

## **Sprucing up the UK's Sitka spruce (*Picea sitchensis*) forests: Can tree species diversification benefit biodiversity?**

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Sitka spruce (*Picea sitchensis* (Bong.) Carr.), is the most common tree species in UK's commercial forests. Tree species diversification of the UK's commercial forests is currently occurring to make them more resilient to new pests and pathogens and climate change. The potential ecosystem implications of this transition are poorly understood. Our aims are to, 1) list the biodiversity known to be supported by Sitka spruce as this has not been collated previously, and 2) assess the changes, in both ecosystem functioning and biodiversity supported, if Sitka spruce forests are diversified with any of 34 other tree species. Using records from across the UK, we identified 564 species that use the Sitka spruce trees as a living space or for feeding. Most of these associated species were non-specialist and found on a wide range of other trees. Data from an extensive literature review showed that diversification with broad-leaved trees would potentially result in faster nutrient cycling and litter decomposition with potential implications for

carbon storage in the litter layer. Diversification with Oak (*Quercus petraea/robur* (Matt.) Liebl.), sycamore (*Acer pseudoplatanus* L.), Scots pine (*Pinus sylvestris* L.), birch (*Betula pendula/pubescens* Roth), beech (*Fagus sylvatica* L.), and Norway spruce (*Picea abies* (L.) H. Karst.) provide the greatest biodiversity benefits both through supporting the biodiversity found on Sitka spruce and additional biodiversity thought to be absent on Sitka spruce. However, except for sycamore, none of these tree species will grow in long-term intimate mixed stands with Sitka spruce. Therefore, we propose that diversification of Sitka spruce plantations should be carried out as 'blocky mixes', i.e. small blocks of single tree species, with tree diversity occurring within a management unit, as a pragmatic approach to support timber production and provide biodiversity benefits. However, the optimal size and spatial arrangement of such blocks requires further assessment.

## Introduction

Sitka spruce (*Picea sitchensis* (Bong.) Carr.) while not native to the UK, is widely planted and the UK's most economically valuable tree species (Forestry Commission, 2014). Historically Sitka spruce was grown in monocultures for the sole purpose of timber production but recently there has been a change of paradigm in UK commercial forestry towards multipurpose forests for provision of other ecological services, such as amenity and biodiversity, in addition to timber. Superimposed on this is the need to manage commercial forests for the increased risk of novel pests and diseases and climate change (Atkinson et al., 2022). Sitka Spruce is at risk from the invasive bark beetle *Ips typographus* (Evans, 2021), which has recently been found in southern England (Inward et al., 2024), and is also vulnerable to drought, which is predicted to increase (Forestry Commission, 2017). One of the ways to meet multipurpose forestry objectives, and to make forests more resilient to threats, is diversification (Atkinson et al., 2022). This diversity can be incorporated at a range of spatial scales and can take the form of a more variable age structure, incorporation of more open spaces, inclusion of more tree species, and greater within species genetic diversity. This study focusses on tree species diversification, while acknowledging that species diversification may also result in structural and age diversification.

With unpredictable biotic and abiotic risks, increasing the diversity of tree species which are established spreads the risk load, since different tree species are likely to have different vulnerabilities to pests and pathogens, drought, frost, wind and wildfire (Atkinson et al., 2022). Thus, if one tree species declines in abundance others may survive ensuring a continued supply of timber alongside

additional or improved ecosystem services (Bradwell, 2021, Felton et al., 2021, Atkinson et al., 2022, Mason et al., 2022). For new plantations in the UK recent guidance has stipulated that in order to obtain grant support “a diverse species composition should be maintained across the forest management unit so that no more than 65% of the area is allocated to a single species” (Forestry Commission, 2023). In addition, the guidance stipulates that new planting should incorporate a minimum of 5% native broadleaved trees or shrubs, 10% other tree species and 10% open ground. This promotes the diversification of tree species.

Current guidance in the UK on diversification focusses on the silvicultural requirements of tree species mixes, with the main aim of timber production i.e., which tree species will grow together, given their shading tolerances and growth rates (Kerr et al., 2020). How tree species diversification influences forest biodiversity and ecosystem functioning is rarely assessed. Forest associated biodiversity is influenced by the tree species present, forest structure and age and site conditions (climate and soils). Here we focus on the changes in tree associated biodiversity and ecosystem functioning following tree species diversification, while acknowledging that these other factors will also influence the biodiversity present.

Tree species diversification may a) provide increased resilience for forest associated biodiversity through functional redundancy, whereby species supported by one tree species are also supported by one or more other tree species, and b) increase the biodiversity supported within the forest due to the greater range of tree species present as different trees will support different species. To assess how tree species diversification may impact the biodiversity of Sitka spruce forests one first needs to know what biodiversity is supported by Sitka spruce. This has not been collated previously, although the biodiversity value of even-aged plantation forests, often Sitka spruce forests, has been discussed (e.g. Quine and Humphrey, 2010, Quine, 2015). Earlier work studying the biodiversity of commercial forests in the UK has either focussed on specific sites (Humphrey et al., 2003a, Quine and Humphrey, 2010) or combined the biodiversity across several different production tree species (Confor, 2020, Barsoum et al., 2024). Thus, our first objective is to produce a list of the biodiversity supported by Sitka spruce within the UK. Our second objective is to assess the changes in biodiversity supported if Sitka spruce forests are diversified with any of 34 other tree species. Specifically: a) if these tree species also support the biodiversity supported by Sitka spruce, this is particularly important if any species are found to be tightly associated with Sitka spruce and b) what additional biodiversity that is not known to be supported by Sitka spruce would be supported by these tree species.

When tree species diversification occurs, we need to understand not only how this drives changes in above-ground biodiversity but also in below-ground functioning. While the objective of diversification may not be to maintain similar ecosystem functioning to that provided by Sitka spruce, it is important to be aware of how the functioning might change, and the consequences of these changes. The 'ecosystem function of a tree species' covers a wide range of processes. This study focused on functional characteristics and ecosystem processes related to decomposition and nutrient cycling which amongst other factors will influence soil carbon storage, often one of the objectives of a multipurpose forest, as more carbon is stored in forest soils than in the trees (Forest Research, 2023). Tree species differ in the chemical composition of their litter and root exudates, their mycorrhizal associations, how they influence the soil microbial community and their influence on other soil properties (e.g. Hobbie et al., 2006, Jacob et al., 2010, Marcos et al., 2010, Berger and Berger, 2012, Mitchell et al., 2016, Benavides et al., 2021), all of which will influence soil carbon. A range of studies have shown that soil carbon stocks differ between different tree species (Andivia et al., 2016, Cremer et al., 2016, Dawud et al., 2016, Steffens et al., 2022). Thus, our third objective was to assess what changes in ecosystem functions related to decomposition and nutrient turnover would occur if diversification with these 34 tree species occurred. We focussed on either direct measures of function (leaf litter decomposition) or related metrics (leaf litter chemistry and soil chemistry). For brevity, both types of measurement are called 'nutrient cycling' throughout.

## **Methods**

### *Assessment of species supported by Sitka spruce*

An extensive search of both published and grey literature, together with biological records data, was conducted in 2023/24 to identify as comprehensively as possible those species that use Sitka spruce in the UK and the nature of this association (termed Sitka spruce-associated species, shortened to SS-associated species throughout). We confined our searches to species that use Sitka spruce as a living space (e.g. epiphytes, or for roosting or breeding in), or for food, either directly eating the tree, or indirectly i.e. feeding on other species found within the tree. We did not include species that only used the wider forest habitat e.g. forest rides or glades or the forest ground flora. The data collation was confined to six taxon groups: birds, bryophytes, invertebrates, fungi, lichens (which were treated as a separate category from non-lichenised fungi), and mammals. Table S1 provides further taxon specific details of the data collation methods and Mitchell et al. (2024) lists all the data sources used. All data were collected under a pre-defined common structure to enable collation across taxon groups into a relational database called Sitka spruce Ecol (Mitchell et al., 2024). The level of association of each SS-associated species with Sitka spruce within the UK was classified as one of the following categories:

'obligate', 'high', 'partial', 'cosmopolitan' or 'uses' defined in Table 1. For fungi and lichens it was possible to define these categories based on the number of records of a species occurring on Sitka spruce compared to other substrates, using data contained within the Fungal Records Database of Britain and Ireland (FRDBI) and the British Lichen Society database (Table S1). Due to the large number of non-lichenised fungi which would be classified as 'cosmopolitan' or 'uses' detailed assessments for these fungi were not made and only 'obligate', 'high' and 'partial' non-lichenised fungi were included in the assessment (Table S1). For bryophytes, birds, invertebrates and mammals numerical occurrence data to assign a level of association was not available and the assessment was made based on the balance of information available in the literature (Table S1). For some species the level of association was only available at the tree genus level (i.e. '*Picea*') (Table 1). The quality of the data used to make the assessment of the level of association of the species with Sitka spruce was recorded with categories, based on whether the literature was peer-reviewed/the database quality controlled and if the data were from the UK or not (Table S2). Where the assessment was made based on multiple sources the quality of the data with the highest level of confidence or relevance to the UK was recorded.

Data on how the SS-associated species used the Sitka spruce tree (feeding directly, feeding indirectly or for use as living space), the part of the tree used (bark, dead wood-standing, dead wood-fallen, dead wood-on live tree, cones, needles, limbs/branches/twigs, roots, seeds, trunk), the age of tree used (seedling/sapling, pole, mature, veteran) and the type of forest structure in which the SS-associated species uses Sitka spruce trees (open or closed canopy) were collated where data was available (see Table S3 for further details and definitions). Information on the conservation status of SS-associated species was recorded, which was broadly grouped as to whether the species was known to have some form of conservation protection, as different taxon groups have different measures of conservation categorisation. Where relevant, according to taxon group, additional information was collated (Table S4) on the IUCN status of the species, if the species was on a UK Red Data book list, or on the priority species list of any of the four countries within the UK. Bird species were also recorded as red, amber or green according to the UK Birds of Conservation Concern list (Stanbury et al., 2021).

#### *Assessment of the biodiversity implications of tree species diversification of Sitka spruce-stands*

Thirty-four tree species (Table 2) were assessed for their potential to a) support the SS-associated species and b) support additional biodiversity not known to be supported by Sitka spruce. These 34 tree species were those recommended to grow in mixtures with Sitka spruce by Kerr et al. (2020), those listed as frequent in Stokes et al. (2023) summary of suitable alternatives to Sitka spruce (Stokes

et al., 2023, Table 5) and those listed as secondary species in Forest Development Types where Sitka spruce is a primary species (Haufe et al., 2021). The suitability of the 34 tree species to grow in a mix with Sitka spruce (Table 2) was based on their growth rate and shade tolerance and taken from Kerr et al. (2020). Kerr et al. (2020) ranked suitability from 1 to 4 where 1 = most compatible with Sitka spruce and in theory could be planted as intimate mixes; 2 = quite compatible mixture combinations that require some element of planting design to ensure the mixture is robust; 3 = the mixture can be robust if specific planting design features are followed; 4 = mixture combinations that are most incompatible, species can be grown in the same management unit but not in intimate mixes, a recommendation of a minimum area of 0.2 ha per species is given. These suitability scores refer to long-term robust mixtures i.e. mixes which will result in a long-term presence of both species on the site. Intimate mixtures of species with compatibility score 4 are possible but they will not persist in the long-term without management intervention due to the shading and growth rate of Sitka spruce.

For all non-obligate and non-parasitic SS-associated species the literature/databases were searched in the same manner as described above to collate evidence of whether the SS-associated species did or did not use these 34 alternative trees. The level of use of the alternative trees was categorised according to whether the species was known to use that tree, or just that genus of tree and if the species regularly used the tree or only rarely (Table 3). In addition, there were categories to record whether a SS-associated species was known not to use the tree in question, if information was unavailable or if only expert judgement drawing on ecological knowledge could be used (Table 3). Again, the quality of the data used to make the assessment (Table S2), and references used, were recorded (Mitchell et al., 2024).

In order to assess the additional biodiversity supported by these 34 tree species that is not known to be supported by Sitka spruce we used the databases OakEcol (Mitchell et al., 2019c, Mitchell et al., 2019b) and Scots Pine Ecol (Mitchell et al., 2025). These databases were constructed in a similar way to the Sitka spruce Ecol database described here but with a focus on the biodiversity found on the UK's native oak species (*Quercus petraea* (Matt.) Liebl. and *Quercus robur* (Matt.) Liebl) and Scots pine (*Pinus sylvestris* L.) and the potential of alternative tree species to support this biodiversity. Both these tree species host more species than Sitka spruce and many of the alternative tree species assessed for oak and Scots pine are also tree species assessed as alternatives in this study. We therefore used the data from OakEcol and Scots Pine Ecol to assess the additional biodiversity that could be hosted if Sitka spruce was planted in mixtures with the 34 alternative trees. In all cases species listed as 'obligate' on either Oak or Scots pine and parasitic species were not included in the assessment. Species were classed as using an alternative based on an optimistic assessment of use i.e. if the use of

the tree was recorded as Yes\_Species, Yes\_Genera, Rarely\_species, Rarely\_genera, or Probable. All 34 alternatives were included in the Scots pine Ecol database and 19 of them were also included in the OakEcol database. For the 19 alternatives present in both datasets, information on whether 2822 species that are not hosted by Sitka spruce would be hosted by these 19 tree species was available. For the remaining 15 tree species information was available on whether 1363 species that are not hosted by Sitka spruce would be hosted by these 15 tree species. We acknowledge this is not a complete assessment of the additional biodiversity supported by these 34 tree species, but given oak is thought to support a greater diversity of species compared to other tree species in the UK (Southwood, 1961, Mitchell et al., 2019a), it provides an approximation, given the limited data available.

*Assessment of how ecosystem functions related to decomposition and nutrient turnover will change with tree species diversification of Sitka spruce forests*

A literature review to identify the decomposition, leaf litter chemistry and soil chemistry of the 34 alternative tree species (Table 2) and Sitka spruce was carried out using key-word driven searches undertaken between June 2023 and March 2024 in Web of Knowledge (<http://wok.mimas.ac.uk/>). Two Boolean searches were conducted for each tree species (Table S5). For each search, the abstracts of all the extracted articles were read and, if the abstract referred to more than one of the 34 tree species, relevant data were extracted, with the aim of producing a matrix of functional data versus tree species for further analysis. The following chemical data were collated for the litter: C, C:N, C:P, Ca, K, Lignin, Lignin:N, Mg, N, P, N:P and for the soil: C, C:N, N. In addition, data on leaf litter decomposition rates and litter and soil pH were also collated. Insufficient information was available to complete the metric for 19 of the tree species, as data were missing for five or more of the variables, so the analysis was conducted on the remaining 15 alternative tree species, plus Sitka spruce (Table 2). As the data were collected in different units, they were first converted so that data for a given variable were in the same units. Decomposition data were all converted, where necessary, to provide values for the decomposition rate constant 'k'. The soil and litter chemistry data were converted into  $\text{mg g}^{-1}$  for concentrations and a log ratio for litter and soil chemical ratios.

In most cases there were multiple values for each tree species/variable combination obtained from different references. The mean value for each tree species-variable combination was calculated using a restricted maximum likelihood model (REML) using nlme (Pinheiro et al., 2018) in R with a fixed factor of tree species and a random factor of 'reference identity'. Means were extracted using the emmeans function (Lenth, 2019). If there were multiple study sites within one reference, then these

were nested within reference as a random factor. There were data for all 16 tree species by variable except for litter pH for Sitka spruce. The missMDA (Husson and Josse 2010) function was used to impute this missing value in the matrix. The matrix was then analysed using PCA in FactoMineR (Husson et al. 2011). All analyses were done in R version 4.4.1 (R Core Team, 2024).

## Results

### *The biodiversity supported by Sitka spruce in the UK*

In total 564 species were found to use Sitka spruce in the UK, composed of 12 birds, 147 bryophytes, 28 non-lichenised fungi, 123 invertebrates, 243 lichens and 11 mammals (Table 4). Initial analysis of the datasets revealed a further 418 fungi listed with Sitka spruce which would be classed as 'cosmopolitan' (Table S1), but it was beyond the scope of this project to scrutinise the entire fungal dataset. Of the 564 species only six are 'obligate', i.e., only found on Sitka spruce. In addition, there was one lichen species that was 'obligate' at the genus level in the UK (having been recorded on '*Picea*'). There were 12 'highly associated' species, composed of 11 fungi and 1 invertebrate species and 28 'partially associated' species. Most species (363) were categorised as 'cosmopolitan' or 'uses' in their level of association.

There was a high level of confidence and regional relevance concerning the level of association of species with Sitka spruce with 79% of the information coming from peer-reviewed data within the UK (Table S6). All the data for 'obligate', 'obligate\_genera', 'high' and 'partial\_genera' SS-associated species came from peer-reviewed data from the UK. For the 'partially associated' species 89% of the data came from peer-reviewed UK data.

Forty-nine of SS-associated species have some form of conservation categorisation, typically indicating that either their populations are small or that their populations are declining. However, none of these species are 'obligate' or 'highly associated' with Sitka spruce and only two of them are 'partially associated' with Sitka spruce, with a further two being 'partially associated' with spruce at the genus level.

### *How the biodiversity uses Sitka*

Most species (70%) use Sitka spruce as a habitat to occupy. The non-lichenised fungi and most of the invertebrates used Sitka spruce for feeding directly on, while birds and mammals used Sitka spruce mainly for feeding, either directly or indirectly with a few species using it to nest or roost in (Figure S1).

The tree bark and dead wood, particularly standing dead wood, were the parts of the tree most frequently used, especially by lichens. Most invertebrates used dead wood or needles, with some species using the bark, cones, limbs/branches/twigs, needles, roots, seeds or trunk. The birds used the live parts of the tree, particularly the limbs/branches/twigs, the needles, seeds and cones. Mammals mainly used the bark and the limbs/branches/twigs (Figure 1). Data on the age and the type of forest structure in which the species uses Sitka spruce trees was lacking for the majority of species with data only available for 122 species and 20 species respectively (Mitchell et al., 2024).

#### *Sitka spruce associated species supported through tree species diversification*

The most precautionary assessment of the potential of the alternative trees to support SS-associated species, uses only information where we know that the species will use that tree, i.e. Yes\_species. Oak, Scots pine, alder (*Alnus glutinosa* (L.) Gaertn), birch and beech (*Fagus sylvatica* L.) are the native trees that would support the greatest number (20-25%) of non-obligate and non-parasitic SS-associated species (Figure 2). Norway spruce (*Picea abies* (L.) H. Karst.), sycamore (*Acer pseudoplatanus* L.) and sweet chestnut (*Castanea sativa* Mill.) (12%) are the most suitable non-native trees hosting 12-19% of the species.

An optimistic assessment of a tree species potential to support SS-associated species is to include all data from Yes\_Species, Yes\_Genera, Rarely\_Species, Rarely\_Genera, and probable (Figure 2). For native trees this gives the same top five native alternative trees as the precautionary assessment (Scots pine, oak, birch, alder, beech), all supporting more than 59% of the SS-associated species. Norway spruce was the non-native tree supporting the greatest number of SS-associated species under these criteria (77%), followed by European larch (*Larix decidua* Mill) (56%), sycamore (56%), lodgepole pine (*Pinus contorta* Douglas) (53%), maritime pine (*Pinus pinaster* Aiton) (50%), radiata pine (*Pinus radiata* D.Don) (49%), Japanese larch (*Larix kaempferi* (Lamb.) Carr.) (53%), and sweet chestnut (42%).

Whether the tree species used in diversification supports the biodiversity found on Sitka spruce may only be considered important for those 40 species whose level of association with Sitka spruce was assessed as 'high' or 'partial', as such species, by definition do not use a wide range of other tree species. Under a precautionary method of assessment Norway spruce and Scots pine support the greatest number of this group of SS-associated species (20 and 13 species respectively) (Figure 3). Under an optimistic assessment Norway spruce supports 38 of these species while European silver fir (*Abies alba* Mill.), Lutz's spruce (*Picea x lutzii* Little), lodgepole pine, maritime pine, ponderosa pine (*Pinus ponderosa* Douglas ex C.Lawson), and radiata pine all support over 20 of these species.

With all the assessment approaches above, the suitability of these tree species to grow in long-term robust mixes with Sitka spruce (Figures 2 & 3) needs to be considered. Of the tree species identified under the different approaches sycamore is the most suitable (score of 1 on a scale of 1 to 4). Norway spruce, which supports the greatest number of 'high' and 'partially associated' SS-associated species has a score of 2, meaning it is a quite compatible mixture combination that require some elements of planting design to ensure the mixture is viable. European and Japanese larch, birch, and beech also have a suitability score of 2. Although oak supports the greatest number of SS-associated species, it is only suitable for growing with Sitka spruce if specific planting design features are followed (score of 3 on a scale of 1 to 4). Alder, Scots pine, lodgepole pine, maritime pine, radiata pine, ponderosa pine and sweet chestnut are all amongst the most unsuitable trees for creating intimate, robust long-term mixes with Sitka spruce (score 4), although they could be planted as blocks within the same management unit.

#### *The additional biodiversity supported due to tree species diversification.*

Species that grow well in mixtures with Sitka spruce do not necessarily host the greatest number of additional species, species not known to occur on Sitka spruce. Of the tree species most compatible in an intimate, robust long-term mixture with Sitka spruce (category 1, Figure 4) sycamore has the potential to bring the greatest additional biodiversity benefits supporting a further 646 species out of a total of 2822 assessed. Of the trees classed as quite compatible with Sitka spruce (category 2, Figure 4) birch and beech would bring the greatest biodiversity benefits, supporting 984 and 939 additional species, respectively, followed by aspen, small leaved lime, Norway spruce and large leaved lime with 540, 536, 536 and 480 additional species, respectively, out of 2822 assessed. Mixtures including oak would bring by far the greatest biodiversity benefits – an additional 2187 species supported (Figure 4). However, oak/Sitka mixtures are silviculturally demanding and oak will only grow in mixtures with Sitka spruce if specific planting design features are followed (see Kerr et al., 2020 for further details). Scots pine and alder will support 1313 and 721 additional species, respectively, out of 2822 assessed, and maritime pine and lodgepole pine will support an additional 732 and 727 species out of 1363 species assessed (category 3, Figure 4). These pine species and alder will only grow in the long-term with Sitka spruce within the same management unit but not in intimate mixes (Kerr et al., 2020).

#### *Changes in decomposition and nutrient turnover because of tree species diversification*

In total, 3155 data points from 154 references (Tables S7 and S8) were extracted for the 16 tree species and 17 variables related to decomposition and nutrient turnover for which data were available (Table 2). Analysis of the data by PCA showed that the first axis explained 48.14% of the variation in nutrient

cycling and the second axis 13.05%. Litter decomposition rate and litter N, Mg, pH, K and P together with soil pH were all positively correlated with the first axis (Figure 5). Litter C, C:N ratio, lignin and lignin:N together with soil C:N ratio and soil C were all negatively correlated with the first axis. The second axis was positively correlated with litter C:P ratio and N:P ratio and soil N. European silver fir, beech, and European larch were intermediate along the first axis and closest to Sitka spruce in ordination space (Figure 5) indicating that if the objective of diversification were to maintain similar nutrient cycling to that occurring under monocultures of Sitka spruce these tree species would be most suitable. Diversification with alder, birch (silver or downy), sycamore, small leaved lime or hornbeam would result in faster litter decomposition rates, litter with higher N, Mg, K and P content and litter and soil with higher pH compared to Sitka spruce, as these species occur at the positive end of the first ordination axis. Diversification with western red cedar, western hemlock, Scots pine and Douglas fir would result in slower decomposition rates and greater C in the litter and the soil, and higher litter and soil C:N ratios compared to Sitka spruce, as these species occur at the negative end of the first ordination axis (Figure 5).

## **Discussion**

This work has shown that diversification of the UK's Sitka spruce plantations may not only provide greater resilience for the 546 species associated with Sitka spruce but will also provide the potential for an overall increase in biodiversity. However, most of the tree species that would provide the greatest increase in biodiversity benefits will not grow in robust long-term intimate mixed stands with Sitka spruce due to the shade cast by Sitka spruce and its fast growth rate (Kerr et al., 2020).

### *The biodiversity found on Sitka spruce*

This work has for the first time tried to collate a list of the species that are known to use Sitka spruce in the UK. We show that Sitka spruce trees can support 546 species across a range of taxon groups, but supports considerably fewer species than native trees, with oak supporting 2300 species (Mitchell et al., 2019a) and ash (*Fraxinus excelsior* L.) 953 species (Mitchell et al., 2014). When considering the importance of Sitka spruce to support biodiversity, consideration needs to be given to not just the number of species that use Sitka spruce but also to their strength of association with Sitka spruce and their conservation status.

The community that uses Sitka spruce is largely composed of common species found on a wide range of other hosts/substrates. The exceptions were six species that are only found on Sitka spruce, that we suggest are non-natives. The Ragged Spruce Gall Adelgid (*Pineus similis*) (Gillette, 1907) was

introduced with Sitka spruce into the UK and the rest of Europe; in the USA, where it is native it has a few other hosts in addition to Sitka spruce, (Cumming, 1962). Our data also suggests that the five 'obligate' fungi *Bankera violascens*, *Endophragmiella resinae*, *Pseudophacidium piceae*, *Dendrostilbella smaragdina*, *Micraspis tetraspora* are also likely to be non-native given their strong association with Sitka spruce and rare occurrence on any other species. Data deficiency, however, is also a problem with these species, for example *Micraspis tetraspora* is only known from the UK type locality in a Sitka spruce forest. In addition, there was one lichen *Epigloea filifera* Döbbeler (1984) recorded as 'obligate' at the tree genus level, i.e. only from '*Picea*'. However, there is only one modern record of this lichen in the UK that had the necessary substratum information. It is a small, inconspicuous species that is expected to be under recorded, and in Europe it is known to grow on a much wider range of hosts. In terms of conservation importance only 49 of the species have some form of conservation designation, none of which appeared to be 'highly' associated with Sitka spruce, indicating that Sitka spruce does not play a pivotal role in their conservation.

In general, conifers are not considered very suitable substrates for bryophytes (Porley and Hodgetts, 2005). The species that are listed in this project as having been recorded growing on Sitka spruce nearly all have their primary substrate elsewhere. Thus, all the bryophytes except one are listed as 'cosmopolitan'. The exception to this is the green shield-moss (*Buxbaumia viridis* (Moug. ex DC.) Brid.) which is recorded as 'partially associated' with Sitka spruce and mostly occurs on dead fallen conifers rather than on living trees.

We listed 12 birds as having an association with Sitka spruce. The widespread planting of Sitka spruce plantations has been identified as the cause of population increases in the UK of some finches that primarily feed on tree seeds such as siskin (*Spinus spinus* Linnaeus), crossbill (*Loxia curvirostra* Linnaeus), parrot crossbill (*Loxia pytyopsittacus* Borkhausen) and Scottish crossbill (*Loxia scotica* Hartert). Several correlative studies show the importance of good Sitka spruce cone crops for breeding success and abundance for these species (Patterson et al., 1995, Watson et al., 2009, Dixon and Haffield, 2013, Furness and Furness, 2021). Increased cone crop and abundance of finches has been linked to increased breeding numbers and productivity of birds of prey, such as the sparrowhawk (*Accipiter nisus* (Linnaeus, 1758)) in spruce habitats (Petty et al., 1995). Other bird species, not on our list, may use the general habitat created by the spruce trees but we have not included them as they don't specifically use the trees, for example willow warblers (*Phylloscopus trochilus* (Linnaeus, 1758)) often nest on the ground within young Sitka spruce plantations, but are generally associated with willows and birch for foraging (Stostad and Menéndez, 2014).

The database from which the non-lichenised fungi data (FRDBI) were extracted records associations with fungal fruit bodies as the nearest living organism (Table S1). In mixed woodlands it is often impossible to be certain what the fungal fruit bodies are associated with. This could result in an over- or underestimation of the number of fungi associated with Sitka spruce, and it is not possible to estimate the error in the data due to this. At present, there are very few UK studies on fungal communities directly associated with Sitka spruce which have utilised molecular metabarcoding approaches to characterise the communities. These have focused on either needle endophytes (Stewart et al., 2019) or the ectomycorrhizal fungi associated with the roots of Sitka spruce (Palfner et al., 2005, O'Hanlon and Harrington, 2011, O'Hanlon and Harrington, 2012). These studies have found small numbers of taxa associated with Sitka spruce, supporting the conclusion from the FRDBI data that the fungal community associated with Sitka spruce is limited.

Both the lichen and the invertebrate data showed the general importance of dead wood for biodiversity. This has been noted previously as an important structural feature of conifer stands, including within the UK's native pine forests (Coppins and Coppins, 2006). However, in commercial plantations deadwood is usually removed to reduce the risk of disease spread and thus rarely found in large quantities. Mammals showed no particular association with Sitka spruce – all being assessed within the category “uses”.

Not all 546 species will be found on any one Sitka spruce tree or in any one forest, in part due to the different distributions of these species within the UK but also because different species will use different ages of trees and different forest structures. Tree age and forest structure are acknowledged as influencing the biodiversity present in forests (Hewson et al., 2011, Herbert et al., 2022, Neal et al., 2024). While data on the age of the tree used was lacking for many species in this study generally older trees, and in particular veteran trees, support more biodiversity, particularly specialist species (Humphrey et al., 2003b, Horák, 2017, Miklín et al., 2017). However, in the UK most Sitka spruce trees are harvested at around forty to sixty years old (Quine, 2015) and although the benefits of old growth Sitka spruce for biodiversity in the UK have been discussed (Humphrey, 2005) the majority of Sitka spruce trees never reach this age. Specifics on how SS-associated species are influenced by forest structure are lacking for many individual species but are known for birds where within both coniferous and deciduous forests an open canopy structure with multiple strata is known to support more key forest species (Hinsley et al., 2009, Broome et al., 2017). This is in contrast to the structure of most Sitka spruce plantations which are usually composed of a closed canopy with few strata (Quine, 2015) unless left to include old growth (Humphrey, 2005). Conversion to continuous cover forestry would change the structure of Sitka spruce plantations bringing potential biodiversity benefits to some taxon

groups (Deal et al., 2014, Calladine et al., 2015, Peura et al., 2018, Cook et al., 2023) and is being trialled in some areas in the UK (Mason, 2020, Kerr et al., 2021).

#### *Potential for increasing biodiversity supported in 'blocky' mixes*

The majority of Sitka spruce dominated forests were planted with the sole objective of timber production but the focus has since changed with a desire for multipurpose forests. As the realities of climate change and the potential of pests and diseases to impact Sitka spruce drive commercial forestry to consider both alternative tree species and tree species diversification, it is important to consider how such multi-purpose objectives can be achieved. Kerr et al. (2020) and Stokes et al. (2023) consider which tree species might grow well with Sitka spruce in the UK, but the biodiversity benefits of diversification are rarely considered. Our analysis has shown that diversification of Sitka spruce forests can in theory provide increased resilience for the biodiversity potentially found on Sitka spruce but can also support additional biodiversity not known to be found on Sitka spruce. However, the tree species that have the potential to support the greatest additional biodiversity do not grow well in long-term intimate mixes with Sitka spruce (Kerr et al., 2020). In the short-term intimate mixtures of species with compatibility score 4 are possible and may bring some biodiversity benefits in the short-term, but these will be transient if the alternative trees are shaded out after a couple of decades. Therefore, we propose that diversification in 'blocky mixes' i.e. blocks of single species, potentially following the minimum 0.2 ha size proposed by Kerr et al. (2020), with tree diversity occurring within a management unit, rather than within an intimate mixed stand, may be an appropriate way to achieve species diversification of Sitka spruce plantations.

Creating forest diversity as blocks within stands (blocky mixes) rather than as intimate mixtures within stands has also been proposed by Tew et al. (2022). It is a pragmatic way forward for forest managers seeking to provide biodiversity benefits, while supporting timber production and avoiding the disadvantages of intimate mixes. Blocky mixes reduce the risk of secondary species being shaded out over time (Haufe et al., 2021) and hence their biodiversity benefits declining with age. Blocks of single species make thinning and harvesting easier, and, if statutory plant health notices are issued, allow for removal of the trees in a more efficient and cost-effective manner than for intimate mixes. However, there may be disadvantages to this approach with respect to wind throw if one block is harvested or thinned before another and visually blocky mixes may not be as appealing as intimate species mixes, depending on their size and shape. In addition, this approach would lose any overyielding opportunities offered by intimate mixtures (Bradwell, 2021, Mason et al., 2022). The challenge from a biodiversity perspective is working out the best spatial pattern of such blocks. The resilience gained

for the associated biodiversity may be dependent on the planting design, (e.g. intimate mixtures, blocky mixes or larger blocks of monoculture), and the dispersal and colonisation rates of associated species. Modelling approaches may help here. From a production view-point, larger blocks may be considered optimal as they could be more cost-effective, whereas from a biodiversity view-point, smaller blocks might be preferable. Bibby et al. (1989) showed that in non-native conifer plantations there were more individual birds if broadleaved trees were dispersed throughout the conifers, rather than concentrated in fewer larger blocks.

This study focussed on the biodiversity implications of diversification of Sitka spruce but when considering tree species diversification other factors will also need to be considered. In particular, the pests and pathogens that may be hosted by the tree species being considered for diversification. In the UK larches are currently not considered a suitable species to plant in many areas due to the risk of *Phytophthora ramorum* (Jones and Wylder, 2012). Pine species are potentially at risk due to Dothistroma needle blight (*Dothistroma septosporum*) (Brown and Webber, 2008). Norway spruce is potentially at greater risk from *Ips typographus* and drought than Sitka spruce is (Evans, 2021). Therefore, careful consideration of the tree pests and diseases potentially hosted by the species used to diversify Sitka spruce is required.

Site specific diversification strategies will need to be developed that identify which of the alternative tree species are most appropriate at a site level. At some sites the combination of the growing conditions, soils and climate, and pest/pathogen risk may mean that few, or perhaps no, other commercial tree species will be appropriate. If the objective of tree species diversification is to maximize the biodiversity benefits, then which species are present within the local area should be considered as the biodiversity listed as “additional species” in this study will not be present at all sites. The data collated during this study and available within Mitchell et al. (2024) would allow selection of tree species targeted to support biodiversity present within the local area.

#### *Impact on nutrient cycling*

Tree species diversification will alter the ecosystem functioning of the forest which may impact, either positively or negatively, on the delivery of other multi-purpose benefits from the forest. Here, we only studied functions related to nutrient cycling with links to soil carbon storage but acknowledge that trees also offer a range of other ecosystem services, which will vary by species. This study showed that diversification with broad-leaved deciduous species, particularly birch, hornbeam, small-leaved lime, sycamore and common alder would result in faster nutrient cycling, with faster decomposition rates. This will result in less carbon being stored in the litter layer within the soil profile which may impact

on the delivery of carbon storage within the forest. However, carbon in the litter layer is particularly vulnerable to being lost through aeration or leaching if disturbed through clear felling (Tew et al., 2021). If the carbon is leached down the soil profile it may have greater longer-term storage, being less at risk from losses due to disturbance, such as clear-felling and fire.

Soil carbon storage may also change if the dominant mycorrhizal association changes from ectomycorrhizal (ECM) with Sitka spruce, to arbuscular mycorrhiza (AM) with species such as sycamore, cypress, cherry, redwoods, rowan or western red cedar (Table 1). Shifts in the dominant tree mycorrhizal association have been shown to be key in controlling root-derived soil C accumulation and hence soil C dynamics in forests (Averill et al., 2014, Brzostek et al., 2015, Keller et al., 2021). Root-derived C inputs are often equal to or greater than leaf litter inputs with these effects being additional to effects of net primary production, temperature, precipitation and soil clay content. However, the outcome can be either an increase or a decrease of soil C, with different studies showing conflicting results (Averill et al., 2014, Brzostek et al., 2015, Keller et al., 2021).

The magnitude of these changes in nutrient cycling and carbon storage within a forest is likely to depend on a range of interacting factors including the planting pattern, e.g. intimate mixes or blocks, the ratio of the different tree species within the mix and their relative growth rates. Our approach here was based on data within the literature and further experimental work is required to better understand how tree species diversification may drive changes in nutrient cycling and carbon storage.

## **Conclusion**

This study has shown how tree species diversification of Sitka spruce forests will lead to biodiversity benefits and changes in ecosystem functioning related to nutrient cycling, but that these changes are dependent on which tree species are included in the mix. Diversification with some broad-leaved deciduous species may result in faster decomposition rates and less carbon storage within the litter layer of the soil profile. The benefits of diversification to the biodiversity of Sitka spruce forests includes a) providing functional redundancy and increased resilience for the Sitka spruce-associated species that may be found there, particularly those that are 'highly' or 'partially associated' with Sitka spruce and b) by supporting a range of additional associated species that are not found on Sitka spruce. Our findings suggest that as most species that use Sitka spruce are common species that utilize a range of other tree species/substrates the greatest biodiversity benefits of tree species diversification at many sites are likely to be realised through the additional species supported rather than support of those species found on Sitka spruce. However, none of the tree species that would bring the greatest biodiversity benefits, except sycamore, will grow in long-term intimate mixes with

Sitka spruce. Therefore, we propose that diversification in ‘blocky mixes’ i.e. blocks of single species with tree diversity occurring within a management unit, rather than within a stand, is the most practical way forward if the aim is to support timber production and to provide biodiversity benefits. While these biodiversity benefits will depend on such factors as the ratio of the different tree species planted, the planting design, forest structure, site characteristics (climate and soils), and the biodiversity present in the local area, our results ultimately clearly show the overall benefits for biodiversity of diversification of Sitka plantations.

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### **Conflict of interest statement**

None declared

### **Data availability statement**

The data is available at the Environmental Information Data Centre: Mitchell, R.J.; Albon, S.D.; Bellamy, P.E.; Ellis, C.J.; Hodgetts, N.G.; Johnstone, C.; Stockan, J.A.; Taylor, A.F.S. (2024). Sitka spruce-associated biodiversity in the UK (Sitka spruce Ecol). NERC EDS Environmental Information Data Centre. <https://doi.org/10.5285/1ce52c10-e3ab-4996-b9b7-052c70b3c1ba>.

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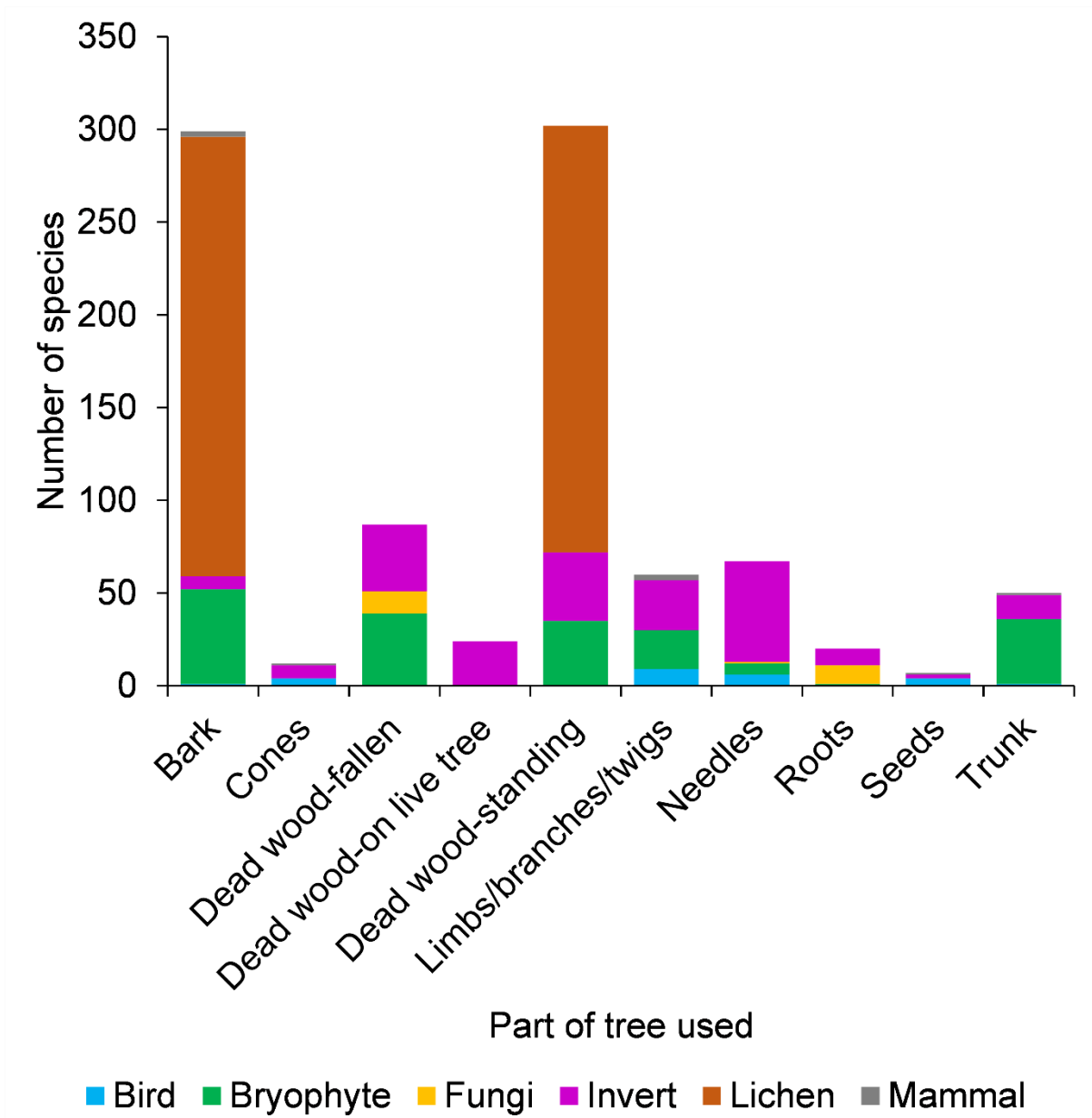
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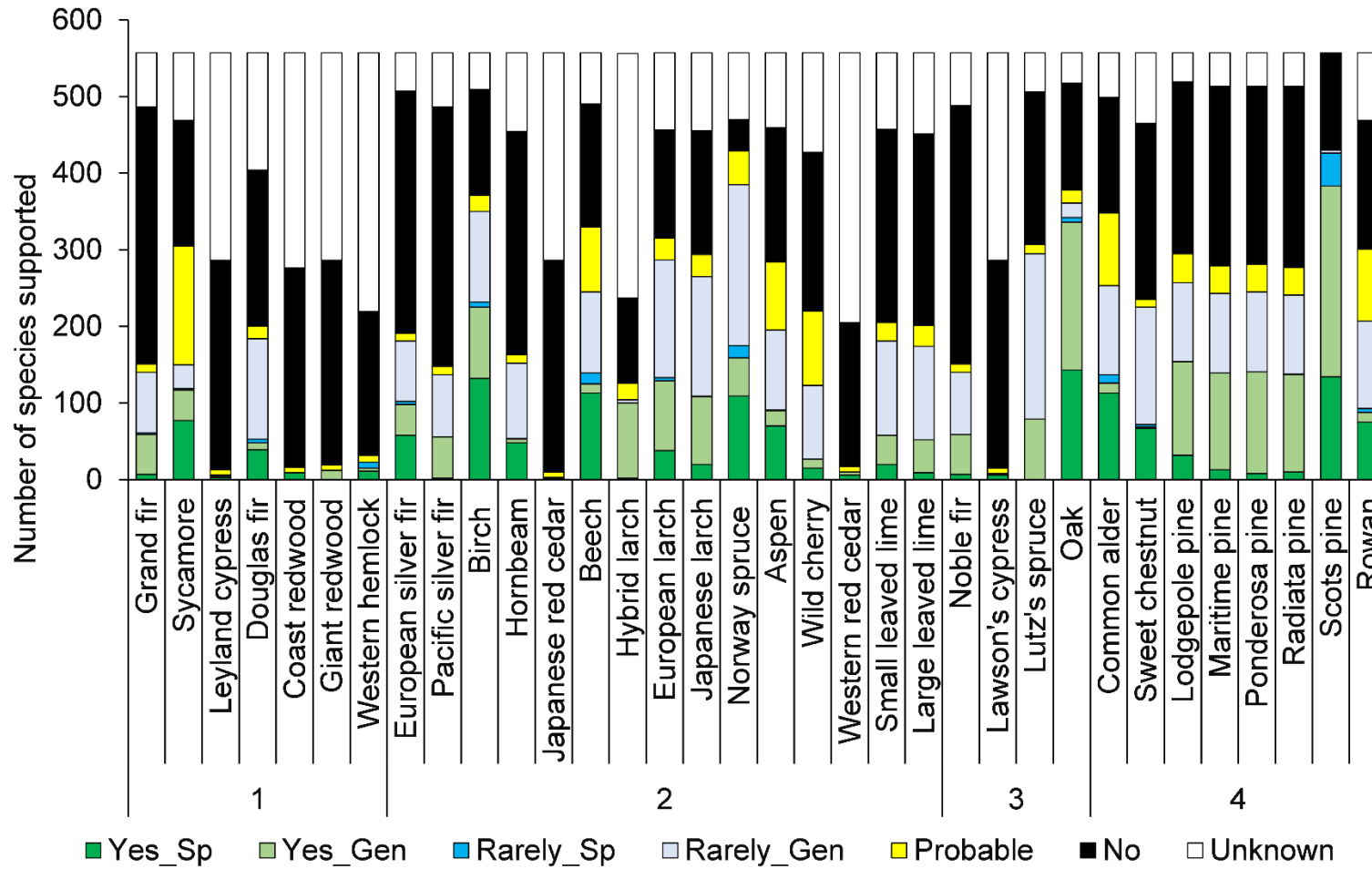
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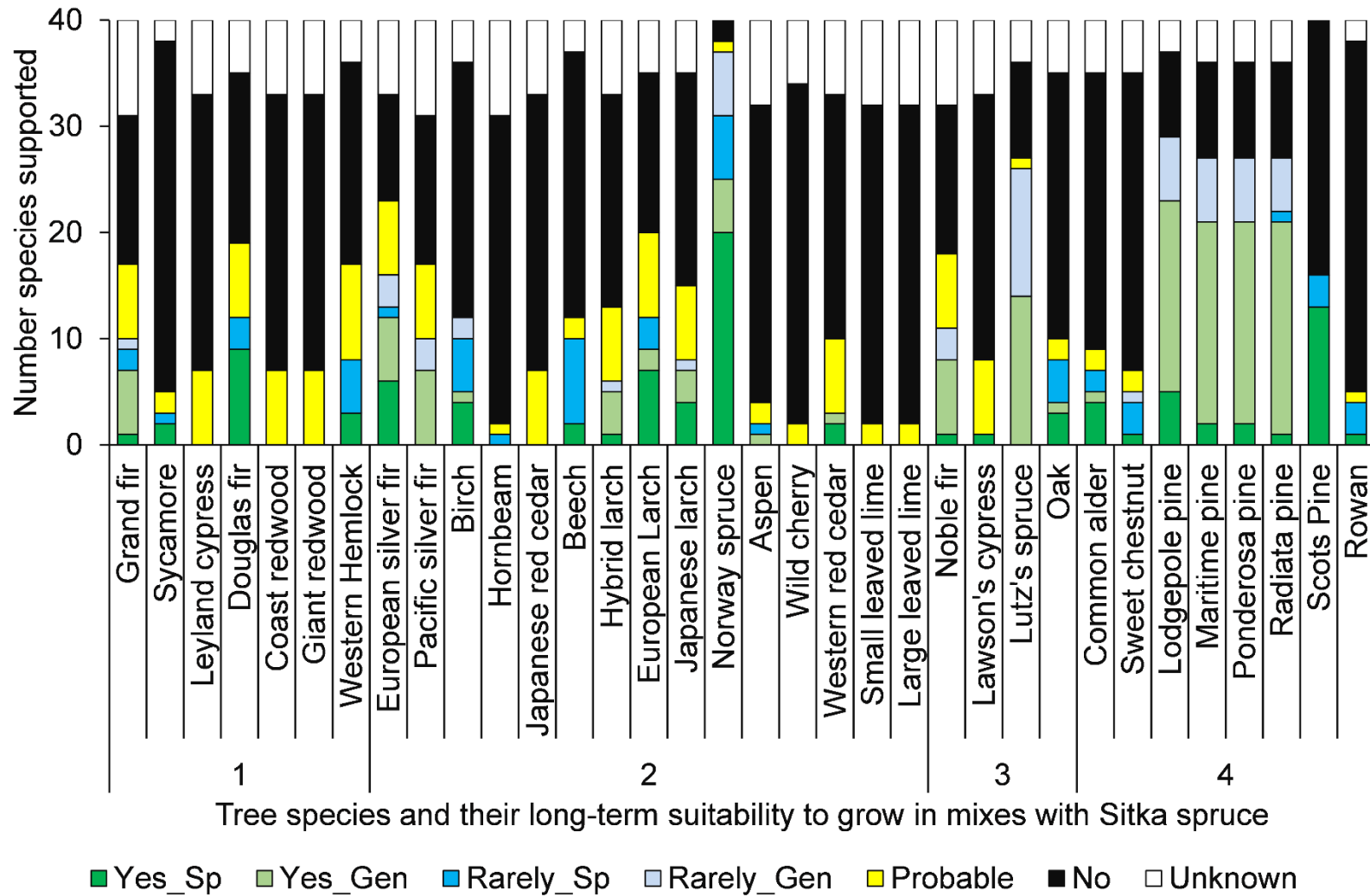


**Figure 1.** The part of the tree used by the 564 Sitka spruce-associated species.

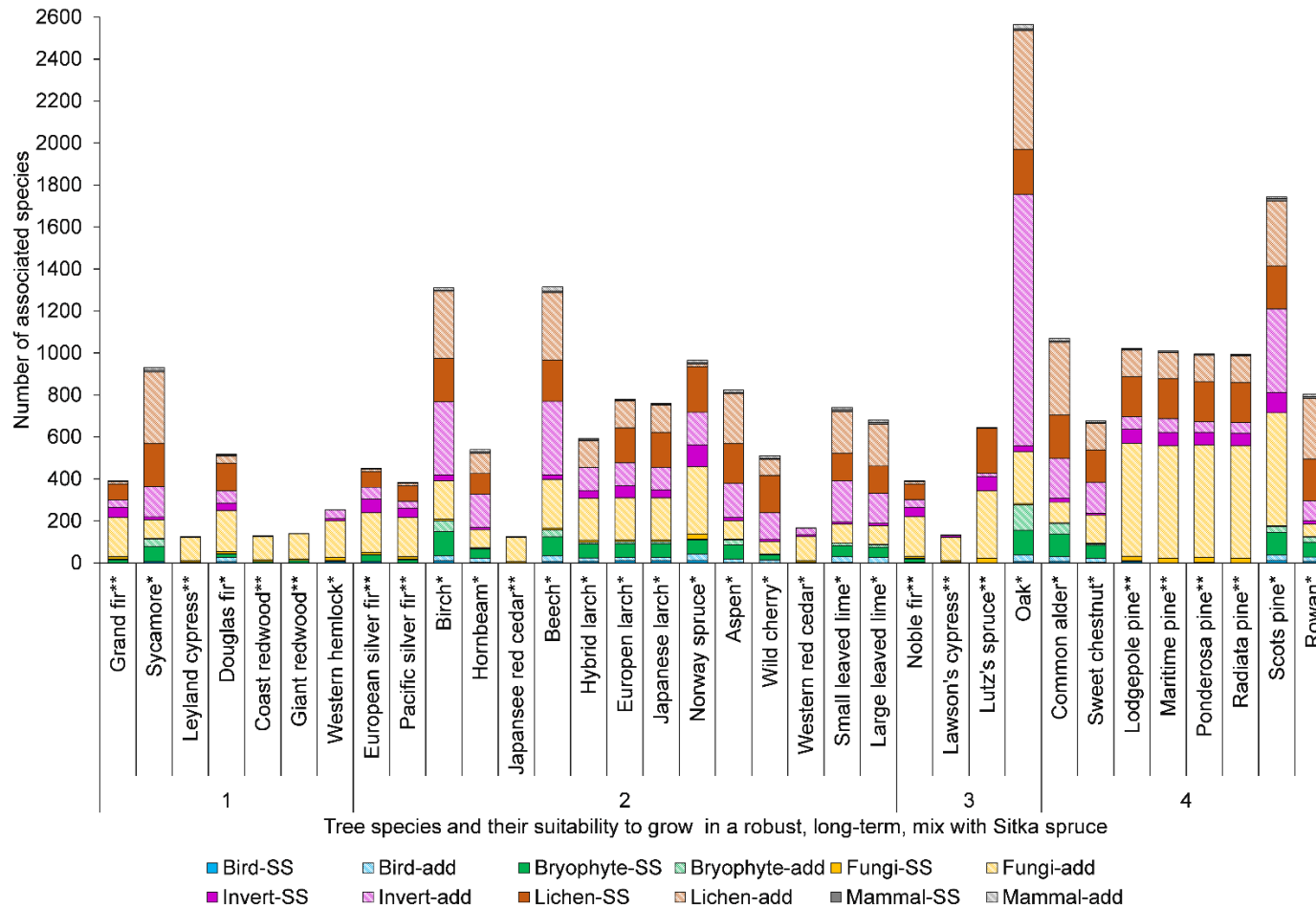


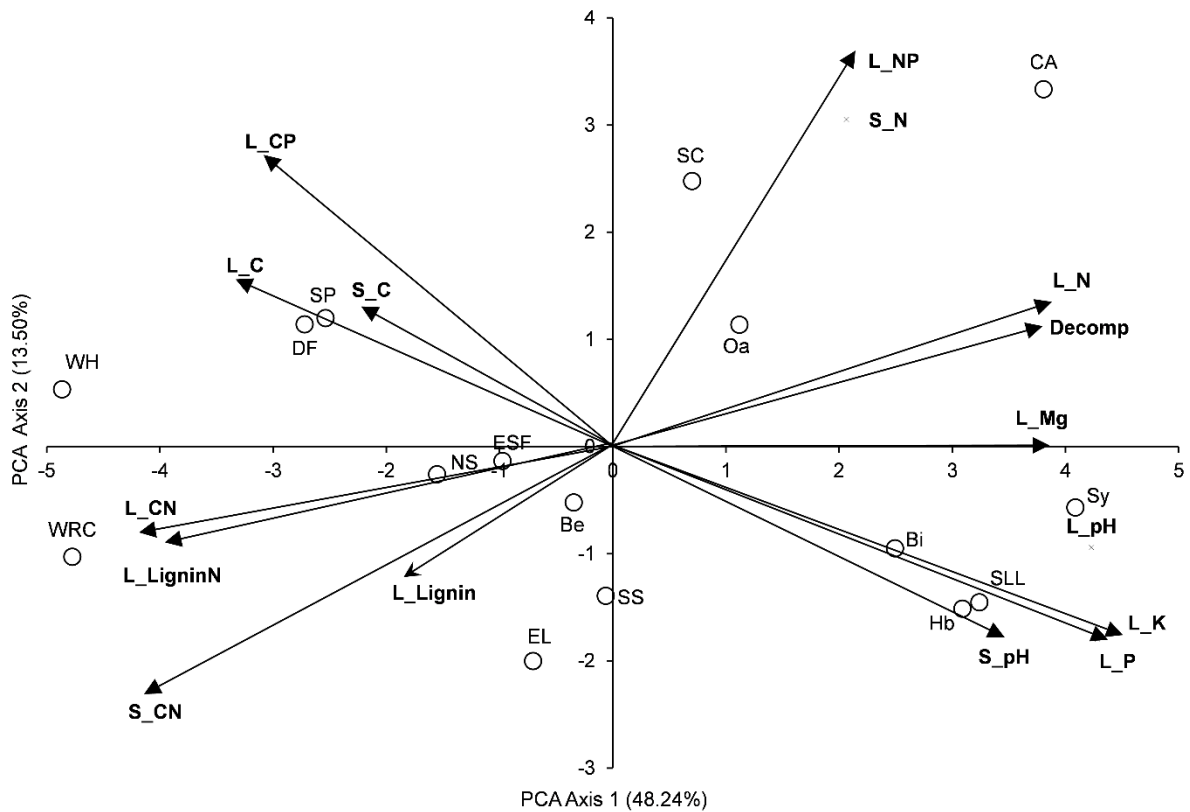
Tree species and their long-term suitability to grow in mixes with Sitka spruce

**Figure 2.** The number of Sitka spruce-associated species supported by other tree species that are suitable for growing in robust long-term mixes with Sitka spruce ranked 1 (high) to 4 (lower) taken from Kerr et al. (2020) see Table 2 for further details. See Table 3 for definitions of levels of association.



**Figure 3.** The number of high and partially associated Sitka spruce-associated species supported by other tree species that are suitable for growing in robust long-term mixes with Sitka spruce ranked 1 (high) to 4 (lower) taken from Kerr et al. (2020) see Table 2 for further details. See Table 3 for definitions of levels of association.





**Figure 5.** Biplot from PCA of analysis of trees (open circles) and their functions related to decomposition and nutrient cycling (arrows). L\_C = carbon content in litter, L\_CN = carbon to nitrogen ratio in litter, L\_Ca = calcium content in litter, L\_K = potassium content in litter, L\_Lignin = lignin content in litter, L\_LigninN = lignin to nitrogen ratio in litter, L\_Mg = magnesium content in litter, L\_N = nitrogen content in litter, L\_Na = sodium content in litter, L\_P = phosphorus content in litter, L\_pH = litter pH, S\_C = carbon content in soil, S\_CN = carbon to nitrogen ratio in soil, S\_N = nitrogen content in soil, S\_pH = soil pH, Decomp = Decomposition rate of litter. Be = beech, Bi = birch (silver & downy), CA = Common alder, DF = Douglas fir, EL = European larch, ESF = European silver fir, Hb = Hornbeam, NS = Norway spruce, Oa = Oak (pedunculate and sessile), SC = Sweet chestnut, SLL = Small leaved lime, SP = Scots pine, SS = Sitka spruce, Sy = Sycamore, WH = Western hemlock, WRC = Western red cedar.

**Table 1.** Criteria used to assess the level of association of biodiversity with Sitka spruce in the UK. This includes species dependent on other species that use Sitka spruce, such as parasites and some of the predatory insects.

Association with Sitka spruce in UK*	Definition**
Obligate	Unknown from other tree species/cannot complete its live cycle without using Sitka spruce.
High	Rarely uses other tree species
Partial	Uses Sitka spruce more frequently than its availability
Cosmopolitan	Uses Sitka spruce as frequently or lower than availability
Uses	Uses Sitka spruce but the importance of Sitka spruce for this species is unknown
Obligate_genera	Unknown from tree genera other than spruces/cannot complete its live cycle without using spruce but information not available about which spruce species is used.
High_genera	Rarely uses tree genera other than spruce but information not available about which spruce species is/are used.
Partial_genera	Uses spruce trees more frequently than their availability but information not available about which spruce species is/are used.
Cosmopolitan_genera	Uses spruce trees as frequently or lower than their availability but information not available about which spruce species is/are used.
Uses_genera	Uses spruce trees but the importance of the spruce for this species is unknown and information is not available about which spruce species is/are used.

\*NOTE: when dealing with parasites the following criteria were used: obligate host + obligate parasite = obligate; obligate host + parasite with multiple hosts = uses; highly associated host + obligate parasite = highly associated; highly associated host + parasite with multiple hosts = uses

\*\*For some taxon groups the level of association could be defined based on the number of records within taxon specific databases, see Table S1 for further information.

**Table 2.** Tree species assessed for their potential to host the biodiversity supported by Sitka spruce. The suitability of the tree species to grow in long-term robust mixes with Sitka spruce is taken from Kerr et al. (2020) where 1 = most compatible with Sitka spruce and 4 = mixture combinations that are most incompatible. The Forest Development Types are taken from Haufe et al. (2021) and are those where Sitka spruce is the primary species listed and the alternative tree assessed is listed as a secondary species. Additional species assessment is the number of species which don't use Sitka spruce but for which an assessment is available as to whether they will or will not use that tree species. Whether there was sufficient information in the literature to collate functional data is indicated as Y (yes) and N (no). The mycorrhizal association is given as ECM = Ectomycorrhiza and AM = arbuscular mycorrhiza.

Suitability in mix with Sitka spruce	English name*	Latin name and authority	Native to UK	Forest Development Type with Sitka Spruce	Additional species assessment	Functional information available	Mycorrhizae association
1	Grand fir	<i>Abies grandis</i> (Douglas ex D. Don) Lindley	No	1.1.5	1363	N	ECM
1	Sycamore	<i>Acer pseudoplatanus</i> L.	No	1.1.7	2822	Y	AM
1	Leyland cypress	<i>Cuprocyparis leylandii</i> A. B. Jacks. & Dallim.	No	1.1.5	1363	N	AM
1	Douglas fir	<i>Pseudotsuga menziesii</i> (Mirbel) Franco	No	1.1.3, 1.1.5	2822	Y	ECM
1	Coast redwood	<i>Sequoia sempervirens</i> (D. Don) Endl.	No	1.1.5	1363	N	AM
1	Giant redwood	<i>Sequoiadendron giganteum</i> (Lindl.) J. Buchh., 1939	No	1.1.5	1363	N	AM
1	Western hemlock	<i>Tsuga heterophylla</i> (Raf.) Sarg.	No	1.1.5	2822	Y	ECM
2	European silver fir	<i>Abies alba</i> Mill.	No	1.1.5	1363	Y	ECM
2	Pacific silver fir	<i>Abies amabilis</i> Douglas ex J. Forbes	No		1363	N	ECM
2	Birch (silver/downy)	<i>Betula pendula/pubescens</i> Roth	Yes	1.1.8	2822	Y	ECM
2	Hornbeam	<i>Carpinus betulus</i> L.	Yes	1.1.7	2822	Y	ECM
2	Japanese red cedar	<i>Cryptomeria japonica</i> (L.f.) D. Don	No	1.1.5	1363	N	AM
2	Beech	<i>Fagus sylvatica</i> L.	Yes	1.1.6	2822	Y	ECM
2	Hybrid larch	<i>Larix × marschlinsii</i>	No	1.1.4	2822	N	ECM
2	European larch	<i>Larix decidua</i> Mill	No	1.1.4	2822	Y	ECM

Suitability in mix with Sitka spruce	English name*	Latin name and authority	Native to UK	Forest Development Type with Sitka Spruce	Additional species assessment	Functional information available	Mycorrhizae association
2	Japanese larch	<i>Larix kaempferi</i> (Lamb.) Carr.	No	1.1.4	2822	N	ECM
2	Norway spruce	<i>Picea abies</i> (L.) H. Karst.	No	1.1.5	2822	Y	ECM
2	Aspen	<i>Populus tremula</i> L.	Yes	1.1.8	2822	N	AM & ECM
2	Wild cherry	<i>Prunus avium</i> L.	Yes	1.1.7	2822	N	AM
2	Western red cedar	<i>Thuja plicata</i> Donn ex D.Don	No	1.1.5	1363	Y	AM
2	Small leaved lime	<i>Tilia cordata</i> Mill.	Yes	1.1.7	2822	Y	ECM
2	Large leaved lime	<i>Tilia platyphyllos</i> Scop.	Yes	1.1.7	2822	N	ECM
3	Noble fir	<i>Abies procera</i> Rehder	No	1.1.5	1363	N	ECM
3	Lawson's cypress	<i>Chamaecyparis lawsoniana</i> (A.Murray bis) Parl.	No	1.1.5	1363	N	AM
3	Lutz's spruce	<i>Picea x lutzii</i> Little	No		1363	N	ECM
3	Oak (sessile/pedunculate)	<i>Quercus petraea/robur</i> (Matt.) Liebl.	Yes	1.1.7	2822	Y	ECM
4	Common alder	<i>Alnus glutinosa</i> (L.) Gaertn	Yes	1.1.7	2822	Y	ECM
4	Sweet chestnut	<i>Castanea sativa</i> Mill.	No	1.1.7	2822	Y	ECM
4	Lodgepole pine	<i>Pinus contorta</i> Douglas	No	1.1.4	1363	N	ECM
4	Maritime pine	<i>Pinus pinaster</i> Aiton	No	1.1.4	1363	N	ECM
4	Ponderosa pine	<i>Pinus ponderosa</i> Douglas ex C.Lawson	No	1.1.4	1363	N	ECM
4	Radiata pine	<i>Pinus radiata</i> D.Don	No	1.1.4	1363	N	ECM
4	Scots pine	<i>Pinus sylvestris</i> L.	Yes	1.1.4	2822	Y	ECM
4	Rowan	<i>Sorbus aucuparia</i> L.	Yes	1.1.8	2822	N	AM

\*The legislation with respect to which non-native tree species can be planted differs between the four countries within the UK. The inclusion of a species in this table does not imply that it can be legally planted and the relevant legislation should be checked.

**Table 3.** Definitions of criteria used to assess association of Sitka spruce-associated species with the 34 alternative tree species listed in Table 2.

Association	Definition
Yes_Sp	Known to use the alternative tree species.
Yes_Gen	No information on if it will use this species of tree but known to use the genera of the alternative tree species.
Rarely_Sp	The associated species has been recorded on this tree species but rarely, so unlikely to be a good alternative tree species
Rarely_Gen	No information on if it will use this species of tree but the associated species has occasionally been recorded on the genera of the alternative tree species. Unlikely to be a good alternative tree species
No	Not known to use this tree species
Parasite	Species is a parasite, so no assessment of alternative tree species made
Probable	Based on ecological knowledge of the species the associated species is thought likely or probable to use this tree species but there are no records of the species using this particular tree species. For example, the species is known to use a wide range of deciduous tree species, thus it is probable that it will also occur on other deciduous tree species, even if no records of its occurrence on this tree species exist.
Unknown	The use (or otherwise) of this tree is unknown

**Table 4.** The number of species in different taxon groups associated with Sitka spruce

Level of association with Sitka spruce*	Taxon group						Total
	Bird	Bryophyte	Fungi	Invertebrate	Lichen	Mammal	
Obligate			5	1			6
Obligate_genera					1		1
High			11	1			12
Partial	4	1	12	11			28
Partial_genera				3	151		154
Cosmopolitan	6	41		31			78
Cosmopolitan_genera		105		9	91		205
Uses	2			48		11	61
Uses_genera				19			19
Total	12	147	28	123	243	11	564

\*See Table 1 for definitions

**Table 5.** Number of species associated with Sitka spruce that have some form of conservation protection and their level of association with Sitka spruce.

Taxon group	Level association with Sitka Spruce	Number of species with some form of conservation protection
Bird	Cosmopolitan	2
Bird	Uses	2
Bryophyte	Partial	1
Invert	Cosmopolitan	9
Invert	Cosmopolitan_genera	4
Invert	Partial	5
Invert	Partial_genera	1
Invert	Uses	10
Invert	Uses_genera	6
Lichen	Partial_genera	2
Mammal	Uses	7
<b>Total</b>		<b>49</b>

# Supplementary material

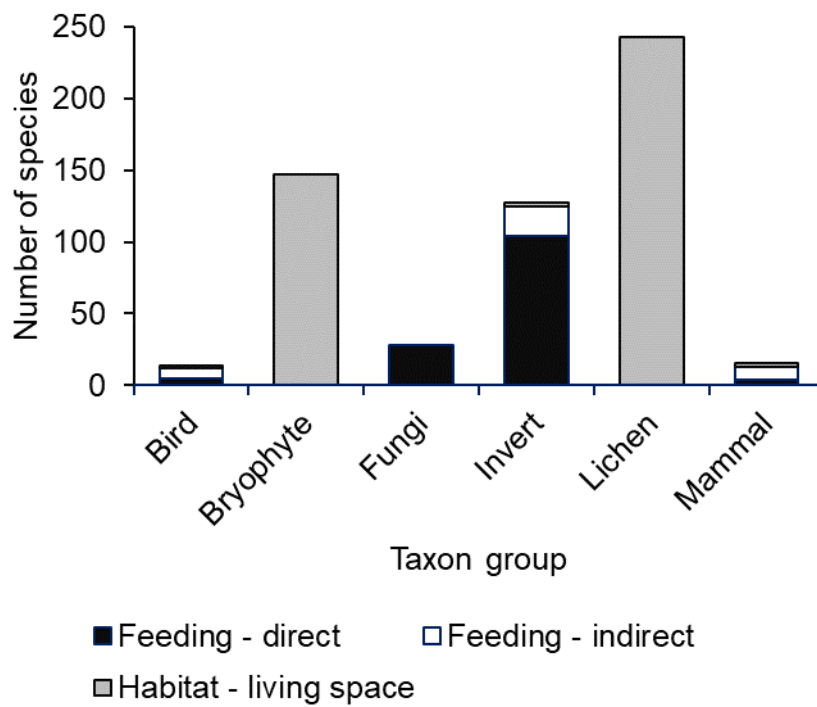


Figure S1. How the 564 species use Sitka spruce

Table S1. Methods used to assess level of species associated with Sitka spruce and alternative trees. For each species the reference used is listed in the SitkaEcol database.

Species group	Data sources and criteria used to assess association
Birds	<p>The assessment of birds associated with <i>Picea sitchensis</i> trees was primarily based on online searches of peer reviewed literature using Web of Science and Google scholar. Search terms used where the scientific name of the Tree species + Birds initially, then for birds associated with that tree further searches for the specific bird species were used to complete all the attributes for the species. Most assessments of level of association were based on studies that directly compared bird use of several tree species within a study. This was supplemented with published observational records of tree use. Further information was sought from unpublished reviews on the habitat associations and requirements for woodland birds. See Sitka spruceEcol data base (Mitchell et al 2024) for a complete list of references. The final list of species was checked against other studies of bird communities in Sitka spruce plantations to identify if there were species likely to be using the trees that were not included elsewhere.</p>
Bryophytes	<p>The British Bryological Society (BBS) records <a href="https://records.nbnatlas.org">https://records.nbnatlas.org</a> and the following references were the primary sources used: Frisvoll, Prestø (1997), Coote et al. (2008) Blockeel et al. (2014), Fudali (2012), Holyoak (2010), Brūmelis et al. (2017) with additional literature used for specific species. See Sitka spruce Ecol data base (Mitchell et al 2024) for a complete list of references.</p>

Species group	Data sources and criteria used to assess association
Fungi	<p>All assessments were made based on data held in the Fungal Records Database of Britain and Ireland (FRDBI). This database is held as two databases - pre and post 2016. Data from both databases were used. In total there were 41120000 records of which 2772000 records had data with an associated organism. The data were cleaned by CJ and AT. Detailed assessments of fungi were limited to those with &gt;30% of records associated with <i>Picea sitchensis</i>. Obligate species were defined as those with 90-100% of records with <i>Picea sitchensis</i>, a criterion of 100% was not used as the method used to record the associated organism within the FRDBI is to record the nearest organism to the fungus, this can result in many erroneous organisms being listed. Highly associated fungi were defined as those with 50-89% of their records associated with <i>Picea sitchensis</i>. Partially associated fungi were defined as those with 30-50% of their records associated with <i>Picea sitchensis</i>. Due to the large number of fungi (418) which would be classified as Cosmopolitan or Uses detailed assessments for these fungi were not made. There were a number of Sitka associated records in the database of ectomycorrhizal fungi known to be highly specific on other tree species: these were removed from the final dataset.</p>
Invertebrates	<p>The principal data sources used were: Ellis, W.N. (2023), Kimber, I. (2023) Dransfield, et al (2023) and references within them and Carter and Maslen (1982) Carter (1971) Clifton and Wheeler 2012, Chinery (2011) Emmet and Heath (1992), Roques (1983) with additional literature searches for specific species. See Sitka spruceEcol data base (Mitchell et al 2024) for a complete list of references.</p>

## Lichens

Data from the British Lichen Society database (1960-2022) was used to identify species associated with *Picea* sp. or spruce. All data was analysed at the genera level of tree host as the majority of host data within the database was recorded as spruce rather than individual species of spruce. Data on substrates was recorded in an inconsistent manner within the database. The data on substrates was cleaned and duplicate records removed by CJ and CE.

The number of times that each species had been recorded on spruce was calculated as a proportion of the total number of all records across all substrata (including corticolous, terricolous and saxicolous records, etc). The 'level of association' for a species was considered obligate if 100% of records were from *Picea*, high if >50% of records were from *Picea*, partial if >2.2% of records are from *Picea*, and cosmopolitan if the number of records from *Picea* trees <2.2%. The 2.2% threshold was calculated by dividing the summed number of records which are from spruce trees (for those species known to occur on spruce) by the summed total number of records for the lichen species across all substratum types.

For assessment of use of alternative trees: trees with fewer than 50 lichen records and lichen species with fewer than 50 records were excluded from analysis. A cluster analysis was performed to determine tree groupings for each tree species; hierarchical analysis was based on flexible beta-linkage ( $\beta = -0.25$ ) applied to a Bray-Curtis coefficient matrix, and with pruning to delimit clusters at a point where the recognition of indicator species is maximised (Dufrêne & Legendre, 1997), implemented using PC-Ord v. 7 (McCune & Mefford, 2018).

Alternative tree categories were assigned to each lichen species based on

1. - Lichen species must have 50 or more total records on tree species assigned to a Tree Genus.
2. Yes\_Gen = at least 10% of the records for this lichen species occur on this tree genus.
3. Probable = the tree genus occurs in a cluster from which at least 25% of the records of the lichen species occur.
4. Probable = at least 5% of the records for this lichen species occur on this tree genus AND the tree genus occurs in a cluster from which 20-25% of the records of the lichen species occur.
5. Rarely = the lichen occurs on the tree AND does not meet the criteria for Yes\_Gen or Probable.
6. Rarely = there is no record on this tree genus in the BLS database AND the tree genus occurs in a cluster from which 15-25% of the records of the lichen species occur.
7. No\_Gen = the lichen does not occur on the tree AND does not meet the criteria for Yes\_Gen, Probable, or Rarely.
8. Unknown = the lichen has <50 total records.

## Mammals

The handbook of British Mammals (Harris and Yalden, 2008). Retrieved from [http://books.google.co.uk/books?id=w\\_UJNAAACAAJ](http://books.google.co.uk/books?id=w_UJNAAACAAJ)

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Species group	Data sources and criteria used to assess association
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was used as the main information supplemented with additional literature searches for specific species (see SitkaEcol for details).

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Table S2. Definitions of criteria used to record the quality of the data used to make assessments of the level of association of species with Sitka spruce or any of the alternative tree species.

Data type	Definition
PR-UK	Information on the level of association between the species and the tree is predominantly based on peer reviewed literature or databases with some form of quality control using data from the UK.
PR-NonUK	This species is known to occur in the UK but information on the level of association between the species and the tree is predominantly based on peer reviewed literature or databases with some form of quality control but uses data from outside the UK.
NR-UK	Information on the level of association between the species and the tree is predominantly based on literature/databases that has a unknown review process but is based on UK data.
NR-NonUK	This species is known to occur in the UK but information on the level of association between the species and the tree is predominantly based on literature/databases that has a unknown review process and uses data from outside the UK.
Anecdotal	Information on the level of association between the species and the tree is predominantly based on anecdotal evidence.

Table S3. Definitions of criteria used to record how the Sitka spruce-associated species uses the tree, the part of the tree used, the age of tree used and the type of forest structure in which the species uses Sitka spruce trees.

Category	Definition
<u>Use of tree</u>	
Feeding - direct	The species eats part of the Sitka spruce (e.g. seeds, needles, wood, bark)
Feeding - indirect	The species eats another organism found on the Sitka Spruce
Habitat - living space	The species uses the Sitka Spruce as a habitat in which to live (e.g. epiphytes, bird nest holes etc.)
<u>Part of tree used</u>	
Bark	The species grows/lives/eats/otherwise uses the bark of Sitka spruce trees. This category was used for lichens/bryophytes that grow on the bark of the tree and birds that hunt for insects on the bark of the tree, for species that nest in holes in the trunk, trunk was used.
Dead wood-standing	The species grows/lives/eats/otherwise uses Sitka spruce standing dead wood
Dead wood-fallen	The species grows/lives/eats/otherwise uses fallen dead wood from Sitka spruce
Dead wood-on live tree	The species grows/lives/eats/otherwise uses dead wood on live Sitka Spruce trees
Cones	The species grows/lives/eats/otherwise uses the cones of Sitka spruce
Needles	The species grows/lives/eats/otherwise uses the needles of Sitka spruce
Limbs/branches/twigs	The species grows/lives/eats/otherwise uses the limbs/branches/twigs of Sitka spruce
Roots	The species grows/lives/eats/otherwise uses the roots of Sitka spruce
Seeds	The species grows/lives/eats/otherwise uses the seeds of Sitka spruce
Trunk	The species grows/lives/eats/otherwise uses the trunk of Sitka spruce trees. This was used for birds/mammals/invertebrates that live/breed inside holes in trees. Bark was used for lichens/bryophytes that grow on the bark of the tree.
<u>Age of tree used</u>	
Seedling/sapling	Species uses Sitka Spruce trees under 2m in height.
Pole	Species uses the pole stage Sitka Spruce trees which are defined as >2m height, younger than 50 years.
Mature	Species uses mature Sitka Spruce trees which are defined as more than 2m in height and under 3m in girth, don't have lots of holes, rotten wood etc - characteristics which are veteran tree characters
Veteran	Species uses Veteran Sitka Spruce trees which includes Veteran, Ancient and Notable trees: defined as large girth (usually over 3m, taking into consideration environmental conditions) with at least 3 veteran attributes (e.g. important habitats visible such as dead wood in the trunk, contain standing dead wood, have fallen wood around base, rot holes, water pockets, seepage lines, hollows in trunk or major limbs etc.).

Category	Definition
<u>The type of forest structure in which the species uses Sitka spruce trees</u>	
Dense low shrub layer	Low complex dense vegetation of shrubs and woody plant structures typically within 2 m of the ground.
Dense high shrub layer	Complex dense vegetation structures in the upper shrub layer typically 2–5 m above the ground.
Open understorey structure	Stands with no or little low shrub or woody vegetation (i.e. <5 m of the ground).
Open canopy structure	Woodland with significant gaps between the crowns of individual trees. Such trees may be open-grown with spreading canopies and often have relatively high amounts of dead/decaying wood.
Closed canopy - few strata	Stands where the canopy layer is relatively simple often associated with single-aged mid-growth phases.
Closed canopy - multiple strata	Stands where the canopy layer is relatively complex forming several foliage strata often associated with more mature growth phases. Multiple strata could be derived from mixtures of trees of different ages or from high canopy depth within individual trees.

Table S4. Definitions of criteria used to record the conservation status of the Sitka spruce-associated species within the SitkaEcol database

Measure	Category	Definition
Conservation status known	Known_protected	Species is listed as being of some conservation concern in one of Red data, IUCN, priority species list
	Known_unprotected	Species is known to be of no conservation concern
	Unknown	The distribution/population of the species is unknown and it is not known whether this species should be of conservation concern
Red data book	Endangered	
	Vulnerable	
	Rare	
	Out of danger	
	Endemic	
	Insufficiently Known	
	Nationally Notable	
IUCN	Endangered	A taxon is Endangered when the best available evidence indicates that it meets any of the criteria A to E for Endangered (see Section V), and it is therefore considered to be facing a very high risk of extinction in the wild.
	Vulnerable	A taxon is Vulnerable when the best available evidence indicates that it meets any of the criteria A to E for Vulnerable (see Section V), and it is therefore considered to be facing a high risk of extinction in the wild.
	Near Threatened	A taxon is Near Threatened when it has been evaluated against the criteria but does not qualify for Critically Endangered, Endangered or Vulnerable now, but is close to qualifying for or is likely to qualify for a threatened category in the near future.
	Least concern	A taxon is Least Concern when it has been evaluated against the criteria and does not qualify for Critically Endangered, Endangered, Vulnerable or Near Threatened. Widespread and abundant taxa are included in this category.
	Data deficient	A taxon is Data Deficient when there is inadequate information to make a direct, or indirect, assessment of its risk of extinction based on its distribution and/or population status.
BoCC5	Red	Birds of conservation concern - red listed <a href="https://www.bto.org/sites/default/files/publications/bocc-5-a5-4pp-single-pages.pdf">https://www.bto.org/sites/default/files/publications/bocc-5-a5-4pp-single-pages.pdf</a>
	Amber	Birds of conservation concern - amber listed <a href="https://www.bto.org/sites/default/files/publications/bocc-5-a5-4pp-single-pages.pdf">https://www.bto.org/sites/default/files/publications/bocc-5-a5-4pp-single-pages.pdf</a>

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	Green	Birds of conservation concern - green listed <a href="https://www.bto.org/sites/default/files/publications/bocc-5-a5-4pp-single-pages.pdf">https://www.bto.org/sites/default/files/publications/bocc-5-a5-4pp-single-pages.pdf</a>
Priority sp_England	Yes	Listed as a Priority species in England (species of principal importance) <a href="https://www.gov.uk/government/publications/habitats-and-species-of-principal-importance-in-england">https://www.gov.uk/government/publications/habitats-and-species-of-principal-importance-in-england</a>
	No	Not listed as a Priority species in England
Priority sp_Wales	Yes	Listed as a Priority species in Wales (Section 7 List) <a href="https://www.biodiversitywales.org.uk/Section-7">https://www.biodiversitywales.org.uk/Section-7</a>
	No	Not listed as a Priority species in Wales
Priority sp_NI	Yes	Listed as a Priority species in Northern Ireland <a href="http://www.habitas.org.uk/priority/types.asp">http://www.habitas.org.uk/priority/types.asp</a>
	No	Not listed as a Priority species in Northern Ireland
Priority sp_Scotland	Yes	Listed as a Priority species in Scotland (Scottish Biodiversity List) <a href="https://www.nature.scot/doc/scottish-biodiversity-list">https://www.nature.scot/doc/scottish-biodiversity-list</a>
	No	Not listed as a Priority species in Scotland

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Table S5. Boolean search strings used to search for literature containing information about the ecosystem functioning of Sitka spruce and alternative trees

Information searched for	Boolean search string
Carbon, nutrient cycling or nitrogen	<p>[Latin name of tree species] AND (carbon OR nutrient cycling OR nitrogen) AND</p> <p>([Abies alba] OR [Abies amabilis] OR [Abies grandis] OR [Abies procera] OR [Acer pseudoplatanus] OR [Alnus glutinosa] OR [Betula pendula] OR [Betula pubescens] [Carpinus betulus] OR [Castanea sativa] OR [Chamaecyparis lawsoniana] OR [Cryptomeria japonica] OR [Cuprocyparis leylandii] OR [Fagus sylvatica] OR [Larix marschlinii] OR [Larix decidua] OR [Larix kaempferi] OR [Picea abies] OR [Picea lutzii] OR [Pinus contorta] OR [Pinus pinaster] OR [Pinus ponderosa] OR [Pinus radiata] OR</p> <p>[Pinus sylvestris] OR [Populus tremula] OR [Prunus avium] OR [Pseudotsuga menziesii] OR [Quercus petraea] OR [Quercus robur] OR [Sequoia sempervirens] OR [Sequoiadendron giganteum] OR [Sorbus aucuparia] OR [Thuja plicata] OR [Tilia cordata] OR [Tilia platyphyllos] OR [Tsuga heterophylla])</p>
Litter chemistry and decomposition	<p>[Latin name of tree species] AND litter AND decomposition AND ([Abies alba] OR [Abies amabilis] OR [Abies grandis] OR [Abies procera] OR [Acer pseudoplatanus] OR [Alnus glutinosa] OR [Betula pendula] OR [Betula pubescens] [Carpinus betulus] OR [Castanea sativa] OR [Chamaecyparis lawsoniana] OR [Cryptomeria japonica] OR [Cuprocyparis leylandii] OR [Fagus sylvatica] OR [Larix marschlinii] OR [Larix decidua] OR [Larix kaempferi] OR [Picea abies] OR [Picea lutzii] OR [Pinus contorta] OR [Pinus pinaster] OR [Pinus ponderosa] OR [Pinus radiata] OR</p> <p>[Pinus sylvestris] OR [Populus tremula] OR [Prunus avium] OR [Pseudotsuga menziesii] OR [Quercus petraea] OR [Quercus robur] OR [Sequoia sempervirens] OR [Sequoiadendron giganteum] OR [Sorbus aucuparia] OR [Thuja plicata] OR [Tilia cordata] OR [Tilia platyphyllos] OR [Tsuga heterophylla])</p>

Table S6. The level of confidence of the association of the species with Sitka spruce. Data are percentage of species within each level of association with Sitka spruce.

Level of association with Sitka spruce*	Confidence in data**				
	Anecdotal	NR-NonUK	NR-UK	PR-NonUK	PR-UK
Obligate	0	0	0	0	100
Obligate_genera	0	0	0	0	100
High	0	0	0	0	100
Partial	0	0	3.6	7.1	89.3
Partial_genera	0	0	0	0	100
Cosmopolitan	1.3	1.3	2.6	17.9	76.9
Cosmopolitan_genera	7.8	0.4	0.4	27.8	63.4
Uses	1.6	3.3	11.5	9.8	73.8
Uses_genera	0	0	10.5	26.3	63.1

\*See Table 1 for definitions

\*\* See Table S2 for definitions

Table S7 Number of references obtained for each tree/function combination for the literature search on soil and litter properties.

Tree species	Decomposition rate	Litter												Soil			
		C	C:N	C:P	Ca	K	Lignin	Lignin:N	Mg	N	N:P	P	pH	C	C:N	N	pH
Beech	45	48	57	16	36	30	20	21	33	76	25	27	2	21	45	28	48
Birch Silver or Downy*	10	28	37	4	14	10	7	6	10	37	10	10	2	19	31	24	38
Common alder	9	6	13	8	7	6	5	3	6	14	12	12	1	11	25	14	25
Douglas fir	10	9	8	1	7	6	6	5	6	9	3	3	1	13	16	17	18
European Larch	2	3	3	1	2	2	2	1	2	3	1	2	2	9	10	12	14
European silver fir	3	3	3	1	2	2	2	1	2	4	1	2	2	12	12	12	12
Hornbeam	8	5	7	1	7	6	2	1	6	18	7	7	2	7	7	6	17
Norway spruce	10	28	32	2	17	12	9	7	14	42	8	8	3	12	25	19	33
Oak (sessile/pedunculate)*	39	43	57	15	27	24	17	16	23	60	26	26	2	27	48	28	43
Sweet chestnut	11	9	10	3	3	3	5	8	3	11	4	4	1	7	6	7	8
Small leaved lime	8	5	14	1	13	9	6	7	9	13	8	8	1	6	12	6	12
Scots pine	11	34	32	4	10	8	8	4	8	41	9	9	1	30	40	31	51
Sitka spruce	3	2	3	1	2	2	3	3	2	3	2	2		2	2	3	3
Sycamore	22	9	18	5	11	6	6	4	7	13	7	8	1	8	15	8	12
Western Hemlock	7	4	4	1	3	3	5	5	3	10	3	3	1	4	4	5	5
Western red cedar	1	4	4	1	3	3	4	4	3	10	3	3	1	4	4	5	5

Data for silver birch (*Betula pendula* Roth) and downy birch (*B. pubescens* Roth) were combined, and data for sessile oak (*Quercus petraea* (Matt.) Liebl.) and pedunculate oak (*Quercus robur* (Matt.) Liebl.) were combined to match the taxonomic level at which the species use data was recorded.

Table S8 List of all references used in collating data on tree soil and litter properties and number of data points from each reference/ecosystem function combination.

	Litter													Soil			
	Decomposition _rate	LitterC	LitterC.N	LitterC.P	LitterCa	LitterK	LitterLignin	LitterLignin.N	LitterMg	LitterN	LitterN.P	LitterP	LitterpH	SoilC	SoilC.N	SoilN	SoilpH
Albers et al. (2004)	2																
Al-Maliki et al. (2017)			3				3	3		3	3	3		3			
Alonso et al. (2022)			2	2						2	2	2					
Anderson (1973)	12																
Andivia et al. (2016)		2	2							2				2	2	2	
Ardanuy et al. (2021)														3	3	3	
Aubert et al. (2010)		2	2							2							
Augusto et al. (1998)			2														
Ayres et al. (2006)	5																
Bayranvand et al. (2017)														2	2	1	2
Benavides et al. (2021)		102	102							102							
Benito-Carnero et al. (2021)		6	6				6			6							
Berger and Berger (2012)	2				4	4	4	4	4	4	4	4					
Berger and Berger (2014)	2				4		4	4	4	4							
Bjornlund and Christensen (2005)	4																
Blonska et al. (2016)														8	8	1	8

	Litter											Soil					
	Decomposition _rate	LitterC	LitterC.N	LitterC.P	LitterCa	LitterK	LitterLignin	LitterLignin.N	LitterMg	LitterN	LitterN.P	LitterP	LitterpH	SoilC	SoilC.N	SoilN	SoilpH
Blonska et al. (2017)														20	20	20	20
Blonska et al. (2021)		3	3	3	3	3			3	3	3	3					
Bluhm et al. (2019)			2							2							
Bolat and Sensoy (2019)														2	2	2	2
Borowik et al. (2022)																5	5
Brandtberg and Lundkvist (2004)			2		2	2			2								
Carnol and Bazgir (2013)			5		5	5			5	5					5		5
Carnol and Bazgir (2013)			5		5	5			5	5							
Castro-Díez et al. (2012)	1	4												4			
Cesarz et al. (2016)		3	3	3	3				3	3	3	3					
Chigineva et al. (2009)	3																
Chodak et al. (2015)																3	6
Chodak et al. (2021)														3	3	3	3
Chodak et al. (2022)															3	3	3
Chodak et al. (2023)		3	3	3						3	3	3		3	3	6	
Chodak and Niklinska (2010)																3	3
Cools et al. (2014)			4												4		
Cortez (1998)	6																

	Litter												Soil				
	Decomposition _rate	LitterC	LitterC.N	LitterC.P	LitterCa	LitterK	LitterLignin	LitterLignin.N	LitterMg	LitterN	LitterN.P	LitterP	LitterpH	SoilC	SoilC.N	SoilN	SoilpH
Cortez et al. (1996)	3		3					3		3							
Cotrufo et al. (1994)	6	3	3	3	3	3	3	3	3	3	2	3					
Cotrufo et al. (1998)	3																
Cremer et al. (2016)															9	9	
Cremer and Prietzel (2017)					6	6			6								6
Cukor et al. (2022)														10	10	10	10
Dawud et al. (2017)															2		2
De Santo et al. (2009)					2		2	2		2							
Don and Kalbitz (2005)	4																
Enez et al. (2016)		2	2				2	2		2							
Ferreira et al. (2012)							3	3		3	3	3					
Fonseca and de Figueiredo (2018)		2	2							2							
Froberg et al. (2011)																	3
Frouz et al. (2015)			2														
Frouz et al. (2020)			2											2	2		
Gao et al. (2023)														6	6	6	6
Gartzia-Bengoetxea et al. (2016)		2	2	2	2	2	2	2	2	2	2	2			2	2	2
Graca and Poquet (2014)							2	2		2	2	2					

	Litter												Soil				
	Decomposition _rate	LitterC	LitterC.N	LitterC.P	LitterCa	LitterK	LitterLignin	LitterLignin.N	LitterMg	LitterN	LitterN.P	LitterP	LitterpH	SoilC	SoilC.N	SoilN	SoilpH
Gurmesa et al. (2013)															3		
Hagen-Thorn et al. (2004)														4	4	4	8
Hatcher (1990)										16							
Herrmann and Bauhus (2013)							11										
Hobbie et al. (2006)	22	11	11		11	11			11	11	11	11					
Holos et al. (2022)																	2
Horodecki et al. (2019)	5	5		5	5	5			5	5	5	5			4	4	4
Horodecki and Jagodzinski (2017)	6	6		6	6	6			6	6	6	6					4
Horodecki and Jagodzinski (2019)	16																
Howard et al. (1998)														5	5	5	5
Jacob et al. (2009)	9		4		4	4			4	4	4	4					
Jacob et al. (2010)	6																
Jagodzinski et al. (2018)															4		4
Jílková et al. (2020)			2												4		2
Johansson (1995)					2	2			2	2	2	2					
Jonard et al. (2008)	2																
Jones et al. (2019)		2	2							2			2				
Kalbitz et al. (2006)	4		4				4										

	Litter													Soil			
	Decomposition _rate	LitterC	LitterC.N	LitterC.P	LitterCa	LitterK	LitterLignin	LitterLignin.N	LitterMg	LitterN	LitterN.P	LitterP	LitterpH	SoilC	SoilC.N	SoilN	SoilpH
Kamczyc et al. (2019)	7																
Kavvadias et al. (2001)																2	2
Keenan et al. (1995)										2	2	2					
Keenan et al. (1996)		2					2	2		2							
Kiikkila et al. (2012)		2	2							2							
Klopatek (2008)	12	2	2				2	2		2							
Klotzbucher et al. (2011)		4	4														
Kooijman (2010)																	4
Kooijman and Martinez-Hernandez (2009)										14							14
Ladegaard-Pedersen et al. (2005)															4		
Langenbruch et al. (2012)		2	3		2			2	2	2					2		2
Larranaga et al. (2020)			3	3													
Lasota et al. (2022)													2				
Likus-Cieslik et al. (2023)														2	2	2	2
Liu et al. (2016)		3		3						3	3	3					
Lorenz et al. (2004)	4		2							2	2	2					
Lorenz and Thiele-Bruhn (2019)														4	4	4	4
Ludley et al. (2009)	3																

	Litter												Soil			
Decomposition _rate	LitterC	LitterC.N	LitterC.P	LitterCa	LitterK	LitterLignin	LitterLignin.N	LitterMg	LitterN	LitterN.P	LitterP	LitterpH	SoilC	SoilC.N	SoilN	SoilpH
Madureira and Ferreira (2022)	2	2	2			2			2	2	2					
Malchair and Carnol (2009)														12	12	24
Marcos et al. (2010)													2			3
Marsalkiene and Nikolajeva (2020)	3	3		3		3	3		3			3				
McTiernan et al. (1997)				5	5			5	5	5	5					
Mitchell et al. (2021)													10	10	10	10
Neiryneck et al. (2000)													6	12	6	
Norden (1994)				17	17			17	17	10	10					
Nunes et al. (2011)															2	2
Oostra et al. (2006)													4	4	1	4
Oulehle et al. (2016)	2	2							2				2	2	2	
Petrillo et al. (2016)	2	2	2	2	2	2	2	2	2		2	2				
Petritan et al. (2010)									2							
Prescott (1995)						2										
Prescott et al. (2000)	3		4	4	4	4	4	4	4	4	4				4	4
Prescott and Preston (1994)	3	3	3	3	3	3	5	3	3	3	3		3	3	3	3
Priha and Smolander (1999)														6		6
Rajapaksha et al. (2013)		2		3					3	3	3					

	Litter												Soil				
	Decomposition _rate	LitterC	LitterC.N	LitterC.P	LitterCa	LitterK	LitterLignin	LitterLignin.N	LitterMg	LitterN	LitterN.P	LitterP	LitterpH	SoilC	SoilC.N	SoilN	SoilpH
Rawlik et al. (2019)														2			2
Rawlik et al. (2021)														2			5
Reich et al. (2005)					9		9	9		9							
Ribbons et al. (2016)														8	8	8	8
Ribbons et al. (2022)														6	6	6	6
Riutta et al. (2012)	4																
Roeder and Meyer (2022)	6																
Rubio-Ríos et al. (2021)		2	2	2	2	2	2		2	2	2	2					
Rutigliano et al. (1996)							2	2		2							
Rutigliano et al. (1998)		2	2	2	2	2			2	2		2					
Sariyildiz (2008)	8	2	2							2							
Sariyildiz and Anderson (2003a)	2	6	6					6		6							
Sariyildiz and Anderson (2003b)	4																
Sariyildiz and Anderson (2005)		11	11	11	11	11	11	11	11	11	11	11					
Schadler and Brandl (2005)	8																
Schelfhout et al. (2017)		5	5	5	5		5	5		5	5	5					5
Schmidt et al. (2015)																	4
Schmidt et al. (2016)			4			4				4	4	4			4		
Schulp et al. (2008)		4												4			

	Litter												Soil				
	Decomposition _rate	LitterC	LitterC.N	LitterC.P	LitterCa	LitterK	LitterLignin	LitterLignin.N	LitterMg	LitterN	LitterN.P	LitterP	LitterpH	SoilC	SoilC.N	SoilN	SoilpH
Setiawan et al. (2016)			5		5	5	5	5	5	5	5	5					
Skorupski et al. (2012)		3	3							3							
Slade and Riutta (2012)	6																
Smolander et al. (2005)													2	2	2	2	
Spasic et al. (2023)													11	11	11	11	
Spulak et al. (2023)				2	2	2			2	2	2	2	2	2	2	2	2
Stasiov et al. (2012)		6	6							6			6	6	5	6	6
Stasiov et al. (2021)		3	3							3			3				3
Stefanowicz et al. (2021)													11	11	11	11	
Steffens et al. (2022)					5		5	5						12			5
Straigyte et al. (2009)	2																
Swiatek and Pietrzykowski (2021)													18	18	18	18	
Tiunov (2009)	4																
Turner et al. (1993)		3	3		3	3			3	3			3	3	3	3	3
Ukonmaanaho et al. (2008)					2	2			2	2	2	2					
Vacek et al. (2021)																	4
Vacek et al. (2022)																	4
Vaidelys et al. (2020)			20														

	Litter												Soil				
	Decomposition _rate	LitterC	LitterC.N	LitterC.P	LitterCa	LitterK	LitterLignin	LitterLignin.N	LitterMg	LitterN	LitterN.P	LitterP	LitterpH	SoilC	SoilC.N	SoilN	SoilpH
van Huysen et al. (2013)		2	2				2	2		2							
Varnagiryte et al. (2005)					3	3			3	3	3	3					
Vesterdal et al. (2008)			3												3		
Vesterdal et al. (2012)					3	3		3	3	3	3	3					
Wang et al. (2021)		3	3	3	3	3			3	3	3	3					
Warlo et al. (2019)														4	4	4	4
Wos et al. (2018)															8	8	8
Wos et al. (2023)															18		18
Yang et al. (2019)	3	3	3		3	3			3	3							
Zheng et al. (2022)															10		10
Zhong and Makeschin (2004)															6	6	6

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