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RESEARCH ARTICLE

The European Forest Plant Species List (EuForPlant): Concept and applications

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Abstract

Question: When evaluating forests in terms of their biodiversity, distinctiveness and naturalness, the affinity of the constituent species to forests is a crucial parameter. Here we ask to what extent are vascular plant species associated with forests, and does species' affinity to forests vary between European regions?

Location: Temperate and boreal forest biome of Northwestern and Central Europe.

Methods: We compiled EuForPlant, a new extensive list of forest vascular plant species in 24 regions spread across 13 European countries using vegetation databases and expert knowledge. Species were region-specifically classified into four categories reflecting the degree of their affinity to forest habitats: 1.1, species of forest interiors; 1.2, species of forest edges and forest openings; 2.1, species that can be found in forest as well as open vegetation; and 2.2, species that can be found partly in forest, but mainly in open vegetation. An additional "O" category was distinguished, covering species typical for non-forest vegetation.

Results: EuForPlant comprises 1,726 species, including 1,437 herb-layer species, 159 shrubs, 107 trees, 19 lianas and 4 epiphytic parasites. Across regions, generalist forest species (with 450 and 777 species classified as 2.1 and 2.2, respectively) significantly outnumbered specialist forest species (with 250 and 137 species classified as 1.1 and 1.2, respectively). Even though the degree of shifting between the categories of forest affinity among regions was relatively low (on average, 17.5%), about one-third of the forest species (especially 1.2 and 2.2) swapped categories in at least one of the study regions.

Conclusions: The proposed list can be used widely in vegetation science and global change ecology related to forest biodiversity and community dynamics. Shifting of forest affinity among regions emphasizes the importance of a continental-scale forest plant species list with regional specificity.

KEYWORDS
biogeographical regions, boreal zone, expert knowledge, forest affinity, forest plant species, habitat shift, nemoral zone, species diversity, vascular flora, woodland

1 | INTRODUCTION

When forests are evaluated in terms of their biodiversity, distinctiveness and naturalness, the question of the forest affinity of each plant species venturing into forest systems is crucial (Hermy et al., 1999; Verheyen et al., 2003; Jaroszewicz et al., 2019; Schneider et al., 2021). For various ecological research questions related to forest ecosystems (e.g., the influence of alien tree species, global changes and land-use legacies on forest biodiversity; Ammer et al., 2018), it is important to separate forest-specific species from habitat generalists and open-land species. This is only possible in a comprehensible way using species lists that are derived from a broad consensus and on a continental scale as a reference.

Approaches to define the affinity of plant species to a given habitat type (e.g., forest, grassland, scrub) or a specific plant community have existed for a long time with different aims. Classical phytosociology is, among other goals, concerned with identifying diagnostic (i.e. differential and character) species for specific vegetation types. Braun-Blanquet (1918, 1964) introduced the term "fidelity" as a measure of the association of a species and a certain vegetation type. Five levels of fidelity were distinguished, ranging from species almost exclusively associated with a given plant community to accidental species (e.g., rare, more or less random sprinklings or relic occurrences from preceding communities). These fidelity levels were modified and further developed by various authors (Barkman, 1989; Bergmeier et al., 1990). Fidelity is also a key concept in up-to-date numerical approaches to define diagnostic species or discriminate species groups in phytosociology (Bruelheide, 2000; Chytrý et al., 2002; Tichý et al., 2019).

Although phytosociological character species (i.e. species that preferably occur in a single vegetation type and thus have high fidelity to it) have often been used to analyse the properties of forest species (Bossuyt & Hermy, 2001; Ewald, 2003) and to quantify forest biodiversity (Dupré, 2000; Willner et al., 2009; Slabejová et al., 2019), this approach has some serious shortcomings in this context. First, a plant species can have a different amplitude towards certain ecological factors in different vegetation formations (forests, scrub, open land). However, assigning a given plant species to a single formation in which it chiefly occurs, as for instance in the classification of sociological behaviour in Ellenberg et al. (1992), does not mirror its ecological behaviour. For example, Ellenberg et al. (1992) assigned *Caltha palustris* exclusively to wet meadows (*Calthion*), although the species also occurs with high frequency in moist forests. The same applies to heliophilous and drought-tolerant plant species such as *Brachypodium pinnatum* and *Polygonatum odoratum*, which were classified as dry grassland (*Festuco-Brometea*) or forest fringe (*Trifolio-Geranietea*) species, respectively. Relying solely on such classification, these species would be excluded from a list of typical forest plants. Contemporary phytosociology partly overcomes this issue by identifying such species as diagnostic for both forest and open-land habitats (Mucina et al., 2016, Chytrý et al., 2020). Yet, even this approach does not offer a direct way of classifying the affinity of plant species to forests as a whole. Second, the species affinity to a given habitat may vary considerably at regional scales due to differences in, for example, (micro-)climate, land use and land-use history, topography, soil and biotic interactions. For example, *Anemone nemorosa* is characteristic of temperate broadleaf forests, albeit under montane conditions, and in northern Europe it is also common in mountain meadows, roadside verges and grasslands (Dierschke, 1997; Peppler-Lisbach & Petersen, 2001; Chytrý, 2007). A potential explanation could be that this species finds more suitable climatic conditions outside forests towards northern latitudes and elevations (i.e. at the cold limit of its distribution range), whereas it needs cooler and more humid growing conditions in the forest understorey of temperate and lowland forests (De Frenne et al., 2019; Zellweger et al., 2020). Such changes in habitat affinity are difficult to consider in the phytosociological system, underscoring the need for a supra-regional classification.

Beyond phytosociology, a myriad of different approaches has been developed over the past decades to define the forest affinity of plant species and use this to assess forest biodiversity or inform conservation decision-making (Peterken, 1974, 1977, Matlack, 1994, Peterken, 1996, Hermy et al., 1999, Honnay et al., 1999, Peterken & Francis, 1999). Such endeavours were, however, based on a limited number of single studies or local observations, limiting their applicability at larger scales. By contrast, Schmidt et al. (2003, 2011) developed the first nationwide and ecologically grounded reference list of vascular plant species occurring in forests across Germany, based on expert knowledge as well as readily available resources of plant diversity monitoring programmes and land-cover data, thus avoiding misinterpretations related to traditional phytosociological classifications. In accordance with the principles of phytosociology, the species listed in this supra-regional forest species list were assigned to different categories of forest affinity, which also allows the evaluation of species that are widespread in both forest and open vegetation as typical forest plants. Moreover, habitat shifts of species were also considered through regionalization. The list was subsequently improved and supplemented with lists of forest-dwelling bryophyte and lichen species by Schmidt et al. (2011). More recently, a list of selected groups of forest animals has also been published for Germany, using a slightly modified approach (Dorow et al., 2019, see also Schneider et al., 2021).

To date, the German forest species list has been applied in ca. 200 scientific publications, including analyses of the effects of management (Heinrichs et al., 2019) and land-use history (Naaf & Kolk, 2015) on forest plant diversity and species composition, analyses of long-term vegetation changes (Naaf & Kolk, 2016), studies of plant dispersal (Brunet, 2007), analyses of the effects of habitat fragmentation (Vanneste et al., 2019; Paal et al., 2020), range size and niche breadth analyses (Michaelis et al., 2016), and conservation network planning (Culmsee et al., 2014). The wide range of possible applications and the frequent use of this list, as well as the potential changes in habitat affinity of many plant species, underpin that there is an urgent need to expand the list towards larger biogeographical scales.

In this study, we aimed to:

1. Develop the first forest plant species list (EuForPlant) for temperate and boreal Europe with a region-specific classification of each species, based on large vegetation surveys and related vegetation databases, regional floras and expert knowledge;
2. Analyse potential shifts in forest affinity of plant species between the study regions;
3. Reflect on the applications and limitations of the list.

2 | METHODS

2.1 | Reference area: countries and biogeographical regions

Forest regions for habitat affinity assessment of vascular plant species were delineated using a combination of country borders with: (a) the Natura 2000 Biogeographical Regions (status 2011, https://ec.europa.eu); and (b) country-specific phytogeographical or geographical classifications of natural landscapes. This resulted in 24 regions from 13 countries, encompassing the nemoral, hemiboreal and boreal vegetation zones as well as lowlands, uplands and high mountains (Figure 1 and Appendix S1).

2.2 | Forest definition

Prior to the species classification, we needed to define forest. We slightly modified the forest definition of the German forest species lists (Schmidt et al., 2003, 2011) containing elements of the forest definitions given by Mueller-Dombois and Ellenberg (1974) and the German Federal Forest Inventory (http://www.bundeswaldinventur.

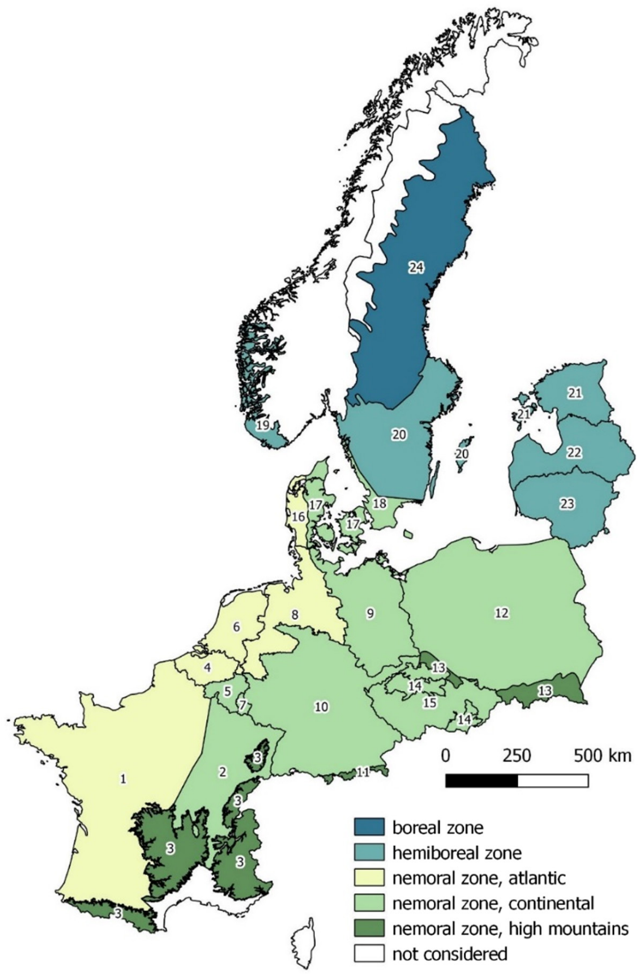

FIGURE 1 Overview of the 24 forest regions for which the European Forest Plant Species List (EuForPlant) has been established: (1) France, Atlantic region; (2) France, continental region; (3) France, mountains; (4) Belgium, lowlands; (5) Belgium, uplands and mountains; (6) Netherlands; (7) Luxembourg; (8) Germany, NW lowlands; (9) Germany, NE lowlands; (10) Germany, uplands and mountains; (11) Germany, Alps; (12) Poland, lowlands; (13) Poland, mountains; (14) Czech Republic, lowlands; (15) Czech Republic, uplands and mountains; (16) Denmark, Atlantic region; (17) Denmark, continental region; (18) Sweden, Nemoral zone; (19) Norway, hemiboreal zone: Atlantic coastline; (20) Sweden, hemiboreal zone; (21) Estonia; (22) Latvia; (23) Lithuania; (24) Sweden, boreal zone (except alpine)

de). We emphasized the ecological context (e.g., stand structure and occurrence of forest species) and reduced the focus on legal definitions (Box 1).

2.3 | Reference list of species

Based on the flora of Germany, Schmidt et al. (2002), Schmidt et al. (2003) developed a regionalized list of potential forest vascular plant taxa (mainly species but in some cases subspecies and a few aggregates; henceforth referred to as "species") as a starting point for discussion in an expert board. This list chiefly included:

BOX 1 Forest definition

Forests are defined as tree-covered areas with normally at least 30% canopy cover (but including, for example, pine forests on sand dunes and bogs, forests on dry rocky slopes, pasture woods). In the case of completely closed canopies, the area of a stand should be equal to at least a circle with the radius of the maximal height of its tree layer. In the case of an open canopy, the minimum area increases proportionally with the decrease in overhead shading.

Forests in our definition include:

- Clear-cuts or temporarily open areas such as forest gaps;
- Stands in the regeneration phase or with shoots from stumps after coppicing;
- Forest edges, including edges of forest tracks.

Forests do not include:

- Scrub, i.e. stands in which the woody component is dominated by shrubs;
- Tree rows and hedgerows;
- Intensively managed parks with forest-like structures;
- Paved forest tracks and forest roads;
- Permanently open areas within forests such as forest aisles (e.g., for power lines, if not under coppice-like management) or forest division, fire break lines, grasslands, cultivated deer pastures and feeding places of game animals;
- Orchards;
- Christmas tree and ornamental twig plantations;
- Short rotation coppices for bioenergy on former arable land;
- Herbaceous fringe vegetation in the phytosociological sense (*Galio-Alliarietalia*, *Trifolio-Geranietea*) without connection to forest stands.

1. All species classified by Ellenberg et al. (1992) as character species of deciduous forests and related scrub (*Alnetea glutinosae*, *Rhamno-Prunetea*, *Quercetea robori-petraeae*, *Querco-Fagetea*, *Salicetea purpureae*), coniferous forests and related heaths (*Erico-Pinetea*, *Pulsatillo-Pinetea*, *Vaccinio-Pinetea*), as well as vegetation of perennial herbs and shrubs in the periphery of forests (*Betulo-Adenostyletea*, *Epilobietea*, *Trifolio-Geranietea*);
2. Species with Ellenberg indicator values for light between 1 and 6 ("deep shade plant" to "between semi-shade plant and semi-light plant");
3. Species selected from an evaluation of forest vegetation surveys, mainly based on larger compilations or databases (for a detailed list see Appendix S1). All species with a relative frequency of at least 10% in at least one forest vegetation type (association or unranked community) were considered.

This list was then sent to a board of 45 experts with a questionnaire concerning the amendment and acceptance of the methodological approach, as well as the category definitions and tentative assignment of the individual species to categories (Figure 2). Chairs for vegetation science and the forest botany chairs at forest faculties were asked to propose experts; further contacts (e.g. retired scientists) were appointed. The assignment was based chiefly on species frequency in vegetation surveys (forest communities according to the forest definition in Box 1 vs open vegetation communities). Species were classified as forest species (category 1) when they have more than double frequency in at least one forest community (association or community with a larger distribution area) compared with in any open vegetation communities. Rare species were classified according to the best available knowledge (for details see Schmidt et al., 2003, 2011).

In an attempt to expand this list to other European regions, the FLEUR network (www.fleur.ugent.be) of forest vegetation ecologists, many of whom are trained originally in phytosociology, took the initiative to establish an international expert board across the 24 European forest regions in Belgium, the Czech Republic, Denmark, Estonia, France, Germany, Latvia, Lithuania, Luxembourg, the Netherlands, Norway, Poland and Sweden (Appendix S1). We restricted ourselves to the nemoral and boreal zones of Europe with the exception of parts of the Alps, Eastern Europe and the Balkans because we were lacking experts in these regions who belonged to or were connected to FLEUR.

The definitions and accompanying explanations (Box 1, Box 2; Figure 3; Appendix S2) together with the German forest species list from 2011 were then sent to all experts as a basis for the delineation of regions and classification of species (Figure 2). In all 24 regions, plant species were assigned to a category reflecting their affinity to forest habitats (see below) following the methodology of Schmidt et al. (2011), that is, wherever possible based on frequency data of species in plant communities in large vegetation surveys or related vegetation-plot databases (for a detailed list see Appendix S1). In the case of the Czech Republic, part of the species information was extracted from a national database of vascular plant species pools in different habitat types (Sádlo et al., 2007), and subsequently matched to our category definitions with some editing. Additional information on rare species and regions where vegetation-plot data were scarce was extracted from regional and national floras (see Appendix S1 for a detailed list) supplemented with expert knowledge. Accordingly, the list was gradually expanded to include new regions and species. In a few cases of striking differences in the classification of single species between adjacent regions, the lead author (TH) made a further personal inquiry of the experts to clarify whether this resulted from an actual habitat shift or from misinterpretations of the basic definitions. Towards the end of this process, the extended list was again sent to all experts for a final check (especially for classification of newly added species) and, if necessary, correction of the classifications.

2.4 | Taxonomy and additional species information

The species concept and nomenclature were based on the Euro+Med PlantBase (Euro+Med, 2006–). Exceptions are some groups of species (mainly composed of apomicts) that are difficult to distinguish and/or lack a consistent taxonomy in floras across the countries involved (*Alchemilla* spp., *Callitriche palustris* aggr., *Hieracium* sect. *Alpestria*, *Rubus fruticosus* aggr.). By contrast, some clearly recognizable hybrids with specific ecology (*Circaea* × *intermedia*, *Polypodium* × *mantoniae*, *Populus* × *canadensis*, *Populus* × *canescens*, *Rhododendron* × *intermedium*, *Salix* × *rubens*, *Spiraea* × *billardii*) were added to the list. In other cases, hybrids were included in one of the parental species. Some subspecies were also distinguished if they are treated as independent species in many floras and differ in their ecology from related subspecies (e.g., *Aconitum lycoctonum* subsp. *lasiostomum*, subsp. *lycoctonum* and subsp. *vulparia*, *Carex muricata* subsp. *muricata* and subsp. *pairae*, *Dactylis glomerata* subsp. *glomerata* and subsp. *lobata*, *Juniperus communis* subsp. *communis* and subsp. *nana*, *Lamium galeobdolon* subsp. *argentatum*, subsp. *flavidum*, subsp. *galeobdolon*, and subsp. *montanum*, *Pinus mugo* subsp. *mugo* and subsp. *rotundata*, *Viscum album* subsp. *abietis*, subsp. *album* and subsp. *austriacum*). Angiosperm plant families follow the nomenclature of the APG IV system (Stevens, 2001), whereas gymnosperm and pteridophyte plant families are according to the Euro+Med PlantBase (Euro+Med, 2006–).

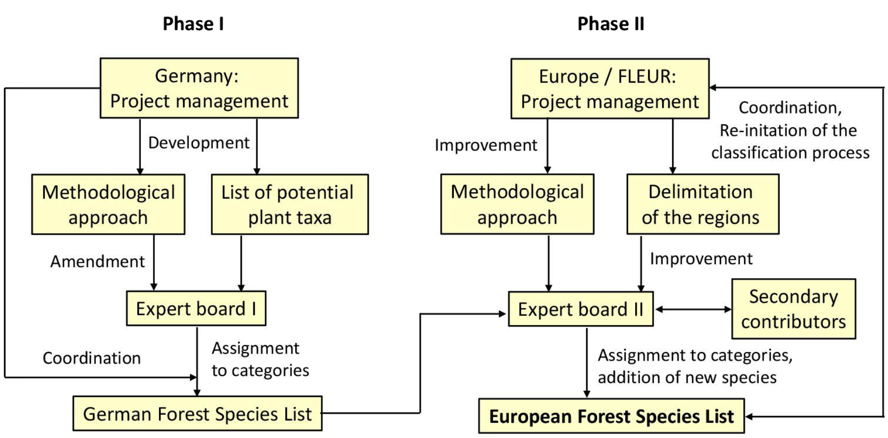

FIGURE 2 Workflow for the creation of the European Forest Plant Species list (EuForPlant)

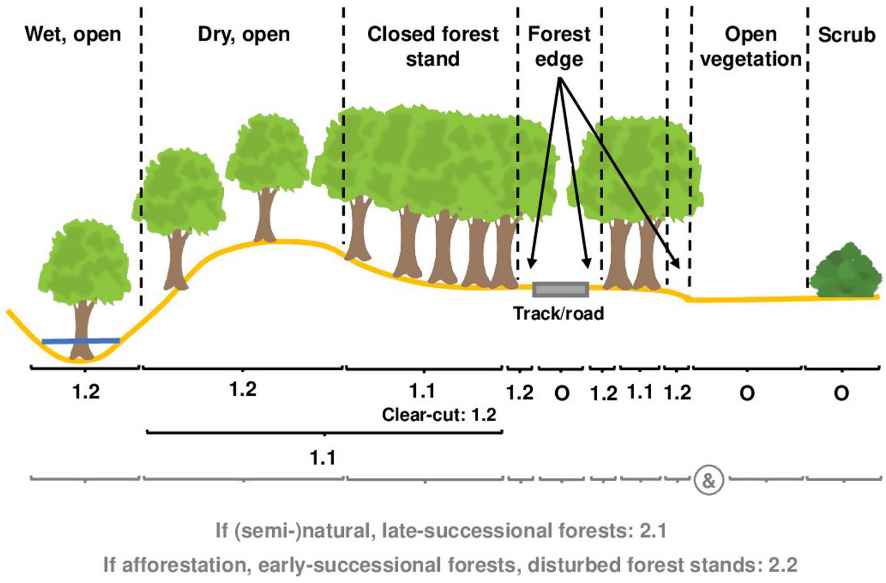

FIGURE 3 Explanation for species assignment to categories of forest species. Plant species may either occur in one habitat type (1.1/1.2/O), or in different combinations of forest and open-landscape habitats (2.1/2.2). If species restricted to forests grow in habitat types 1.1 and 1.2, they belong to category 1.1. Category 1.1 includes species that can be found mainly in closed forests, whereas 1.2 species occur predominantly along forest edges and in forest openings. Category 2.1 includes species that are part of at least one near-natural (late-successional) forest type. The majority of 2.1 species probably have their primary occurrences in forests, surviving and regenerating in open (cultural) landscape habitats, but also in remnant forests. Species are assigned to category 2.2 if they only enter (open) forests created by afforestation or during succession of open vegetation (dwarf-shrub heaths, calcareous and sand grasslands, wet meadows). All species that do not meet the requirements for the four forest affinity categories are classified as "species of open landscape" (category O) (Box 2)

We distinguished the following life forms and assigned species to vegetation layers:

- Trees – woody perennial plants, typically having a single stem or trunk contributing to the upper canopy layer(s) of a forest (>7 m);
- Epiphytic parasites – plants that grow as hemiparasites in the crown of trees;
- Lianas – long-stemmed, woody or rarely herbaceous vines that are rooted in the soil and use trees or shrubs to climb up to the canopy;
- Shrubs – medium-sized perennial woody plants which are distinguished from trees by their multiple stems, shorter stature (≤7 m) and regularly surmount the herb layer;
- Herb-layer species – annual, biennial or perennial herbaceous species as well as woody dwarf shrubs (chamaephytes).

For all regions separately, we distinguished between native species including archaeophytes (i.e. species established before AD 1500) and alien species (i.e. neophytes, introduced after AD 1500), based on regional and national floras or reference lists. Native species and archaeophytes could not be clearly separated because the status of archaeophytes is poorly known in some countries (see also Wagner et al., 2017). We defined alien species that were native in at least one of the study regions as "regionally alien species" and species that were not native in any of the study regions as "alien species" (mainly non-European neophytes).

2.5 | Classification of plant species according to forest affinity

Following Schmidt et al. (2003, 2011), our forest species list distinguishes five categories of forest affinity referring to the forest definition above. This region-specific classification scheme was applied to each species. The categories are nested within two larger groups, i.e. specialist forest species and generalist forest species (Box 2).

2.6 | Data analysis

First, we calculated the number of native, regionally alien and alien species for each life form (trees, epiphytic parasites, lianas, shrubs and herb-layer species) as well as for the different forest affinity categories (1.1, 1.2, 2.1 and 2.2/O). Second, we computed the distribution of the forest affinity categories across the 24 study regions, and determined the representation of plant families within each category. Differences in the distribution of forest affinity categories among study regions were then tested using a Kruskal–Wallis non-parametric analysis of variance (ANOVA) with the "kruskal.test" function in the *stats* package, followed by Dunn–Bonferroni post-hoc tests using "dunnTest" function in the *FSA* package (version 0.8; R Core Team, R Foundation for Statistical Computing, Vienna, AT). Third, for all species, we calculated the probability of assignment to each of the four forest affinity categories (1.1, 1.2, 2.1 or 2.2) or the O category in the 24 study regions (e.g., if a species was assigned to

BOX 2 Categories of forest affinity

Group 1. Specialist forest species (species that occur only in forests)

- Category 1.1 – Species that can be found mainly in the closed-canopy forest;
- Category 1.2 – Species that occur predominantly along forest edges and in forest openings, including: (a) species of forest edges (both sunny and shaded, both outside and inside the forest); (b) species of windthrow, burned or clear-cut areas; (c) species that mainly occur on skid trails and unpaved forest paths; and (d) species that are restricted to open forests found under extreme site conditions (shallow soils on slopes, rock outcrops, boulder and scree slopes, extremely wet forests).

Group 2. Generalist forest species (species that occur both in and outside forests)

- Category 2.1 – Species that can be equally found in forest and open vegetation;
- Category 2.2 – Species that can be found mainly in open vegetation, but also in forest.

The following explanations are important for the assignment of plant species to the four categories (Figure 3 and Appendix S2).

Group 1 vs 2. The species with the highest degree of forest affinity are classified into group 1, whereas those assigned to group 2 are typical forest species that also occur regularly in one or several non-forest, open-landscape habitats. Some of the group 1 species may also occur occasionally in woody habitats outside the forest such as hedgerows, coppices, mountain pine and green alder scrub (krummholz). The abundance of species in forest vs open vegetation was considered irrelevant for assignment to the main groups because this is highly dependent on the landscape configuration, the naturalness of forests in a region and other factors.

Category 1.1 vs 1.2. Many category 1.1 species may show a positive response to management, i.e. they flower and set fruit especially on sites of 1.2 with less shady conditions, but are not included in this group if they regularly occur in closed-canopy forests (e.g., *Milium effusum*). On the other hand, any species classified to category 1.2 may also occur in a closed-canopy forest, but usually only in small numbers and with lower vitality (often non-flowering).

Category 2.1 vs 2.2.

Category 2.1 includes species that are part of at least one near-natural (late-successional) forest community. The majority of species probably have their primary occurrences in forests, surviving and regenerating in open habitats of (cultural) landscape, but also in remnant forests. Examples of this group include: several species of wet (spring) forests and wet grasslands such as *Angelica sylvestris*, *Caltha palustris* and *Crepis paludosa*; and several species of thermophytic forests and dry grasslands (e.g., *Anthericum liliago*, *Polygonatum odoratum*, *Sesleria caerulea*). Even if there are very few remnant populations of these species in near-natural forests of a region, they were assigned to category 2.1.

Category 2.2 includes species that are not part of near-natural (late-successional) forest communities. Species are assigned to category 2.2 if they only enter (open) forests created by afforestation or during the succession of open vegetation (dwarf-shrub heaths, calcareous and sand grasslands, wet meadows). Also included are species of pastured forests, stands of alien trees (e.g., *Robinia pseudoacacia*) and severely disturbed forest stands such as many alluvial forests (*Salicion albae*). In general, most 2.2 species are characterized by high light requirements. The category considers that a significant part of European forest is recent, and their flora still shows signs of former land uses.

Category O. All species that do not meet the requirements for the four forest species categories are classified as "species of open landscape" (category O). These are only included in the forest species list if they are categorized as forest species in at least one of the regions. Whether a species is classified as 2.1/2.2 or O depends on its relative abundance in certain types of forest vs open vegetation, and not its general frequency in a region (see Group 1 vs 2). Accidental occurrences of a particular species in a forest are thus not sufficient for assignment to categories 2.1 or 2.2. The same is true for the occurrence of open-landscape species in forests.

category 1.1 in 23 regions and to 1.2 in one region, its probabilities of assignment to 1.1 and 1.2 were 96% and 4%, respectively). We also calculated the probability that each species was consistently assigned to the same category across all study regions, or whether it shifted to another category. For instance, if a species was assigned to 1.1 in five regions, to 1.2 in three regions and to 2.1 in two regions, the probability of assignment to its main category 1.1 was 50%, whereas the probability of 1.1 → 1.2 or 1.1 → 2.1 shifts were 33% and 22%, respectively. Probability distributions of habitat consistency (i.e. assignment to its main category across the study area) or shifts were then computed across all 1,726 forest species, and visualized using the "geom_density" function in the *ggplot2* package (Wickham, 2016). All statistical analyses were performed in R version 3.5.1 (R Core Team, R Foundation for Statistical Computing, Vienna, AT).

3 | RESULTS

3.1 | Overview

EuForPlant comprises a total of 1,726 vascular plant species (Table 1), most of them (1,621; 94%) native in at least some of the studied regions. The majority of species (1,437; 83%) are part of the herb layer, followed by tree and shrub species. Only a few species are lianas and epiphytic parasites. Life forms differ between native and alien forest species (Figure 4a); whereas nearly 90% of native and archaeophytic species are herb-layer species, ca. 50% of the species classified as alien in the whole study area are trees, lianas and shrubs.

Of the 1,726 species, 250 were exclusively (or in more than 50% of the regions) classified as species of closed-canopy forest (category 1.1; e.g., *Elymus caninus*, *Fagus sylvatica*, *Gymnocarpium dryopteris*, *Oxalis acetosella*; see Appendix S3 for a complete list). Forest edge, open forest and clear-cut species of category 1.2 were the smallest group with 137 species (e.g., *Cardamine flexuosa*, *Digitalis purpurea*, *Humulus lupulus*). Note that many *Trifolio-Geranietea* species such as *Peucedanum oreoselinum* and *Polygonatum odoratum* are also found in other habitats than forest edges, and are therefore usually not classified as category 1.2. Much larger than the groups of specialist forest species were the generalist forest and open-landscape groups, with 450 species classified as 2.1 (e.g., *Caltha palustris*, *Deschampsia cespitosa*, *Pteridium aquilinum*, *Quercus robur*) and 777 species classified as 2.2/O (e.g., *Aesculus hippocastanum*, *Festuca rubra*, *Silene flos-cuculi*). Many typical widespread species that occur both in closed-canopy forest and in open landscape were shrubs and trees because they rejuvenate and establish themselves in open vegetation outside the forest (Appendix S3).

Prevailing habitat preference differed between native and regionally alien species, on the one hand, and other (mostly non-European) alien species, on the other hand (Figure 4b). Whereas ca. 15% of native and regionally alien species were almost exclusively species of closed-canopy forest (category 1.1), this was true only for 5% of the other alien species. The latter were mainly comprised of the group of open-landscape species (groups 2.2 and O).

Many vascular plant species (260) occurred in all 24 studied regions (e.g., *Adoxa moschatellina*, *Carex elongata*, *Athyrium filix-femina*, *Ribes nigrum*, *Ulmus glabra*; see Figure 5). Yet, many other species had limited distribution and occurred in only one or a few regions. This pattern was similar for all forest affinity categories except 1.2 species, occurring significantly less frequently across the study regions than species of the other categories (median of 6 regions compared with 17 for 1.1, 16 for 2.1 and 15 regions for 2.2/O species; Kruskal–Wallis test, χ^2 = 79.6, *df* = 4, *p* < 0.001, with Dunn–Bonferroni post-hoc tests; Figure 5). The number of forest species varied substantially between regions; the highest number was encountered in the French mountain areas (1,220 species), whereas the lowest number was found in the Netherlands (442). Focusing exclusively on specialist forest species (1.1 and 1.2), the most species-rich region was the German uplands and mountains (300 species), whereas the boreal zone of Sweden (103) appeared to be the most species-poor region (see also Appendix S4).

The majority of forest species were dicots (1,261) and monocots (379), whereas gymnosperms (16) and pteridophytes (70) were of minor importance. Among the 117 plant families represented in the list, the largest were the Asteraceae (194 species), Rosaceae (144) and Poaceae (115). The 23 plant families with at least 20 forest species are listed in Table 2. There were remarkable differences in family representation between the forest species groups. Species only occurring in closed-canopy forests (1.1) were comparatively rare among Apiaceae, Asteraceae, Fabaceae and Rosaceae, whereas no Salicaceae were part of this group. For example, families with disproportionally high species numbers among category 1.1 were Orchidaceae (e.g., *Cephalanthera* spp., *Epipactis helleborine*, *Goodyera repens*, *Neottia nidus-avis*), Juncaceae (*Luzula* spp.) and Violaceae (*Viola* spp.). This was also the case for pteridophytes (e.g., *Athyrium filix-femina*, *Lycopodium annotinum*, *Phegopteris connectilis*) and some spermatophyte families such as Pinaceae (e.g., *Abies alba*, *Larix decidua*, *Pseudotsuga menziesii*) and Papaveraceae (e.g., *Corydalis* spp). Conversely, only two 1.1 species were present among Asteraceae (*Aposeris foetida* and *Prenanthes purpurea*) and only one among Fabaceae (*Lathyrus vernus*). Apiaceae (e.g., *Chaerophyllum temulum*, *Torilis japonica*) and Fabaceae (e.g., *Lathyrus niger*, *Vicia sylvatica*) were especially well represented in category 1.2. Among generalist forest species (2.1 and 2.2), Asteraceae (e.g., *Centaurea scabiosa*, *Cirsium oleraceum*, *Hieracium murorum*, *Tussilago farfara*) outnumbered the other families.

TABLE 1 Overview of the total number of species and relative frequency in the European Forest Species List (EuForPlant), grouped by their native status and life form

	Number of species	Percentage
All forest species	**1,726**	**100**
Nativeness		
Native species (incl. archaeophytes)	1,339	77.6
Regionally alien species	282	16.3
Alien species (across all study regions)	105	6.1
Life form		
Trees	107	6.2
Epiphytic parasites	4	0.2
Lianas	19	1.1
Shrubs	159	9.2
Herb-layer species	1,437	83.3

3.2 | Habitat shifts

Despite the relatively low probability of shifting categories between regions (on average there was a 17.5% ± 4.2% *SE* probability of an among-region shift compared with a 75.6% ± 6.8% *SE* probability of no shift; Figure 6), only about one-third of all species (594) had a constant habitat preference, which implies that they were consistently assigned to the same category across all the study regions. Species with a constant habitat preference mainly belonged to categories 1.1 and 2.1. The majority of species, however, showed a habitat shift throughout their distribution range. The most common shifts were those in which species swapped between two categories (776 species) or species either shifted from one habitat to another (e.g., 1.1→1.2; 30 species) or occupied an additional habitat (e.g., 1.1→2.1;

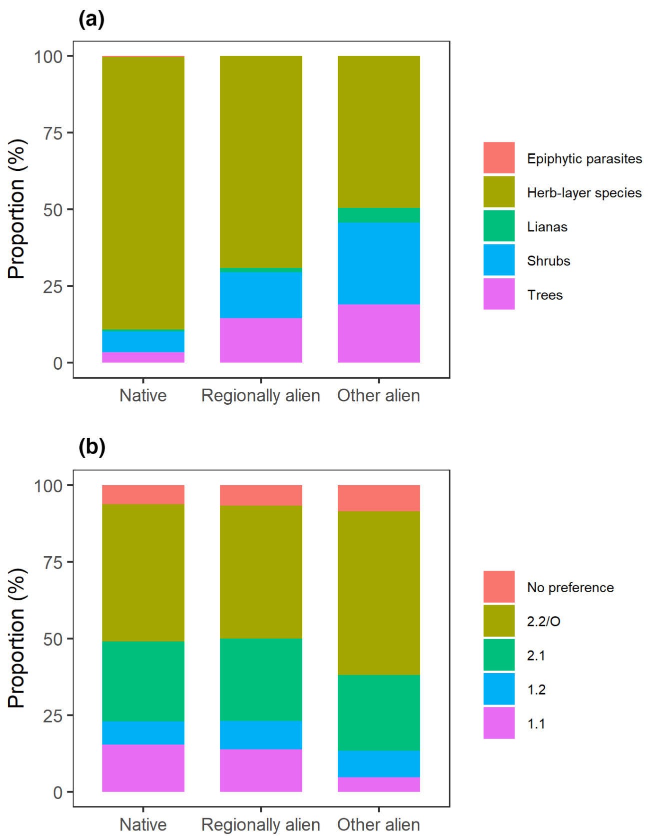

FIGURE 4 Proportion of different (a) life forms and (b) forest affinity categories (1.1, species of closed-canopy forests; 1.2, species of forest edges and forest clearings; 2.1, species of forests and open vegetation; 2.2/O, species of mainly open vegetation (but sporadically occurring in forests) of the 1,726 forest species in EuForPlant among the 1,339 native species (incl. archaeophytes), 282 regionally alien species and other 105 (mostly non-European) alien species. For each species, the most common category across the 24 study regions was considered. If two or more categories were equally frequent, the species was ranked as "no preference". When summarizing across all regions, we did not distinguish among 2.2 and O species because these are the only categories including species that are rarely found in forests. Moreover, species classified as O necessarily have a 2.2 habitat preference in at least one region, otherwise they would not be part of this forest species list

72 species). A remarkably common habitat shift was from 2.2 to O (451 species); in some regions, the species also occurred in open, early-successional forests, whereas in other regions, they were restricted to open landscape (e.g., *Artemisia campestris*, *Carex lasiocarpa*, *Galium verum*, *Linum catharticum*, *Sanguisorba minor*; Appendix S3). Another common shift was from 2.1 to 2.2 (108 species); in some regions, the species also occurred in (semi-)natural, late-successional forests, whereas in other regions, they were restricted to early-successional forests (e.g., *Agrostis capillaris*, *Brachypodium pinnatum*, *Carex nigra*, *C. pseudocyperus*, *Potentilla erecta*; Appendix S3).

Finally, 1.1 → 2.1 shifts also occurred; although species were restricted to closed forests in some regions, they also occurred in open landscape in others (e.g., *Anemone nemorosa*, *Convallaria majalis*, *Dryopteris* spp., *Vaccinium myrtillus*). A considerable number of forest species (356) were assigned to three or more categories over the 24 regions. Among these, a habitat shift 2.1 → 2.2 → O (179 species) was especially well represented, implying a different ability of those species to grow in forests with different degrees of canopy openness.

4 | DISCUSSION

4.1 | A new approach to defining the forest affinity of European plant species

EuForPlant comprises nearly 2,000 vascular plant species in 24 different regions, covering a large part of Europe's temperate and boreal forest flora. The species were categorized according to their affinity to forests, and this classification was applied by region. The list goes significantly beyond existing local and supra-regional lists of forest species in providing an expert-based approach using a standard protocol. Where possible, vegetation databases were used to assess the linkage of plant species to forests across large geographical scales.

EuForPlant encompasses a variety of life forms (chiefly understorey herb, shrub and tree species, but also lianas and epiphytic parasites such as *Viscum* spp.), and covers 117 plant families. Among all vascular plant species on this list, 386 were alien in at least one of the study regions, with phanerophytes (trees, shrubs and lianas) being the most species-rich life form among aliens. These numbers are in accordance with Wagner et al. (2017) for woodlands across the entire European continent, albeit the representation of alien species in terms of relative frequency was three times higher (23.7% of all species) in our data set compared with Wagner et al. (2017) (7%). Interestingly, some plant families were either over- or underrepresented in our forest species list compared with the whole flora of the regions of the European Forest Plant Species List. To illustrate, in Germany, in the centre of the study area, plant families that were overrepresented on the list, thus having strong affinity to forests, were: Campanulaceae, Caprifoliaceae, Ericaceae, Orchidaceae, Ranunculaceae, Rosaceae, Rubiaceae, Salicaceae and Violaceae. Of these families, Ericaceae and Orchidaceae were particularly well represented among the 1.1 species. This is not surprising given that many pyroloids (Ericaceae, Pyroleae tribe) and orchids from temperate and boreal forests associate with fungi that form ectomycorrhizas on surrounding trees (Bidartondo et al., 2004; Tedersoo et al., 2007). One of the ecological attributes of such plants with myco-heterotrophy (e.g., *Corallorhiza trifida* or *Neottia nidus-avis*) or mixotrophy (e.g., *Cephalanthera* spp. or *Epipactis* spp.) is that they are independent of solar radiation and are able to colonize deeply shaded forest habitats (Zimmer et al., 2007). Moreover, many Ericaceae are known to thrive on nutrient-poor soils with acid humus (mor), and are often a prominent feature of the vegetation in heathlands, bogs and moors, but also in forests (Schwery et al., 2015; Olleck et al., 2020). Some other species-rich families were underrepresented or hardly present among forest species: Amaranthaceae, Asteraceae, Brassicaceae, Caryophyllaceae Gentianaceae and Plantaginaceae.

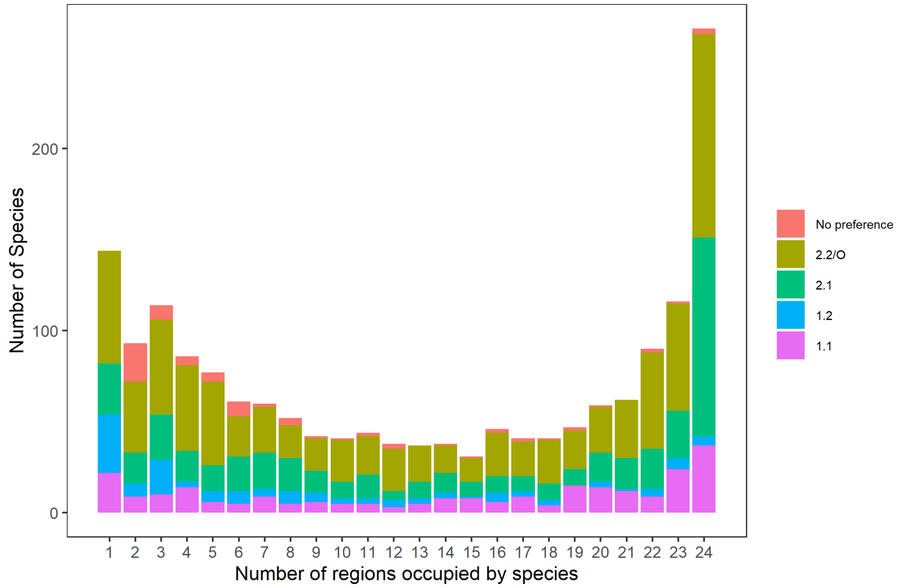

FIGURE 5 Species range size distribution of the 1,726 vascular plant species over the 24 forest regions in temperate and boreal Europe. The *x*-axis indicates the number of regions that are occupied by the respective species. Forest species are divided according to the forest affinity categories (1.1, species of closed-canopy forests; 1.2, species of forest edges and forest clearings; 2.1, species of forests and open vegetation; 2.2/O, species of mainly open vegetation, but sporadically in forests). For each species, the most common category across the 24 study regions was considered. If two or more categories were equally frequent, the species was ranked as "no preference". See Figure 4 for the reason of merging the categories 2.2 and O. Moreover, species classified as O necessarily have a 2.2 habitat preference in at least one region, otherwise they would not be part of this forest species list

Amaranthaceae, for instance, are known to prefer warm, open habitats such as temperate grasslands, sand dunes and agricultural habitats (Kadereit et al., 2003), and were therefore nearly absent from this list of forest species. However, some of these families, such as Asteraceae, Brassicaceae and Gentianaceae, are more strongly represented in forest vegetation in the southeastern part of Europe (Večeřa et al., 2021) that is not covered by the forest species list, probably reflecting the evolutionary history of the families.

4.2 | Importance of the regionally specific classification system

Despite the relatively low proportion of between-region habitat shifts, a remarkable number of species (nearly 75%) swapped categories in at least one of the study regions. The most common shifts were from category 2.1 to 2.2 or from 2.2 to O, although a shift from 1.1 to 2.1 was also detected in 12% of category 1.1 species. Thus, although species may be restricted to early-successional forests, afforestations or even to open vegetation in some regions, they may also occur in (semi-)natural, late-successional forests in others. Although some bias due to differences in judgement between experts cannot be ruled out, such changes in a species' ecological niche over broad geographical areas can most likely be attributed to large-scale gradients in climatic conditions, land use and deposition of airborne pollutants, as well as local variation in topography, microclimate and biotic interactions (see, for example, Wasof et al., 2013). This phenomenon is partly referred to the "law of relative site constancy" (Walter & Walter, 1953), implying that a species' individual physiological requirements can be met in different types of vegetation under varying climatic conditions. Similar microclimatic conditions can, for instance, be found in highly different ambient climates owing to the complex interplay between macroclimate and vegetation (Lenoir, 2020). As a result, the observed shift of several typical forest plant species (e.g., *Anemone nemorosa* and *Convallaria majalis*) from 1.1 to 2.1 towards higher latitudes, mountainous regions and coastal areas may arise from the fact that local climatic conditions outside forests in these northern, high-elevation and Atlantic regions tend to be similar to microclimatic conditions below the forest canopy in temperate, lowland and continental regions (De Frenne et al., 2019; Lenoir, 2020). Occasionally, however, the assignment of species to forest affinity categories may simply depend on the occurrence of certain forest habitats in the respective regions. In sum, these habitat shifts illustrate that the affinity of vascular plant species to forests strongly depends on region. They underpin the importance of applying the classification at a regional level across broad spatial scales.

4.3 | Expected impact, limitations and ways forward

The current list was made publicly available on figshare in 2019 (Heinken et al., 2019, https://doi.org/10.6084/m9.figshare.8095217.v1), and has since been applied in several scientific publications,

TABLE 2 Family representation among vascular plant species in the European Forest Plant Species List (EuForPlant)

	All species		Occurrence mainly in category								No preference	
			1.1		1.2		2.1		2.2/O			
Families	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Asteraceae	194	11.2	2	0.8	11	8	44	9.8	126	15.5	11	14.5
Rosaceae	144	8.3	5	2	20	14.6	62	13.8	50	6.2	7	9.2
Poaceae	115	6.7	23	9.2	0	0	29	6.4	59	7.3	4	5.3
Fabaceae	88	5.1	1	0.4	13	9.5	13	2.9	59	7.3	2	2.6
Cyperaceae	97	5.6	12	4.8	3	2.2	25	5.6	52	6.4	5	6.6
Ranunculaceae	65	3.8	14	5.6	7	5.1	23	5.1	20	2.5	1	1.3
Apiaceae	61	3.5	3	1.2	8	5.8	17	3.8	30	3.7	3	3.9
Lamiaceae	56	3.2	7	2.8	3	2.2	13	2.9	31	3.8	2	2.6
Orchidaceae	53	3.1	23	9.2	5	3.6	11	2.4	13	1.6	1	1.3
Caryophyllaceae	49	2.8	7	2.8	5	3.6	9	2	25	3.1	3	3.9
Ericaceae	39	2.3	9	3.6	0	0	12	2.7	16	2	2	2.6
Brassicaceae	35	2.0	7	2.8	4	2.9	7	1.6	17	2.1	0	0
Salicaceae	33	1.9	0	0	0	0	11	2.4	21	2.6	1	1.3
Orobanchaceae	32	1.9	5	2	5	3.6	4	0.9	13	1.6	5	6.6
Boraginaceae	29	1.7	7	2.8	5	3.6	7	1.6	8	1	2	2.6
Caprifoliaceae	29	1.7	4	1.6	7	5.1	8	1.8	10	1.2	0	0
Asparagaceae	27	1.6	7	2.8	0	0	8	1.8	8	1	4	5.3
Juncaceae	27	1.6	7	2.8	1	0.7	5	1.1	14	1.7	0	0
Plantaginaceae	27	1.6	2	0.8	2	1.5	4	0.9	19	2.3	0	0
Rubiaceae	27	1.6	7	2.8	1	0.7	5	1.1	13	1.6	1	1.3
Campanulaceae	24	1.4	3	1.2	2	1.5	3	0.7	14	1.7	2	2.6
Violaceae	22	1.3	7	2.8	0	0	8	1.8	6	0.7	1	1.3
Primulaceae	20	1.2	6	2.4	1	0.7	7	1.6	5	0.6	1	1.3
Other 94 families	433	25.1	82	32.8	34	24.8	115	25.6	184	22.6	18	23.7

Note: Shown are the total number of species and relative frequency for the 23 families with at least 20 species, grouped by forest affinity categories (1.1, species of closed-canopy forests; 1.2, species of forest edges and forest clearings; 2.1, species of forests and open vegetation; 2.2/O, species of mainly open vegetation, but sporadically in forests). For each species, the most common category across the 24 study regions was considered. If two or more categories were equally frequent, the species was ranked as "no preference".

e.g., to assess the variation in plant species diversity and composition along edge-to-interior gradients in forests across Europe (Govaert et al., 2020), to study the migration of forest herbs along hedgerow corridors (Vanneste et al., 2020), to assess functional diversity of understorey plant communities in fragmented landscapes (Vanneste et al., 2019), to experimentally assess the effects of both macro- and microclimatic changes on understorey plants with contrasting degree of forest affinity (De Pauw et al., 2021), to model their population growth rates under a changing climate system (Sanczuk et al., 2021), and to characterize the seed bank in forests along various environmental gradients (Gasperini et al., 2021). Other potential applications of this list are:

1. To study the effects of global environmental change (climate change, land-use change, atmospheric pollution, biological invasions, etc.) on forest biodiversity; for example, by linking the distribution of forest affinity categories (e.g., in terms of relative frequency) in European forests to various environmental variables such as macroclimatic temperature and precipitation (e.g., from CHELSA; Karger et al., 2017), atmospheric nitrogen (N) deposition and acidification (e.g., from EMEP; http://www.emep.int) and land-use changes (e.g., from historical landscape analyses);
2. To unravel how forest structure and microclimate gradients influence understorey plant community dynamics; for example, by assessing the relationship between temporal shifts in the distribution of forest affinity categories in European forests (e.g., using resurvey databases such as forestREplot; https://forestreplot.ugent.be) to changes in forest canopy cover and subcanopy temperatures over time;
3. To study the ecology of forest plants; for example, by comparing Ellenberg indicator and thermal tolerance values among the forest affinity categories. For instance, it is expected that species of closed forests (1.1) would have lower Ellenberg indicators

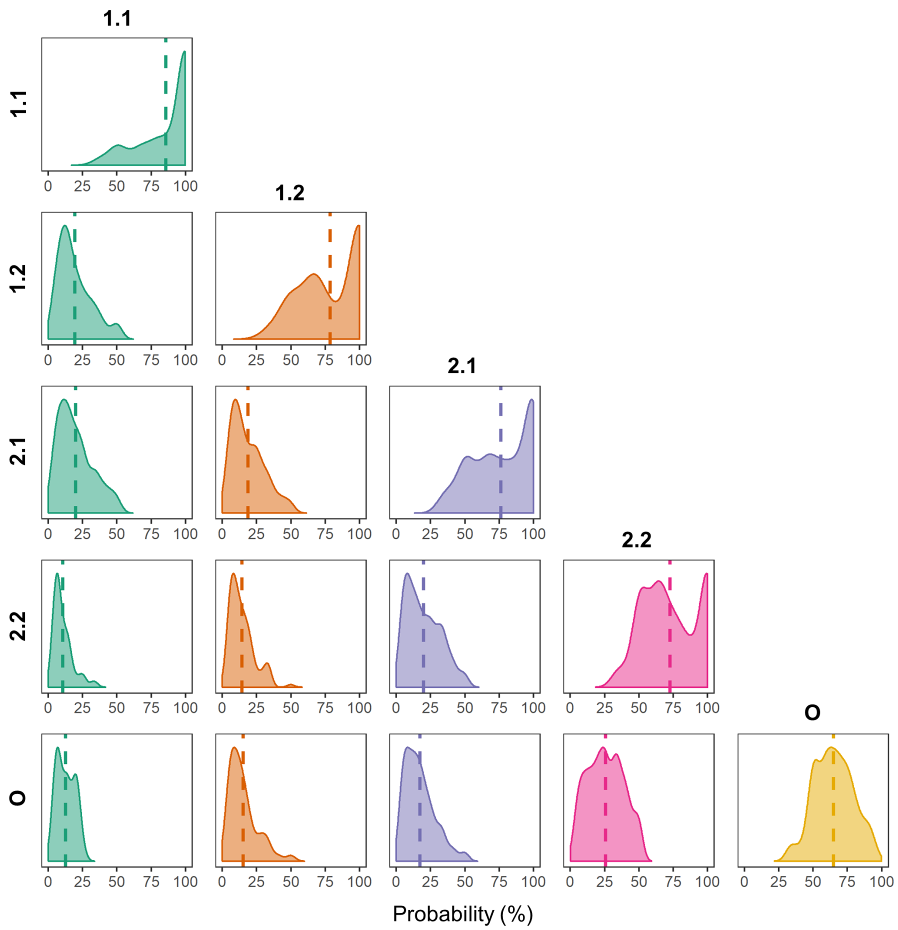

FIGURE 6 Distribution of probability across the 1,726 forest species in EuForPlant that a species (a) stays within the same category (graphs on the diagonal) or (b) shifts to another category in the 24 study regions. Categories of forest affinity are: 1.1, species of closed-canopy forests; 1.2, species of forest edges and forest clearings; 2.1, species of forests and open vegetation; 2.2, species of mainly open vegetation, but sporadically also occurring in forests. All species that do not meet the requirements for the four forest affinity categories are classified as O species (Box 2). For each species, the most common category across the 24 study regions was considered. If two or more categories were equally frequent, the species was ranked as "no preference"

for light, nitrogen and reaction than species of open vegetation (Dzwonko, 2002; Schmidt et al., 2014). In addition, the list can be used to explore the evolutionary ecology of forest plant species;

4. Trait-based analyses; for example, by establishing the link between forest affinity categories and functional life-history traits that are related to their competitiveness or dispersal ability. For instance, Vanneste et al. (2019) demonstrated that the 1.1 species were significantly shorter, produced heavier seeds and displayed lower specific leaf area than species in the other categories;
5. Use in conservation planning and decision-making; for example, to evaluate biodiversity status of forests and to identify most valuable, least-transformed forests remaining in Europe. For instance, Culmsee et al. (2014) previously used the forest plant species list developed by Schmidt et al. (2011) to determine the distribution of high-nature-value forests in Lower Saxony, Germany. In turn, this approach contributed to the identification of new conservation areas and to monitor the success of existing forest conservation measures within the framework of Natura 2000.

Despite the extensiveness of the data set and its potential suitability for ecological research, several shortcomings must be considered when using the EuForPlant. Most importantly, analyses of vegetation databases or comprehensive vegetation surveys based on databases were the primary source of the classification of forest species only in some regions (e.g., the Czech Republic, Germany and the Netherlands), whereas expert knowledge was a central methodology of classification in other regions. This is because in the European Vegetation Archive (Chytrý et al., 2016) or other databases: (1) some of the included countries, especially in northern Europe, are not adequately covered; (2) the structural information needed to assign species to categories is often not available in the databases; and (3) many rare species are not sufficiently represented to classify them using fidelity measures. Following expert-based evaluation and correction of errors due to different interpretations of the definitions by experts, the classification of forest species has mainly been based on expert knowledge rather than an objective mathematical algorithm. Expert assessments have been demonstrated to be invaluable and are still gaining momentum in ecological applications and conservation decision-making (Kuhnert et al., 2010). Skilled experts have acquired extensive knowledge and experience, allowing them to perform a multicriteria analysis of the most relevant information for a given context in order to find the most appropriate solution. However, groups of experts are not free from biases and blind spots, and the usefulness of such expert judgements fluctuates (Burgman, 2005). For this reason, we looked for ways to independently support the expert assessments of the forest affinity categories using clear definitions and, as far as possible, vegetation databases. Moreover, the classification was coordinated by the FLEUR network, a group of scientists who have met annually for over 15 years and have local knowledge of the broad range of forest communities and habitat types covered in this list. Another potential limitation related to this list is that intra-regional shifts in forest affinity are not considered. Even within regions, large climatic variability may be encountered, for instance, in mountainous areas where gradients from lowland conditions to montane or (sub-)alpine climate occur. Finally, to date, our list covers only part of Europe, albeit a significant one, but not Southern and Eastern Europe. Filling in data from these areas will be an important task for the future.

5 | CONCLUSION

EuForPlant is a unique database of forest vascular plant species covering the European temperate and boreal biome with a region-specific classification scheme of their forest affinity. The list has many possible applications in vegetation science, and is equally instrumental in forest monitoring and conservation decision-making. EuForPlant can be readily linked to other large vegetation-plot databases such as EVA (Chytrý et al., 2016) and sPlot (Bruelheide et al., 2019; Sabatini et al., 2021), to plant trait data sets such as TRY (Kattge et al., 2020) and ClimPlant (Vangansbeke et al., 2021), as well as to climate databases such as CHELSA (Karger et al., 2017) and SoilTemp (Lembrechts et al., 2020). The links between these databases can help answer questions related to forest plant diversity patterns, structure and dynamics of understorey plant communities, long-term vegetation changes in forests in response to global environmental change, plant species niche breadth and range sizes, plant dispersal and colonization, and many others. Users of EuForPlant need to be aware of its limitations and potential biases that might affect answers to specific research questions. Finally, we see this list as dynamic and underpin the importance of expanding it towards other regions and biomes (e.g., the Mediterranean and the Balkans) to create the most comprehensive compilation of forest plant species at a pan-European scale. The latest version of EuForPlant will always be available on igshare (https://doi.org/10.6084/m9.figshare.8095217.v1).

AUTHOR CONTRIBUTIONS

Thilo Heinken conceived and designed the study in close collaboration with the FLEUR network and regional collaborators. All authors were involved in the region delineation and species classification. Thomas Vanneste and Thilo Heinken conducted the statistical analyses. Thilo Heinken and Thomas Vanneste wrote the first draft of the paper, while all authors contributed to revisions.

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DATA AVAILABILITY STATEMENT

The complete database and accompanying metadata are available from the Figshare repository, with the identifier https://doi.org/10.6084/m9.figshare.8095217.v1 (Heinken et al., 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix S1. The 24 regions for which the EuForPlant was established, the responsible coordinators and contributors, and the main information sources used for the delimitation of natural regions and assignment of species

Appendix S2. Explanatory materials for forest definitions and forest affinity categories as an assistance for the regional contributors

Appendix S3. Widespread plant species of different forest species categories

Appendix S4. Species numbers of forest species groups in the European Forest Plant Species List across the 24 regions in temperate and boreal Europe, sorted by the total number of species

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