



# Article Assessment of Drought-Tolerant Provenances of Austria's Indigenous Tree Species

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**Abstract:** (1) Background: Forestry will have to react to climate change because many tree species suffer. Mitigation can be realized either by planting non-native trees from regions with high climatic stress or by utilizing native tree provenances already adapted to stressful environments. Non-native trees have often generated problems in the past due to uncontrolled invasiveness. The use of native trees pre-adapted to the prospective climatic conditions is far less risky for the respective ecosystems. We offer a tool for selecting ecotypes of native trees as provenances for future forestry. (2) Methods: We propose the selection of tree species native to Middle Europe from a database of vegetation relevés of  $\pm$  natural forest stands. By calculating the mean ecological indicator values of stands from their vegetation, cover sites can be elected that can provide seeds of provenances well adapted to future climatic conditions. (3) Results: By selecting the 10% partition of the most extreme stands of European tree species, seeds can be sampled and propagated for re-cultivating forests fit for future climate. (4) Conclusions: One can expect ecotypes of tree species that grow well on dry sites, since generations have faced evolutionary selection, for survival under stressful environments. This approach helps to avoid ecological risks of non-native trees.

**Keywords:** ecological indicator values; drought resistance; native trees; Central Europe; tree breeding; forestry; climate change

# 1. Introduction

Climate change dynamics will have a strong impact on forest ecosystems and timber production [1,2]. Due to the most recent IPCC report, hot extremes as well as heavy precipitation will cause considerable damages to the world's ecosystems [3]. In managed as well as natural forests, increased temperature and lower rainfall will induce problems for the survival of several tree species [4–6]. As an example, the managed forests at lower and medium altitudes of Europe dominated by Norway spruce or European beech suffer seriously from the consequences of more frequent droughts [7,8]. Consequently, individual trees are more prone to being attacked by pest insects (i.e., bark beetle) or pathogens [9,10].

Specific problems arise for European trees with increasing mean annual temperatures (plus 1.7–1.9 °C, compared to pre-industrial times [11]) and raising water stress. In the last two decades, summer droughts have led to serious impacts on European forests that ended up with extensive dieback in spruce, pine and beech forests [2,12,13]. The main problem of the trees under drought stress is hydraulic dysfunction and subsequent deficit of carbon storage [14]. The capacity to manage drought periods might be increased in populations that experience drought relative to their species specific normal physiological range. Tree species that arrived to Middle Europe in the postglacial period have occupied various habitats that represent the range of site conditions that the respective species were able to conquer under the given climate and the given competitors. Human influence on



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**Copyright:** © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). this process was rather indirect in that man changed habitat structure and soil by logging but ignoring the need of regeneration [15]. Reforestation—if ever strived for in former times—was not so much aiming at high quality timber. During the period of optimizing the quantity and quality of wood higher attention was led on reforestation with provenances that grew fast and gave high yield [16]. The general use of very productive provenances on sites of various water supply has led to the problem of extensive diebacks of cultivated forests along with dry summers during the last two decades [12,13].

In some tropic regions, the strategies of forestry tend to change by fostering native tree regeneration and gaining finally a rather multifunctional forest ecosystem with differentiated options of human utilization [17,18]. The idea to preferably use native tree species for the transformation of forests according to climate change was also considered in temperate regions [19]. The use of native species is ecologically sound and does not include risks of planting non-native trees that might become invasive and alter ecosystem services [20,21]. Native trees have co-evolved over thousands of years and contribute to the ecosystem functioning in a balanced way.

In European countries, forest management underlies legal regulations, e.g., with respect to reforestation after logging or keeping forests at healthy state [22–24]. Unfortunately, in Austria, the regulations for afforestation by use of seed material and saplings from local to regional tree nurseries [18] are nowadays not as strict as they were in the second half of the 20th century [25]. Reforestation was only allowed by use of locally produced saplings [18,26]. This regulation guaranteed that forestry should use generally trees that were adapted to the local climate. In practice, these rules were not always based on the most up-to-date knowledge of forest ecology. In Middle Europe specifically, Norway spruce was planted also far beyond its natural range. In consequence, this species suffers a lot from the recent climatic stressors, especially in case of non-natural stands.

Forest ecology has promoted the establishment of mixed forests to overcome the problems of monospecific stands for decades [27]. Mixed forests favoring native trees have been pointed out as most appropriate to fulfill the multiple functions of productive ecosystems under future climatic conditions [28–31]. Due to the accelerated climate change dynamics, traditional forest management will not have time to let the natural regeneration work until the fittest individuals made it [32–34]. In the tropics, reforestation of a mixed forest with native species is already applied to overcome environmental problems and to guarantee forest multifunctionality [35]. Few attempts to favor native trees were also made in parts of Europe [36,37]. Spatial limitations (natural or cultural land-use types) often prohibit the spread of suitable ecotypes of trees that were locally selected on regional substrate and dry habitat conditions. Forest managers might have problems finding such preadapted populations of native trees at the local or regional scale [38].

Therefore, we aim in this study to provide a tool for detecting drought-resistant ecotypes of the desired native trees at the local or regional scale. Specifically, we (1) compile a data pool that unites knowledge from forest site ecology and vegetation ecology (vegetation surveys), we (2) perform data mining by extracting site ecological information from the vegetation cover, we (3) select the percentile of the driest stands covered by the more common tree species and we (4) provide maps and metadata of stands of Austrian tree species capable of surviving under relatively dry conditions.

#### 2. Materials and Methods

The basic idea in this paper is to select tree species provenances that are preadapted to future (dryer) site conditions by vegetation metadata analysis. Information on site conditions of forest stands is manifold but far-scattered. However, there is a high number of relevés published in vegetation ecology that can be used as indirect estimates of the respective site conditions.

Austrian forests were classified by the last author [39] based on a database comprising more than 20,000 relevés, with 19,058 of these relevés selected after a floristic quality-check for those that contain significant coverage of the more common Austrian tree species in

the tree layer. The selected relevés represent plot-wise species lists of tree and herb layers, including data on coverage of species quantified by the Braun-Blanquet scale [40]. The geographical localization, aspect and altitude of all plots were stored in the metadata of this database.

Out of the 164 woody plant species in Austria, 73 taxa show tree-like shape. Some of them are rare and were not represented in the database. In order to get statistically sound results, we considered only those relevés where the given tree species covered at least 25% of the ground in one of the tree layers. This process resulted in 46 tree species to be represented in at least one relevé (Table 1). Finally, 16 species were selected for detailed analysis due to their relevancy for silviculture under recent policy constraints.

**Table 1.** Number of relevés for each tree species present at coverages of 25% minimum in at least one vegetation relevé.

Species	Number of Relevés	Species	Number of Relevés
Picea abies	4700	Ulmus glabra	95
Fagus sylvatica	2707	Salix fragilis	86
Pinus sylvatica	1145	Pinus cembra	83
Fraxinus excelsior	1133	Populus $ imes$ canadensis	62
Alnus incana	890	Prunus padus	42
Quercus petraea s.lat.	809	Betula pendula	37
Alnus glutinosa	799	Populus nigra	35
Carpinus betulus	681	Acer platanoides	32
Abies alba	636	Prunus avium	29
Acer pseudoplatanus	475	Betula pubescens	25
Quercus robur	395	Robinia pseudacacia	24
Larix decidua	323	Ulmus minor	17
Pinus nigra	227	Fraxinus ornus	15
Salix alba	210	Populus $ imes$ canescens	14
Tilia cordata	206	Ulmus laevis	10
Ostrya carpinifolia	183	Quercus dalechampii	5
Qercus pubescens s. lat.	175	Castanea sativa	4
Populus alba	170	Populus tremula	4
Quercus cerris	156	Salix caprea	2
Tilia platyphyllos	123	Acer tataricum	1
Acer campestre	113	Sorbus aucuparia	1
Fraxinus angustifolia	109	Sorbus torminalis	1
Pinus uncinata	105	Tilia x vulgaris	1

Several trees in Table 1 are widespread in Austria and ecotypes are mentioned for some of them [38]. Some tree species can grow well under a very broad amplitude of climatic or edaphic factors and are cultivated in various habitats [27], e.g., *Pinus sylvestris, Fagus sylvatica* and *Quercus robur*. In this paper, we focus only on the most relevant tree species for Austrian forestry. In the full report of our StartClim20011D-project, even more tree species are discussed [38].

Ellenberg's ecological indicator values (EIV) have been well-established in ecology for decades [41] and serve as an indirect estimate of the site conditions under which a plant species preferentially grows [42–44]. EIVs characterize the mean conditions at the species' optimal performance and are defined for distinct geographical regions. The EIVs for Austria are available from BOKU [45]. They are based on the ratings by Ellenberg [46] and adapted for Austria [47–49].

The indicator for water supply ('moisture' = M) considers the availability of water for the plants on site irrespective of the source of water either from rainfall, air moisture or soil water. The ordinal scale for M spans from level 1 to level 12 [46]. Almost all of the plant species from Austrian forests are assigned an EIV for moisture [45]. Species that have no clear optimum along the gradient are classified as "indifferent" and do not contribute to the mean. By calculating the arithmetic means of the EIVs of the species growing at a site a rough estimate of the site conditions can be given [42,44]. Calculating means of EIVs for relevés is sensitive to the number of species present in the plot and contributing to the means [50,51]. Such relevés often represent sites where light conditions at the forest floor are very poor, with only very shade tolerant species occurring. Therefore, means were calculated only for relevés that contained more than five vascular plant species. Furthermore, the species of interest was excluded from the calculation of the mean moisture values (mM).

The mM-values of relevés of a respective species vary around a mean for all relevés. We decided to affiliate the 10th percentile of the relevés with the relatively lowest mM-values as useful to pick drought-resistant populations of the respective tree species. We illustrate the distribution of all relevés comprising the respective species along environmental gradients such as altitude and aspect in comparison with the 10th percentile of the driest relevés of those species. Practitioners in forestry will find helpful the spatial positioning of the 10% relevés, where the most drought-resistant populations of tree species can be found for future forestry under climate change conditions (Appendix A).

The relevés were linked to climatic factors (mean annual precipitation and mean annual temperature for the period 1971–2000). We aligned the floristic mapping grids [52] of the corresponding relevés (if coordinates for the relevé were available) with grid-based means of annual precipitation and annual mean temperature data using ARCGIS 10.2 (Figure 1).



**Figure 1.** Grid-based values of annual precipitation (above) and annual mean temperature (below) for Austria averaged over the period 1971–2010; adapted from [38]. Data source: Zamg-ÖKLIM [53].

#### 3. Results

## 3.1. Means and Amplitudes of Drought Tolerance of Selected Austrian Tree Species

In this subsection, we demonstrate the amplitude and means of ecological factors of plots where the respective tree species plays a significant role in the tree layer. mM-means of relevés indicate the average water availability for the tree species on the respective sites

and can be used to define the 10% driest relevés of the respective tree species (e.g., Figure 2). In addition, the distribution of the 10% driest and the remaining 90% relevés along the gradient of environmental factors such as altitude and aspect confirm the selection of just the populations with the most drought-resistant populations of the respective tree species (e.g., Figures 3 and 4). Furthermore, we projected the distribution of the 10% driest and the remaining 90% relevés of the analyzed tree species against the factors annual sum of precipitation and annual mean temperature at the respective sites of the relevés comprising our selected tree species (e.g., Figure 5). In this way, we can expect to provide sites with tree provenances that would fit to the expected future temperature and precipitation situation.



**Figure 2.** Distribution of relevés along the gradient of mean moisture values calculated from vegetation relevés for the six selected Conifer species ( $\bar{x}$ : arithmetic mean of all relevés, P 10: 10th percentile cutline of the 10% driest relevés, n: number of relevés).



**Figure 3.** Distribution of the relevés for six selected Conifer species along the altitudinal gradient (red bars: no. of relevés belonging to the driest 10%, green bars: 90% residual relevés).



Figure 4. Cont.



**Figure 4.** Distribution of the relevés for six selected Conifer species between aspect classes (exposition class  $<5^{\circ}$  refers to  $\pm$  flat sites with a slope of less than 5°; red bars: number of relevés belonging to the driest 10%, green bars: number of residual relevés).



**Figure 5.** Thirty-year means of annual mean temperature (to the left,  $^{\circ}$ C) and annual precipitation (to the right, mm) for the 10% driest relevés (red) and residual 90% relevés (green) for six selected Conifer species (Abialb: Silver Fir, Lardec: European Larch, Picabi: Norway spruce, Pimcem: Stone Pine, Pinnig: Austrian Pine, Pinsyl: Scots pine); significant differences between the dry and residual relevés represented as: \* *p* < 0.05, \*\*\* *p* < 0.0001; no symbol indicating no significant difference.

The first group of tree species consists of six Conifers with high silvicultural relevancy for Austria. The second group comprises of ten Angiosperm species that are also most relevant for actual as well as future silviculture from the ecological point of view. The species are ranked within the group according to the number of relevés in which they are reported (Table 1). We calculated a mean mM-value of 5.41 for Norway spruce (*Picea abies*) and, similar to Silver fir (*Abies alba*), its optimum appeared to be represented by sites with an mM between 5 and 6. However, the wider distribution of mM-values over the moisture scale (3.6–8.8) suggests a larger amplitude in drought tolerance than that of Fir (Figure 2).

While the altitudes of the Spruce relevés range from 120 to 2000 m a.s.l., a substantial proportion of relevés were located between 1300 to 1500 m. The driest relevés, however, showed a more restricted range and more uniform distribution along the altitudinal gradient (Figure 3). While the general pattern was similar to Fir, the dominance of SE-, S- and SW-exposed sites in the dry relevés was more pronounced for Spruce (Figure 4). Furthermore, relevés belonging to the driest 10% demonstrated significantly higher mean annual mean temperatures (6.3 °C compared to 5.6 °C) and lower mean annual precipitation (1289 mm compared to 1379 mm) than the residual relevés (Figure 5).

Scots pine (*Pinus sylvestris*) is in general a light demanding species, although in terms of water requirements this species can be found at both ends of the moisture spectrum. This is represented to some extent by the wide distribution observed here: mM between 2.7 and 8.5. The mM-value of 10th percentile was, at 3.37, very low (Figure 2).

Scots pine also demonstrated a wide range in elevation, from 220 to 1890 m a.s.l., with elevations of around 700 m a.s.l. the most frequent. The range of the dry relevés was more restricted to lower elevations between 200 and 900 m a.s.l. (Figure 3).

Like Austrian pine (*Pinus nigra*), the distributions between aspect of both the dry and residual relevés were similar although compared to the residual relevés, the dry relevés with Scots pine showed a stronger preference for SE- rather than SW-exposures (Figure 4). However, unlike Austrian pine, Scots pine relevés belonging to the driest 10% demonstrated significantly lower annual precipitation (698 mm compared to 999 mm) than the residual relevés. The difference in annual mean temperature was statistically insignificant (Figure 5).

Silver fir was found occupying sites with an mM between 4 and just above 7, although the distribution indicates optimal sites with mM-values between 5 and 6 and a general avoidance of dry sites (Figure 2). The general avoidance of dry conditions is also indicated by the prevalence of W-, N- and NE-facing locations within the residual relevés (i.e., those not belonging to the 10th driest percentile) (Figure 4), where, due to less intense incident radiation, evaporative demand is typically lower. The driest 10% recorded mM-values of 4.93 and below and were strongly represented by SE- to SW-aspects. However, there was no significant difference in either annual precipitation or annual mean temperature between the driest 10% (the dry relevés) and the remaining 90% (the residual relevés) (Figure 5).

Silver fir is generally classified as a montane/submontane tree species, which is rather well illustrated by the elevation distribution of the relevés, with Silver fir of both the dry and the residual relevés (Figure 3). The fir relevés ranged from 300 to 1700 m a.s.l., with the highest dry relevés found at 1400 m).

The relevés comprising European larch (*Larix decidua*) showed a slightly skewed distribution along the moisture gradient: a few relevés indicating considerable presence on dry soils, moist sites (mM > 6.25) almost completely avoided and an optimum mM of 5.4 (Figure 2).

Apart from a difference in range, there was no clear distinction with respect to distribution over elevation between the dry and residual relevés. As Larch is an alpine species, often found in forest communities at the timber line, the range of the residual relevés reached just above 2000 m a.s.l. (Figure 3). The dominance of southern exposures was very clear in the dry relevés of larch (almost half were either S-/SW-exposed sites), despite a clear preference of the residual relevés for north-facing sites (Figure 4). Due to insufficient allocation of climate data to the Larch relevés, statistical comparison of temperature and precipitation values of the dry and residual relevés could not be performed.

Austrian pine is a very drought-tolerant species, which is well reflected by the distribution in mM-values: range in mM from 2.6 to 4.8 and dominance of relevés with mM of between 3 and 4. The mM of the 10th percentile was 3.15 (Figure 2). Consequently, the Austrian pine relevés were generally located at lower elevations. The distribution ranged from 250 to 1330 m a.s.l., with the majority lying within submontane elevations. This elevation zone was also dominated by the dry relevés, although their distribution beyond this range, particularly at higher elevations (>900 m a.s.l.), was more limited (Figure 3).

As a drought-resistant species, the distribution between aspect of both the dry and residual relevés demonstrated a clear preference for the S- to W-aspects, where, all other site characters being equal, evaporative demand is generally higher (Figure 4). There was no significant difference in either annual precipitation or annual mean temperature between the dry relevés and the residual relevés (Figure 5), perhaps due to the similar geographical distribution of both the dry and residual relevés (Figure A1 in Appendix A).

The rather narrow range in the mM-values indicates a clear preference of Stone pine (*Pinus cembra*) for fresh soils: the optimum was an mM of just above 5 (Figure 2).

Together with Larch, Stone pine is a common species found at the timber line of the Alps, although, unlike Larch, its range in elevation is more limited to higher altitudes: the residual relevés ranged from 1500 to 2270 m a.s.l., with the optimum lying between 1800 and 2000 m. The range of the dry relevés was narrower: 1700–2100 m a.s.l. (Figure 3). Of the dry relevés, SW-exposed sites were the most represented, although the general distribution over the different aspects was rather uniform (Figure 4). This was perhaps a result of the small number of dry relevés detailing the sites aspect (n = 83). Due to insufficient allocation of climate data to Larch and Stone pine relevés, statistical comparison of temperature and precipitation values of the dry and residual relevés could not be performed.

There are several broadleaved tree species in Austria that are the most valuable for sustainable forestry. We illustrate the distribution of the 10th percentile of driest relevés for deciduous trees in Figure 6 and project the relevés against ecological factors in Figures 7–10).



Figure 6. Cont.



**Figure 6.** Distribution of relevés along the gradient of mean moisture values calculated from vegetation relevés for 10 Angiosperm tree species ( $\bar{x}$ : arithmetic mean of all relevés, P 10: 10th percentile cutline of the 10% driest relevés, n: number of relevés).







**Figure 7.** Distribution of the relevés for 10 Angiosperm species along the altitudinal gradient (red bars: number of relevés belonging to the driest 10%, green bars: number of residual relevés).



**Figure 8.** Distribution of the relevés for 10 Angiosperm species between aspect classes (elevation class  $< 5^{\circ}$  refers to flat sites with a slope of less than 5°; red bars: number of relevés belonging to the driest 10%, green bars: number of residual relevés).



**Figure 9.** Thirty-year means of annual precipitation (mm) for the 10% driest relevés (red) and residual 90% relevés (green) for 10 Angiosperm species (Acecam: Field Maple, Acepse: Sycamore, Carbet: Hornbeam, Fagsyl: European beech, Fraexc: Ash, Quecer: Turkey oak, Quepet: Sessile oak, Quepub: Downy oak, Querob: Pendunculate oak, Tilcor: Small-leaved lime); significant differences between the dry and residual relevés represented as: \* = p < 0.05, \*\*\* = p < 0.0001; no symbol indicating no significant difference.



**Figure 10.** Thirty-year means of annual mean temperature (°C) for the 10% driest relevés (red) and residual relevés (green) for 10 Angiosperm species (Acecam: Field Maple, Acepse: Sycamore, Carbet: Hornbeam, Fagsyl: European beech, Fraexc: Ash, Quecer: Turkey oak, Quepet: Sessile oak, Quepub: Downy oak, Querob: Pendunculate oak, Tilcor: Small-leaved lime); significant differences between the dry and residual relevés represented as: \* = p < 0.05, \*\*\* = p < 0.0001; no symbol indicating no significant difference.

Most prominent for ecologically sound forest management is European beech (*Fagus sylvatica*). With respect to distribution over the moisture gradient (mM-values), Beech shows a similar pattern to Hornbeam (*Carpinus betulus*) (Figure 6). However, the slightly higher mean mM-value of all relevés (5.2) and that of the 10th percentile (4.73) indicates that Beech is—on average—less tolerant against dry conditions than Hornbeam. The residual relevés of Beech spanned from the lowest elevations up to 1640 m (Figure 7). In the

Northern Calcareous Alps, Beech can often be found in the forest communities at the timber line. However, the most drought-tolerant provenances seem to be distributed further down slope, between 300 and 1000 m a.s.l.

North-facing sites were most frequently represented by the residual relevés, while dry sites were more evenly distributed (Figure 8). Furthermore, both mean annual mean temperature (7.8/6.3 °C) and annual precipitation (962/1307 mm) were significantly different between the dry and the residual sites (Figures 9 and 10).

The distribution of relevés with Ash (*Fraxinus excelsior*, Figure 6) illustrates a preference for rather fresh site conditions: a fairly wide normal distribution (mM between 3.8 and 7.5) around a mean of 5.57, with a 10th percentile of 4.9. The elevations recorded for the Ash relevés ranged right up to 1340 m a.s.l., although the dry provenances appear to occupy lower elevations (generally below 500 m a.s.l., Figure 7).

While all aspects were well represented by Ash relevés, flat/slightly inclined sites were the most frequent. Flat sites were also frequent among the dry sites, although of the aspects, southern exposed sites were more common (Figure 8). As with Beech, both mean annual mean temperature (9.1/7.7 °C) and annual precipitation (657/1121 mm) were significantly different between the dry and residual sites (Figures 9 and 10).

The slightly skewed distribution of Sessile oak (*Quercus petraea* s.lat.) relevés means that while most frequently represented mM-values (4.5–4.75) lay close to the moist end of its range (5.7), the dry limit of this species distribution stretched right into the very dry parts of the moisture gradient (mM of 2.5) (Figure 6). Most of the residual Sessile oak relevés and all of the dry sites were located below 500 m, with the majority at around 350 m a.s.l. However, residual relevés from sites as high as 1200 m a.s.l. were also present (Figure 8). Apart from the dominance of the flat sites among the residual relevés, SE- to SW-aspects were most common among both the dry and residual sites. Finally, both mean annual mean temperature (8.2/8.7 °C) and annual precipitation (557/643 mm) were significantly different between the dry and the residual sites of Sessile oak (Figures 9 and 10).

The mean mM-values derived for Hornbeam showed a normal distribution around a mean of 5, ranging from 3.9 to 6.5 (Figure 6). The 10th percentile value of 4.54 demonstrates some degree of drought tolerance within Austrian Hornbeam populations. The residual relevés of Hornbeam ranged from the lowest elevations in Austria up to 1300 m a.s.l., with elevations between 200 m and 400 m the most frequent. The relative distribution of the dry relevés also mirrored this pattern (Figure 7). Generally, Hornbeam relevés on flat or only slightly inclined sites were the most common, although all aspect classes were well represented within the residual relevés. Flat or slightly inclined sites were also common among the dry relevés, though of the inclined sites, southern aspects (SE, S, SW) occurred more frequently (Figure 8).

Of the compared climatic variables, the dry relevés were shown to receive significantly less annual precipitation (686) over the last 30 years than the residual sites (778 mm) (Figures 9 and 10).

In comparison to Field maple (*Acer campestre*), the distribution of Sycamore (*Acer pseudoplatanus*) is rather narrower and finds itself more towards the moist part of the gradient. The mM-values ranged from 4.7 to 6.5, with values around 5.5 the most frequent (Figure 6). This species clearly prefers more fresh site conditions, as illustrated by the rather high 10th percentile value (5.26).

Both the dry and residual relevés of Sycamore also demonstrate a wide range in elevation (Figure 7). The elevation of the residual relevés ranged from 100 to 1700 m a.s.l., while those of the dry relevés were restricted to lower elevations (200 to 1000 m a.s.l.). Generally, the N-and NE-aspect classes were strongly represented by the Sycamore residual relevés, although the distribution for the dry relevés was comparatively more uniform (Figure 8). Relevés belonging to the driest 10% demonstrated significantly lower mean annual precipitation than the residual relevés (1339 mm compared to 1423 mm). Meanwhile the difference in mean annual mean temperature was statistically insignificant (Figures 9 and 10).

Of the Oaks, Pendunculate oak (*Quercus robur*) is the most competitive on moist sites, though the wide distribution over the moisture gradient illustrates the wide range in moisture tolerance within its Austrian population. This species demonstrated a normal distribution (between 3.2 and 8.0) around a mean of mM = 5.1, with a 10th percentile of 4.48 (Figure 6). In terms of elevation, Pendunculate oak relevés were found as high as 1100 m a.s.l., though the majority of the distribution of both the dry and residual relevés was restricted to the foothill zones (below 500 m) (Figure 7). Many of the sites were found on rather flat terrain, though the frequency of southern exposed slopes was clearly larger for the dry relevés (Figure 8). Again, as with Sessile oak, only the difference in mean annual precipitation between the dry and residual sites (562/580 mm) was significant (Figure 9 and 10).

The distribution of the Small-leaved lime (*Tilia cordata*) showed a clear general preference for fresh sites (i.e., soils with a balanced water budget). A rather normal distribution around a mean mM-value of about 5 (5.08) was observed, spanning a range from 3.4 to 6.3. The 10th percentile was 4.59 (Figure 6). While the relevés ranged from the foothills to montane elevations (maximum of 910 m a.s.l.), the dry sites were restricted to the foothills and submontane zones (Figure 7). The residual relevés indicated a tolerance of most aspects and inclinations, though N-exposed sites appear to be preferred. The more drought-adapted provenances seem to be found more often on S- to SW-exposed sites (Figure 8). There was no significant difference in either mean annual precipitation or mean annual mean temperature between the dry relevés and the residual relevés (Figures 9 and 10).

Downy oak (*Quercus pubescens* s.lat.) exhibited a very similar distribution to that of Turkey oak (*Quercus cerris*), except for being shifted slightly further towards the drier end of the moisture gradient. The distribution ranged from 3.1 to 4.8, with a mean mM-value and 10th percentile of 3.9 and 3.43, respectively (Figure 6). Both the dry and residual relevés demonstrated very similar ranges in elevation, though the distribution within this range was opposite to one another: relative dominance of lower elevations among the residual sites, and vice-versa for the dry sites (Figure 7). In both cases, the south-exposed sites were most frequent for Downy oak (Figure 8). Although no significant difference in mean annual mean temperature was observed, the difference in mean annual precipitation between the dry and residual sites (562/580 mm) was significant (Figures 9 and 10).

The mM-values of Turkey oak were distributed between 3.2 and 5.6 (Figure 6). The mean mM-value was calculated at 4.4, indicating an optimum on dry to slightly desiccating soils. While elevations ranged from 180 to 570 m a.s.l., the majority of both the dry and residual relevés were found to be 200 and 300 m a.s.l. (Figure 7).

For both the dry and residual relevés, a similar distribution among the aspects was observed; a dominance of flat/slightly inclined sites, with southern exposures the next most frequent (Figure 8). A significant difference in mean annual precipitation was also observed between the dry (561 mm) and residual (628 mm) relevés (Figures 9 and 10).

The mM-values of relevés with Field maple ranged from 3.4 to 6.6, although as the histogram depicts (Figure 6), the lower mM-values are poorly represented. The optimum appears to be around 5, while the mean mM-value of the 10th percentile was 4.5. The distributions between elevation classes revealed that Field maple generally occurs at lower elevations, with elevations of around 300 m most common (Figure 7). Furthermore, although data on aspect was limited for this species, the distribution of the residual relevés between aspect classes indicates that this species prefers  $\pm$  flat sites with an inclination less than 5° (Figure 8). There was no significant difference in either annual precipitation or annual mean temperature between the driest 10% and the residual relevés (Figures 9 and 10).

### 3.2. Geographical Distribution of the Relevés and Locations of Potentially Drought-Tolerant Provenances

Details of the geographical distribution of the relevés with interesting tree provenances are given in Appendix A. Figure A1 demonstrates the distribution of relevés comprising of four important Austrian Conifer trees, whereas Figures A2 and A3 show the same for ten Angiosperm trees.

The selected tree species are economically and ecologically important for actual forest management in Austria. From these maps one can deduce in which parts of Austria source populations can be sampled for the proliferation of trees adapted to climate change in tree nurseries.

In case of Norway spruce the map of evaluable relevés (Figure A1, green symbols) does not reflect exactly the natural distribution within Austria. This map fails to illustrate the very hotspot of natural Spruce occurrences in the Central Alps. Unfortunately, 75% of all relevés with Spruce missed detailed geographical coordinates and cannot be shown in our map. Nevertheless, one can forage for the red dotted source populations of Spruce in the northern and eastern parts of the Alps and the Hercynian region. The lowland spruce forests cannot provide pre-adapted spruce, due to the fact that all these stands are planted.

The map for Scots pine (Figure A1) illustrates that its occurrences in Austria are scattered and bound to dolomitic or acidic substrates. Like with Spruce, Scots pine is mostly planted in the lowlands and suffers from the drought periods. Drought-adapted provenances can be expected to the west in the Tyrolean Inn valley, in some dolomitic outcrops of the northeastern and southeastern Alps, and in the easternmost part of the Hercynian region at the border to the Pannonian lowlands.

In case of Silver fir (Figure A1), there can be seen also a gap of relevés in the Central Alps that can be called  $\pm$  natural. High rainfall areas in the Alps and the Hercynian region serve several relevés with fir, and the corresponding 10% of the driest sites are to be found throughout the whole distribution area. This allows a representative selection of drought-adapted ecotypes for Silver fir nurseries.

The Austrian pine is documented naturally only from few dolomitic sites towards the eastern edge of the Alps (Figure A1). There are more plantations on extreme soils such as in the plains south of Vienna and in some sand dune systems east of Vienna. Austrian pine is well adapted to soil generated drought and was, therefore, planted far from its natural area, such as the Vinschgau in South Tyrol or the dolomitic and sand hills in Slovakia and Hungary. Foresters experienced pest problems in plantations outside the natural area [54]. Therefore, planting of this species sounds very interesting due to its high drought resistance, but needs more empirical exploration and testing.

We found in the database also many relevés with Stone pine, which occur preferably in the subalpine zone of the central Alps and a few places in the Northern Calcareous Alps of Austria. There were not enough relevés from the 10th percentile of the lowest mM-value that were assigned coordinates, which would allow exact positioning in our map. In consequence, we cannot provide a separate map. The same problem of too few relevés for mapping holds true for European Larch, which is generally more widespread throughout the Alps. Detailed descriptions of both relevé pools are given in Appendix A.

From the deciduous native trees, some Oak species were specifically promoted and propagated by foresters in some regions. More widespread trees such as European beech are not so much kept in nurseries. Indeed, European beech is the most widespread deciduous tree in Austria (Figure 11), avoiding the central parts of the Alps and the very flat plains of the Pannonian lowlands because of rather continental climate [55]. This species grows on all kinds of basic to acidic soils and is currently expanding its local range towards the lowlands as well as upwards to the timberline. Beech is a tree dominating wherever it can grow undisturbed. Skeletal dolomitic soils throughout the Northern Calcareous Alps and sites at the dry edge of the Alps and the Hercynian region provoke the establishment of several populations showing awesome survival under dry conditions (Figure A2). The example of Beech illustrates the practical use of the results of this dataset and other such studies. We could select drought-tolerant populations in all forest ecoregions [26] where Beech represents a focus species in Austrian forestry. Specifically, there are several relevés with low mM-values filtered in the forest ecoregions 4.1 and 4.2 (Figure 12) that represent the center of beech forestry. The identification of potentially drought-adapted provenances for the different forest ecoregions will help identify and collect seeds from source populations for nurseries to help Austrian forestry adapting to the projected changes in climate.



**Figure 11.** Distribution of European beech (*Fagus sylvatica*) in Austria; grid-based occurrences of different status, grids according to [52].



**Figure 12.** Grid cells corresponding to the driest 10% relevés with dominant or subdominant European beech (*Fagus sylvatica*) located within Austrian Forest Ecoregions 4.1 (to the **left**) and 4.2 (to the **right**).

Ash is very specific, as it is a formerly widespread but rarely dominating species, but it is suffering enormous from pest attacks at stand level [56] causing serious diebacks. The potential for the selection of drought-tolerant populations is obviously higher in the eastern part of Austria (Figure A2). In this species, the search for drought tolerance is probably less important than the search for pest resistant progeny [57].

From the oaks, Sessile oak is commonly used by lowland forestry in eastern Austria. Several relevés on dry sites are aggregated at the border between the Hercynian Region and the northern part of the Pannonian lowland (Figure A2). In case of Pedunculate oak (Figure A3), several ecotypes differing by their need of water are known and commercially used in forestry. Though there is a 10th percentile of relevés from dry habitats, it seems unclear if they would fit to other site parameters as well. The remaining two oak species are of low frequency at the moment, and their areas are restricted to the east (Turkey oak) and to the east and south of Austria (Downey Oak), respectively (see Figure A3). Both species are widespread towards the south of Europe, and one can expect that the 10th percentile of the driest sites may provide very drought- and heat-resistant provenances.

Hornbeam is known in forestry, i.e., for its high ecological input by stimulating nice humus conditions. It is widespread throughout Austria's lowlands and peripheral parts of the Alps. Consequently, also the 10th percentile of driest relevés is to be found outside or towards the edge of the Alps (Figure A2).

Scyamore grows from the lowlands up to the subalpine zone, preferring nutrient-rich and relatively moist sites (Figures 13 and A2). The driest 10% of relevés cover quite nicely the whole distribution area.



**Figure 13.** Moisture indicator values (Box-plot) for the driest 10% relevés representing relatively sites of 16 Austrian tree species (Pinnig: Austrian pine, Pinsyl: Scots pine, Qerpub: Downey oak, Quepet: Sessile oak, Quecer: Turkey oak, Querob: Pendunculate oak, Acecam: Field maple, Tilcor: Small-leaved lime, Carbet: Hornbeam, Lardec: Larch, Fagsyl: European beech, Fraexc: Ash, Picabi: Norway spruce, Pincem: Stone pine, Abialb: Silver fir, Acepse: Sycamore); arranged according to increasing mM-values. \* = p < 0.05, \*\*\* = p < 0.0001.

From the maple species, Field maple is the second most important in Austrian forestry. Its natural area covers the Pannonian lowland, where it is widespread (Figure A3). There are several populations that could serve as drought-resistant source populations for propagation of seedlings well adapted to climate warming.

Finally, the Small-leaved lime is valuable also for increasing the quality of humus even on dry sites. Source populations for drought-tolerant provenances are to be found mostly in the lowlands, but few are also available in the continental parts of the alpine Inn Valley in Tyrol (Figure A3).

#### 4. Discussion

According to the Austrian Forest Act [22], provenances from the same forest ecoregion represent those best adapted to the respective site conditions, i.e., soil and climate conditions. The Forest Reproductive Material Act [25,58], subsequently, states that these provenances represent the best sources of reproductive material to maintain the optimal performance of Austria's forests, i.e., the optimal provision of production, welfare and protective functions. However, with the ongoing climate change it seems questionable whether these provenances will be the best adapted under future site conditions.

Currently, there are relatively few data sources that forest managers can consult when selecting the most appropriate reproductive material for a given site. Regarding performance in terms of timber production (i.e., yield potential), extensive data on yield and increment from several thousand plots in Austria, covering the main production forest species, are made available by the national forest inventory [59]. However, these data only provide an indication of production potential, and, importantly, production potential under current site conditions; the dataset gives no indication of performance under future site conditions. Austrian forestry is therefore in need of additional data so as to select the provenances best suited to the likely changes in climate, i.e., increases in mean temperatures and drought incidence [60].

This study demonstrates the potential of using the Austrian Vegetation Database [61] in identifying the provenances likely to be best adapted to future climate conditions. Like the Austrian forest inventory, this database is very extensive in its spatial coverage, with

over 36,000 vegetation relevés taken from all over Austria. By deriving ecological indicator values of site moisture, our study demonstrates the relative range in site moisture conditions where 16 Austrian tree species occur. Furthermore, the driest sites identified here (i.e., the driest 10%) potentially represent the provenances of each species that are most adapted to drought conditions (Figure 13). While inter-population variations in phenotype may result from acclimation mechanisms [62], site-specific selection pressures (natural or even artificial, e.g., negative selection thinning based on vitality), if allowed to proceed over several generations, are likely to have facilitated some adaptation to drought due to the high within-population genetic variation typical for trees [63]. While the derived indirect ecological indicator values give no indication of yield potential, the data may help managers promote stability by identifying drought-tolerant provenances. This represents a key objective within the emerging sustainable forest management paradigm, where the optimal provision of functions and products (e.g., promoting biodiversity and protective functions)

and promoting biodiversity in forests even under climate change prospects [65,66]. Modeling can help to understand the general future processes of stand dynamics in forests under climate change [67,68], but distribution models are commonly based on the actual or formerly used and widespread provenances of trees [69]. The potential of pre-adapted ecotypes of native tree species is not included in any model. According to these models, European beech might disappear from the Middle European lowlands and withdraw to higher mountain regions [69]. This scenario could possibly be avoided if drought-tolerant provenances were used for reforestation.

is delivered by maximizing ecosystem function rather than maximizing yield [30,33,64]

As expected, many of the identified potentially drought-adapted populations identified (i.e., the driest 10%) were, as expected, located in the warm and dry regions of Austria (Figure 1). Many were found, for instance, in the Pannonian region of the Vienna Basin. As this area is subject to rather intensive agriculture, most of the dry sites were located on the margins of this area, e.g., along the Manhartsberglinie, the area of Wachau or the Thermenlinie, where due to the higher reliefs, these areas are less suitable for agriculture purposes than say the foot of the Leiser and Hainburg Mountains or the Leithagebirge. The dry sites of Turkey and Downy oak, Field maple and Austrian pine were found limited to these particular areas. In addition to the Pannonian areas, other dry areas such as the inner Alps, the Styrian Fringe Alps and the South-eastern foothills were also identified as potential locations for drought-adapted provenances of Pendunculate oak and Hornbeam. Furthermore, the dry sites of Scots pine were also restricted to the drier eastern parts of the country.

The two-sample *t*-tests indicated that reduced precipitation (thirty-year mean annual precipitation) was a decisive factor distinguishing between the dry and residual sites of Norway spruce, Scots pine, European beech, Hornbeam, Sycamore, Ash, and Large-leaved lime, as well as Turkey-, Sessile- and Downy oak (Figures 5 and 9). Furthermore, due to increasing evaporative demand with increasing temperature, it was also shown that the dry sites of European beech, Norway spruce, Ash, Sessile oak and Large-leaved lime were on average significantly warmer than the corresponding residual sites (Figures 5 and 10).

Despite the often-significant difference in the mean climatic variables between the dry and residual sites, it was also evident that topographical features such as aspect are equally relevant in terms of site dryness. For example, southern-exposed (SW, SE, S) slopes where due to higher incident radiation, evaporative demand is typically higher, were particularly frequent amongst the dry sites of Silver fir, Norway spruce, Larch, Hornbeam, European beech, Ash and Small-leaved lime as well as Turkey-, Pendunculate and Sessile oak, (Figures 4 and 8). The data also revealed a role played by elevation; the dry sites of Stone-, Austrian-, Scots pine, Field maple, Sycamore, European beech, Ash and Smallleaved lime as were, typically, more frequent at lower and, therefore, warmer elevations with higher evapotranspiration than the corresponding residual sites (Figures 3 and 7). However, this may indirectly correspond to a precipitation effect due to increased orographic precipitation with increasing elevation. Finally, the data may also indicate a relationship between hydrological soil properties and the ecological

indicator values derived. For example, many of the dry sites of European beech, Norway spruce, Silver fir and Sycamore were found within the Northern and Southern Calcareous Alps, where precipitation is relatively high. This observation may be due to the low water holding capacity of the thin rendzina soils typical of these regions [38]. Nevertheless, the dry sites of the Small-leaved lime and Ash were, despite their wide distribution, limited almost exclusively to areas of low rainfall, despite the wide distribution of these species.

These variations in dryness, due to factors such as topography and hydrologicallyrelevant soil properties, may be particularly significant when identifying drought-adapted provenances within areas with a rather homogenous climate, such as forest ecoregions [26]. Due to the wide distribution of Beech and, thus, the number of available relevés, it was possible to identify potentially drought-adapted populations for different forest ecoregions (Figure 12). Given the uncertainty posed by the introduction of new untested provenances [33], the identification of potentially drought-adapted provenances in the different ecoregions would at very least provide greater flexibility to forest managers who want to foster adaptation to climate change. However, these provenances must nonetheless be screened themselves via provenance trials/pot experiments to confirm whether or not they are superior with respect to drought resistance [66].

While our results illustrate the potential of the Austrian Vegetation Database to facilitate the adaptation of Austrian forestry to climate change, there are significant weaknesses in the database, particularly concerning the geographic location of the relevés. In some cases, precise geographic coordinates have been assigned to the relevés. However, in many cases, the relevés have only been assigned to quadrants of the floristic mapping according to [52], i.e., grid cells of  $5 \times 3$  geographic minutes. A substantial number of relevés currently bear no geographic information at all, except for a verbal description of the sample region. In many cases, the spatial accuracy of the data could be improved by consulting the original sources, which is, however, a time-consuming task. Another disadvantage of the database is the age of some relevés, so that one has to check if the described stands even still exist.

If an identified autochthonous provenance still proves to be inadequate in terms of adapting to climate change, forest management may nonetheless look at provenances of the same species from abroad or new exotic species [33,70]. However, as the data of this study indicates, forest managers may not need to look abroad for alternative species more resistant to drought stress. As Figure 13 shows, rather drought-tolerant provenances for a number species already exist here in Austria, e.g., Austrian- and Scots pine and Downy-, Sessile- and Turkey oak. While their suitability to other site-specific factors must of course be considered (e.g., soil pH, light and nutrient requirements etc.), the data nevertheless illustrate that there is enough potential within Austria's autochthonous tree species for them to be at least be considered alongside alternative adaptation strategies such as exotic provenances or species. First research projects are conducted, e.g., for Sessile oak in the national park Thayatal [71]. This area belongs to the Manhartsberglinie where several of the 10% driest relevés of this species are situated. Furthermore, stands of Pendunculate oak, which are identified as vulnerable to climate change, could be steadily adapted to climate change by steadily introducing more drought-tolerant Oak species such as Sessile oak or Downey oak. The well-known hybridization of those Oak species [72] may support the natural introgression of drought-tolerance traits into former less resistant Pedunculate oak populations [73].

## 5. Conclusions

While the pressure of climate change continues to push the case for foreign provenances or exotic species [19,70], their introduction, particularly that of exotic species, may have negative ecological effects [33,74,75]. Forestry should, therefore, not ignore the autochthonous options available to adapt to the projected changes in climate. Our study illustrates that a potentially significant amount of inter- and intraspecific variation in drought tolerance is available within Austrian tree populations. The next steps are to assess this potential and to design effective ways of incorporating it into the strategies aimed at helping the Austrian forestry to adapt to climate change. Seed material from droughtresistant populations designated by our selection strategy can be cultivated in tree nurseries to be planted on sites that are expected to be more prone to water deficiency under future climate scenarios. However, the potential of more sustainable water management in some tree provenances cannot guarantee the overcome of other hazards, such as unexpected pest waves [9,10,54].

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#### Appendix A

## Geographical Distribution of the Relevés and Locations of Potentially Drought-Tolerant Provenances

Figure A1 demonstrates the distribution of relevés comprising of six important Austrian Conifer trees, whereas Figures A2 and A3 show the same for 10 Angiosperm trees.

There were 4452 relevés with dominant or subdominant Norway spruce (*Picea abies*) available for analysis. As only 24% could be assigned grid cells (Figure A1), a more precise written description of the real distribution over Austria is given below.

Burgenland: a few relevés came from the Günser Mountains.

Carinthia: southern slopes of the Hohe Tauern, Weißensee area, Spittal an der Drau, Karawanken, Nockberge, St. Veit an der Glan, Villach (Dobratsch, Gerlitzen, Kanzianiberg), Carinthian Basin (Gurkniederung, Hermagor, Klopeiner lake Lavant valley), Loibl area, Lesachtal (Gailtaler und Karnische Alpen), Koralpe.

Lower Austria: Waldviertel (Weinsberger Forest, Litschau, Heidenreichstein, Gmünd, Zwettl, Waidhofen an der Thaya, Thaya valley near Hardegg, Wild, Kamptal, Ostrong and Jauerling), foothills of the Alps (Amstetten), Northern Calcareous Alps (Dürrenstein, Lunz, Göller, Neuwald, Rothwald, Hohe Wand, Rax-Schneeberg), and Wechsel.

Upper Austria: Northern Calcareous Alps (Dachstein Nord, Bad Aussee, Gmunden, Traunstein, Höllengebirge, surrounding of Molln, Kirchdorf an der Krems, Sengsengebirge,), Mühlviertel (Böhmerwald, Freistadt, Windhaag, Rohrbach, Wegscheider Bergland), Alpine foothills (Braunau am Inn, Mondsee, Mattighofen, Ranshofen).

Salzburg: Hohe Tauern (Ammertal, Hollersbachtal, Obersulzbachtal), Northern Calcareous Alps (Leoganger Steinberge, Untersberg, Gaisberg, Hochkönig, Tennengebirge, Steinernes Meer), Lungau (Tamsweg, Gerlosplatte), Zell am See.

Styria: Northern Calcareous Alps (Ennstaler Alps, Aflenzer Staritzen, Mitterbach, Bruck an der Mur, Veitsch, Hochschwab), Ennstal, Mürztal (Krieglach), Wechsel, Fischbacher Alps, Joglland, Murtal (Murau, Unzmarkt, Judenburg), Murauer Nockberge, Neumarkter Sattel, Hartberg, Graz, Schöckl, Hochlantsch, Koralpe, Gleinalm, Bad Radkersburg, Hebalm, and East-Styrian Hügeland.

Tyrol: Northern Calcareous Alps (Außerfern, Karwendel, Kaisergebirge, Lechtaler Alps, Außerfern, Mieminger Kette), Kitzbühel, Nauders Reschenpass, Landeck, Imst, Innsbruck Schwaz, Kufstein, Interior Alps (Pitztal, Ötztal, Tuxer Alpen), East Tyrol (Lienz).

Vorarlberg: Bludenz, Brandnertal, Bregenz, Dornbirn, Gamperdonatal, Gadental, Kleines Walsertal, Walgau.

The 10% driest sites with Norway spruce are well distributed widely over Austria, though noticeable absentees include Vorarlberg, Mühlviertel and Koralpe. Interestingly, relevés from the lowlands commonly comprising of more thermophilous species are not represented therein.

A total of 1064 relevés with dominant or subdominant Scots pine (*Pinus sylvestris*) were available from the database. As the map (Figure A1) illustrates, the geographical distribution is dominated by the eastern Waldviertel, the Oberinntal of Tyrol, the northern edge of the Alps, the Thermenalpen, Southern Carinthia, West-Styrian Bergland, and Southern Burgenland. Of the relevés not assigned grid cells, the following areas are represented: Mühlviertel (including the Bohemian Forest), Sauwald, Waldviertel (Weinsberger Forst, Waidhofen an der Thaya), the Northern Foothills (Trauntal bei Wels), the Northern Calcareous Alps in Salzburg, Styria and Lower Austria, the Interior Alps of Tyrol (Ötztal), Villach, the Lavant valley and Koralpe.

Considering the known range of Scots pine in Austria, the areas of Nockberge, the Gailtaler Alps, Bucklige Welt, Central Burgenland and Innviertel were conspicuous by their absence.

Many of the 10% (106) dry sites with Scots pine occurred in the dry areas of the Interior Alps, such as along the Upper Inn valley. Nevertheless, areas such as the Manhartsberglinie, the Mur valley north of Graz and Southern Carinthia were also represented.

The majority of the 632 relevés with dominant or subdominant Scots pine were located around the northern, southern and eastern borders of the Alps (Figure A1). Due to missing data regarding the coordinates of relevés from Zwettl, Obersulzbachtal, Sauwald, and Mühlviertel, many of these could not be assigned to grids on the map. Furthermore, in comparison to the actual distribution of Fir within Austria, regions such as Waldviertel, Innviertel and East-Styrian Hügelland are also underrepresented by the relevés.

The 10% relevés on relatively dry sites were scattered rather widely across Austria, though they generally avoided the zones of the northeastern Alps with very high rainfall. However, a large proportion can be found in the Gamperdona valley, the Lech valley Alps, the Leogang Mountains the "Thermenregion" and the East- and West-Styrian mountains. Several of the dry relevés can also found in the dry regions south of the Alps (between Lienz and the Lavant valley), while two relevés were also sourced from dry regions of the Waldviertel.

The 323 relevés with European Larch (*Larix decidua*) were distributed rather well over the Alpine regions of Austria, with the exception of Vorarlberg, where only 3 were present (e.g., the Brander valley). The Tyrolean regions of the Northern Calcareous Alps (Lechtaler Alps, Karwendel and the Mieminger Range) are well represented, while contributions from the Styrian (Ennstaler Alps, Gesäuse, Hochschwab, Schneealpe), Salzburg (Steinernes Meer, Kleinarltal, Postalm, Osterhorn, Untersberg, Schafberg, Tennengebirge), Upper Austrian (Dachstein, Höllengebirge, Sengsengebirge) and Lower Austrian (Rax, Göller) parts of the Northern Calcareous Alps were also significant. Contributions were also made by the Central Alps (Stubaier Alps, the Samnaun, Langau, Knittelfeld, and the Koralpe) and the Southern Calcareous Alps (the Karawanken, the Karnische Alps and the Villacher Alps). When compared to the actual distribution within Austria, areas such as Pinzgau, the Nock Mountains, the Niedere Tauern and the southern slopes of Hohe Tauern, Mühl- and Waldviertel were rather underrepresented by the relevés of the data pool.

Due to the lack of assignment of grid cells to the relevés, a graphical representation is not given.

The majority of the 10% dry relevés were located in the dry stands in the Virgen valley/East Tyrol, the Tyrolean Interior Alps and several in the Northern Limestone Alps (Lechtaler Alps, Mieminger Range).

The 227 relevés of dominant or subdominant Austrian pine (*Pinus nigra*) were almost completely concentrated around the eastern edge of the Alps. Natural sites are found in the Thermenalpen, secondary sites found in Steinfeld. Exactly 55 of the Austrian pine relevés came from Carinthia, though these are not shown on the map below (Figure A1), as these relevés could not be assigned to grid cells. The sporadic occurrence of Austrian pine observed in Burgenland was, however, not represented by the Austrian pine relevés.

The distribution of the 105 dry sites was also limited to the Eastern edge of the Alps.

The 80 relevés of Stone pine (*Pinus cembra*) were mainly distributed between the edge of the intermediate and interior Alps of Tyrol (including Ampass, Weerberg), the Central Alps of Salzburg (Pinzgau: Obersulzbachtal), parts of the Northern Calcareous Alps (Totes Gebirge, the Dachstein massif, the Ennstaler Alps) and, to some extent, the Eastern Alps (the Murauer Nockbergeand the Nockberge National Park).

Due to impossible assignment of grid cells to the relevés, a graphical representation is not given.

The eight relevés on very dry sites demonstrate a rather scattered distribution: Ampass, Weerberg, the Obersulzbach valley, the Nockberge National Park and the Murauer Nockberge.

Of the total 2681 relevés with European beech (*Fagus sylvatica*) as either dominant or subdominant tree, 91% were assigned grid cells. Consequently, the geographical distribution of the relevés is well illustrated by Figure A2. The Beech relevés as shown were distributed over much of Austria. From Vorarlberg, through the Northern Calcareous Alps right to the Wienerwald, Beech occurrence is almost continuous. A concentrated area of occurrence around the Southern Alps is conspicuous. Gaps in the distribution are caused by the limits to the natural range of Beech (e.g., in the foothills and Interior Alps) and by anthropogenic interventions in the Bohemian Massif. Furthermore, comparison with the actual distribution (Figure 11) illustrates the underrepresentation of, e.g., the Mühl- and Waldviertel and the East-Styrian Hügelland.

Relatively few of the 10% rather dry sites with Beech were found in the West. Significant clusters are located rather in the Eastern part of the country: the Danube valley near Aschach, Wachau, the eastern Waldviertel, the Dunkelsteiner Wood and Wienerwald, the Thermenregion, the Mur valley between Bruck und Graz, and the Leithagebirge (Figure A2). Beech stands on dry sites can also be found in the Carinthian Basin and the Karawanken.

A total of 1097 relevés with Ash (*Fraxinus excelsior*) were available, of which 58% could be assigned with grid cells. The majority were sourced from the parts of the Northern Calcareous Alps (Vorarlberg, Salzburg, Upper Austria, and the Wienerwald), areas where Ash most often occurs (Figure A2). The rest of the relevés were generally scattered between the Bohemian Massif, the northern Foothills, South-west-Styrian Hügelland and the Koralpe. However, the areas of Nockberge and the East-Styrian Hügelland were conspicuous by their absence.

The 10% driest sites of Ash were almost only found in Eastern Austria (Thermenregion, the Leithagebirge, the Wienerwald, Kamp valley, and the Traun valley near Wels), though two sites were found far west: Montafon and the Upper Inn valley.

A total of 798 relevés with dominant or subdominant Sessile Oak (*Quercus petraea*) were available. As above, the distribution of the relevés was confined to Eastern Austria, though its range spread further than just the Pannonian area. A minority of western relevés were found in the Upper Inn and Gail valleys. The upper Danube valley, the Wald- and Weinviertel, the Wienerwald and the hills of Burgenland and Styria were represented by the relevés. The distribution also stretched into the Alps and the northern foothills, though these particular relevés could not be assigned grid cells and are, thus, not illustrated in Figure A2.

Of the 10% (79) relevés on dry sites, the majority were confined to the eastern Waldviertel (Thaya Valley National Park, Manhartsberglinie, and Wachau), though several were also present outside this region (Weinviertel, Bruck an der Mur and the Kanzianiberg near Villach).

Of the total 679 relevés where Hornbeam (*Carpinus betulus*) was either dominant or subdominant, 85% were assigned grid cells. Consequently, the geographical distribution of the relevés is well illustrated by Figure A2. The distribution ranges from the Salzburg Flachgau to the upper Danube valley, through the southern and eastern Waldviertel, towards the Weinviertel. Significant numbers of relevés also came from the Wienerwald, the Leithagebirge, Central and Southern Burgenland, the Mur valley north of Graz and the East- and West-Styrian Hügelland.

The 10% dry sites of Hornbeam were located in the Danube valley near Aschach, the eastern Waldviertel, Wachau, the Thermenregion, the Leithagebirge, the Mur valley north of Graz and the hills south of Graz (Figure A2).

Particularly large contributions to the Sycamore (*Acer pseudoplatanus*) relevés came from the Northern Calcareous Alps of Vorarlberg (Klostertal, Bregenzerwald), Salzburg, Upper Austria (Höllengebirge) and Lower Austria (Ötscher region), as well as several sites from the Bohemian Massif (Sauwald). Styria contributed sites from the Niedere Tauern and the Western Hügelland, as well as from the East- and Central-Styrian Mountains. Isolated sites from the Interior and Intermediate Alps, as well as sites from the Lavant valley in Carinthia, also contributed (Figure A2).

The 10% (47) dry sites were scattered over an area from Vorarlberg in the West right over to the Hainburg range in the East. Nevertheless, a concentration of sites just south of Vienna was observed.

The native Pendunculate oak (*Quercus robur*) enters deepest into the Oceanic regions of Austria (Figure A3). The 385 relevés with Pedunculate oak are widespread between Montafon, the Inn valley, Flachgau, the Mühlviertel, the northern Waldviertel, the Weinviertel, the Industrieviertel, Northern and Southern Burgenland, the upper Mur valley, Southern Styria and the Carinthian Basin.

The majority of the 38 driest sites were distributed along an almost straight transect that stretched from the Manhartsberg mountain range to the Traisen valley. Nevertheless, a considerable number of sites were concentrated around the eastern Weinviertel and Leithagebirge. Isolated sites were also located in the Inn valley, the Carinthian Basin and the Mur valley north of Graz.

Most of the 200 relevés where Small-leaved lime (*Tilia cordata*) was either dominant or subdominant generally came from Vorarlberg (Rhein valley and Montafon), the Inn valley and Flachgau (Figure A3). Nevertheless, the Alpine foothills (Traun floodplains), the Mühl-, Wald- and Weinviertel, the Danube floodplains, the Leithagebirge, the Mur valley north of Graz and Southern Styria also contributed a number of relevés.

Apart from one site in the Inn valley, the 10% driest sites of Small-leaved lime were restricted to the east of Austria: Wachau, the Danube floodplains, the Mur valley and the Carinthian Basin.

As with Turkey oak, the relevés of Downy oak (*Quercus pubescens*) seem to favor the Pannonian plain (Figure A3). Though significant numbers were found in the Wachau and Thaya Valley National Park, the majority came from the Weinviertel, Wienerwald, Thermenregion and Northern and Central Burgenland. Some relevés were, however, found in the Carinthian basin, from Kanzel near Graz and the central Inn valley near Zirl, though grid cells could not be assigned to these relevés.

The 10% driest sites of Downy oak were located in the Thaya Valley National Park, Wachau, the Weinviertel (e.g., the Bisamberg), the Thermenregion, and the Leithagebirge (Figure A3). Dry sites were also found in parts of Carinthia, Styria and Tyrol, though these sites could not be assigned to grid cells on the map above.

All the 156 relevés with dominant or subdominant Turkey oak (*Quercus cerris*) came from the Pannonian regions (westernmost plots from the Pulkau- and Lower Traisen

valley). The majority are gathered around the Leiser Mountains, Wienerwald, Vienna Basin, Leithagebirge and Central Burgenland (Figure A3).

The 10% specifically dry sites were located in the Pulkau valley, the St. Pölten area, the Leithagebirge and the Weinviertel (Zaya, Hochleitenwald).

The 113 relevés where Field maple (*Acer campestre*) was dominant/subdominant were distributed between Lower Austria and Burgenland (Figure A3). Many were located in the Wachau region, with contributions also coming from the Weinviertel, Vienna, the Thermenregion, the Leitha Mountains, Leitha floodplain, the March and Danube floodplains, the Hainburg Mountains, the southern Vienna Basin and Central Burgenland.

The 10% dry sites are found in the Wachau region (Dürnstein), Vienna (Leopoldsberg), the Leitha Mountains, the Weinviertel and central Burgenland.



**Figure A1.** Grid cells representing vegetation relevés of Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), Silver fir (*Abies alba*), and Austrian pine (*Pinus nigra*); to the left, green: grids corresponding to all locatable relevés (52% of the total relevés were assigned grids); to the right, red: grids corresponding to the locations of the relevés of the driest 10% (90% were assigned grids).



**Figure A2.** Grid cells representing vegetation relevés of European beech (*Fagus sylvatica*), Ash (*Fraxinus excelsior*), Sessile oak (*Quercus petraea*), Hornbeam (*Carpinus betulus*), and Scyamore (*Acer pseudoplatanus*); to the left, green: grids corresponding to all locatable relevés (52% of the total relevés were assigned grids); to the right, red: grids corresponding to the locations of the relevés of the driest 10% (90% were assigned grids).



**Figure A3.** Grid cells representing vegetation relevés of Pedunculate oak (*Quercus robur*), Smallleaved lime (*Tilia cordata*), Downy oak (*Quercus pubescens*), Turkey oak (*Quercus cerris*), and Field maple (*Acer campestre*); to the left, green: grids corresponding to all locatable relevés (52% of the total relevés were assigned grids); to the right, red: grids corresponding to the locations of the relevés of the driest 10% (90% were assigned grids).

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