**2**								**29**	11			**27**	24			**4**	1	1		**1**	
Picea abies	**1093**	377	114	51	**8**	7	2		**5**				**34**	1	1	1	**558**	232	84	27	**402**	104	16	23	**85**	33	11		**1**	
Pinus sylvestris	**920**	328	89	53	**10**	6	3	1	**11**	4	2		**28**				**396**	146	45	12	**424**	148	28	35	**50**	24	11	5	**1**	
Populus	**629**	202	29	20	**5**	5			**7**	2	1		**33**	1			**173**	42	6	4	**348**	125	17	16	**62**	26	5		**1**	1
Quercus	**880**	355	94	35	**6**	3	3		**6**	2	1		**10**				**341**	97	39	4	**454**	233	42	31	**62**	20	9		**1**	
Salix	**638**	333	21	1	**6**	6	1		**1**				**14**				**219**	75	2	1	**367**	248	17		**31**	4	1			
Sorbus	**88**	27	2	1	**3**	3			**4**	3			**1**				**33**	7	1	1	**34**	12			**12**	2	1		**1**	
Tilia	**143**	26	5	2	**5**	4			**1**				**5**				**49**	6	1	1	**80**	16	4	1	**2**				**1**	
Ulmus	**250**	57	23	6	**2**	2							**36**				**73**	18	11	6	**101**	37	12		**38**					

*Includes vascular plants, mammals and other organisms.



	Acer	*Alnus*	*Betula*	*Carpinus betulus*	*Coryllus avellana*	*Crataegus*	*Fagus sylvatica*	*Fraxinus excelsior*	*Juniperus communis*	*Picea abies*	*Pinus sylvestris*	*Populus tremula*	*Prunus*	*Quercus*	*Salix caprea*	*Sorbus*	*Taxus baccata*	*Tilia*	*Ulmus*
■ Bryophytes	0	2	4	0	0	0	0	0	0	9	2	1	0	0	1	0	0	0	0
■ Lichens	0	0	0	0	0	0	0	0	1	10	10	0	0	3	0	1	2	0	0
■ Fungi	9	44	44	0	18	2	35	22	10	105	107	44	0	36	27	8	0	8	17
■ Insects	1	14	45	1	5	0	31	6	0	83	74	28	1	58	7	1	0	7	8
■ Vertebrates	0	0	2	0	0	0	0	0	0	0	4	4	0	4	0	1	0	0	0

Tree species or genera

Figure 1. Number of dead wood-dependent species showing preference for a single tree species or genus (Dahlberg and Stokland 2004). Please note that the species numbers differ from the data by Sundberg et al. (2019), provided in Table 5, due to the different definitions used for when a dead-wood dependent species should be considered associated with a particular tree species. Data points were obtained using WebPlotDigitizer (Rohatgi 2022).

Red listed specialist species constitute 1–11 % of the strongly host-dependent species. *P. abies*, *P. sylvestris* and *Quercus* had the highest total number of red listed specialist species. The distribution patterns of red listed specialists varies across Sweden. In northern regions, the highest number of red listed specialists is associated with *Betula*, *P. abies* and *P. sylvestris.* In southern parts of the country red listed specialists are mainly associated with *Quercus, F. sylvatica*, *Ulmus* and *F. excelsior* (Sundberg et al. 2019). A large proportion of the red listed species is dependent on large old trees, which have become uncommon in current landscapes (e.g., Lindenmayer et al. 2014, Eide et al. 2020).

The last group of species consists of specialist species in dead wood. The proportion of dead wood specialists associated with different tree species varies from zero to six percent of the strongly tree-associated species. Fungi and insects are the primary groups among the dead wood-specialists, while other organism groups are less represented.

Regarding dead wood, the total number of dead-wood dependent species in Sweden is estimated to be between six and seven thousand species, with insects and fungi as the most represented groups (de Jong and Almstedt 2005). Generally, many species exhibit a preference for either broad-leaf or conifer wood, or both, while only a small portion of them show a clear preference for a specific tree species. For example, among beetles (Coleoptera), only 26 % of the species showed a preference for individual tree species (Stokland et al. 2012). The association of dead wood-dependent species with particular tree species has also been reviewed in Dahlberg and Stokland (2004) and the number of these species is shown in Figure 1. It is important to note that the species numbers differ from those reported by Sundberg et al. (2019) (Table 5). The reason for the difference is that different definitions were used for the association of dead-wood dependent species with a particular tree species.

4.2.2 Habitat provisioning

Old-growth forests

Old-growth forests, or forests with long continuity, are important for biodiversity conservation. Many species of plants, lichens, bryophytes and invertebrates have limited dispersal abilities and depend on structures and conditions that develop over long periods of time (e.g., old large trees, coarse dead wood, or specific microclimates) (Nordén et al. 2014).

According to the Swedish environmental target, the indicator 'Old Forests' in the boreal region is defined as forests older than 140 years, whereas in the hemi-boreal and nemoral regions, 'Old Forests' are defined as being older than 120 years. (Skogsdata 2023). The largest areas of 'Old Forests' in Sweden are currently found in the boreal region, with 905 000 hectares in northern Norrland and 518 000 hectares in western Norrland. In the southern parts of Sweden, these old forests comprise 333 000 hectares in Svealand and 208 000 hectares in Götaland (Skogsdata 2023).

Long-term data from the Swedish NFI shows that over the past century, the area of old-growth forests (according to NFIs definition[11]) has declined considerably, primarily within boreal regions in the central and northern parts of Sweden (Skogsdata 2014, 2023). In contrast, in the hemi-boreal and nemoral regions of the southern parts of the country, the area of old-growth forests was already low one hundred years ago and has subsequently experienced an increase. Since the 1990s, however, there has been an overall increasing trend in the area of old-growth forest in productive forest land, including boreal, hemi-boreal and nemoral regions of the country. Concerning 'Old Forests', despite a portion of these forests being

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[11] In the Swedish NFI, old-growth forests are classified as those that are older than 160 years in the northern and southern boreal regions, and those that are older than 120 years in the hemi-boreal and nemoral regions.

harvested, a larger portion of forest areas has been estimated to transition from not-old to old forest during this period (Skogsdata 2023).

Coniferous forests represent the largest proportion of old forests ('Old Forests' or old-growth forests) in productive forests (Skogsdata 2014, Westling et al. 2020a). Among other forest types, older deciduous forests[12], mostly dominated by *Betula* and other deciduous trees (constituting over 65 % of the basal area), were estimated to cover approximately 25 000 hectares in the boreal region and around 80 000 hectares in the hemi-boreal and nemoral regions. Additionally, the area of old hardwood deciduous forests[13] (>120 years old), covers approximately 20 000 hectares in the hemi-boreal and nemoral regions (Skogsdata 2014). Areas of specific forest types are detailed in the section on Habitat types below.

Protected areas

Given their importance in supporting biodiversity, formally protected forests are essential for the long-term survival of many threatened species today (Angelstam and Andersson 2001). Currently, 2.4 million hectares of forest land in Sweden are formally protected. Of this, 1.3 million hectares consist of productive forest land. These forests are protected as nature reserves and national parks (SCB 2022, Skogsdata 2022).

Much like the distribution of 'Old Forests', these protected forests are mainly located in alpine and near-alpine regions of northern Sweden, accounting for about 57 % of the total forest in that area. Protected forests in the remaining boreal region, i.e., northern boreal, southern boreal and hemi-boreal comprise around 5 %, 2.9 % and 4 % of the total forest area, respectively. In the nemoral region, approximately 4.5 % of the forest area is formally protected. In addition, the estimated areas of voluntary forest set-asides and consideration patches cover approximately 1.4 and 0.5 million hectares of forest area, respectively (SCB 2022). Of the 'Old Forests' mentioned above, ca. 45 % of the area is located within protected areas (29 %), voluntary set-asides (12 %) and consideration patches (4 %), while 55 % of the area is situated outside these areas (Skogsdata 2023).

The NFI identified several general patterns distinguishing protected areas from unprotected managed forests. In terms of tree species distribution, forests dominated by *P. abies* and *Betula* are relatively more common in protected forests,

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[12] The classification of older deciduous forests varies depending on the region: in the boreal zone, they are defined as forests that are over 80 years old, while in the hemi-boreal and nemoral zones, the threshold is set at 60 years of age or older.

[13] Hardwood forest trees (“ädellövträd” in Swedish) is a term used to describe a group of tree species that are valued for their high-quality wood and include e.g., *Ulmus* sp., *F. excelsior*, *F. sylvatica*, *C. betulus*, *Quercus sp.*, *P. avium*, *T. cordata* and *A. platanoides.* In the National forest inventory, these forests are defined as forests dominated by deciduous trees (>65 % of basal area), with hardwood tree species constituting more than 50 % of the basal area (Skogsdata 2014).

while *P. sylvestris* forests and other deciduous forest types are relatively less common in protected areas compared to in unprotected forests (Skogsdata 2006, 2022).

Habitat types defined in the EU Habitats Directive

Habitat types listed under the Habitats Directive[14] encompass a variety of forest and other tree-bearing habitats (European Council 1992, Westling et al. 2020a). Given that these habitats are clearly defined in terms of species composition, such detailed categorization can, in the context of pest risk management, provide further understanding on the distribution of tree species in valuable habitats across Sweden.

Sweden has a total of 89 such habitat types, out of which 31 are characterized by the presence of trees or shrubs. These tree-bearing habitat types are primarily found in forests (15 habitat types), but they also occur among wetlands, grasslands, alpine, and coastal habitats (Naturvårdsverket 2011). Among these habitat types, eleven habitats have been given priority status in the Habitats Directive [9].

For many habitat types, a specific tree species composition is a defining feature for their classification. These tree species are then defined as *characteristic* species, i.e., common species that help define different habitat types, but they can also serve as important habitats for a variety of other species. Forest tree species are a notable example of such characteristic species. Further, habitat types also include a set of *typical species*, i.e., species associated with a certain habitat quality. In the context of environmental monitoring, they can indicate good conditions or favourable conservation status of the respective site or habitat (Aronsson 2008).

Habitat types where trees constitute *characteristic* or *typical* species are listed in Supplementary table 3 and Supplementary table 4. The categorization follows the Swedish interpretation of the habitat types (Naturvårdsverket 2011). Habitat types containing trees and shrubs as characteristic species can be divided into two groups: (1) those with a canopy cover generally higher than 30 %, typically forest habitats, and (2) open habitat types with lower (<30 %) or varying canopy cover.

In the first group of habitats, which primarily include forest types, the number of characteristic tree and shrub species ranges from one to eight, as shown in Supplementary table 3. Furthermore, in several instances a minimum basal area of specific tree species is required for classification as a particular habitat type or its subcategory. In addition to forest habitat types, tree cover is also described as a

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[14] EU's Habitats Directive aims to protect a selected number of valuable and threatened habitat types, and guidelines have been established for protection and sustainable use of these habitats (European Council 1992). Designated sites are chosen in different countries based on a set of criteria that aims to ensure that the sites are representative and valuable for the conservation of habitats and species of interest within their respective territories. These sites are then included within Natura 2000 network, often situated within protected areas, such as nature reserves and national parks. However, it is important to note that sites qualifying as habitat types can also be found outside designated Natura 2000 sites, as identified, for example, by the National Forest Inventory.

defining feature in Wooded dunes (2180) and Wooded pastures (9070). According to the guidelines, while *P. sylvestris* is not defined as a characteristic species, it is the main tree species in Wooded Dunes. In Wooded Pastures, old deciduous trees are typical, but conifer species may also be present (Naturvårdsverket 2011).

The second group primarily consists of open habitats, in which tree or shrub species can be defining or characteristic species for each habitat type (see Supplementary table 4). For example, several species of *Salix* are defining species (with more than 50 % area cover) in two dune habitats (2170, 2190) and one alpine habitat (4080). *Juniperus communis* is a defining feature, and a characteristic species, in one grassland habitat (5130). Fennoscandian wooded meadows (6530) host the highest number of characteristic tree species. However, these trees do not form a continuous canopy cover, but instead contribute to the overall structure of this partly open habitat type. Wetland habitat types are generally classified as open, although tree cover can be present in varying degrees, in some cases defining habitat subgroups (7110, 7120, 7230). Small shrubs like *Betula nana* and *Salix* are identified as characteristic species within several wetland and alpine habitats.

In some cases, tree and shrub species are also recognized as typical species (in contrast to characteristic species (see definitions above)). For example, *Hippophaë rhamnoides* is a typical species in two coastal habitats (1220 and 1610) and *Salix caprea* in Nordic subalpine/subarctic forests with *Betula pubescens* ssp. *czerepanovii* (9040). Several other species of *Salix* are identified as typical species in various habitat types, including freshwater, grassland, wetland, alpine and forest habitats (3220, 6430, 7220, 7240, and 9040).

Current area estimates of forest and other tree-bearing habitat types are summarized in Supplementary table 5. The largest forest habitat types in terms of area include subalpine birch forests (9040), Western taiga (9010) and Bog woodlands (91D0). On the other hand, several habitat types, including hardwood deciduous forests, alluvial forests, and wooded meadows, are relatively uncommon.

For most forest habitats, stand age is an important criterion for classification of these forests as habitat types[15] (Gardfjell and Hagner 2019). Similarly to 'Old forests' mentioned previously, when considering the total area, the majority (about 75 %) of forest habitat types are situated in forests outside of protected areas (Berglund 2019, Westling et al. 2020a, Skogsdata 2022). There are, however, considerable regional differences in distribution of forest habitat types. In the alpine region for example, nearly half of the forest area qualify as a forest habitat type. In contrast, the proportion of forest land classified as a particular habitat decreases considerably in the boreal and continental (nemoral) regions, where only 7 % and

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[15] According to the guidelines for NFI/NILS inventory, a forest qualifies as a habitat if it exceeds its site-specific minimum harvest age by at least 40 years. This age requirement is reduced to 20 years if the forest contains over 10 m^3 of dead wood per hectare, or if the forest structure is multi-layered. Additionally, criteria for qualifying a forest as a habitat type can include a specific number of overstory trees, or the forest's succession stages following a disturbance.

5 % of forest land, respectively, are classified as habitat types (Westling et al. 2020a).

The results of an overall assessment of habitat types in Sweden showed that very few tree-bearing habitat types have a favourable conservation status (summarized in Supplementary table 5) (Westling et al. 2020a). The assessment of conservation status for the habitat types includes several factors, such as area, habitat structure and functions, as well as main current and future risks to these habitats, including both human-induced and natural factors. Forests and other wooded habitats with favourable conservation status are primarily located in the alpine biogeographical region. On the other hand, habitats in other regions are mostly evaluated as having unfavourable conservation status, largely due to insufficient or decreasing area and unfavourable quality (for more details, see Eionet 2024). Within forest habitat types, 12 out of 15 habitats are found to have insufficient area, and 14 out of 15 habitats have insufficient quality. The assessment of conservation status shows a similar pattern for the other groups of habitat types (Westling et al. 2020a, Eionet 2024).

Large old trees as indicators for biodiversity

Large and old trees provide specific microhabitats (e.g., hollows, coarse bark, coarse woody debris) that are important for many species, including lichens and insects (Hultengren et al. 1994, Axelsson Linkowski and Svensson 2009).

In Sweden, an inventory of large old trees has been conducted as part of the regional environmental monitoring program for valuable trees (Jansson et al. 2017). This program is coordinated by several county boards in southern Sweden, and the investigated area encompasses a large portion of the country's hemi-boreal and nemoral regions. In this inventory, large old trees were defined as those with a diameter greater than 80 cm or trees with hollows with a diameter greater than 40 cm. In terms of the number of trees, *Quercus* was the most commonly found among large old trees, with approximately 600 000 trees. This was followed by *P. tremula* and *Betula* (each with around 400 000 trees), *F. sylvatica* and *P. abies* (ca 300 000 trees), *Acer*, *F. excelsior*, and *Tilia* (ca 200 000 trees) and *P. sylvestris* (ca 100 000 trees). Other tree species including *A. glutinosa*, *Malus*, *P. avium*, *Sorbus*, *S. caprea* and *Ulmus* were each represented by approximately 50 000 trees. These valuable trees were mostly found in deciduous forests and grasslands (including meadows and pastures), with approximately 900 000 and 600 000 trees, respectively. They were also found in other forest types (coniferous, mixed forests, or clear-cuts) and residential properties (gardens, yards, or similar), where the number of trees ranged between 200 000 and 400 000. A smaller portion of large old trees was found in alleys, parks, and agricultural land, each represented by approximately 100 000 trees or less (Jansson et al. 2017).

Data on large old trees have also been collected by other inventories. Although the definitions of large old trees may vary, these inventories can provide more detailed insights into the occurrence and distribution of these trees, which are valuable for conservation. For example, in the productive forest land in hemi-boreal and nemoral regions, the National Forest Inventory (NFI) has estimated the numbers of large trees of *Quercus*, *F. sylvatica*, and other hardwood deciduous species (with a diameter at breast height >50 cm) to be 44, 26, and 7 trees per km², respectively (Skogsdata 2014). Additionally, the NFI's inventory of near-urban forests (defined as forests located in urban areas and in the surrounding zones extending 0.2 to 7.5 km from these areas) revealed that large-diameter *P. tremula* and *S. aucuparia* trees are more common in these areas compared to in non-urban forests (Skogsdata 2009). On average, *P. tremula* trees with a diameter larger than 30 cm were represented by three trees per hectare in near-urban forests, compared to 0.5 trees per hectare in productive non-urban forests. For *S. aucuparia* trees with a diameter between 10 and 19 cm, an average of three trees per hectare was found in urban and near-urban forests, compared to one tree per hectare in productive non-urban forests.

Outside of forests, the National survey of semi-natural pastures and meadows categorized valuable trees into three groups: large trees (with diameter at breast height > 1m), pollarded trees, and other valuable trees (Swedish Board of Agriculture 2005, 2017a, 2021). In the survey, the total number of valuable trees at each site was recorded. However, specific tree species/genera were recorded only as present or absent, so the exact numbers of individual trees within each species or genus are not documented (Table 6). *Quercus* was the most common among large trees present within the sites, followed by *F. sylvatica*, *F. excelsior*, and *Tilia*, though these were present in significantly fewer sites. *F. excelsior* was the most commonly occurring species among pollarded trees, found in 63 % of the 4559 sites with the occurrence of pollarded trees. Pollarded trees of *Tilia, Acer* and *Betula* were also recorded, but in far fewer sites. Among other valuable trees, *Betula*, *Quercus*, *P. tremula* and *P. sylvestris* were the most commonly represented species/genera.

In agricultural land, large trees[16] have been surveyed as part of a regional environmental monitoring program alongside field margins in southern and central Sweden (Glimskär et al. 2016). The most common large-diameter trees were *Quercus* (ca. 0.2 trees per km of field margin), followed by *P. tremula*, *F. excelsior*, *P. sylvestris* and *P. abies* (each with around 0.1 trees per km of field margin) and *S. caprea* and *Betula* (each with ca. 0.05 trees per km of field margin). Other tree species, *F. sylvatica*, *A. platanoides*, *Tilia*, *Ulmus*, *Salix* and *S. intermedia*, collectively accounted for ca 0.1 trees per km of field margin. The occurrence of

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[16] Large trees were defined as trees with a trunk diameter greater than 50 cm, except for *Quercus* and *F. sylvatica* which should have reached a diameter of 70 cm.

tree species differed considerably among landscape types. For example, large diameter *Quercus* and *P. tremula* were more common in landscapes dominated by cultivated land, while *P. abies* and *P. sylvestris* were more common in landscapes dominated by a mix of forest and cultivated land or forest and pastures. *Fraxinus excelsior*, *Betula* and *S. caprea* were distributed relatively evenly among different landscape types.

Table 6. Occurrence of valuable trees (large trees, pollarded trees, and other valuable trees) in semi-natural pastures and meadows. Data from The Swedish Board of Agriculture (2021).

	Large trees (DBH > 1m)	**Pollarded trees**	**Other valuable trees***
General overview			
Total number of trees	30 893	55 313	106 108
number of dead/dying trees	2 256	5 019	30 229
number of hollow trees	6 669	8 651	23 811
number of large trees	-	1 683	-
Total number of sites	8 161	4 559	20 648
Total area of the sites (km^2)	478	210	1 003
Tree species/genera	**Number of sites with recorded tree species**		
Acer	201	468	676
Alnus	89	-	770
Betula	294	442	7 917
Corylus avellana	180	-	535
Crataegus	6	-	168
Fagus sylvatica	502	-	450
Fraxinus excelsior	681	2 887	1 609
Juniperus communis	-	-	585
Malus sylvestris	15	-	816
Picea abies	121	-	1 032
Pinus sylvestris	257	-	2 814
Populus tremula	156	-	3 572
Prunus	49	-	950
Prunus padus	5	-	150
Prunus spinosa	-	-	12
Quercus	6 049	-	7 002
Salix	86	-	190
Salix caprea	281	282	2 199
Sorbus	146	-	1 496
Sorbus aucuparia	37	-	1 898
Tilia	409	1 063	893
Ulmus	247	254	489
Other	2	489	19

*e.g., multi-stemmed trees affected by grazing, old slow-growing trees, trees with occurrence of indicator species, and trees with cultural importance.

Effects of tree pests

Pests can significantly alter the structure of forests, impacting the diversity of other species within the ecosystem. Non-native pests introduced to or spreading into new areas may cause large-scale damage that can have a negative impact on the forest and tree associated ecosystems. However, it is important to note that natural disturbances, including outbreaks of native pests, are essential components of forest ecosystem dynamics (Angelstam and Kuuluvainen 2004). For example, in natural coniferous forests, outbreaks of native bark beetles have been demonstrated to create forest gaps, which positively affect the diversity of several groups of forest insects, such as saproxylic beetles, hemipterans, bees, and wasps (Müller et al. 2008).

In North America, the native mountain pine beetle *Dendroctonus ponderosae* has expanded its geographic range, causing large outbreaks at epidemic levels in areas it previously did not occupy. These outbreaks therefore share many characteristics with those caused by non-native pest species (Cudmore et al. 2010). The effects of mountain pine beetle outbreaks are generally positive for biodiversity, with beetle outbreaks leading to more structurally diversified forest stands and increased understory species richness and productivity (reviewed in Dhar et al. 2016). However, these outbreaks may negatively impact species dependent on shaded conditions, and salvage logging of infested forests leads to adverse effects on the biodiversity of both terrestrial and aquatic species (Dhar et al. 2016). Further, whitebark pine (*Pinus albicaulis*) is now considered endangered partly as a result of extensive outbreaks of the mountain pine beetle in areas where the beetle previously did not occur (Buotte et al. 2017).

Examples of the far-reaching impacts of non-native pest species on forest structure and biodiversity can be illustrated by the significant declines of hemlock (*Tsuga canadensis*) and American chestnut (*Castanea dentata*) in North America. These declines have been caused by the hemlock woolly adelgid (*Adelges tsugae*) and chestnut blight (*Cryphonectria parasitica*), respectively (Ellison et al. 2005). As these trees declined, they have been replaced by other tree species throughout their geographic ranges, leading to long-term effects on various ecological processes and biodiversity. The decline of hemlock has resulted in significant reductions in the populations of several bird species that use hemlock trees as a habitat. Further, the structural changes of tree canopies resulting from the decline has increased the establishment rate of saplings and increased undulate browsing compared to conditions under healthy hemlock stands (Ellison et al. 2018). On the other hand, highly affected sites also had a higher herbaceous plant and invertebrate species richness compared to healthy hemlock stands (Ingwell et al. 2012). American chestnut trees have been severely impacted by the pathogen, transforming the once-dominant tree species into an understory shrub across its range. While the specific effects of the decline of the American chestnut have been less investigated, potential consequences include impacts on aquatic ecosystems, including negative effects on aquatic macroinvertebrates due to lower quality litter provided by the replacing hardwood species. Additionally, the decline of American chestnut could in the long term lead to a decreased provisioning of slowly decomposing dead wood in streams, which in the long term, will affect water flow, and provide less available habitat for fish and other invertebrate species (Ellison et al. 2005, Lovett et al. 2016).

An increased mortality of tree species can have, at least in the short-term, positive effects on several rare and threatened species that benefit from increased amounts of dead wood. For example, the predatory beetle (*Aulonium trisulcum,* Coleoptera: Zoopheridae) has reportedly increased in numbers in England, likely due to the rise in newly dead *Ulmus,* potentially linked to the occurrence of Dutch elm disease (caused by the non-native fungus *Ophiostoma novo-ulmi*) (Marshall 1978). However, in the long term, numerous species may face the risk of coextinction, since they are strongly dependent on specific tree species for survival. For example, recent declines in the populations of *Ulmus* spp. and *F. excelsior* due to the impacts of Dutch elm disease and ash dieback (caused by fungus *Hymenoscyphus fraxineus*) serve as notable examples of this issue. Both *Ulmus* and *Fraxinus* have similar habitat requirements, predominantly growing in nutrient-rich stand types in southern Sweden (Diekmann 1999). A recent study compared current forest tree composition with that from before the arrival of tree pathogens. The study found a shift in species composition towards an increased presence of *T. cordata* and *C. betulus* in richer sites, and an increase in *F. sylvatica* in less nutrient-rich sites. Additionally, in wetter sites, there was an increase in the proportions of *A. glutinosa* and *P. padus* in current stands compared to before pathogen establishment (Brunet et al. 2023).

Furthermore, a recent study indicated that many tree-associated species are shared between *F. excelsior* and *U. glabra*, and in total more than one hundred species are experiencing high risk of regional extinction due to the tree population decline caused by these tree pathogens (Hultberg et al. 2020). On an national level, thirty species of lichens and fungi are currently red listed mainly due to decreased populations of these two tree genera (Sundberg et al. 2015, Eide et al. 2020). In a related study analyzing the decline of *Fraxinus excelsior* in the UK, Mitchell et al. (2022) found that up to 45 associated species could be negatively impacted.

Several studies have also closely examined the patterns and processes related to the spread of these pathogens. In a study from the island of Gotland, eastern Sweden, Jönsson and Thor (2012) investigated the effects of ash dieback on the diversity of epiphytic lichens. They visited sites that had been inventoried for epiphytic lichens before the establishment of the pathogen and estimated local and regional co-extinction risks of tree associated lichen species. On average, 70 % of *F. excelsior* showed symptoms of infection, with the infection rate being relatively higher in traditionally managed sites with pollarded trees (84 %) compared to grazed or unmanaged sites (ca. 65 %). The average local co-extinction probability for epiphytic lichens associated with *F. excelsior* was around 40 %. The study demonstrated that severe dieback of *F. excelsior* (mortality >60 %) resulted in significant changes in the species composition of associated lichen species. Lichen species that depend on specific environmental conditions or have small population sizes were found to be most likely to become locally extinct (Jönsson and Thor 2012).

Regarding the spread rates of this pathogen, in a study on old-growth *F. excelsior*-trees in the county of Västra Götaland, 94 % of the trees showed symptoms of ash dieback in 2020, as compared to 62 % in 2009, and the symptoms in affected trees had become more severe (Bengtsson et al. 2021). Smaller trees and trees in shaded areas were generally more affected than larger trees and those standing in open conditions. The annual average mortality was around 2 %, but trees pollarded within the last ten years exhibited a higher death rate (about 3.3 % per year). This is in contrast to unpollarded trees and trees pollarded more than 30 years ago, which had lower mortality rates, i.e., 1.6 % and 1.4 %, per year, respectively.

In summary, non-native pests can have a profound impact on forest structure and biodiversity. The decline of old trees and old-growth forests is currently an important conservation issue, with many species being red listed due to the loss of these habitats. Non-native tree pests may present an additional, considerable threat to these already vulnerable species. It is therefore important not only to closely monitor and manage non-native pests that have already established but also to prevent the introduction and establishment of new pests.

4.3 Ecosystem services

4.3.1 Provisioning of timber and non-timber products

Forests are considered a key ecosystem for providing timber, energy and fibres, and contributing to the provisioning of ornamental resources (e.g., Christmas trees, hunting trophies etc.) and biochemicals (Harrison et al. 2010). In Sweden, forest trees are primarily used for sawn wood products, pulp, paper, various other wood-based products, bioenergy, and ornamental purposes. Sweden plays a significant role in the international market for these wood-based products, contributing approximately 9 % to global sawn timber trade, 8 % to paper, and around 6 % to pulp (KSLA 2015, Skogsindustrierna 2024). Forests also provide non-timber products, such as various edible items like berries, mushrooms, and game meat. It should be noted that many of the provisioning ecosystem services are typically included in assessments of economic impact, and detailed information on harvested amounts and associated monetary value for Sweden is provided in Widenfalk et al. (2022).

Wood-based products and material for bioenergy

The total growing stock of trees in Sweden has been estimated at approximately 3500 million m^3 standing volume in forest land (Table 3) (Skogsdata 2022). The average annual harvest of timber in Swedish production forests has been continuously increasing, and in the period 2008–2018, it was estimated at 80–90 million m^3 of standing wood volume. During this period, the average annual area of final felling, thinning, and clearing was estimated at 196, 337, and 261 thousand hectares, respectively. *Picea abies*, *P. sylvestris*, and deciduous trees contributed, on average, around 55 %, 33 %, and 13 % of the total harvest volume, respectively (Skogsdata 2022).

According to statistics from 2018, more than half (53 %) of the harvested wood in Swedish forestry was used as sawn timber, 38 % as pulpwood, and 9 % as fuelwood, corresponding to 18, 13, and 3 million tons of dry biomass, respectively. Additionally, 2 million tons of forest fuel (tops and branches) were harvested and used in heating plants (Agestam et al. 2022). Approximately 45 % of the sawn timber became sawn goods, while the remaining 55 % were by-products, with half being wood chips used for pulp and paper production. About 60 % of the pulpwood was used in pulp and paper mills, and a smaller portion was used for other purposes, such as textile production. By-products from the paper and pulp industries were mainly used as a source of bioenergy (e.g., pellets or black liquor) within the industry (Agestam et al. 2022).

Both *P. sylvestris* and *P. abies* are used extensively in the sawn timber industry as well as in the pulp and paper industry. Approximately two-thirds of the sawn timber is traded from Sweden, and *P. abies* and *P. sylvestris* are represented roughly equally in the traded coniferous sawn timber. In the paper industry, spruce fibre is typically used for newsprint, intermediate layers in packaging, and certain hygiene products. Stronger paper, cardboard, and fine printing paper are primarily based on coniferous fibres (mainly from *P. abies*, *P. sylvestris* and *P. contorta*). Deciduous fibres are also utilized to some degree in several of these products (Agestam et al. 2022).

Edible products

Forest environments provide a variety of edible products. Among these, bilberry (*Vaccinium myrtillus*), lingonberry (*Vaccinium vitis-idaea*), cloudberry (*Rubus chamaemorus*), and cranberry (*Vaccinium oxycoccos*) are important edible berry species. Bilberry mainly grows in semi-shaded and shaded forest stands dominated by conifers, while lingonberry prefers conifer forests with a partly open canopy cover. Cloudberry and cranberry mostly grow in mires (Svensson 2017, Bohlin et al. 2021).

Bilberries and lingonberries are the most prevalent of the edible berry species in Sweden. The cover of bilberries and lingonberries in forest land is estimated at around 10 % and 7 %, representing approximately 350 and 250 million ha of forest land, respectively. The distribution of other berry species is lower, covering 1–2 % of forest land (Skogsdata 2022).

Production of berries can vary considerably among years, but the average annual production of bilberries and lingonberries in 2017–2021 was estimated to be around 318 and 389 thousand tons, respectively (Skogsdata 2022). Bilberry is the most commonly collected berry species in Sweden (Salo 1995). Berries are picked mostly for domestic use, and it is estimated that about 58 % of Swedish households collect berries, resulting in around 15 000 tons of berries collected annually (Jonsson and Uddstål 2002). Bilberries are also picked commercially, with an estimated 10 700 tons collected in 2012 for commercial purposes (Livsmedelföretagen 2013). A closer analysis of NFI data reveals that bilberry production is positively associated with the amount of *P. sylvestris* trees in the stand (as biomass) (Gamfeldt et al. 2013).

The most popular edible mushrooms collected in Sweden, both by households and commercially, are chanterelle (*Cantharellus cibarius*), funnel chanterelle (*Craterellus tubaeformis*), and porcini mushrooms (*Boletus edulis*) (Salo 1995, Stryamets et al. 2015). Most of the edible mushrooms collected in forests form mycorrhiza with common tree species. Chanterelle and porcini grow in forests with both coniferous and deciduous trees, while funnel chanterelle is associated with *P. abies*, *P. sylvestris*, and *F. sylvatica* (Hallingbäck and Aronsson 1998).

Game meat is another important forest resource. Based on information from questionnaires completed by hunters in Sweden, the annual harvest of game meat was around 15 million kg in 2005/2006, corresponding to an estimated gross recreation and meat value of 3.1 billion SEK (Boman and Mattsson 2012). Moose (*Alces alces*) is the most commonly hunted game species, with approximately 100 000 animals hunted annually, accounting for around 2 % of the meat consumed in Sweden (Skogsstyrelsen 2018). In this context, moose are known to browse on a variety of vegetation. Among trees, foliage and shoots of *P. sylvestris* and *Betula* are commonly consumed food sources. Other tree species, such as *Salix*, are preferred but are less common food sources in their environment (Shipley et al. 1998, Hörnberg 2001, Månsson 2007).

Historically, the sap from mainly *B. pendula*, *B. pubescens*, and *A. platanoides* was an important forest resource, as it was used as a drink, an ingredient in various foods, or processed into alcoholic beverages (Svanberg et al. 2012). Today, however, the use of tree sap is less common.

Ornamental products

Forests also provide various tree-related materials for decorative purposes. For example, *P. abies* is the most common tree species used as a Christmas tree in Sweden (Salo 1995). Although there is no official statistics on the total production of Christmas trees in Sweden, it is estimated that in 2016, approximately 3.3 million Swedish households purchased Christmas trees, with around 60 % being *P. abies* (Pettersson 2018). In 2017, 447 hectares of agricultural land were used for

Christmas tree production, which roughly corresponds to the production of about 250 000 trees (Paulmann 2002, Swedish Board of Agriculture 2017b). Considering that the annual importation of Christmas trees into Sweden was around 270 000 trees (an average yearly value for the period 2014–2022 (SCB 2023)), it appears that a large portion of the Christmas trees used in Sweden is produced domestically.

Another type of ornamental product from forests is reindeer lichen (*Cladonia* sp.), which is used for decorative purposes. Lichen-rich areas are typically associated with *P. sylvestris*-dominated forests in the northern parts of the country (Kauppi 2007, Roturier et al. 2017). However, reindeer lichens are also found in dry-site forest types across the country (Arnborg 1990, SLU Artdatabanken 2018).

Effects of tree pests

The damage caused by tree pests to wood products is commonly valued in terms of loss of forest yield or stumpage value, costs of treatment, removal and replacement of damaged trees, and also in terms of economic impacts on property values or recreation (Montagne-Huck and Brunette 2018). The most damaging non-native forest tree pests can be found across several species groups such as insects, fungi, or nematodes. Further, they can be found among several different feeding guilds of insects, such as phloem and wood borers, sap feeders, and foliage feeders, causing considerable damage to their host trees, thus affecting wood fibre production due to growth losses (reviewed in Kenis et al. 2017).

For example, three of the most damaging non-native insect pests in the United States, i.e., emerald ash borer (*Agrilus planipennis*), spongy moth (*Lymantria dispar*) and hemlock adelgid (*Adelges tsugae*), have caused timber losses worth on average 60, 4.6 and 1.1, million US dollars per year, respectively (Aukema et al. 2011). However, the relative economic value of timber losses due to these specific pests was relatively low compared to other expenditures, such as tree removal, replacement and treatment by local governments and households, as well as residential property value losses (Aukema et al. 2011, Fei et al. 2019).

In Canada, the outbreaks of mountain pine beetle have killed more than 50 % of the total merchantable volume of lodgepole pine, which initially led to an increase of around 11 % in timber production at the national level. However, logging activity is expected to decrease in areas that experienced beetle outbreaks, and it is estimated that this will lead to a decrease in timber supply of approximately 20 %, 7.5 %, and 1.5 % at regional, national, and global levels, respectively. The recovery time for regional timber production is estimated to be 60–80 years (Dhar et al. 2016).

In Europe, the potential economic impact on timber production is posed by several non-native pest species, notably the pine wood nematode (*Bursaphelenchus xylophilus*), which is indigenous to North America. The nematode is spread by vector beetles, specifically longhorn beetles from the genus *Monochamus*, with several species occurring in Sweden. The pine wood nematode is currently present in Portugal, and control measures have been implemented to combat its spread to other areas. If not successfully controlled, the potential economic impact of pine wood nematode in the European Union has been estimated at €22 billion over the period from 2008 to 2030. In Japan, where the species has established, wood losses caused by this nematode are estimated to be more than 2 million m^3 of timber per year (reviewed in Kenis et al. 2017).

The indirect effects of non-native tree pests on the provisioning of berries, mushrooms, and wild game are less known. The production of common ectomycorrhizal mushrooms in Canada has been estimated to recover in about 15 years in forests attacked by mountain pine beetle, but the recovery time was estimated to be longer for forests that have been clear-cut (Dhar et al. 2016). Bilberry production is known to be associated with semi-shaded conditions. Partial canopy openings in attacked forests may, at least in the short term, be beneficial for berry production. However, many other site-specific factors, including clear-cutting and regenerating trees, may also affect berry production (Dhar et al. 2016). For other berry species, high infestation levels of spruce beetle (*Dendroctonus rufipennis*) in Alaska were associated with higher production of several species of wild berries, including lingonberry (*Vaccinium vitis-idaea*) (Suring et al. 2006). Forest cutting, however, has been shown to have strong negative effects on berry production (Johnson 2014, Dhar et al. 2016).

For other tree-associated species, as discussed in the previous section on biodiversity, the potential impact of non-native pests will likely be greatest on species that have a strong association with the affected tree species or that rely on habitat conditions where, e.g., tree cover or specific tree species constitute a key element in the habitat (see Section 4.2).

4.3.2 Provisioning of drinking water

Forests, mountains, rivers and lakes are ecosystems that are of key importance for provisioning of fresh water (Harrison et al. 2010). Recent research highlights the importance of upstream ecosystems and the role of land use management in provisioning freshwater. Specifically, the concept of "green-blue water flows" has been established, which describes the impact of land use on water distribution in soils (green water) and in rivers and aquifers (blue water) (Falkenmark and Rockström 2010).

In Sweden, approximately half of the drinking water comes from surface water, with the remainder originating from ground water or artificially recharged groundwater (Svenskt Vatten 2017). Surface water is the main source in Sweden's most populated areas, notably in the country's three largest cities - Stockholm, Göteborg, and Malmö. Surface water, however, often requires treatment to remove contaminants, before it can be safely consumed. Groundwater, on the other hand, generally requires no or less purification due to lower organic content (Svenskt Vatten 2017).

Most of the surface water used as drinking water in the Nordic countries originates from forested catchments (Harrison et al. 2010). This is also true for the three major urban regions in Sweden, where forest land constitutes approximately 60 % of the total catchment area. Specifically, these areas are Lake Mälaren, Göta älv, and Lake Bolmen, which serve as the main sources of drinking water for Stockholm, Göteborg and Malmö, respectively (Sonesten et al. 2004, Vattenmyndigheterna 2008, Ledesma et al. 2012, Borgström 2020). Forests influence how water flows from precipitation to water bodies through several interconnected hydrological and ecological processes. These processes include the interception of precipitation, soil infiltration, reduction of soil erosion (and thus sedimentation in water bodies), and filtering water pollutants (Hamilton and Dudley 2008).

Forests within watersheds are generally recognized as beneficial for water quality. They reduce the runoff of pollutants (including nitrogen, phosphorus, and pathogens) into water bodies more effectively compared to other land covers, such as agricultural or urban areas, thereby reducing water treatment costs (Westling et al. 2020b). Conversely, forest harvesting, other forestry operations, and severe disturbances like wildfires can adversely affect water quality, leading to increased turbidity, sediment delivery, and organic carbon leaching (Kuglerová et al. 2021, Chen and Chang 2022, Shah et al. 2022, Härkönen et al. 2023). In this context, the role of riparian forests, i.e., forests situated close to water bodies, has also been highlighted, as they act as nutrient sinks, thereby reducing nutrient output to surface waters (Gundersen et al. 2010). A study from North America reported that riparian or streamside buffers can retain up to 97 % of eroded sediment from harvested areas, thereby protecting streams (Lakel et al. 2010).

Groundwater, as a source of drinking water, is dependent on sufficient recharge of groundwater aquifers, and is therefore sensitive to droughts, which can lead to water scarcity (Barthel et al. 2021). Regarding the contribution of trees to hydrological processes, during the summer season in northern Europe coniferous forests intercept approximately one third of the precipitation and increase transpiration rates, thereby influencing the overall net precipitation in forests. This leads to a decreased groundwater recharge during the growing season and groundwater recharge occurs mainly during winter rains in southern Sweden, or during snowmelt in northern parts of the country (Nygren et al. 2020).

Effects of tree pests

The effects of biotic disturbances on water quality were studied in North America during outbreaks of mountain pine beetle (Mikkelson et al. 2013b, Brouillard et al. 2016). The studies showed that tree mortality led to increased concentrations of total organic carbon in water-treatment facilities in areas infested with mountain pine beetles compared to non-infested areas (Mikkelson et al. 2013b, Brouillard et al. 2016). Increased levels of organic carbon led to higher concentrations of disinfection by-products (DBPs) in treated water, such as trihalomethanes, which are considered harmful to human health (Mikkelson et al. 2013a). The impact of tree mortality on water quality was found mainly in areas where the infestation exceeded 50 % of the forest in the watershed area. In the most affected areas, the concentrations of DBPs continued to increase during a ten-year period after the outbreak (Brouillard et al. 2016). This increase in organic carbon has been attributed to a destabilization of the bacterial community and microbial processes when tree mortality exceeds a 30–40 % threshold, which in turn affects downstream water quality (Mikkelson et al. 2017).

Similarly, large-scale infestations of native bark beetles (*Ips typographus*) in Bavaria led to a significant increase in nitrate concentrations in the runoff water used as drinking water. The elevated nitrate levels persisted for up to 17 years post-infestation; however, levels remained within the WHO safety limits for drinking water (Huber 2005, Beudert et al. 2015).

4.3.3 Climate regulation

Forests, mountains and wetlands are considered key ecosystems contributing to climate regulation (Harrison et al. 2010). Forest ecosystems contribute to climate regulation at the global scale by long-term storage of carbon (C) in soils, living trees and dead wood. Scandinavian forests acted as a C sink of ca. 0.03 Pg C per year during the period 2000–2007 (Pan et al. 2011).

Growing forests are generally considered to act as C sinks (Peichl et al. 2022, Grelle et al. 2023), but large scale disturbances, insect infestations, and forest harvests can transform them into C sources. However, the forests return to being C sinks as they regrow, although it may take several decades (Amiro et al. 2010). Old-growth forests can continue to serve as C sinks (Luyssaert et al. 2008, Peichl et al. 2022), though some studies suggest that primary old-growth forests can sometimes act as C sources (Gough et al. 2007, Hadden and Grelle 2017). This is likely due to respiration of coarse woody debris, which is more abundant in these forests, thereby impacting overall C sequestration.

Since the C-storing capacity of boreal forests is significant, the long-term impacts of forests and forest management strategies on climate are at the focus of ongoing scientific discussions. The uncertainties about forest-management impacts on climate involve differing views on the effectiveness of various management strategies, such as high harvest levels versus reduced harvests, and the potential of increased wood usage as a substitute for fossil-derived products (Gustavsson et al. 2017, Gustavsson et al. 2021, Skytt et al. 2021, Petersson et al. 2022, Schulte et al. 2022, Hurmekoski et al. 2023). Furthermore, there are uncertainties regarding the influence of differing albedo effects between coniferous and deciduous forests, and across different seasons, as well as the role of aerosols emitted from different forest types (Betts 2000, Spracklen et al. 2008, Wickham et al. 2013, Landry and Ramankutty 2015, Popkin 2019).

Carbon in forest soils

The majority of C in boreal forest ecosystems is stored in the soil. The total amount of soil organic carbon (SOC) in Swedish productive forest land is estimated at 1870 million tons (comprising 1360 million tons in mineral soils and an additional 510 million tons in peat soils). The average C store is estimated at 65 tons ha^{-1} in the mineral soils, 82 ton ha^{-1} if peat soils are included (Skogsdata 2017). Many factors influence the C stock in the soil, such as soil type, soil moisture, humus type, climate, and the associated soil organisms, along with the processes to which they contribute. Forests on mesic and mesic-moist soils, which are the most common soil types in Sweden, store the highest amounts of SOC. In the inventory 2003–2012, forests dominated by *P. sylvestris*, *P. abies*, and deciduous trees growing on these soils stored approximately 40, 40, and 15 percent of total SOC, respectively. These forests covered about 45, 35, and 13 percent of productive forest land, respectively. The remaining stock of SOC (around 5 %) is stored in forests on wet or dry soils, primarily in forests with *P. sylvestris* on dry soils (Skogsdata 2017). In this context, fungi play an important role in regulating C sequestration, with specific fungal communities driving the decomposition and transformation of organic matter, hence influencing the C storage capacity of these soil types in Swedish forests (Kyaschenko et al. 2017).

The effects of tree species on SOC stocks have been found to be most pronounced in the organic forest floor layer, while the effects of tree species on C stocks in mineral soil showed less consistent results (Vesterdal et al. 2013). In general, conifer tree species have higher forest floor C stocks compared to deciduous tree species, and consistent differences in forest floor C stocks have been documented among tree genera in both boreal (*Picea*, *Pinus*, *Betula*, *Populus*) and temperate forests (*Picea*, *Pinus*, *Fagus*, *Quercus*, *Fraxinus*, *Acer*, and *Tilia*). A study by Hansson et al. (2011), investigating three common forest species from Sweden, estimated that the total amount of C in the soil (depth 0–30 cm) was largest in forests with *P. abies* (7270 g m^{-2}), followed by *P. sylvestris* (4922 g m^{-2}) and *B. pendula* (4084 g m^{-2}). The differences in SOC stocks were most pronounced in the humus layer, and the forest floor C stocks for the three species accounted for a relatively large part of the total C in a soil profile, i.e., 44, 34, and 15 percent, respectively.

Carbon storage in tree biomass

The C stock of living tree biomass comprises approximately 50 % of total tree biomass, with somewhat higher values found in coniferous compared to deciduous tree species (Thomas and Martin 2012). The accumulation of C is typically highest in younger forests, with the rate of C accumulation levelling out, or gradually declining as the forest matures (Peichl et al. 2022, Hoover and Smith 2023). The total biomass of living trees in forest land in Sweden has been estimated at roughly 2500 million tons (dry weight), and the three most common forest tree species, *P. abies*, *P. sylvestris* and *Betula*, account for more than 90 percent of total standing volume (Skogsdata 2022). The average C storage in tree biomass, including dead wood, stumps and roots, is estimated to be approximately 50 t C ha^{-1} in productive forests on mineral soils (Skogsdata 2017).

Climate regulation of forest and trees on local scales

The effects of trees on climate regulation have also been studied at local scales such as urban and agricultural areas, which are known to contribute significantly to C emissions (Smith 2004, Moran et al. 2018). For example, natural ecosystems, including forests, wetlands, and lakes in Stockholm county, have been shown to sequester 17 % of total CO_2 emissions caused by human activities in the area (Jansson and Nohrstedt 2001). Regarding urban areas, in a study conducted in Leicester, a mid-sized city in Great Britain, it was found that aboveground vegetation stored approximately 3000 tons of C per square kilometre of urban area. The majority of this C (approximately 97 %) was stored in trees, with only a small fraction in other types of herbaceous and woody vegetation (Davies et al. 2011).

In the Swedish inventory of urban trees' contributions to ecosystem services, the trees' role in C sequestration in urban environments was also examined (Deak Sjöman and Östberg 2020). Carbon storage within urban areas was estimated to range between ca. 500 and 3700 tons of C per square kilometre. Generally, higher C levels were found in cities with a greater proportion of forest cover, which contributes to the total canopy cover. Similarly, the economic value of C storage in trees in urban areas was estimated to range from approximately 2.0 to 15.5 million SEK per square kilometre. The highest levels of C storage in urban areas were typically associated with the most common tree species found within the cities (e.g., *Picea*, *Quercus*, *Betula*) (Table 4). However, in some cases, the greatest C storage levels were associated with species that were not the most abundant in the city's tree population. For example, in Stockholm, the highest C storage was estimated in *Q. robur*, which comprises only 13 % of the tree population, in contrast to the most common species, *P. sylvestris*, representing 31 %. In these cases, total C storage was influenced by other factors, such as the size of the trees or the total leaf biomass (Deak Sjöman and Östberg 2020).

Moreover, in agricultural land, the presence of trees can significantly enhance C sequestration. For example, a study from France suggests that hedgerows have the potential to sequester up to 1 ton of C per kilometre of hedge per year. The C sequestration rates depend on various characteristics, such as the size of the hedgerow and its location in the landscape (Aertsens et al. 2013).

Effects of tree pests

In a global literature review, Thom and Seidl (2016) found that stand-replacing disturbances in boreal and temperate forests, caused by fire, wind or bark beetles, on average result in a roughly 40 % decrease in total ecosystem C. These disturbances thereby significantly reduce aboveground C in biomass and SOC, while increasing dead aboveground C. The impacts of tree pests on C stocks depend largely on the type of pest, number of affected trees and the extent of tree mortality (Hicke et al. 2012). In a study of biotic disturbances across the United States during 1997–2015, insect outbreaks led to approximately five times larger C fluxes from live to dead biomass pools compared to other tree pests and pathogens. Bark beetles were the most important disturbance agents, accounting for approximately 60 % of the total biotic disturbance-induced C fluxes, with impacts comparable to that of fire (Kautz et al. 2018).

Extensive tree mortality can turn ecosystems into a net C source, while a lower fraction of killed trees may only reduce the C sequestration capacity of a forest ecosystem without necessarily turning it into a net C source. In general, the recovery of aboveground C stocks in boreal forests following disturbances or harvest is estimated to take several decades to return to pre-disturbance levels (Amiro et al. 2010, Peichl et al. 2022).

In the context of bark beetle impact, research regarding the effects of disturbances caused by the mountain pine beetle *Dendroctonus ponderosae* in Canada on C storage has yielded mixed results (reviewed in Dhar et al. 2016). Some studies have suggested that these outbreaks lead to increased CO_2 emissions due to the decomposition of dead trees. Others have reported that the growth of new trees may offset these losses, resulting in a net positive effect on the climate. Moreover, other studies have not observed any significant changes in CO_2 uptake between infested and undisturbed forests.

Replacement of dominant forest tree species due to infestation by pests has been the subject of several studies. For instance, coniferous forests in northeastern USA, dominated by hemlock (*Tsuga canadensis*), have been replaced by deciduous forests of black birch (*Betula lenta*) following an infestation of the hemlock adelgid (*Adelges tsugae*). While the C stocks in living trees of mature deciduous forests were found to be comparable to those of coniferous forests, the soils in mature deciduous forests exhibited higher respiration rates and increased decomposition. This could potentially lead to a significant decrease in soil C storage compared to pre-infestation levels. The process is, however, slow and the full impacts on C storage may take decades to become evident (Raymer et al. 2013, Ignace et al. 2018).

In Europe, several already established non-native pest species could potentially have a significant impact on C storage in forests throughout this century. The pine wood nematode (*Bursaphelenchus xylophilus*) and Asian longhorned beetle (*Anoplophora glabripennis*) are among the species with the potential to cause substantial losses of *P. sylvestris* and *Betula*, respectively. According to Seidl et al. (2018), approximately 10 % of total European C stocks, equivalent to 1027 Tg C, are at risk due to these non-native species. Furthermore, the authors estimate that the recovery time from these impacts in the boreal zone would be approximately 40 years.

4.3.4 Pest regulation services

Pest regulation is an important ecosystem service in agro-ecosystems. However, the importance of other ecosystems for this service, including forests, is not sufficiently understood or acknowledged (Harrison et al. 2010).

In agricultural landscapes, trees and shrubs can play an important role in controlling pest species by offering habitats, shelter, or food sources for their natural enemies (Garratt et al. 2017, Gontijo 2019). Woody habitats, including hedgerows or forests have been shown to support high diversity of invertebrate species. Hedgerows act as important sources of pollen and nectar, while woodlands can support populations of e.g., parasitoid wasps, aphid-eating hoverflies and serve as an overwintering habitat for ladybird beetles (Coccinellidae) (Holland et al. 2016).

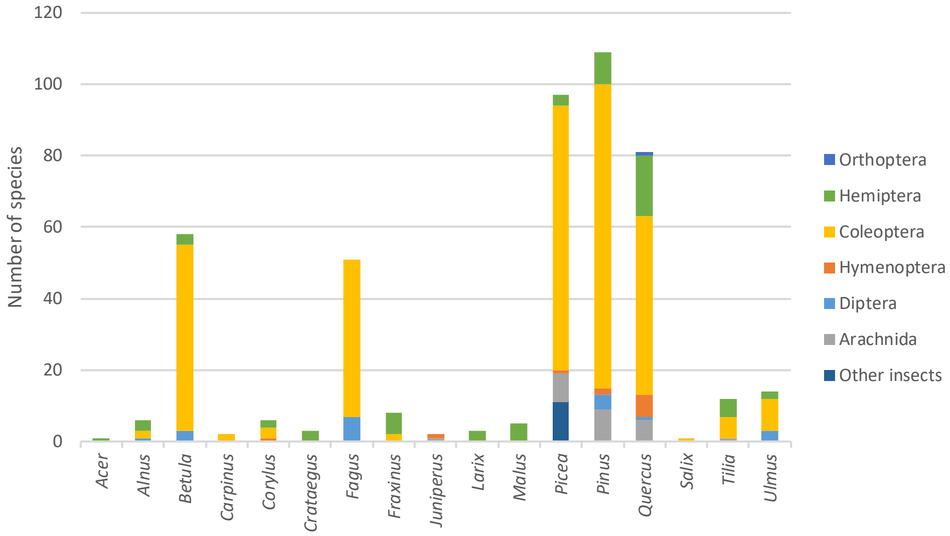
The role of specific tree and shrub species on the abundance of important natural enemies in agricultural landscapes, including ladybird beetles, hoverflies (Syrphidae), and lacewings (*Chrysoperla* sp.), was examined in a study from the Netherlands (Van Rijn 2014). The study revealed that multiple factors, including tree or shrub species, as well as the abundance of flowers and aphids (which serve as an alternative prey), had significant impacts on the abundance of different groups of natural enemies. Ladybirds were most frequently observed on *P. padus*, *P. spinosa*, *A. pseudoplatanus* and *S. cinerea*. Further, the abundance of ladybirds rose with an increasing number of aphids and the proportion of blooming flowers. Hoverflies showed a preference for woody species with a high abundance of aphids, such as *E. europaeus*, *P. padus*, *P. spinosa*, and *A. pseudoplatanus*. Ladybirds were found on woody plants throughout the entire spring, whereas hoverflies only appeared during certain periods of the season. The occurrence of lacewings, on the other hand, was not influenced by any specific tree or shrub species.

In terms of species associations with specific tree species, the highest number of strongly associated predator, parasitoid, and omnivorous invertebrates can be found in *P. sylvestris*, *P. abies*, *Quercus*, *Betula*, and *F. sylvatica*. These species host approximately 50–100 species, while the number of species associated with other tree species is markedly lower (< 20 associated species per tree species) (Figure 2) (Artdatabanken 2018). The predator and parasitoid species are mostly represented by beetles, but they also include arachnids, dipterans, and hymenopteran species. The species numbers presented here only reflect the count of associated host-dependent species, and do not provide information on the abundance and behaviour of these predatory and parasitic insects, or their impacts on specific pests. As such, these numbers should be interpreted with care. Nevertheless, there is some evidence suggesting that species-rich communities associated with old-growth, e.g., veteran oak trees, can enhance predator diversity and activity around these trees, indicating that old-growth trees may serve as a source of natural enemies (Wetherbee et al. 2020).

A review by Holland et al. (2016) concludes that there is limited data on the effects of woody habitats for pest control in adjacent crops, with most evidence originating from a small set of studies. The research suggests that the impact of linear woody habitats, such as trees and shrubs alongside field boundaries, on pest control in adjacent crops is relatively weak, particularly when compared to that of semi-natural grasslands or other flower-rich areas. Furthermore, the effects of woodlands/forests on pest control are also poorly documented in the literature.

Moreover, trees in agricultural landscapes can also present a disservice, as they can host pest species. For instance, *E. europaeus* serves as a winter host for the black bean aphid (*Aphis fabae*), a pest in sugar beets and beans, while *P. padus* acts as a winter host for the cherry-oat aphid (*Rhopalosiphum padi*), a pest in cereal crops (Way and Banks 1968, Wiktelius 1984). A study from North America showed that the density of woody species, which serve as winter hosts for aphids, in the field area was the most important factor in predicting aphid colonization rates in soybean crops in early spring (Bahlai et al. 2010). Woodlands can also influence pest regulation in both positive and negative ways. For instance, pollen beetles (*Meligethes aeneus*) overwinter in woodlands, potentially increasing the infestation rates of adjacent oilseed rape fields. On the other hand, a higher proportion of woodland in a landscape has been shown to increase the parasitism rates of pollen beetles, thus reducing their impact (Rusch et al. 2012).

In forest ecosystems, research has shown that tree diversity can have a significant impact on pest control. Increased diversity of trees has been linked to decreased susceptibility to pests in temperate and boreal zones (Jactel et al. 2005, Pautasso et al. 2005). Jactel and Brockerhoff's (2007) meta-analysis showed that the effect of mixed forests on herbivore damage was most pronounced in oligophagous herbivores, with the impact on polyphagous insects showing more variation. The most pronounced effects were observed in forest stands composed of taxonomically diverse species, and in forests where the associated (non-host) tree species were represented in higher numbers than the host tree species. In another review concerning forest tree mixtures, research indicates that mixed forests, compared to pure spruce forests, have the potential to decrease damage from common *P. abies* pest species such as the *Heterobasidion annosum* fungus and the spruce bark beetle (*Ips typographus*) (reviewed in Felton et al. (2016)). However, several studies also acknowledge that the effect of forest mixtures on herbivore damage, and activity of natural enemies is highly variable and context-dependent, and more research is therefore needed to fill the knowledge gaps (Vehviläinen et al. 2007, Staab and Schuldt 2020).



	Acer	Alnus	Betula	Carpinus	Corylus	Crataegus	Fagus	Fraxinus	Juniperus	Larix	Malus	Picea	Pinus	Quercus	Salix	Tilia	Ulmus
Orthoptera	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Hemiptera	1	3	3	0	2	3	0	6	0	3	5	3	9	17	0	5	2
Coleoptera	0	2	52	2	3	0	44	2	0	0	0	74	85	50	1	6	9
Hymenoptera	0	0	0	0	1	0	0	0	1	0	0	1	2	6	0	0	0
Diptera	0	1	3	0	0	0	7	0	0	0	0	0	4	1	0	0	3
Arachnida	0	0	0	0	0	0	0	0	1	0	0	8	9	6	0	1	0
Other insects	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0

Figure 2. Number of predator, parasitoid and omnivorous invertebrates with a strong association to a particular tree species or genus (SLU Artdatabanken 2018).

Effects of tree pests

To our knowledge, no study has yet investigated the effects of non-native tree pests on the provisioning of pest regulation services by trees. Instead, the efforts have primarily been focused on controlling the non-native species themselves, often through the use of biological control (i.e. Nuss 1992, Turbé et al. 2011). A recent analysis of over one hundred studies showed that the surrounding non-crop habitats, such as forests or grasslands, account for variation in the abundance and activity of natural enemies, but they do not consistently provide pest regulation services (Karp et al. 2018). Therefore, an increased understanding of landscape effects is required when assessing the biocontrol potential of non-crop habitats in agricultural lands.

4.3.5 Pollination

Pollination is a key ecosystem service provided by agricultural systems. However, adjacent land types such as semi-natural grasslands, forest edges, and heathland/shrubland, also play an important role as they support diverse pollinator communities (Öckinger and Smith 2007, Harrison et al. 2010). Pollination, primarily mediated by insects, can be regarded both as a regulating service, contributing to the production of food crops, and as a supporting service, as it helps to maintain populations of pollination-dependent plant species which can serve, for example, as habitats for biodiversity. Additionally, the production of honey by honey bees can be considered a provisioning service (Jha et al. 2013, Borgström et al. 2018).

In Swedish agriculture, large areas are cultivated for grass or clover ley and cereal production, which are not directly dependent on insect pollination. However, the production of several agricultural crops, such as oilseed crops and legumes, benefit significantly from insect pollination. Additionally, production of clover seeds, used in ley seed mixtures, as well as horticultural crops like fruits, vegetables, and berries, rely largely on insect pollination (Bartomeus et al. 2014, Lindström et al. 2016, Borgström et al. 2018). The land area used for the production of these pollinated crops comprises approximately 5 % of the total cultivated land area in Sweden (SCB 2018).

Honey bees (*Apis mellifera*) are the most common pollinator species. In 2019, the economic value of honey bee pollination in Sweden was estimated to between 315 and 641 million SEK, with the highest benefits estimated in production of apples, oilseed rape, and strawberries (Pedersen et al. 2020). However, wild pollinators, such as bumble bees and wild bees (Apoidea), butterflies and moths (Lepidoptera), and hoverflies (Syrphidae), have been shown to improve the yields of many crops, significantly supplementing pollination by honey bees (Garibaldi et al. 2013, Rader et al. 2016, Reilly et al. 2020).

Trees can support pollinating insects in several ways. They provide pollinators with nesting habitats, shelter, and food resources in the form of pollen, nectar, or honeydew (i.e., sweet secretions from aphids when they are abundant on trees). Additionally, they serve as landmarks for honey bees, facilitating their orientation to food sources (Donkersley 2019). While herbaceous plants have been traditionally considered as the major source of a bee’s diet, recent studies have discovered that honey bees collect a significant proportion of their diet from trees, especially *Acer*, *Crataegus*, *Prunus avium*, *Salix*, and *Tilia*. Further, tree pollen has been consistently found in bees located in areas with open land, suggesting that bees travel long distances to reach this food source (Donkersley et al. 2017, Donkersley 2019). Moreover, the presence of mixed forests (i.e., clusters of deciduous and coniferous stands) and mixed coniferous forests in the landscape correlated with low honey bee colony losses. In contrast, landscapes with high proportion of agricultural, urban, and industrial areas were associated with high honeybee colony losses (Clermont et al. 2015).

In the case of wild pollinators, a study by Wood et al. (2016) found that the pollen of woody plants frequently appeared in the pollen loads of solitary bees, concluding that the role of trees and shrubs for wild bees in farmlands has likely been underestimated in observational studies, due to the difficulty of directly observing bee feeding behaviour in trees. Furthermore, in a comprehensive European study, the abundance of wild bees benefitted from an increase in the area of deciduous forests, while it was negatively affected by an increase in the area of coniferous forests (Carre et al. 2009).

The composition of the landscape in Sweden's agricultural land has been examined through an inventory of habitats along field margins in southern and middle Sweden. Coniferous forests, cultivated land, and pastures were the most common adjacent land types along field margins. They constituted about 38 %, 10 %, and 23 % of the total length of field margins, respectively (Glimskär et al. 2016). Deciduous forests constituted only a small fraction of field margins (about 4 % of the field margin length), and they were most frequently in southernmost Sweden. However, flowering and fruiting trees were commonly found at field margins. *Prunus spinosa* and *Salix caprea* were the most frequently represented tree species, each occupying approximately 8 to 9 meters of field margin per kilometre. They were followed by *Corylus avellana*, *Sorbus aucuparia*, and *Prunus padus*/*Prunus* spp., each represented approximately 5 to 7 meters of field margin per kilometre (Glimskär et al. 2016).

Species-specific contributions of trees to pollinator support

Different tree species play varying roles in supporting pollinators. The differences are determined by the trees' production of nectar, pollen, and honeydew, as well as their flowering times (Hill and Webster 1995). Nectar and pollen serve as critical resources for pollinators. Nectar is a sugar-rich solution that plants produce to attract and reward animal pollinators, thereby promoting outcrossing. Honey bees, in particular, transform the nectar they collect into honey within their hives. Pollen, on the other hand, is a protein-rich food source that primarily serves as food for the offspring. The protein content of pollen plays a significant role in determining its nutritional value for bees. Studies have shown that a diet low in protein can negatively affect colony growth and survival (Rahbek Pedersen et al. 2009).

Pollen and nectar production in different tree species is summarized in Table 7, based on the information from Mattson and Lang (2001), Kryger et al. (2011) and Janssens et al. (2006). Important nectar producers for honey bees include *A. platanoides*, *F. alnus*, *M. sylvestris*, *P. avium*, *P. spinosa*, and *Tilia*. The honey production potential of these tree species is estimated to range between 100–400 kg/ha. *Corylus avellana*, *M. sylvestris*, *P. spinosa* and *S. aucuparia* are also considered important pollen sources for honey bees. While common, wind-pollinated forest trees, such as *P. abies*, *P. sylvestris*, *Betula*, and *P. tremula,* have negligible nectar production, bees can collect honeydew from these trees. The honey production potential of mature forest stands from this honey-dew source is estimated to be approximately 25 kg/ha.

Regarding flowering times, some tree species, such as *S. caprea* and *A. platanoides*, flower early in the season, providing valuable nectar resources for bees during colony establishment. A study by Svensson (2002) indicated that at a landscape level, areas with a high volume of *S. caprea* harboured a greater abundance of bumblebees compared to areas with low volumes. Further, *C. avellana* and *Alnus* produce pollen that attracts flower visitors early in the season (Hansson 1980). While pollen from several early-flowering trees like *C. avellana* or *Quercus* is considered to be of low nutritional value for honey bees (Kryger et al. 2011), it can support other flower visiting species. For example, *Quercus* has been identified as an essential early-season pollen source for a solitary bee species (*Osmia bicornis*, Hymenoptera, Megachilidae), in pasture-rich farmlands and agricultural areas in southern Sweden. In agricultural areas, the presence of *Quercus* and other tree species, likely serving as a source of pollen and nectar or as natural nesting habitat, has also been shown to positively affect the reproduction of this bee species (Persson et al. 2018, Yourstone et al. 2021).

Other trees species, such as *F. alnus*, *S. aucuparia*, and *Tilia* bloom later in the summer, providing bees with essential food resources towards the end of their active season. *Tilia*, in particular, can host large numbers of aphids that produce honeydew, an attractive food source for bees (Hansson 1980). However, *Tilia* also presents a potential disservice: it has been associated with mass bumble bee mortality, observed late in the summer in numerous cities across Europe. This phenomenon has mainly been observed in the non-native silver linden (*Tilia tomentosa*), but has also occurred in native species such as *T. cordata* and the common linden *Tilia* × *europaea*. The causes of this mortality have been unclear, previously attributed to natural factors, starvation, or potential chemical deception by compounds present in the nectar of linden (Koch and Stevenson 2017). However, a recent study has revealed that linden nectar contains trigonelline, an alkaloid that may, alone or in combination with other alkaloids, influence bee memory and learning behaviour. This could lead to bees persistently foraging on linden late in the summer, despite a diminishing nectar supply and lower air temperatures, potentially leading to an energy deficit. However, a direct link between this alkaloid and bees feeding behaviour remains to be investigated (Lande et al. 2019).

Table 7. Relative importance of nectar, pollen, and honeydew production by different tree species for honey bees (+++ High Importance, ++ Medium Importance, + Low Importance). Parentheses denote low nutritional quality. Data compiled from Kryger et al. (2011) and Mattson and Lang (2001), with additional information from Allt om biodling (2018) and the Swedish Museum of Natural History (2018). The theoretical average honey production potential of several tree species is based on data from Janssens et al. (2006). For some tree species, honey production is estimated based on the production of honeydew (marked with 'hd').

Scientific name	**Nectar**	**Pollen**	**Honeydew**	**Theoretical honey production potential (kg/ha)**	**Flowering month**
Acer platanoides	+++	++		200	IV, V
Alnus		++		-	III, IV
Betula		+	++	0	V
Carpinus betulus		++		-	V
Corylus avellana		(+++)	+	0	III, IV
Crataegus	+++	++		100	V, VI
Euonymus europaeus	+	+		-	V, VI
Fagus sylvatica		++	+	-	V
Frangula alnus	+++	+		200	VI, VII, VIII
Fraxinus excelsior		+		-	V, VI
Hippophaë rhamnoides	+	+		-	V
Juniperus communis		+		-	V, VI
Larix decidua	+	++		25	V
Malus sylvestris	+++	+++		100	V, VI
Picea abies		(+)	++	25 (hd)	V, VI
Pinus sylvestris		(+)	++	25 (hd)	V, VI
Populus tremula		(+)	+	25 (hd)	IV, V
Prunus avium	+++	++		-	V, VI
Prunus padus	++	++		-	V, VI
Prunus spinosa	+++	+++	+++	50	V
Quercus		(++)	+	25 (hd)	V
Rhamnus cathartica	+	+		-	VI
Salix caprea	+++	+++	+++	100	IV, V
Sambucus nigra		+		-	VI, VII
Sorbus	++	+++		-	V, VI
Taxus baccata		+		-	IV
Tilia cordata	+++	+	++	400	VII, VIII
Ulmus		+	+	-	IV, V
Viburnum opulus	+	+		50	VI, VII

Pollination in forests

In forest ecosystems, the production of bilberries and lingonberries represents an important provisioning ecosystem service that relies on insect pollination. Bumble bees and wild bees are the primary pollinators of these berries. Wild bees are mainly associated with open habitats within forest lands, with many species utilizing standing dead wood as a nesting resource (Rubene et al. 2015, Westerfelt et al. 2015). In a study by Peltola et al. (2014), nesting habitats for wood-nesting bees were experimentally increased in open forest habitats. Preliminary results suggested that the bees that were attracted to these nests also led to increased number of pollinated bilberry flowers.

Effects of tree pests

To our knowledge, there are no specific studies where the impact of non-native tree pests on trees' ability to support pollinators has been investigated. The ongoing decline of *F. excelsior* and *Ulmus* is likely to have a minimal impact on pollination services, since these trees represent relatively low value for pollinators (Kryger et al. 2011). However, the decline of other tree species may have a more pronounced negative effect on both honeybees and wild bees. This is because many tree species provide vital food resources for adult bees and their offspring during different parts of the season (Donkersley 2019).

In forest ecosystems, openings in the tree canopy due to tree mortality caused by non-native pests could potentially have a positive effect on local pollinator communities, at least in the short term. Several studies have found that pollinator abundance and diversity are higher in open forest habitats, as these provide more flowering and nesting resources for pollinators (Rubene et al. 2015, Westerfelt et al. 2015, Rodríguez and Kouki 2017).

4.3.6 Soil erosion regulation

Forests and mountains are key ecosystems for soil erosion regulation. Disturbances to vegetation cover in these ecosystems can lead to soil instability and an increased risk of landslides and soil erosion (Harrison et al. 2010).

Soil erosion is a naturally occurring process that refers to the detachment and movement of soil caused by rain, wind, running water, surface thaws or snowmelt (Morgan 2005). Soil erosion produces both on-site and off-site effects. On-site effects include the loss of soil from the site, breakdown of soil structure, and loss of nutrients and organic matter. Off-site effects, for instance, include increased sedimentation in streams, which can lead to eutrophication of aquatic habitats, reduced river flow capacity, and an increased risk of flooding. Soil erosion is influenced by several factors, including site topography, soil conditions, groundwater levels, precipitation, and vegetation cover (Lundström et al. 2017).

Forests, shrublands, and grasslands are land cover types that generally exhibit relatively small soil losses with estimated rain-induced erosion rates of 0.14, 0.51, and 0.30 t ha^{-1} year^{-1}, respectively. On the other hand, bare soils and agricultural land are types of land cover where soil erosion is significantly higher, with rates of 15.1 t ha^{-1} year^{-1}and 4.4 t ha^{-1} year^{-1}, respectively (Cerdan et al. 2010). The likelihood of soil erosion and landslides is also higher on unstable slopes. It has been estimated that approximately 0.3 % of Sweden's land area (around 160 000 ha) and about 5 % of all watercourses are located in areas with high erosion risk (slopes of $\geq$ 25°, height >15 m, area >500 m^2) (Lundström et al. 2017). Most of these areas are situated in forest land, which is stabilized by forest trees and other vegetation and these areas also require adaptations to forest management practices to minimize the risk of landslides and soil erosion (Skogsstyrelsen 2018).

Plant roots play a critical role in slope stabilization and erosion control. However, assessing the relative contributions of woody and herbaceous vegetation is challenging due to methodological complexities and the large size and heterogeneity of woody plant roots (reviewed in Reubens et al. (2007)). Fine roots (<3 mm in diameter) are considered more important for soil fixation than coarse roots, but several studies have demonstrated that coarser roots also contribute to soil stabilization on shallow slopes. Woody species possess strong vertical roots and fine roots branching from lateral roots, potentially stabilizing soils in both deeper layers and surface soil. Moreover, forests and trees intercept rainfall, reducing the amount and speed of raindrops reaching the soil, thereby decreasing surface runoff and the detachment rate of soil particles, compared to areas without tree cover. Furthermore, vegetation roots enhance the water infiltration capacity of soils, which can reduce surface runoff. It is generally concluded that a combination of woody and herbaceous plant species, providing variation in distribution, depth, strength, and root pattern, is beneficial for controlling soil erosion (Reubens et al. 2007, Ellison et al. 2017).

Species-specific contributions of trees to soil stability

Different tree species vary in their root architecture, affecting the potential for stabilizing effects on soils and slopes. For instance, among common forest tree species, *P. sylvestris* often develops a taproot for anchorage, *P. abies* shows pronounced growth of proximal roots, and *Betula*, being a deciduous species with a greater demand for water, has the most extensive root system (Kalliokoski et al. 2008). In an overview presented by Norris et al. (2008), tree species are categorized based on their root architecture and suitability for soil and slope stabilization (Table 8). Tree species are classified according to their root characteristics into (1) species with anchoring and buttressing of deep tap roots, (2) species suitable for bank and channel reinforcement, (3) species suitable for deep reinforcement and soil strength enhancement, (4) species suitable for removing soil moisture, and (5) species suitable for surface protection, shallow reinforcement, and erosion control (Norris et al. 2008).

In mountain regions, intact vegetation is crucial for regulating soil erosion, due to the instability of elevated areas and the slow regeneration of soils in these areas (Harrison et al. 2010). For example, mountain birch (*B. pubescens* subsp. *czerepanovii*) woodlands is considered to play an important role in preventing soil erosion in Iceland, where soils are particularly susceptible to erosion. Degradation of these woodlands, for instance, due to grazing of domestic animals, has been shown to cause substantial increases in soil erosion (Aradóttir and Arnalds 2001, Wielgolaski 2005). Additionally, a recent study indicated that the shrub cover, composed mainly of *Alnus* and *Salix* species, is reducing soil erosion alongside riverbanks in arctic Canada, which in turn will counteract the effects of the warming climate and permafrost thawing (Ielpi et al. 2023).

Table 8. Classification of different tree and shrub species present in Sweden based on their role in soil and slope stabilization, according to Norris et al. (2008).

Tree species	**Root system type**	**Root description**	**Anchoring and buttressing of deep tap roots**	**Bank and channel reinforcement**	**Deep reinforcement and soil strength enhancement**	**Phreatophytes removing soil moisture**	**Surface protection, shallow reinforcement and erosion control**
Acer platanoides	Heart	Deep rooted			x		
Alnus glutinosa	Heart	Deeper rooted than *A. incana* (but habitat dependent)		x	x	x	
Alnus incana	Heart	Shallow rooted				x	x
Betula pendula	Plate*	Intensive shallow root system			x		x
Betula pubescens		Intensive shallow root system					x
Carpinus betulus	Heart		x				
Corylus avellana		Extensive strong root system					x
Crataegus monogyna	Heart	Deep rooted			x	x	
Euonymus europaeus		Extensive root system					x
Fagus sylvatica	Heart*						
Frangula alnus		Shallow rooted					x
Fraxinus excelsior	Plate	Extensive, deep root systems, strong roots			x		
*Hippophaë rhamnoides**					x		x
Juniperus communis	Tap						
Larix decidua	Heart	Deciduous taproot system			x		
Picea abies	Plate	Dominant, widespread shallow roots, in very deep soil some vertical roots	x^				x
Pinus contorta	Tap						
Pinus sylvestris	Tap		x		x		
Populus tremula	Plate	Extensive and aggressive root systems			x		
Prunus avium	Heart	Deep rooted			x		
Prunus padus		Extensive root system with strong roots			x		
Prunus spinosa					x		
Quercus petraea	Heart				x		
Quercus robur	Heart*	Deep taproot	x		x	x	
Rhamnus cathartica		Extensive root system					x
Salix caprea					x	x	x
Sambucus nigra		Shallow rooted					x
Sorbus aucuparia	Plate*	Deep rooted in deep soil, otherwise shallow			x		
Taxus baccata	Heart						
Tilia cordata	Heart				x		x
Tilia platyphyllos	Heart						
Ulmus glabra	Heart						x
Ulmus minor							x

* variable root type

^ in certain deep soils

Effects of tree pests

To our knowledge, few studies have addressed the impact of non-native tree pests on the ability of tree species to provide soil regulation services. In general, forestry practices, including clear-cutting, road construction, soil compaction, and exposure of mineral soil, are known to augment soil erosion, particularly on slopes (Lundström et al. 2017). Consequently, it is possible that forest practices, such as salvage logging or felling to prevent the spread of non-native tree pests, could negatively impact soil erosion control, potentially increasing sedimentation in streams (Dhar et al. 2016). However, an increased risk of soil erosion has been identified in unmanaged mountainous forests attacked by (native) spruce bark beetle (*Ips typographus*), particularly on high slopes (Weslien and Schröter 2000).

Furthermore, the decline of *Alnus* along riparian ecosystems, due to the infestations of non-native *Phytophthora alni* species complex, could disrupt the trees' ecological functioning. This may lead to the destabilization of riverbanks, especially along small streams (Černý and Strnadová 2010).

4.3.7 Natural hazard regulation

Mountains, rivers, lakes, and wetlands are key ecosystems for natural hazard regulation (Harrison et al. 2010). Although not the primary contributors, forests also play a role in this service. In particular, characteristics of forests can influence the provisioning of various ecosystem services, including the regulation of natural hazards (Turner et al. 2013).

In forest ecosystems, windstorms and wildfires represent the most common natural hazard risks. These events have immediate impacts on forest stands and can have significant human and economic consequences (Spinoni et al. 2020). Although wind and fire disturbances are part of the natural dynamics in boreal forests (Esseen et al. 1997), these disturbances are viewed as economic risks in managed forests. These risks are also expected to increase due to climate change (Ou 2017). Recent literature has investigated some aspects of reducing these risks, for example by means of varying forest composition to reduce the consequences of fire and storm events in production forests (Felton et al. 2016).

Storm resistance in forests

Several factors contribute to the stability of forest stands, as reviewed by Dhôte (2005) and Gardiner et al. (2010). These include climatic factors, such as wind speed, the occurrence of ground frost, and the amount of rainfall or snowfall prior to a storm event, all of which influence the probability of storm damage. Site characteristics, such as soil depth, texture, and water content, as well as elevation and exposure to winds, also play significant roles. The probability of storm damage increases with tree height, with mature stands running the highest risk for storm damage. At the individual tree level, factors such as rooting depth, the area of the exposed crown, and proximity to the nearest edge contribute to the probability of storm damage.

The resistance of specific tree species to wind storms is difficult to assess due to the variety of factors listed above and the lack of literature directly comparing tree species grown in controlled conditions. However, deciduous tree species are generally considered more resistant to storms compared to conifer species. Gardiner et al. (2010) rank *Q. robur, Q. petraea*, *T. cordata*, *F. excelsior*, A. *pseudoplatanus* and *C. betulus* as storm-resistant tree species. *Pinus sylvestris*, *F. sylvatica*, *P. avium*, *B. pendula* and *B. pubescens* are ranked as intermediate, while *P. abies, P. tremula* and *P. contorta* are ranked as vulnerable. Furthermore, according to the Finnish National Forest Inventory, signs of wind damage in northern Finland from 1982–1994 were most evident in *P. abies* (4.8 %), followed by *P. sylvestris* (2.2 %), and least noticeable in *Betula* (0.5 %) (Dhôte 2005).

In line with these findings, damage was overrepresented in *P. abies*-dominated forests during major storm events in recent decades in Sweden (Valinger 2006, Gardiner et al. 2010, Blennow 2013). For example, investigations after the 2005 storm "Gudrun" revealed that *P. abies* accounted for 80 % of the volume of damaged trees, while *P. sylvestris* and deciduous trees made up 18 % and 2 %, respectively. In contrast, the growing stock of *P. abies*, *P. sylvestris* and deciduous trees in the region prior to the storm was 50 %, 25 %, and 19 % respectively (Fridh 2006). Several factors contributed to an increased probability of damage. These included an increased proportion of *P. abies* in the stands, but also increasing stand age, with mature managed stands being more susceptible compared to younger stands. Moreover, it was found that recently thinned stands were at a higher risk for storm damage (Valinger and Fridman 2011).

The susceptibility of different species mixtures in forest stands to wind storms has been analysed after several storm events in Europe. The underlying concept is that forest stands composed of susceptible tree species can become more resistant to wind throws when mixed with other, more stable, tree species. For example, the analysis of the 2005 "Gudrun" storm event showed that the probability of storm damage was lower in mixed stands compared to pure stands of *P. abies*. Moreover, mixtures that included deciduous trees, particularly birch, were more resistant to damage. Although less pronounced, lower damage levels were also observed in mixtures with *P. sylvestris* (Valinger and Fridman 2011). Positive effects of admixtures compared to pure stands of *P. abies* were also observed in other studies conducted in Europe (Griess et al. 2012, Felton et al. 2016). However, the effects of tree mixtures have shown inconsistent results among different studies, making it difficult to draw general conclusions about the mitigating effects of mixtures on storm damage (Dhôte 2005, Gardiner et al. 2010, Blennow 2013).

Fire resistance in forests

Diverse factors, such as site conditions, stand structure, and climatic factors like temperature and rainfall, all influence a stand's susceptibility to fire (Kuuluvainen

2002, Aalto and Venäläinen 2021). The surface fuels in the bottom of the forest are the most important for ignition and fire spread. Generally, the risk of fire is considered higher in conifer stands compared to deciduous stands (Jactel et al. 2009, Bernier et al. 2016, Felton et al. 2016). Conifer trees are considered more flammable due to their high resin and essential oil content, whereas deciduous trees, with their higher leaf moisture content, are less flammable (Astrup et al. 2018). Some tree species, such as *P. sylvestris* and likely *Quercus* as well, have adapted to fire regimes. These adaptations have led to increased survivability and regeneration in forests with naturally occurring fire dynamics (Kuuluvainen and Aakala 2011, Drobyshev et al. 2021).

In Fennoscandia, open and dry *P. sylvestris* dominated forests have highest risk for ignition and surface fire, while the risk is lowest in moist forests with *P. abies* and in deciduous forest (Granström 2005, Tanskanen et al. 2005, Tanskanen et al. 2006, Aalto and Venäläinen 2021). Inclusion (>20 %) of deciduous tree species (*Betula, P. tremula*) into forests leads to changes in the surface fuel structure, resulting in more compact leaf litter. This alteration likely reduces both the intensity and spread of forest fires compared to pure coniferous forests (Vermina Plathner et al. 2022). In addition, ignition experiments conducted with *Pinus contorta* litter have shown that the flammability of this species' litter is higher compared to that of the native *P. sylvestris*, thus potentially increasing the risk of forest fires in managed forests where this species is planted (Granström 1998).

Effects of tree pests

We have not found any studies specifically investigating the impact of non-native pest species on subsequent storm risk in forests. However, in general, tree pests can kill groups of trees and thereby create forest gaps. This, in turn, exposes previously sheltered trees, making them more vulnerable to wind felling (Gardiner et al. 2013). For example, it has been shown that wood decay caused by the native fungal pathogen *Heterobasidion annosum* increases the probability of wind damage, such as uprooting and stem breakage, in forests dominated by *P. abies* (Honkaniemi et al. 2017). Moreover, a simulation study of boreal forests revealed that, at the landscape level, the presence of gaps in coniferous forests has a greater impact on storm damage, while variation in species composition (stands with *P. abies* and/or *P. sylvestris*) have a smaller impact on potential storm damage to the forests (Zeng et al. 2010).

Regarding risk of fire, tree mortality due to pests can increase the amounts of flammable fuel both in tree canopies and on the forest floor (Valachovic et al. 2011, Page et al. 2013). Mortality of conifer trees results in decrease of moisture content in needles, and alters carbohydrate and fat content, which in turn increases flammability. When the needles fall from the trees, the amounts of fuel also increase on the forest floor (Dhar et al. 2016). However, long-term and simulation studies of several types of tree pests, such as mountain pine beetle (*Dendroctonus ponderosae*), spruce beetle (*Dendroctonus rufipennis*) (Derose and Long 2009, Andrus et al. 2016), western spruce budworm (*Choristoneura freemani*) (Meigs et al. 2015) and sudden oak death (*Phytophthora ramorum*) (Metz et al. 2011), have shown that the likelihood of subsequent forest fires generally does not increase following infestation by these species. Besides pest infestations, other contributing factors, such as site topography and climatic conditions, can also play significant roles in determining the probability of forest fire occurrence (Dhar et al. 2016).

However, some studies have found lagged responses of tree mortality on forest fires. In the case of eastern spruce budworm (*Choristoneura fumiferana*) infestations, the probability of fire decreased directly after the disturbance, but the risk increased at intermediate time scales (about 10 years) after a defoliation event caused by the insects (James et al. 2017). Furthermore, long-term accumulation of fuel on the forest floor has also been shown to increase the probability of wildfires in oak stands infested by *P. ramorum*. As the disease progresses and more fuel accumulates in the stands, the risk of higher-severity fires increases in these areas (Metz et al. 2011).

4.3.8 Regulation of peak water flows

Forests, mountains, rivers, lakes, and wetlands are key ecosystems in regulating water flow (Harrison et al. 2010). Forests, in particular, can store and recycle large amounts of water through several processes. Trees contribute through transpiration, interception, and evapotranspiration, while also enhancing soil properties, thus improving infiltration and groundwater recharge (Ellison et al. 2017).

In terms of peak water flow management, a review by Cooper et al. (2021) categorized woodlands into four types: (1) Catchment forests, which include all woodland within a catchment area, (2) Cross-slope forests, i.e., sections of forests across slopes in open landscapes that can slow down surface water runoff, (3) Floodplain forests, i.e., deciduous forests located in flat areas adjacent to water streams, and (4) Riparian woodlands, which are narrow, linear wooded areas adjacent to rivers. Much of the research has focused on forests at the catchment area scale. Other types of woodlands, particularly riparian woodlands, have received less attention in terms of water flow management, and thus, further research is needed to understand their role. Moreover, large areas of floodplain forests have historically been lost due to deforestation and human activities.

At the catchment area scale, a decrease in forest cover generally increases water flows, while afforestation decreases it. This has been observed primarily in conifer forests (Cooper et al. 2021). Research from boreal forests, including studies from Sweden, indicates that the effects of forest harvesting lead to increased spring and high flows at the stand level and in small watersheds. However, in larger watersheds, the responses of high water flow to cumulative disturbances become more complex and can result in varied outcomes (Wei et al. 2022). Furthermore, the characteristics of flood events can influence forests' ability to mitigate flooding, with the pre-event soil moisture identified as an important factor that limits the absorption potential of forest soils (Wahren et al. 2012). During periods of prolonged rainfall, forest soils can become saturated and any subsequent rain would then result in surface runoff (Cooper et al. 2021).

In the Swedish inventory of urban trees' contributions to ecosystem services, the trees' role in runoff water retention was also examined (Deak Sjöman and Östberg 2020). The decrease in surface water runoff was calculated using i-Tree tool, based on the trees' capabilities for evaporation, transpiration, and interception. The average annual water retention by trees in urban areas was estimated to range from approximately 2400 to 8600 cubic meters per square kilometre. Generally, water retention rates increase with a higher proportion of tree cover at the city scale. Among the tree species in urban areas, those with the highest total leaf area across the tree population, typically the most common species, were associated with the highest levels of runoff retention at the city level (Deak Sjöman and Östberg 2020) (Table 4).

Effects of tree pests

Research has been conducted on the impact of biotic disturbances in the context of mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in Canada (as reviewed by Mikkelson et al. (2013a)). Tree dieback caused by beetle outbreaks led to increased runoff at the stand scale. However, the total outflow at a larger scale was dependent on various factors such as the size of the catchment, the extent of the forested and impacted areas, and the degree of forest regeneration. Bark beetle outbreaks have been shown to affect peak flows in watersheds, with a minimum threshold of 20–25 % canopy reduction proposed to lead to increased runoff. However, streamflow exhibited a delayed response to bark beetle outbreaks, with maximum streamflow observed approximately 15 years after the outbreak. Furthermore, the combined effects of bark beetle outbreaks and logging in infested areas have been demonstrated to increase water yield and peak flow in these areas (Dhar et al. 2016).

4.3.9 Air quality regulation

Forests and mountains are considered key ecosystems that contribute to air quality regulation (Harrison et al. 2010). For example, studies have shown that forests and trees in the United States removed approximately 17 million tons of air pollution during one year (Nowak et al. 2006, Nowak et al. 2014). Though the total pollutant removal accounted for less than one percent improvement in overall air quality, this removal led to significant health benefits in urban areas. These benefits include reduced incidences of acute respiratory symptoms, fewer hospital admissions, and fewer lost school days (Nowak et al. 2014). Moreover, in urban areas, short-term (one hour) tree-related improvements in air quality have been found to be more significant, depending on the type of pollutant and the extent of tree cover (Nowak et al. 2006).

Due to the potential health benefits of trees in urban environments, the role of urban trees in pollutant removal has been studied extensively. For example, several experimental studies have demonstrated the positive effects of trees on improving air quality at the street level, showing reductions in pollutant concentrations ranging from 15 % to 65 % along open roads (reviewed in Abhijith et al. 2017). Both street trees and urban woodlands reduce pollutants such as particulate matter pollution (PM), ozone (O_3), nitrogen dioxide (NO_2), sulphur dioxide (SO_2), and carbon monoxide (CO) (Roy et al. 2012). Particulate matter pollution, consisting of various types of fine particles (PM10, PM2.5, ultrafine particles) and liquid droplets, can be intercepted by the surfaces of tree leaves and bark. Vegetation retains particle pollutants temporarily until they are either washed off by rain, re-enter the atmosphere, or fall to the ground with leaf litter. Additionally, specific canopy and leaf characteristics influence surface retention of particulate matter (Lindén et al. 2023). On the other hand, gaseous pollutants like O_3, NO_2, SO_2, and CO can be absorbed through leaf stomata and metabolized by leaf tissues. The reduction of O_3, SO_2, and NO_2 emissions primarily occurs during the daytime, whereas the removal of PM and CO by trees occurs diurnally (Nowak et al. 2006).

However, urban trees also have potential disadvantages, such as the emission of allergens and volatile organic compounds (VOCs). While the majority of urban tree species can cause moderate allergic reactions, several species, including *Betula*, *C. betulus*, and *C. avellana*, are considered highly allergenic. On the other hand, species like *Tilia*, *Acer* and *P. abies* are associated with low allergenicity (Cariñanos et al. 2016, Grote et al. 2016). VOCs emitted by trees in urban environments can potentially react with urban pollutants, leading to the formation of harmful ground-level ozone. Certain tree species, such as *Quercus* and *P. tremula*, emit large quantities of VOCs and can, therefore, contribute to ozone formation (Karl et al. 2009, Grote et al. 2016). Another potential disadvantage of trees, especially in narrow street environments, is that they can reduce air exchange between the street and the air above the buildings, potentially leading to increased pollutant levels locally (Abhijith et al. 2017).

In a review, Sicard et al. (2018) evaluated various urban tree species regarding the aforementioned services and disservices in terms of improving air quality, as well as their resistance to diseases, pests, and ozone. Among the tree genera commonly found in Swedish cities, *Acer*, *Crataegus*, and *Prunus* were considered the most effective for improving air quality. Other genera, including *Fraxinus*, *Malus*, *Tilia*, *Fagus*, *Pinus*, *Platanus*, *Sorbus*, *Ulmus*, *Aesculus*, *Taxus*, and *Betula*, were rated as intermediate, listed in decreasing order of effectiveness. Lastly, *Populus*, *Quercus*, and *Salix* were ranked as being of low value for air quality improvement, primarily due to their low O_3 removal capabilities and high emission potential. *Picea abies*, a common tree species in urban forests not included in this list, is recognized for its high efficiency in removing particulate matter (PM) but is considered to have a low potential for ozone (O_3) removal and studies present varying figures regarding its emission of monoterpenes (Grote et al. 2016, Sicard et al. 2018). However, due to the year-round presence of foliage, evergreen conifer species can play a significant role in removing air pollution during the winter months, when pollution levels in urban areas are generally higher (Pleijel et al. 2022).

In the Swedish inventory of urban trees' contributions to ecosystem services (based on the i-Tree tool), the analysis of air quality regulation was based on several factors, including the trees' net absorption of NO_2, SO_2, $PM_{2.5}$ and VOCs, as well as trees proximity to city inhabitants (Deak Sjöman and Östberg 2020). At the city scale, the average net absorption of NO_2, SO_2, $PM_{2.5}$ and VOCs by trees corresponded to approximately 320, 160, 70 and 400 kg per km^2 urban area per year, respectively. Urban areas with high levels of canopy cover generally exhibited higher levels of pollutant absorption (Table 4). The highest efficiency of pollutant reduction was estimated during the summer months, which corresponds to the period of the largest leaf biomass, i.e., when both deciduous and conifer contribute to total leaf biomass during the season (Deak Sjöman and Östberg 2020).

Effects of tree pests

The ecological impact of tree pests on the air pollution removal capacity of trees has not been extensively studied (Raum et al. 2023). A study by Jones and McDermott (2018) modelled the impacts of the emerald ash borer (*Agrilus planipennis*) infestations on air quality and public health in urban areas in the United States. In these areas, the host trees, *Fraxinus*, can make up 10 to 40 % of the total canopy cover. The results showed that the loss of urban trees has led to increased concentrations of pollutants over time. The study further concluded that an increase in air pollution, associated with tree loss, corresponded with a higher incidence of cardiovascular diseases, thus highlighting the role of urban trees for human health.

4.3.10 Cultural services

A wide range of ecosystems, such as forests, agricultural land, and semi-natural grasslands, play an important role in providing cultural services (Harrison et al. 2010). While "cultural services" is a term widely used in literature, it primarily encompasses values associated with recreation, education, inspiration, cultural heritage, aesthetic appreciation, sense of place, and spiritual and religious values (Millennium Ecosystem Assessment 2005a, Blicharska et al. 2017).

In Sweden, hiking and mushroom picking are the most common outdoor recreation activities in forests. According to survey results, the majority of respondents report that they frequently visit forests, and many also perceive the forest as important for their well-being (Fredman et al. 2013, Fredman and Hedblom 2015). Concerning forest structure, older forests characterized by good visibility and the presence of large, old-growth trees are generally preferred for outdoor activities. In contrast, young forests, clear-cut areas, or forests with dead wood, wind-felled trees, or abundant undergrowth tend to be less favoured (Lindhagen and Hörnsten 2000, Gundersen and Frivold 2008, Fredman and Hedblom 2015, Fredman et al. 2023). Among specific forest types, older deciduous forests are perceived as the most attractive for outdoor activities, followed by coniferous forests, a conclusion mostly based on the visual impression from photos (Fredman and Hedblom 2015, Fredman et al. 2023). Forests dominated by *P. abies* gain recreational qualities in later stages of development, with managed mature forests 80–100 years old being the most preferred. These mature forests offer good visibility and have low amounts of dead wood, which allow for better accessibility. Forests dominated by *P. sylvestris* may have some recreational advantages over those dominated by *P. abies*, as they allow for more sunlight, thus increasing visibility, and maintain these qualities for longer periods of time as the accumulation of dead wood is slower in pine forests (Hannerz 2016). Moreover, the environment of the forests, including proximity to water bodies, noise levels, hiking trails, and other recreational facilities, influences their recreational value (Fredman et al. 2023).

Given that the majority of the world's population, including that of Sweden, lives in urban areas (SCB 2021), these areas thus become increasingly important for people's contact with nature (Chen 2017). In fact, a recent study from Sweden found that the majority (57 %) of recreation occurs in urban and peri-urban areas, which cover only about 5 % of the total land area (Lehto et al. 2022). In urban environments, trees have been shown to have several social and aesthetic benefits, including enhancing the living environment, offering recreational opportunities, improving scenic quality, and providing privacy (Roy et al. 2012). Urban trees also offer psychological benefits, such as reducing stress and promoting emotional well-being (Nesbitt et al. 2017). Furthermore, urban areas with high tree cover were associated with several additional benefits. These included increased interactions among citizens, reduced crime rates, and higher residential property values (Roy et al. 2012, Mullaney et al. 2015).

Moreover, people value the proximity of forests. According to the surveys, the preferred distance to the nearest forest area is typically very short (less than 1 km), emphasizing the importance of forests located close to residential areas (Hörnsten and Fredman 2000, Skogsdata 2009). According to the Swedish NFI (2009), approximately 30 % of urban forests, i.e., forests in or near urban areas (distances ranging from 200 to 7500 m from urban boundaries) located on productive forest land, possess recreational qualities. Recreational coniferous and deciduous forests account for approximately 20 % and 10 % of urban forests, respectively. Notably, deciduous forests with recreational qualities were four times more common in urban areas as compared to non-urban forests.

Additionally, large old trees hold significant aesthetic, symbolic, religious, and historical values (Blicharska and Mikusiński 2014). These trees, however, are rather uncommon in contemporary landscapes, and are mostly found in specific areas such as farm environments, parks, cemeteries, alleys, or along roadsides (Höjer and Hultengren 2004). Urban tree inventories reveal that large diameter trees (dbh >0.9–1.2m) constitute only a small proportion (0.5–2 %) of the total urban trees in certain cities such as Stockholm, Borås, and Hässleholm Deak Sjöman and Östberg 2020 In pastures and meadows, these large trees often bear signs of traditional land-use, like pollarding, coppicing, or grazing by animals (Hultengren et al. 1994, Torralba et al. 2018). A portion of large old trees is formally protected as natural monuments ("naturminne" in Swedish), either as individual trees or as tree groups (Naturvårdsverket 2018, 2022). In total, there are approximately 1400 of these protected sites scattered throughout Sweden. The database provides a description of the tree species for approximately 60% of these sites. The most commonly represented species are *Quercus* (at around 380 sites), *P. sylvestris* (around 190 sites), and *P. abies* (approximately 60 sites). These are followed by *F. sylvatica*, *Tilia*, *J. communis*, *T. baccata*, *Ulmus*, and *F. excelsior*, which are found at about 10–50 sites each (Naturvårdsverket 2018, 2022).

Effects of tree pests

The impacts of non-native tree pests on various aspects of cultural services have been examined in several studies. For example, widespread mortality of lodgepole pine in western Canada due to outbreaks of the mountain pine beetle (*Dendroctonus ponderosae*) has affected a large number of recreational sites (Dhar et al. 2016). Tourist attitudes towards bark beetle damage were generally negative (Arnberger et al. 2018), yet the overall impact of beetle outbreaks on tourism and recreational revenue has been minimal (Dhar et al. 2016). Similarly, visitors to recreational forests infested by the emerald ash borer (*Agrilus planipennis*) have reported a preference for mature forest stands and a dislike for dead wood and the removal of dead trees. However, other factors, such as the view of the surrounding landscape or the number of co-visitors, had a more substantial impact on people’s choice of hiking trails compared to tree mortality caused by the insects (Arnberger et al. 2017).

Further, a study by Jones (2017) evaluated the impact of tree mortality caused by *A. planipennis* on people’s well-being by combining data from local tree inventories with a nationwide survey on life satisfaction. The study demonstrated that tree mortality had a small but measurable effect on people's self-reported life satisfaction. The effects were most significant five years after the initial detection of the insect pest and were particularly pronounced in young adults. Interestingly, another study showed that people in areas affected by *A. planipennis* tended to spend less time on leisure activities and more time at work, thereby affecting decisions about daily activities (Jones 2016). Further, tree mortality caused by *A. planipennis* has also been linked to changes in the aesthetic perception of urban environments, which subsequently led to reduced property values in urban and residential areas. The short-term economic impact on property values in these areas has been estimated to exceed the economic impacts on timber products (Aukema et al. 2011, Lovett et al. 2016).

5. Summary

In this report, we aimed to provide information for estimating the potential impact of non-native plant pests on different tree species in the context of pest risk assessments. Here, we summarized the primary values provided by trees, particularly in terms of biodiversity and ecosystem services, which are potentially at risk. To estimate these values at risk, we performed a literature review that included all major native tree species occurring in Sweden. Additionally, we identified studies evaluating the effects of non-native pests on tree-related biodiversity and ecosystem services.

Sweden has most of its tree cover concentrated in forests, but some portion of trees also occurs in non-forested areas such as agricultural and urban landscapes. Regarding tree species composition, a few species are predominant. Namely, the two conifer species *Picea abies* and *Pinus sylvestris*, followed by two species of *Betula* (*B. pendula* and *B. pubescens*). Together, these tree species constitute more than 90 % of the growing tree stock in Sweden. Other tree species in Sweden are much less common, with each accounting for less than two percent of the total growing stock.

In terms of biodiversity, quantitative information on the species richness of organisms associated with various tree species was available for most of the included tree species or genera. Additionally, different general indicators of habitat provisioning were available, including the extent of old forests, protected areas, and specific habitat types characterized by various tree species.

In terms of ecosystem services, trees were found to contribute to several provisioning, regulating, and cultural services. However, the data availability on the contributions of individual species or genera of trees to these ecosystem services varied among these different categories of ecosystem services.

Since most of Sweden's trees are concentrated in forests, numerous ecosystem services are also associated with these environments. For example, forests are a primary source of timber and other wood materials but also for other non-timber products, such as the production of berries and mushrooms, as well as hunting opportunities. Forests also contribute to other ecosystem services, including the provisioning of drinking water and regulatory services like climate regulation, soil erosion control, managing peak water flows, as well as cultural services such as recreation. Several ecosystem services in urban areas, such as the regulation of water peaks and air quality, are also positively associated with increasing tree cover.

While many forest-associated ecosystem services are related to common forest tree species, such as *P. abies*, *P. sylvestris* and *Betula*, other tree species also offer specific qualities essential for the provisioning of ecosystem services. Pollination is one example where several deciduous tree species are a critical food source for pollinators. For example, several tree species provide valuable nutrients for both honey bees and wild bees. Additionally, some tree species support pollinating insects during parts of the year when other flower sources are scarce.

Impacts of non-native pests on biodiversity can yield various outcomes. For instance, biotic disturbances caused by range expanding bark beetles in North America have been shown to diversify forest stands, generally having positive effects on biodiversity. However, other non-native pests lead to tree dieback, resulting in negative impacts on biodiversity as a result of changes in the structure and composition of forests. For example, tree dieback can affects many species associated with these tree species.

Several studies have estimated the impact of non-native tree pests on ecosystem services, mostly in forest ecosystems. Provision of timber products is primarily affected by mortality of trees, which can decrease the availability of mature forests for wood production. Additionally, large-scale mortality of forest trees can impact other services, including the provision of drinking water, carbon sequestration, and water flow regulation. Several studies have estimated thresholds of tree mortality that impact these ecosystem services, examined temporal aspects of service disruption following disturbances, and estimated the recovery of these services. Additionally, in urban environments, tree mortality due to non-native plant pests has been linked to the deterioration of air quality, potentially affecting human health. Tree dieback can also impacts cultural services, such as the visual quality of urban environments, which can have further effects on human well-being. Although not studied specifically in terms of their impact, non-native tree pests could potentially also influence other ecosystem services such as pollination and pest regulation.

In conclusion, non-native plants pests can have an impact on a very large number of tree-related biodiversity and ecosystem services and this impact should be considered when conducting pest risk assessments. To support such efforts this report provides an overview of the numerous values associated with biodiversity and ecosystem services that are linked to trees, forests, and specific tree species.

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Supplementary information

Supplementary table 1. Search string for identifying studies on the effects of non-native species on biodiversity and ecosystem services. Species list follows Kenis and Branco (2010) and Santini et al. (2013), including pests on trees that are regulated under the EU Council Directive 2000/29/EC (European Council 2000).

“*Acleris*“ OR “*Agrilus anxius*” OR “*Agrilus fleischeri*” OR “*Agrilus planipennis*” OR “*Anisogramma anomala*” OR “*Annulohypoxylon cohaerens*” OR “*Anoplophora chinensis*” OR “*Anoplophora glabripennis*” OR “*Anthonomus quadrigibbus*” OR “*Apiognomonia veneta*” OR “*Apiosporina morbosa*” OR “*Argyresthia thuiella*” OR “*Aromia bungii*” OR “*Arrhenodes minutus*” OR “*Aschitonyx eppoi*” OR “*Athelia rolfsii*” OR “*Atropellis“ OR “Bactericera cockerelli*” OR “*Biscogniauxia mediterranea*” OR “*Biscogniauxia nummularia*” OR “*Blumeriella jaapii*” OR “*Botryosphaeria dothidea*” OR “*Botryosphaeria laricina*” OR “*Botryosphaeria parva*” OR “*Botryosphaeria stevensii*” OR “*Bursaphelenchus xylophilus*” OR “*Calonectria kyotensis*” OR “*Calonectria pauciramosa*” OR “*Cameraria ohridella*” OR “*Candidatus Phytoplasma ulmi*” OR “*Ceratobasidium bicorne*” OR “*Ceratocystis fagacearum*” OR “*Ceratocystis laricicola*” OR “*Ceratocystis platani*” OR “*Ceratocystis virescens*” OR “*Chalara populi*” OR “*Choristoneura“ OR “Chrysomyxa abietis*” OR “*Chrysomyxa arctostaphyli*” OR “*Coniferiporia sulphurascens*” OR “*Coniferiporia weirii*” OR “*Contarinia pseudotsugae*” OR “*Corythucha ciliata*” OR “*Cristulariella depraedans*” OR “*Cronartium ribicola*” OR “*Cronartium“ OR “Cryphonectria parasitica*” OR “*Cryptostroma corticale*” OR “*Cylindrocladium buxicola*” OR “*Delphinella abietis*” OR “*Dendroctonus micans*” OR “*Dendroctonus rufipennis*” OR “*Dendroctonus valen*” OR “*Dendrolimus sibiricus*” OR “*Diaporthe oncostoma*” OR “*Dicarpella dryina*” OR “*Didymascella thujina*” OR “*Diplodia pinea*” OR “*Discula destructiva*” OR “*Dothistroma pini*” OR “*Drepanopeziza punctiformis*” OR “*Drepanopeziza sphaerioides*” OR “*Dryocosmus kuriphilus “ OR “Elatobium abietinum*” OR “*Endocronartium“ OR “Entoleuca mammata*” OR “*Erwinia amylovora*” OR “*Erysiphe adunca*” OR “*Erysiphe alphitoides*” OR “*Erysiphe arcuata*” OR “*Erysiphe azaleae*” OR “*Erysiphe flexuosa*” OR “*Erysiphe hypophylla*” OR “*Erysiphe platani*” OR “*Erysiphe syringae*” OR “*Erysiphe vanbruntiana*” OR “*Eutypa lata*” OR “*Eutypella parasitica*” OR “*Gibberella circinata*” OR “*Glomerella acutata*” OR “*Glomerella cingulata*” OR “*Glomerella miyabeana*” OR “*Gnomonia leptostyla*” OR “*Gremmeniella abietina*” OR “*Guignardia aesculi*” OR “*Gymnosporangium sabinae*” OR “*Gymnosporangium“ OR “Gymnosporangium tremelloides*” OR “*Heterobasidion irregulare*” OR “*Hymenoscyphus pseudoalbidus*” OR “*Hyphantria cunea*” OR “*Inonotus rickii*” OR “*Ips confusus*” OR “*Ips hauseri*” OR “*Kabatina abietis*” OR “*Kabatina juniperi*” OR “*Kabatina thujae*” OR “*Lachnellula willkommii*” OR “*Lepteutypa cupressi*” OR “*Matsucoccus feytaudi*” OR “*Megaplatypus mutatus*” OR “*Melampsora farlowii*” OR “*Melampsora laricis-populina*” OR “*Melampsora medusae*” OR “*Melampsoridium hiratsukanum*” OR “*Meria laricis*” OR “*Monochamus “ OR “Mycosphaerella castaneicola*” OR “*Mycosphaerella dearnessii*” OR “*Mycosphaerella gibsonii*” OR “*Mycosphaerella laricis-leptolepidis*” OR “*Mycosphaerella pini*” OR “*Mycosphaerella populorum*” OR “*Nematospora coryli*” OR “*Nematostoma parasiticum*” OR “*Neodiprion abietis*” OR “*Neofabraea populi*” OR “*Oidium lauracearum*” OR “*Oligonychus perditus*” OR “*Ophiostoma novo-ulmi*” OR “*Ophiostoma ulmi*” OR “*Passalora sequoiae*” OR “*Pestalotiopsis guepinii*” OR “*Petrakia echinata*” OR “*Phacidium coniferarum*” OR “*Phacidium infestans*” OR “*Phaeocryptopus gaeumanni*” OR “*Phloeospora robiniae*” OR “*Phomopsis juniperivora*” OR “*Phyllonorycter platani*” OR “*Phyllosticta concentrica*” OR “*Phytophthora alni*” OR “*Phytophthora cactorum*” OR “*Phytophthora cambivora*” OR “*Phytophthora cinnamomi*” OR “*Phytophthora citricola*” OR “*Phytophthora citrophthora*” OR “*Phytophthora cryptogea*” OR “*Phytophthora drechsleri*” OR “*Phytophthora europaea*” OR “*Phytophthora gonapodyides*” OR “*Phytophthora hedraiandra*” OR “*Phytophthora hibernalis*” OR “*Phytophthora ilicis*” OR “*Phytophthora inflata*” OR “*Phytophthora inundata*” OR “*Phytophthora italica*” OR “*Phytophthora kernoviae*” OR “*Phytophthora megasperma*” OR “*Phytophthora polonica*” OR “*Phytophthora pseudosyringae*” OR “*Phytophthora quercina*” OR “*Phytophthora ramorum*” OR “*Phytophthora syringae*” OR “*Pissodes nemorensis*” OR “*Pissodes strobi*” OR “*Pissodes terminalis*” OR “*Pithya cupressi*” OR “*Polygraphus proximus*” OR “*Popillia japonica*” OR “*Pseudaulacaspis pentagona*” OR “*Pseudopityophthorus minutissimus*” OR “*Pseudopityophthorus pruinosus*” OR “*Pulvinaria regalis*” OR “*Ramichloridium pini*” OR “*Rhabdocline pseudotsugae*” OR “*Rhynchophorus ferrugineus*” OR “*Rhytisma acerinum*” OR “*Saperda candida*” OR “*Scaphoideus luteolus*” OR “*Seiridium cardinale*” OR “*Septoria betulae*” OR “*Septotis podophyllina*” OR “*Sphaceloma murrayae*” OR “*Splanchnonema platani*” OR “*Stegophora ulmea*” OR “*Stigmina pulvinata*” OR “*Stigmina thujina*” OR “*Tetropium gracilicorne“ OR “Thyriopsis halepensis*” OR “*Trechispora brinkmannii*” OR “*Venturia nashicola*” OR “*Xylosandrus compactus*” OR “*Xylosandrus crassiusculus*”

Supplementary table 2. Occurrences of different tree species and genera in the National survey of semi-natural pastures and meadows (Swedish Board of Agriculture 2023).

Genus/species	**Proportion of all sites**	**Total number of sites**	**Coverage of trees** **<10 %**	**10–30 %**	**>30 %**
Acer	12 %	10 835	9 946	745	144
Alnus	20 %	17 675	14 068	2 817	790
Betula	53 %	46 798	30 088	10 867	5 843
Corylus avellana	21 %	18 250	14 104	2 936	1 210
Crataegus	15 %	13 571	12 575	805	191
Fagus sylvatica	4 %	3 287	2 817	383	87
Fraxinus excelsior	18 %	15 995	13 453	1 859	683
Juniperus communis	48 %	42 076	31 469	6 873	3 734
Malus sylvestris	20 %	17 275	16 242	850	183
Picea abies	33 %	28 610	23 449	3 590	1 571
Pinus sylvestris	34 %	29 841	22 414	4 680	2 747
Populus tremula	29 %	25 246	20 691	3 576	979
Prunus padus	7 %	5 869	5 440	325	104
Prunus spinosa	15 %	12 819	10 104	1 981	734
*Prunus*sp.	12 %	10 365	9 613	631	121
Quercus	35 %	30 382	19 768	6 534	4 080
Salix caprea	15 %	13 549	12 870	582	97
Salix sp.	16 %	14 196	12 651	1 217	328
Sorbus aucuparia	34 %	30 240	27 538	2 145	557
Sorbus sp.	13 %	11 268	10 689	492	87
Tilia	6 %	4 877	4 137	557	183
Ulmus	4 %	3 822	3 443	297	82

Supplementary table 3. Habitat types listed in the Habitat Directive's Annex I, defined by tree cover (>30%, less in alpine regions) and the presence of tree and shrub species as characteristic or defining elements of the habitat. For specifications of habitat type ID, refer to Supplementary table 5.

Habitat type ID	**Canopy Cover (%)**	**Defining tree species (% basal area)**	**Total number of characteristic tree and shrub species**	*Acer platanoides*	*Alnus glutinosa*	*Alnus incana*	*Betula nana*	*Betula pendula*	*Betula pubescens*	*Carpinus betulus*	*Corylus avellana*	*Crataegus spp.*	*Fagus sylvatica*	*Frangula alnus*	*Fraxinus excelsior*	*Hippophae rhamnoides*	*Juniperus communis*	*Malus sylvestris*	*Picea abies*	*Pinus sylvestris*	*Populus tremula*	*Prunus padus*	*Prunus spinosa*	*Quercus petraea*	*Quercus robur*	*Salix caprea*	*Salix* spp.	*Sorbus aucuparia*	*Sorbus intermedia*	*Tilia cordata*	*Ulmus glabra*	*Ulmus minor*
Sand dune habitats																																
2180	>30	Mainly *P. sylvestris* (pioneer tree species *Alnus* sp., *Quercus*)	**0**																													
Grassland habitats																																
9070	30 - 100	Presence of native tree species	**0**																													
Forest habitats																																
9010	30 - 100 (<30% in alpine region)	Habitat subgroups: spruce forest (>70% *P. abies*) pine forest (>70% *P. sylvestris)* , coniferous mixed forest (>70% *P. abies* and *P. sylvestris*), mixed forest (>30% deciduous and >30% coniferous) and trivial deciduous forest (>70% trivial deciduous)	**5**					x	x										x	x	x											
9020	50 - 100	Hardwood forest trees (normally >50%, but at least). Important species: *Q. robur* , *U. glabra* , *F. excelsior* , *T. cordata* and *A. platanoides*	**6**	x							x				x										x					x	x	
9030	30 - 100	Coniferous or trivial deciduous >50%	**8**			x			x							x	x					x				x	x	x				
9040	10 - 100	*Betula pubescens* subsp. *czerepanovii* (>50%)	**1**						x																							
9050	50 - 100	*P. abies* >50% of basal area	**1**																x													
9060	30 - 100	Coniferous trees (>50%). Often, *P. sylvestris* >50% on top of the ridge, *P. abies* >50% in lower parts)	**2**														x			x												

Habitat type ID	**Canopy Cover (%)**	**Defining tree species (% basal area)**	**Total number of characteristic tree and shrub species**	*Acer platanoides*	*Alnus glutinosa*	*Alnus incana*	*Betula nana*	*Betula pendula*	*Betula pubescens*	*Carpinus betulus*	*Corylus avellana*	*Crataegus spp.*	*Fagus sylvatica*	*Frangula alnus*	*Fraxinus excelsior*	*Hippophae rhamnoides*	*Juniperus communis*	*Malus sylvestris*	*Picea abies*	*Pinus sylvestris*	*Populus tremula*	*Prunus padus*	*Prunus spinosa*	*Quercus petraea*	*Quercus robur*	*Salix caprea*	*Salix* spp.	*Sorbus aucuparia*	*Sorbus intermedia*	*Tilia cordata*	*Ulmus glabra*	*Ulmus minor*
9080	50 - 100	*F. excelsior* / trivial deciduous trees (>50%, together or separately), varying species composition between the northermost and southermost parts.	**5**		x	x			x						x												x					
9110	30 - 100	*F. sylvestris* (>50%)	**1**										x																			
9130	30 - 100	*F. sylvestris* (>50%)	**1**										x																			
9160	50 - 100	*Quercus* , *C. betulus* (>50%, together or separately)	**4**							x														x	x					x		
9180	30 - 100	hardwood tree species (*F. excelsior* , *U. glabra* , *T. cordata* , *A. platanoides* , *Q. robur* are important) normally > 50%, but at least 30%)	**8**	x						x	x				x									x	x					x	x	
9190	30 - 100	*Q. robur* , *C. betulus* and/or *Q. petrea*) (normally >50% together or separately, or at least 30% *Quercus* sp.)	**6**					x	x					x							x				x			x				
91D0	30 - 70	*B. pubescens* , *P. sylvestris* , *P. abies* (dominate)	**4**						x					x					x	x												
91E0	30 - 100	*F. excelsior* and trivial deciduous trees (together or separately >50%). *F. excelsior* , *A. glutinosa* and *A. incana* most common species	**6**		x	x			x						x							x									x	
91F0	30 - 100	*Q. robur* , *U. glabra* , *F. excelsior* (together) (>50%)	**6**		x										x						x	x			x						x	
Total number of habitat types featuring a characteristic tree or shrub species				**2**	**3**	**3**	**0**	**2**	**7**	**2**	**2**	**0**	**2**	**2**	**5**	**1**	**2**	**0**	**3**	**3**	**3**	**3**	**0**	**2**	**5**	**1**	**2**	**2**	**0**	**3**	**4**	**0**

Supplementary table 4. Habitat types listed in the Habitat Directive's Annex I, with low (<30%) or variable tree cover, and the presence of tree and shrub species as characteristic or defining elements of the habitat. For specifications of habitat type ID, refer to Supplementary table 5.

Habitat type ID	**Canopy Cover (%)**	**Defining species (% area cover)**	**Total number of characteristic tree and shrub species**	*Acer platanoides*	*Alnus glutinosa*	*Alnus incana*	*Betula nana*	*Betula pendula*	*Betula pubescens*	*Carpinus betulus*	*Corylus avellana*	*Crataegus spp.*	*Fagus sylvatica*	*Frangula alnus*	*Fraxinus excelsior*	*Hippophae rhamnoides*	*Juniperus communis*	*Malus sylvestris*	*Picea abies*	*Pinus sylvestris*	*Populus tremula*	*Prunus padus*	*Prunus spinosa*	*Quercus petraea*	*Quercus robur*	*Salix caprea*	*Salix* spp.	*Sorbus aucuparia*	*Sorbus intermedia*	*Tilia cordata*	*Ulmus glabra*	*Ulmus minor*
Coastal habitats																																
1610	n.a.	n.a.	**1**														x															
Sand dune habitats																																
2170	< 30	*Salix repens* ssp. *repens* var. *argentea* (>50%)	**1**																								*x*					
2190	< 30	*Salix repens* , *Salix repens* ssp. *rosmarinifolia* (>50%)	**1**																								x					
Freshwater habitats																																
3210	n.a.	n.a.	**1**																								x					
Alpine habitats																																
4060	<10	n.a.	**3**				x										x										*x*					
4080	<10	*Salix* spp. (> 50%)	**1**																								*x*					
6150	<10	n.a.	**1**																								*x*					
Grassland habitats																																
5130	0 - 30	Significant presence of *J. communis*	**3**									x					x						x									
6450	0 - 30	n.a.	**1**																								*x*					
6530	n.a.	Presence of deciduous trees and shrubs	**12**					x	x	x	x	x			x			x					x		x				x	x	x	x

Habitat type ID	Canopy Cover (%)	Defining species (% area cover)	Total number of characteristic tree and shrub species	*Acer platanoides*	*Alnus glutinosa*	*Alnus incana*	*Betula nana*	*Betula pendula*	*Betula pubescens*	*Carpinus betulus*	*Corylus avellana*	*Crataegus spp.*	*Fagus sylvatica*	*Frangula alnus*	*Fraxinus excelsior*	*Hippophae rhamnoides*	*Juniperus communis*	*Malus sylvestris*	*Picea abies*	*Pinus sylvestris*	*Populus tremula*	*Prunus padus*	*Prunus spinosa*	*Quercus petraea*	*Quercus robur*	*Salix caprea*	*Salix* spp.	*Sorbus aucuparia*	*Sorbus intermedia*	*Tilia cordata*	*Ulmus glabra*	*Ulmus minor*
Wetland habitats																																
7110 (7120)	0 - 100	n.a.	**1**				x																									
7230	n.a.	n.a.	**0**																								*x*					
7310	0 - 100	n.a.	**1**				x																									
7320	n.a.	n.a.	**1**				x																									
Total number of habitat types featuring a characteristic tree or shrub species				**0**	**0**	**0**	**4**	**1**	**1**	**1**	**1**	**2**	**0**	**0**	**1**	**0**	**3**	**1**	**0**	**0**	**0**	**0**	**2**	**0**	**1**	**0**	**8**	**0**	**1**	**1**	**1**	**1**

Supplementary table 5. Current area estimates and conservation status of habitat types listed in the Habitats Directive's Annex I, which include tree or shrub species as characteristic or defining elements of the habitat. Habitats are selected based on definitions by the Swedish EPA (Naturvårdsverket 2011). "P" denotes priority habitat types. The table presents current area estimates (km^2) and conservation status (FV - favourable, U1 - inadequate, U2 - unfavourable, empty cells - not present) of habitat types in alpine (ALP), boreal (BOR), and continental (CON) biogeographical regions in Sweden in 2019, as reported by Westling et al. (2020a). For details and information on favourable reference areas, see Eionet (2024).

				Area in km^2 (2019)			**Conservation status (2019)**		
ID		**Habitat name**	**Swedish name**	**ALP**	**BOR**	**CON**	**ALP**	**BOR**	**CON**
Coastal habitats									
1610		Baltic esker islands with sandy, rocky and shingle beach vegetation and sublittoral vegetation	Rullstensåsöar i Östersjön	-	55	-	-	U2	-
Sand dune habitats									
2170		Dunes with *Salix repens* ssp. argentea (*Salicion arenariae*)	Sandvidedyner	-	0.1	0.2		U2	U2
2180		Wooded dunes of the Atlantic, Continental and Boreal region	Trädklädda dyner	-	53	16	-	U2	U2
2190		Humid dune slacks	Dynvåtmarker	-	0.6	0.7	-	U2	U2
Freshwater habitats									
3210		Fennoscandian natural rivers	Större vattendrag	15	190	4.0	U1	U1	U1
Alpine habitat types									
4060		Alpine and boreal heaths	Alpina rishedar	18 500	300	-	FV	FV	-
4080		Sub-Arctic *Salix* spp. scrub	Alpina videbuskmarker	1 100	15	-	FV	FV	
6150		Siliceous alpine and boreal grasslands	Alpina silikatgräsmarker	4 450	75	-	FV	FV	
Grassland habitats									
5130		*Juniperus communis* formations on heaths or calcareous grasslands	Enbuskmarker	-	22	22	-	U2	U2
6450		Northern boreal alluvial meadows	Svämängar	30	20	-	U2	U2	
6530	P	Fennoscandian wooded meadows	Lövängar	-	17	0.1	-	U2	U2
9070		Fennoscandian wooded pastures	Trädklädd betesmark	33	650	65	U2	U2	U2
Wetland habitats									
7110	P	Active raised bogs	Högmossar	-	1 250	9.0	-	U1	U2
7120		Degraded raised bogs still capable of natural regeneration	Skadade högmossar	-	7	3.0	-	U2	U2
7230		Alkaline fens	Rikkärr	1 500	720	2.5	FV	U1	U2
7310	P	Aapamires	Aapamyrar	4 000	10 400	-	FV	U1	-
7320	P	Palsa mires	Palsmyrar	127	-	-	U2	-	-

				Area in km^2 (2019)			**Conservation status (2019)**		
ID		**Habitat name**	**Swedish name**	**ALP**	**BOR**	**CON**	**ALP**	**BOR**	**CON**
Forest habitats									
9010	P	Western taiga	Taiga	7 400	14 000	30	U1	U2	U2
9020	P	Fennoscandian hemiboreal natural old broad-leaved deciduous (*Quercus, Tilia*, *Acer, Fraxinus* or *Ulmus*) forests rich in epiphytes	Nordlig ädellövskog	-	60	10	-	U2	U2
9030	P	Natural forests of primary succession stages of landupheavel coast	Landhöjningsskog	-	170	-	-	U1	-
9040		Nordic subalpine/subarctic forests with *Betula pubescens* ssp. *czerepanovii*	Fjällbjörkskog	15 000	-	-	FV	-	-
9050		Fennoscandian herb-rich forests with *Picea abies*	Näringsrika granskogar	650	750	-	U1	U2	-
9060		Coniferous forests on, or connected to, glaciofluvial eskers	Åsbarrskog	-	60	-	-	U2	-
9080	P	Fennoscandian deciduous swamp woods	Lövsumpskog	-	230	60	-	U2	U2
9110		*Luzulo-Fagetum* beech forests	Näringsfattig bokskog	-	20	50	-	U1	U2
9130		*Asperulo-Fagetum* beech forests	Näringsrik bokskog	-	10	40	-	U2	U2
9160		Sub-Atlantic and medio-European oak or oak-hornbeam forests of the Carpinion betuli	Näringsrik ekskog	-	120	30	-	U2	U2
9180	P	*Tilio-Acerion* forests of slopes, screes and ravines	Ädellövskogsbranter	-	20	1.4	-	U2	U2
9190		Old acidophilous oak woods with *Quercus robur* on sandy plains	Näringsfattig ekskog	-	40	20	-	U1	U2
91D0	P	Bog woodland	Skogsbevuxen myr	2 000	20 000	150	FV	U1	U1
91E0	P	Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior*	Svämlövskog	10	40	10	U1	U2	U2
91F0		Riparian mixed forests of *Quercus robur*, *Ulmus laevis* and *Ulmus minor*, *Fraxinus excelsior* or *Fraxinus angustifolia*, along the great rivers	Svämädellövskog	-	8.0	0.4	-	U1	U2