Identifying Replacement Tree Species for Maintaining Bryophyte Diversity: A Novel Method for Assessing Community Similarity

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Highlights

- A novel method, using normalised species abundances and Euclidean distance, effectively quantifies similarity between two communities.
- Bark water holding capacity and pH are factors which affect the abundance of epiphytic bryophytes.
- The native trees *Quercus petraea* and *Q. robur* could be jointly managed for conservation.
- Either *F. sylvatica* or *Q. rubra* could be a good replacement for *Q. petraea*/*robur*.
- A combination of *A. pseudoplatanus* and *T. europaea* could support many *F. excelsior*-associated bryophytes.

Abstract

Climate change and a recent surge in global trade are increasing the range of various pests and pathogens of trees, leading to the decline of many keystone tree species worldwide. In the UK, three native oak and ash species (*Quercus. petraea, Q. robur* and *Fraxinus excelsior*) are dying due to numerous pests and pathogens, threatening hundreds of obligate and highly associated species. Epiphytic bryophytes are just one example of organisms whose survival depends on that of their host tree, and they play crucial roles within the ecosystem. The replacement of diseased trees with alternative species has been put forward as a potential solution to mitigate the effects of losing keystone tree species and their associated biodiversity. This study compared the three native declining trees with six potential substitutes in an attempt to identify replacement tree species which host similar bryophyte communities to the native trees. The study analysed three bark chemistry properties (water holding capacity, pH and conductivity) and proposed a novel method (NEDI) for assessing community similarity, which uses normalised abundances and Euclidean distance. Bark water holding capacity and pH both emerged as significant factors determining the abundance of bryophytes. This information and that gained from NEDI suggested that *F. sylvatica* or *Q. rubra* are similar to both *Q. petraea* and *Q. robur*; and *A. pseudoplatanus* and *T. europaea* are similar to *F. excelsior*. These tree species could therefore represent potential replacements for the three threatened native species. Future work should extensively test these predictions to see whether they hold real value for conservation.

Keywords

Native trees; Epiphytes; Bryophyte communities; Community similarity; Euclidean distance; Bark chemistry; Replacement species; Conservation.

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List of Acronyms and Abbreviations

ANOVA	Analysis of Variance
Chao1	Chao's Non-Parametric Diversity Estimator
NEDI	Normalised Euclidean Distance Index
Shannon	Shannon's Diversity Index
Simpson	Simpson's Diversity Index
SSI	Sørensen Similarity Index
WHC	Water Holding Capacity

1. Introduction

As the Earth undergoes warming and climates shift, many diseases and pests of trees will likely expand their range into newly favourable zones, presenting significant threats to native woodlands (Sturrock et al., 2011). Simultaneously, abiotic changes can alter the ability of trees to withstand disturbance by submitting them to stress, resulting in increased likelihood of outbreaks (Hennon et al., 2020). These issues have been exacerbated by a concurrent increase in global trade, which has facilitated the expansion of numerous pests and diseases. Indeed, it has been found that the majority of emerging infectious tree diseases have been disseminated through the commercial transportation of wood (Boyd et al., 2013; Ghelardini et al., 2016).

Understanding the patterns of disease emergence and spread is complex, as outcomes are influenced by a number of interacting factors (Sturrock et al., 2011). For example, under different projected global warming scenarios, whether *Phytophthora cinnamomic* will remain a widespread, highly invasive, and destructive plant pathogen (or become less prevalent) depends on whether regions become wetter or drier, the fertility of their soils, the efficiency of detection methods, and on the inherent susceptibility of local plant species and communities (Burgess et al., 2016). In certain instances, forest decline has been caused by a combination of factors which resulted in the ideal conditions for outbreak. For example, in recent years, Norway spruce forests in Europe have been devastated by the spruce bark beetle due to storm events which caused large-scale felling, and periodic episodes of drought (Kärvemo et al., 2023). With climate change persisting, and an anticipated increase in occurrence of droughts, floods, storms and extreme temperatures, such scenarios are likely to become more frequent (Boyd et al., 2013).

The broader impact of these outbreaks and associated forest declines, although tricky to quantify, has been studied. In addition to their recreational, cultural, and economic value, woodlands provide numerous ecosystem services, including carbon sequestration, flood mitigation, water purification, and crucially, they support high levels of biodiversity. If an outbreak results in the decline of certain foundation or keystone tree species, there can be severe negative consequences for the whole ecosystem and all of its services (Boyd et al., 2013). For example, in Slovenian montane temperate forests, the decline of the foundation species *Abies alba* (due to dieback) resulted in its replacement by *Fagus sylvatica*. This led to decreased understory light penetration, alterations in litter characteristics, and consequently, a homogenisation of, and significant decline in, understory plant diversity (Nagel et al., 2019). Outbreaks of two non-native invasive species in box tree (*Buxus* spp.) forests in Europe and the Caucuses threatens 63 obligate species with extinction, which may also lead to increases in other pests and diseases, as their natural enemies decline (Mitchell et al., 2018). The loss of Eastern hemlock (*Tsuga canadensis* (L.) Carr.) in the southern Appalachian Mountains (due to

hemlock woolly adelgid) has led to reductions in transpiration which could significantly alter the hydrological cycle of the ecosystem (Ford and Vose, 2007). Furthermore, no other species in the region is known to adequately replicate the ecohydrological role of Eastern hemlock, highlighting the significance of its loss (Ford and Vose, 2007). These examples illustrate some of the cascading effects resulting from the loss of foundation and keystone tree species in forest ecosystems.

In UK woodlands, native species are facing similar threats. Oak (*Quercus* spp.) and ash (*Fraxinus excelsior*) are the first and second most abundant tree species in Great Britain, respectively (Hill et al., 2017), and they are currently affected by several pests and pathogens. The ascomycete *Hymenoscyphus fraxineus* (the causative agent of ash dieback) has devastated *F. excelsior* stands throughout the UK and Europe (Thomas, 2016), with recorded tree mortality rates as high as 100% over a period of less than 15 years (George et al., 2022). The native trees *Q. robur* and *Q. petraea* are facing declines due to numerous pests and diseases. Most notably: Acute Oak Decline, Chronic Oak Decline (Denman and Webber, 2009) – both of which are thought to have multiple interacting causes (Denman et al., 2017) – Oak Processionary Moth (Godefroid et al., 2019), and a number of powdery mildews (Topalidou and Shaw, 2015).

In the UK, a total of 953 species of birds, mammals, bryophytes, fungi, invertebrates and lichens have been identified as "associated" with *F. excelsior* – 44 of these are considered to be obligate, and 62 highly associated (Mitchell et al., 2014). Similarly, 2300 species have been identified as associated with *Q. petraea* and *Q. robur,* with 326 of those found to be obligate and 229 highly associated (Mitchell et al., 2019). The loss of these keystone species carries significant repercussions for the biodiversity they support. This is because trees not only provide a physical habitat for many species, but they also play a crucial role in shaping the specific environmental conditions within their ecosystems, for instance by regulating the amount of light that penetrates the forest floor (Mitchell et al., 2014).

Epiphytes are an example of commensal organisms whose survival strongly depends on the health of their hosts, as they utilise the trunk of trees as their platform for growth (J. Ellis et al., 2015). Due to their strong sensitivity to environmental disturbance, epiphytes are frequently used as biological indicators of environmental pollution, heavy metal accumulation, and general habitat quality (Giordani et al., 2012; Löbel, Snäll and Rydin, 2012; Mohan Bahuguna et al., 2014; Shi et al., 2017). Moreover, epiphytes also play key roles in ecosystem functions such as water regulation, nutrient cycling, soil stabilisation and nitrogen fixation. Therefore, the loss of these organisms (e.g., due to habitat loss/fragmentation, industrialisation, or climate change) could have severe consequences for the entire ecosystem, especially if this coincides with the loss of ecologically significant tree species (Mohan Bahuguna et al., 2014; J. Ellis et al., 2015).

The replacement of diseased trees with alternative tree species has been put forward as a potential solution to mitigate the effects of losing keystone tree species (and their associated biodiversity) to pests and disease (Ennos et al., 2019). Determining what tree may be a suitable candidate for the replacement of a native species is not a simple task. It demands efforts to minimise the loss of tree-associated biodiversity, uphold ecological functions, reduce the occurrence of diseases and pests, and account for compatibility within the specific environment (Mitchell et al., 2014; Mitchell et al., 2019; Mitchell et al., 2020). Planting the "wrong" trees could have adverse effects if for example they significantly alter soil nutrient (Hong et al., 2020) or hydrological processes (Jia et al., 2017), have the potential to become invasive (Ennos et al., 2019), or if their planting produces no benefits for local livelihoods (Coleman et al., 2021).

The tree species *Acer pseudoplatanus, Castanea sativa, F. sylvatica, Q. cerris, Q. rubra,* and *Tilia x europaea* have been previously suggested as ecological replacements for either *Q. petraea, Q. robur* or *F. excelsior* owing to their similarities related to biodiversity and ecological functions. These species are also already found growing within the UK, thus we can with some certainty say they are fit to grow within the climate and will not act as invasive (Mitchell et al., 2014; Mitchell et al., 2019; Mitchell et al., 2020). Therefore, these six tree species have been selected as possible candidates for the replacement of the native declining tree species, *Q. petraea, Q. robur* and *F. excelsior*.

A comprehensive assessment of all the similarities in biodiversity and ecosystem functioning between all nine tree species is beyond the scope of this study. Instead, the primary focus will be on investigating variations in diversity across the different tree species. Concurrently, the study will evaluate different methods for comparing diversity and their potential utility in identifying replacement trees for three native species affected by disease. Specifically, I will compare three commonly used diversity metrics and relative diversity. Then I will look at a popular similarity metric and compare that with my proposed novel method for comparing similarity between communities. Information on bark chemistry will also be incorporated, since factors such as bark water holding capacity, pH, and conductivity have all been shown to influence the diversity of epiphyte communities (Becker, Dobson and Howard, 2019; Kubiak and Osyczka, 2020; Zarate-García et al., 2020). The assessment will focus on specifically epiphytic bryophyte communities which, as previously mentioned, serve as indicators of a forest's health (J. Ellis et al., 2015). Hence, they will serve as a valuable proxy for evaluating the biodiversity status of the tree species being studied, aiding in the identification of potential alternatives to the three native tree species under threat.

The hypotheses for this study are as follows: (1) tree species will exhibit distinct differences in both bryophyte diversity and bark chemistry.; (2) *Quercus* species will be most similar in terms of

bryophyte diversity and bark chemistry (since they belong to the same genus), thus proposed replacement *Quercus* species will emerge as good substitutes for the two natives; (3) *F. excelsior* (which has many highly associated species) will exhibit the highest bryophyte diversity, thus finding a singular replacement will be challenging (although a combination of substitutes may maintain diversity); and (4) there will be relationships between the bark chemistry properties (WHC, pH and conductivity) and bryophyte abundance.

2. Materials and Methods

The dataset used in this study was produced by Mitchell et al. (2020). Data were selected on the basis that they could give information on the studied trees, bryophytes, and factors influencing bryophyte cover. All statistical analyses and figure production were done using Microsoft Excel (version 16.82) and Python 3.

2.1. Study Site

The data used in this project were collected from six protected sites spanning the United Kingdom and located in rural, low pollution areas (Mitchell et al., 2021a). These include three National Trust gardens (Knightshayes Court in England, Bodnant in Wales, and Dinefwr in Wales) as well as the national arboretum at Westonbirt in England, the National Trust for Scotland's garden at Crathes, and the private garden at Mount Stuart in Scotland (see Figure 1). These sites have been historically managed so that they contain old trees, often more than 150 years old, and they were picked on the basis that they home many of the trees of interest to this study. A total of 230 trees were included in the study with around 35-40 originating from each site. See Mitchell et al. (2020) Metadata for more information on the study sites.

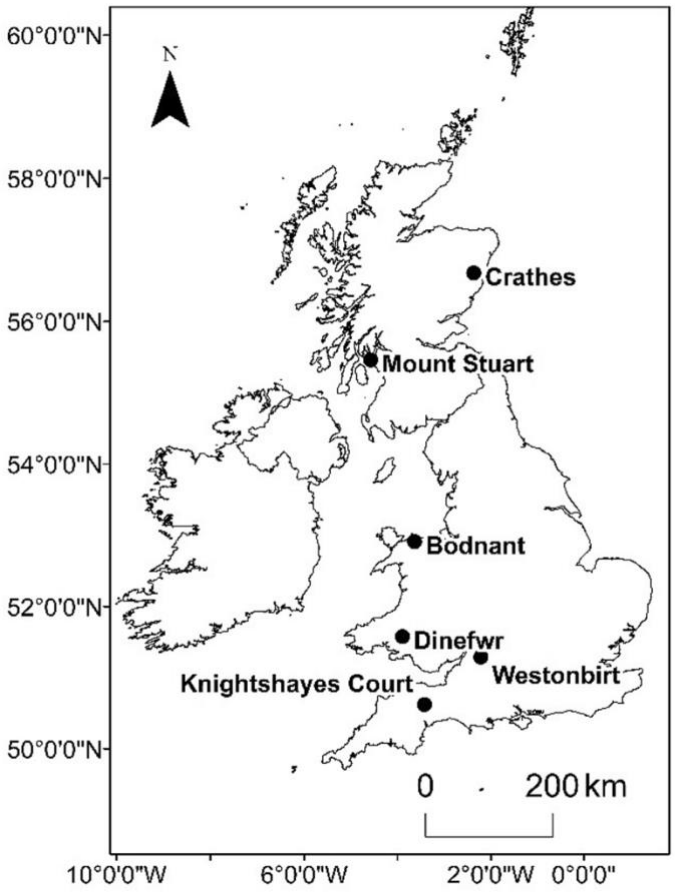

Figure 1: Location of study sites. Taken from Mitchell et al. (2021b).

2.2. Data Collection

2.2.1. Bryophyte data

All bryophyte species from 0-1.75 m on tree trunks were identified and recorded. See Appendix A for information regarding the bryophyte names, authorities and codes, and for incidence and abundance of each bryophyte species. Furthermore, see Mitchell et al. (2020) Metadata for more information on epiphyte sampling.

2.2.2. Bark Chemistry Data

A sample of bark was collected from each tree (height not specified). The samples were then sent to the lab for analysis of water holding capacity, pH and conductivity. For more information on the methods used for measuring bark chemistry, see Mitchell et al. (2020) Metadata.

2.3 Data Analysis

2.3.1. Measures of Diversity

For the purpose of this study, a community refers to the collection of bryophyte species residing on a particular tree species. While species richness (number of species) and diversity (number of individuals) offer insights into community composition, they may not provide a comprehensive assessment due to sampling biases and the influence of sample size (Roswell, Dushoff, & Winfree, 2021). I suggest employing *relative* richness/diversity (calculated as absolute richness/diversity divided by the number of sampled trees), for a more robust measure less affected by sample size. To compare absolute and relative richness/diversity, two barplots were generated with Python (Numpy and Matplotlib packages). Refer to Appendix B for the code.

Moreover, diversity metrics which incorporate relative abundances, or which take into consideration elusive species, can further address those biases. Three popular diversity metrics were utilised in this study, each employing a different method to evaluate diversity (Andermann et al., 2022). The three metrics used were the Simpson's diversity index (Simpson, 1949), the Shannon index (Shannon, 1948), and Chao's non-parametric diversity estimator (Chao, 1984). All calculations for the diversity indices were performed using Excel.

Simpson's index measures to what degree a community is dominated by one or a couple of species; therefore, it is a measure of community evenness (Magurran, 2013). Specifically, it represents the probability that two individuals sampled at random will belong to the same species. The index is commonly rewritten to represent the probability that two randomly chosen individuals will be of *different* species (Morris et al., 2014) – this is referred to as the Gini-Simpson Diversity Index (Daly, Baetens and De Baets, 2018). This reformulation offers a more intuitive assessment of diversity, where higher values correspond to greater diversity. The latter is given by the following equation:

$$D = 1 - \sum_{i=1}^{R} {p_i}^2 \quad (1)$$

where R is the richness and p_i represents the proportion of the i-th species.

The Shannon index is similar to Simpson's index, in that it also considers both composition and relative abundance (Kim et al., 2017), and it essentially represents the uncertainty associated with predicting the next letter in a string of letters (Spellerberg and Fedor, 2003). In a community, if relative proportions are similar among all species, the uncertainty in identifying an unknown

individual will be high. Conversely, if one or a few species dominate, the likelihood of predicting the species identity is higher. Therefore, these communities represent high and low diversity, respectively (Morris et al., 2014). Shannon's index is calculated using the following formula:

$$H = \sum_{i=1}^{R} p_i \, ln \, p_i \tag{2}$$

where the notation is consistent with that used for Simpson's index. Normalisation of species abundances were performed for all communities prior to calculations of diversity, as both *H* and *D* are influenced by community size (Kim et al., 2017).

So, while Simpson and Shannon are both measures of diversity, they consider different features of a community. Fundamentally, Simpson is a measure of probability and Shannon a measure of entropy or disorder (Daly, Baetens and De Baets, 2018).

A measure which may be more suitable for the data presented is Chao's Nonparametric Diversity Estimator (Chao, 1984), aka. Chao1. It is used to assess the diversity of a community based on the assumption that the presence of rare species can inform how well sampling has been performed and how many undetected species there are. The basis of this assumption is that dominant species are easily detectable and thus tell us very little about any undiscovered taxa. Conversely, rare species, which are harder to detect, supply most of the information about missing species (Branco, Figueiras and Cermeño, 2018). Therefore, Chao1 is based on counts of singletons (i.e., species with one count) and doubletons. Calculations of Chao1 were done via an equivalent formula (Wolf and Alejandro, 2003) which was employed for ease of use. It is as follows:

$$S_{Chao} = S_{obs} + \frac{{F_1}^2}{2F_2} \tag{3}$$

where S_{obs} is the number of observed species, and F_1 and F_2 are the number of singletons and doubletons, respectively.

If information regarding the species accumulation and sampling effort were available, the applicability of Chao1 in this situation may be assessed more effectively, as such estimators are useful for predicting the asymptote of rising species accumulation curves (Chao and Chiu, 2016). However,

its application in this context is justified by the high proportion of low abundance counts in the dataset.

2.3.2. Measures of Similarity

The Sørensen Similarity Index (SSI) (Sørensen, 1948) is a commonly used metric for comparing similarity/dissimilarity between two samples or communities. The formula is as follows:

$$SSI = \frac{2w}{m + n} \tag{4}$$

where *m* is the total number of species in the first sample, *n* is the number of species in the second sample, and *w* is the number of species common to both samples. Calculations of SSI were done using Excel.

SSI compares communities based on incidence data, by considering presence or absence, but it does not take into account the abundance of different species within the communities. Thus, rare and common species are given the same weight (Chao et al., 2006). Another issue arises when two communities vary greatly in size. For example, if community *n* is richer than community *m*, then the difference between the two will appear very large, even if the composition of the two communities is actually very similar.

In an attempt to focus on compositional similarities between communities, I propose a method which measures similarity through relative counts of bryophyte species and Euclidean distance, hereafter referred to as Normalised Euclidean Distance Index (NEDI). First the proportion *p* of each species in the community is calculated:

$$p_{c,s} = \frac{a_{c,s}}{\sum_s a_{c,s}} \tag{5}$$

where *c* is the focal community, *s* is a particular species within that community and *a* is abundance. Then the Euclidean distance (*D*) of the corresponding species of the two communities being compared is calculated using the formula below:

$$D(c_1, c_2) = \sqrt{\sum_s \left(p_{c_1,s} - p_{c_2,s}\right)^2} \tag{6}$$

The computed distances will indicate how similar two points are i.e., a low Euclidean distance between two tree species will indicate similar species abundances.

Although it has been suggested that there are issues with using methods centred around Euclidean distance (Ricotta and Podani 2017; Ricotta and Pavoine 2022), the key reason for the objections is that they utilise absolute values of abundance instead of relative values of abundance. Ricotta and Podani (2017) illustrate the issue through a hypothetical situation where there are three communities (*U, V* and *W*) made up of four species (*S1-S4*) (see Table 1). When we calculate the similarity using Euclidean distance (without normalising), we find that *U* is closer to *V* than it is to *W*, despite having no species in common ($D_{UV} = 3.162$; $D_{UW} = 4.472$; $D_{VW} = 7.071$). However, when we account for the sample size, by dividing by abundance (see Eq. 5), we find that the distances *do* reflect the observable similarities/differences in composition ($D_{UV} = 1.054$; $D_{UW} = 0.0$; $D_{VW} = 1.054$). Now, $D_{UW} = 0$ because they have the same relative proportion of species. Thus, they are also equidistant from community *V*.

Table 1: Example situation with three communities (U, V, W) and four species (S1-S4), where values within the table indicate abundances. Taken from Ricotta and Podani (2017).

	U	V	W
S1	1	0	3
S2	2	0	6
S3	0	1	0
S4	0	2	0

NEDI also resolves the other issue associated with using SSI, where all species are erroneously given equal importance (as species are either present or absent), and a species' dominance or rarity is not a consideration. By using Euclidean distance, an individual within a community is represented by $\frac{1}{\sum_s a_{c,s}}$. Therefore, if this individual is rare within the community, it will have little impact on the distance. The opposite applies to species which are common in the community.

Pairwise distances between each tree species were computed to assess similarity between relative abundances of each bryophyte species. To visualise NEDI, a graph was defined using Python (Numpy, Pandas, Pylab and Networkx packages) where each tree species represents a mass which is attracted by a "spring" to the other masses, with the strength of the spring being proportional to the trees' similarity (i.e., the Euclidean distance). The trees/masses are placed on the graph in a random

configuration and the system "relaxes" to a state of minimal energy (i.e., minimal tension in the springs). Since the final configuration is influenced by the random seed (i.e., the starting configuration), the code was run multiple times with different configurations to observe the results and find the "best fit". See Appendix B for the code. The same method was used for SSI for the purpose of comparing NEDI with a commonly used metric of similarity.

2.3.3. Bark Chemistry

One-way analysis of variance (ANOVA) was performed using Excel between all nine tree species for bark conductivity, pH and water holding capacity (WHC), respectively. To visualise those differences, three barplots were produced using Python (Matplotlib package), representing bark conductivity, pH and WHC. For the code see Appendix B. Furthermore, pairwise independent *t*-tests were performed (with Bonferroni correction) on Excel to find which tree species were significantly different from one another.

Linear regressions were also performed for each of the bark properties and individual tree bryophyte abundances, with Pearson's correlations computed for each property, respectively, and the variables were plotted using Python (Numpy, Matplotlib and Scipy packages). See Appendix B for the code.

3. Results

3.1. Measures of Diversity

The results from the calculations of absolute richness/diversity and relative richness/diversity are summarised in Table 2 and visualisations of these results are provided in Figure 2.

Table 2. Values of absolute (i.e., total recorded) richness, absolute diversity, relative (i.e., per tree) richness and relative diversity calculations for all nine tree species.

	Absolute Richness	Absolute Diversity	Relative Richness	Relative Diversity
Q. petraea	17	46	1.30769231	3.53846154
Q. robur	29	166	0.85294118	4.88235294
F. excelsior	43	251	1.34375	7.84375
A. pseudoplatanus	34	195	1.0625	6.09375
C. sativa	21	90	0.875	3.75
F. sylvatica	33	220	0.94285714	6.28571429
Q. cerris	24	70	1.71428571	5
Q. rubra	25	73	1.66666667	4.86666667
T. europaea	32	194	1.03225806	6.25806452

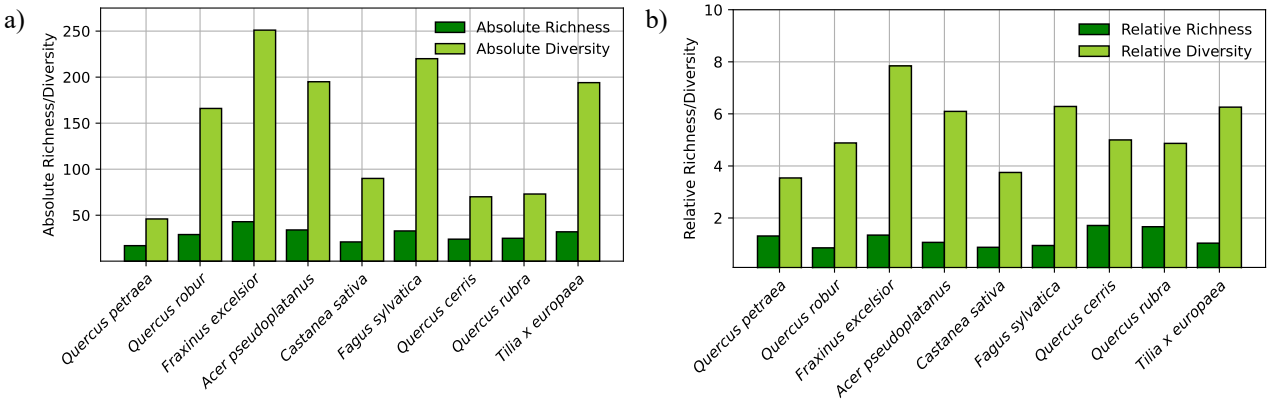

Figure 2. Barplot of bryophyte richness and diversity with (a) showing absolute richness and diversity and (b) showing relative richness and diversity, for all nine tree species.

Compared to absolute richness, calculating relative richness revealed the following: (1) *Q. cerris* has the highest number of species per tree; (2) *Q. petraea* has more than *Q. robur, A. pseudoplatanus, C. sativa, F. sylvatica,* and *T. europaea*; (3) *Q. cerris* and *Q. rubra* have more than *Q. robur, F. excelsior, A. pseudoplatanus, F. sylvatica* and *T. europaea*; and (4) that *Q. robur* has the least bryophytes per tree overall.

Compared to absolute diversity, by studying relative diversity, I found that (1) *F. excelsior* continues to have the most bryophyte individuals per tree; (2) *Q. petraea* and *Q. robur* have less than *A. pseudoplatanus, F. sylvatica, Q. cerris* and *T. europaea*; (3) *Q. robur* and *Q. rubra* have very similar relative diversity (difference of ~0.016); (4) *F. sylvatica* and *T. europaea* have very similar relative diversity (difference of ~0.028); and (5) *C. sativa* has lower relative diversity than both *Q. cerris* and *Q. rubra*. In general, calculating relative diversity makes the differences between trees less pronounced, confirming that looking at relative diversity is important for removing biases brought about by unequal sample sizes.

The results from the three common diversity indices are presented in Table 3 alongside values of relative diversity. Across all metrics, *F. excelsior* exhibited the highest diversity. However, the ranking of all other tree species varied depending on the metric employed. In general, Chao1 showed the most variability between tree species, with values between 49-718. Conversely, Simpson showed little variability, with values between 0.912-0.945.

Table 3. Comparison of relative diversity, Simpson diversity, Shannon-Weiner diversity and Chao1, between all nine tree species.

	Relative Diversity	Simpson	Shannon	Chao
Q. petraea	3.54	0.92	2.48	49
Q. robur	4.88	0.93	2.86	176
F. excelsior	7.84	0.95	3.17	718
A. pseudoplatanus	6.09	0.94	3.03	334
C. sativa	3.75	0.91	2.62	111
F. sylvatica	6.29	0.93	2.94	335.5
Q. cerris	5.00	0.94	2.86	168
Q. rubra	4.87	0.94	2.86	241
T. europaea	6.26	0.93	2.90	382

3.2. Measures of Similarity

The results from SSI calculations are summarised in Table 4. Pairwise calculations for each of the native tree species with the potential replacement species suggested that *Q. petraea* is most similar to *Q. rubra, Q. cerris* and *T. europaea*; *Q. robur* is most similar to *Q. rubra, T. europaea* and *F. sylvatica*; and *F. excelsior* is most similar to *A. pseudoplatanus*, *T. europaea* and *F.* sylvatica (listed in descending order of similarity with each native tree, respectively). Overall, *F. excelsior* and *A. pseudoplatanus* showed the highest degree of similarity, while *C. sativa* was the least similar to every native species. A graphical representation of these relationships is shown in Figure 3.

Table 4. Pairwise SSI results between the three native species (Q. petraea, Q. robur and F. excelsior) and the six potential replacements (A. pseudoplatanus, C. sativa, F. sylvatica, Q. cerris, Q. rubra, T. europaea).

	Q. petraea	*Q. robur*	*F. excelsior*
A. pseudoplatanus	0.5491	0.635	0.7793
C. sativa	0.5264	0.52	0.4063
F. sylvatica	0.5715	0.7214	0.6134
Q. cerris	0.6342	0.6793	0.5971
Q. rubra	0.6667	0.7408	0.5
T. europaea	0.6123	0.7214	0.6934

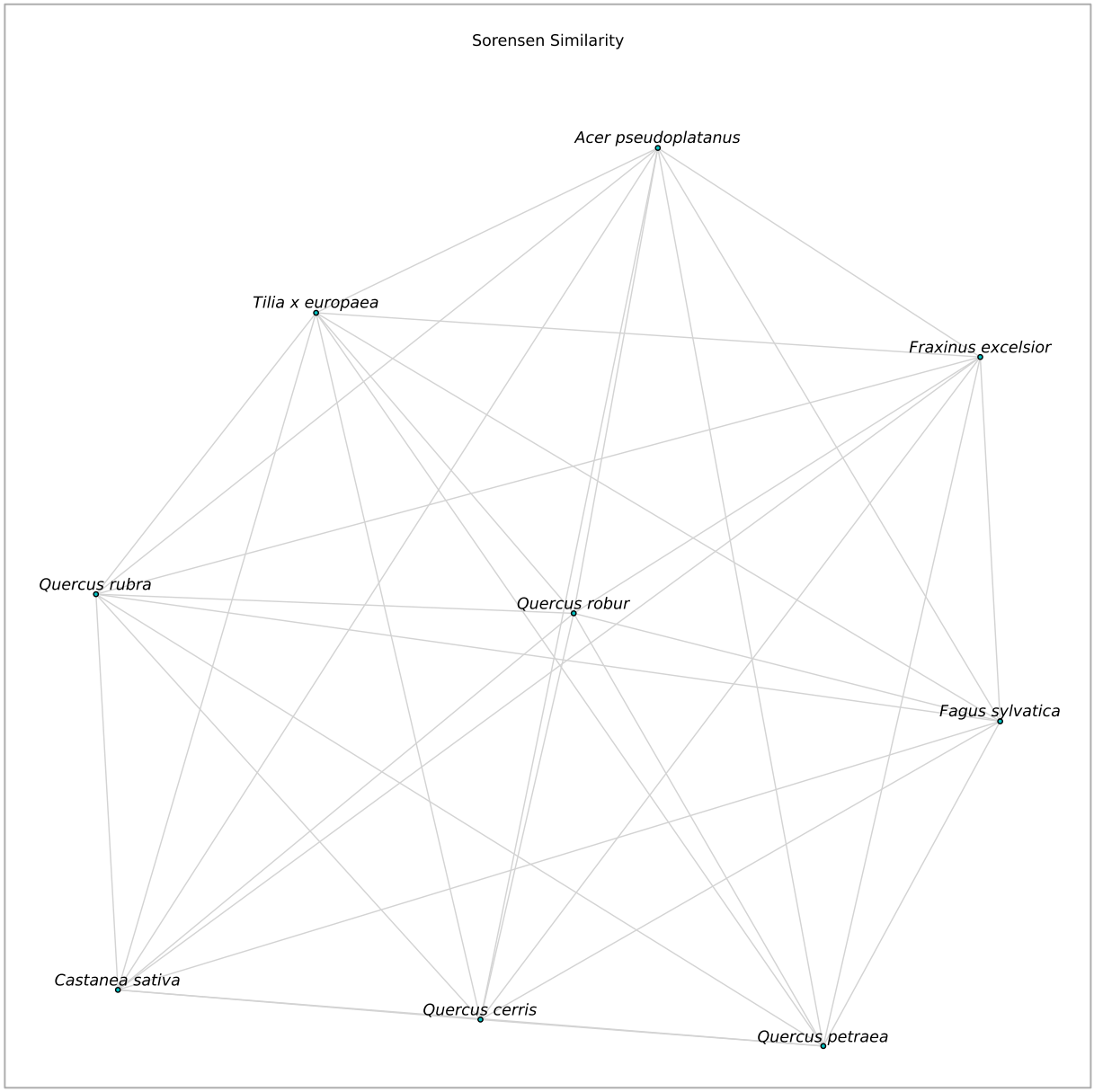

Figure 3. Graphical representation of SSI shown by a graph with tree species "attracted" to other trees species in proportion to SSI. The output is dependent on the starting configuration. Thus, this is only one visualisation of several other potential outputs.

The results from NEDI are reported in Table 5. The values suggest that *Q. petraea* is most similar to *Q. cerris, F. sylvatica* and *Q. rubra*; that *Q. robur* is most similar to *Q. cerris*, *F. sylvatica* and *Q. rubra*; and that *F. excelsior* is most similar to *T. europaea*, *A. pseudoplatanus* and *F. sylvatica*. Overall, *Q. robur* and *Q. cerris* show the highest degree of similarity, but *Q. petraea* and *Q. cerris* are also highly similar (difference of 0.003). Additionally, *A. pseudoplatanus* was least similar to *Q. petraea* and *Q. robur*, and *C. sativa* was least similar to *F. excelsior*. A graphical representation of these relationships is shown in Figure 4.

Table 5. Pairwise NEDI results between the three native species (Q. petraea, Q. robur and F. excelsior) and the six potential replacements (A. pseudoplatanus, C. sativa, F. sylvatica, Q. cerris, Q. rubra, T. europaea).

	Q. petraea	*Q. robur*	*F. excelsior*
A. pseudoplatanus	1.288907698	1.086169977	0.861503047
C. sativa	1.026882262	1.01111185	1.787088385
F. sylvatica	0.742434368	0.615333803	1.043386378
Q. cerris	0.567984124	0.565434454	1.270879509
Q. rubra	0.797217383	0.689956509	1.404260939
T. europaea	0.973761263	0.765798655	0.719484819

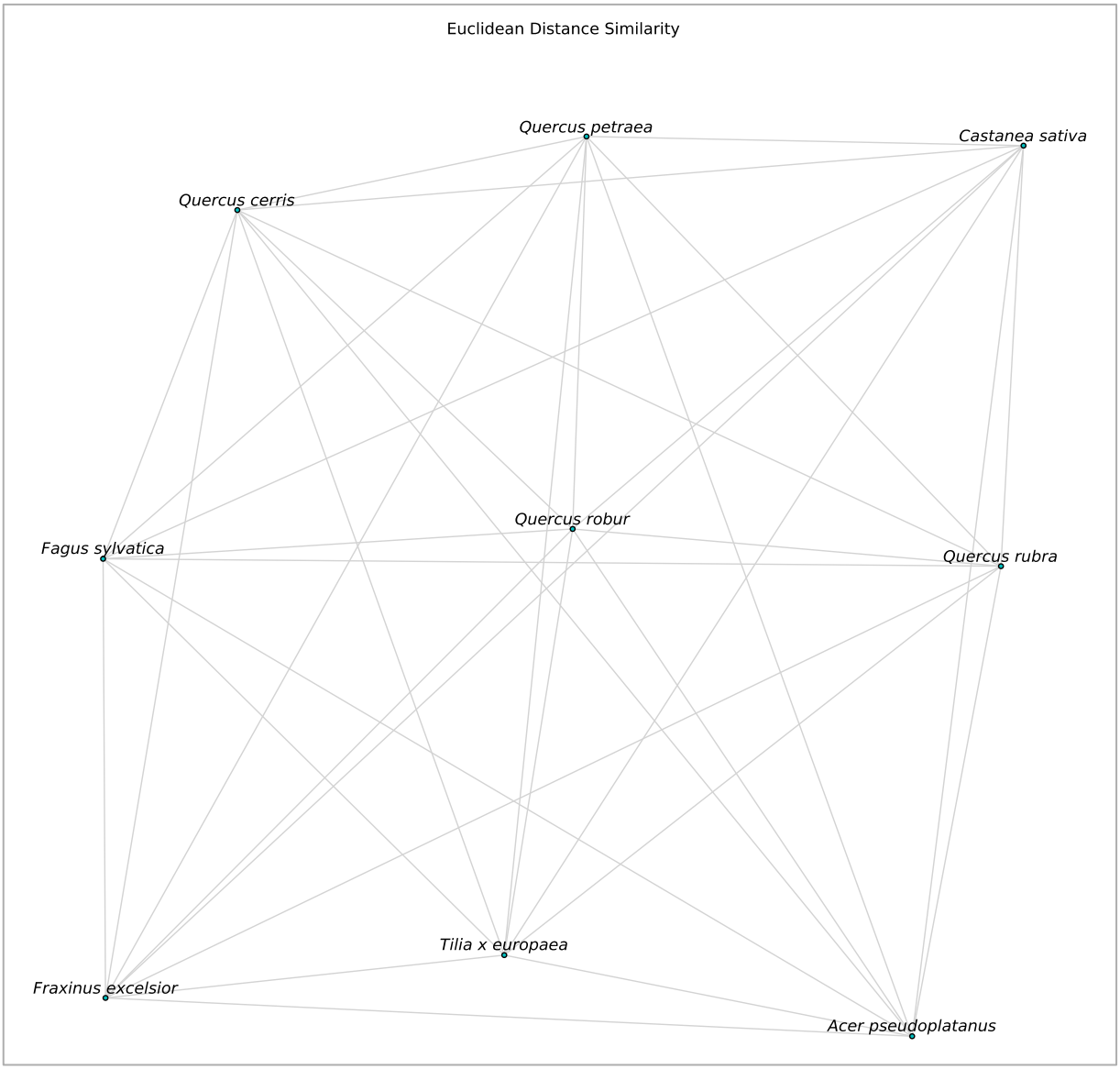

Figure 4. Graphical representation of NEDI shown by a graph with tree species "attracted" to other trees species in proportion to their similarity (i.e., the Euclidean distances). The output is dependent on the starting configuration. Thus, this is only one visualisation of several other potential outputs

3.3. Bark Chemistry

3.3.1 Bark Water Holding Capacity

The results from the ANOVA show that WHC differed significantly between tree species ($F(8, 221) = [13.82]$, $p < 0.001$). The barplot (see Figure 5a) – where error bars represent standard error of the means – offers a visualisation of these differences. Pairwise independent *t*-tests (with Bonferroni correction) were then performed among the three native trees (*Q. petraea, Q. robur,* and *F. excelsior*) and between each of the three natives and the six potential replacements (*A. pseudoplatanus, C. sativa, F. sylvatica, Q. cerris, Q. rubra,* and *T. europaea*).

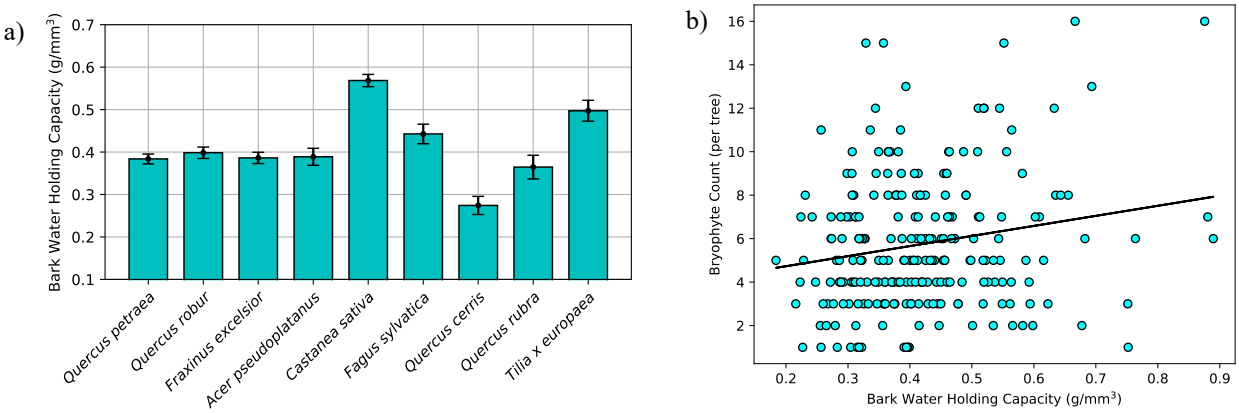

Figure 5. (a) Barplot representing mean bark WHC (g/mm³) for each of the nine tree species with standard error bars representing standard error of the mean. (b) Individual tree bryophyte count plotted against bark WHC with a regression line (y = 4.63x + 3.81).

This revealed that: (1) the three native species are not significantly different from one another; (2) none of the three native species are significantly different from either *A. pseudoplatanus* or *F. sylvatica*; (3) *Q. petraea* and *Q. robur* are not significantly different from *Q. rubra*; (4) all three native species are significantly different from *C. sativa*, *Q. cerris* and *T. europaea*; and (5) *F. excelsior* is significantly different from *Q. rubra*.

The regression line ($y = 4.63x + 3.81$), shown in Figure 5b, suggests a fair relation between the two variables, which was confirmed by a Pearson's correlation test showing a weak, but statistically significant, positive relationship between individual tree bryophyte abundance and bark WHC ($r = 0.186$, $p = 0.00467$).

3.3.2. Bark pH

The results from the ANOVA showed that pH differed significantly between tree species (F(8, 221) = [68.43], p < 0.001). The barplot (see Figure 6a) offers a visualisation of these differences. Pairwise independent *t*-tests (with Bonferroni correction) revealed the following relationships: (1) *Q. petraea* and *Q. robur* were not significantly different from one another; (2) both *Q. petraea* and *Q. robur* were not significantly different from *Q. cerris* or *Q. rubra*; (3) *F. excelsior* was not significantly different from *T. europaea*; (4) *F. excelsior* was significantly different from *Q. cerris* and *Q. rubra*; and (5) all three of the native trees were significantly different from *A. pseudoplatanus*, *C. sativa* and *F. sylvatica*.

The regression line ($y = 0.83x + 1.32$), shown in Figure 6b, suggests a fair relation between the two variables, which was confirmed by a Pearson's correlation test showing a weak, but statistically significant, positive relationship between individual tree bryophyte abundance and pH (r = 0.226, p = 0.000491).

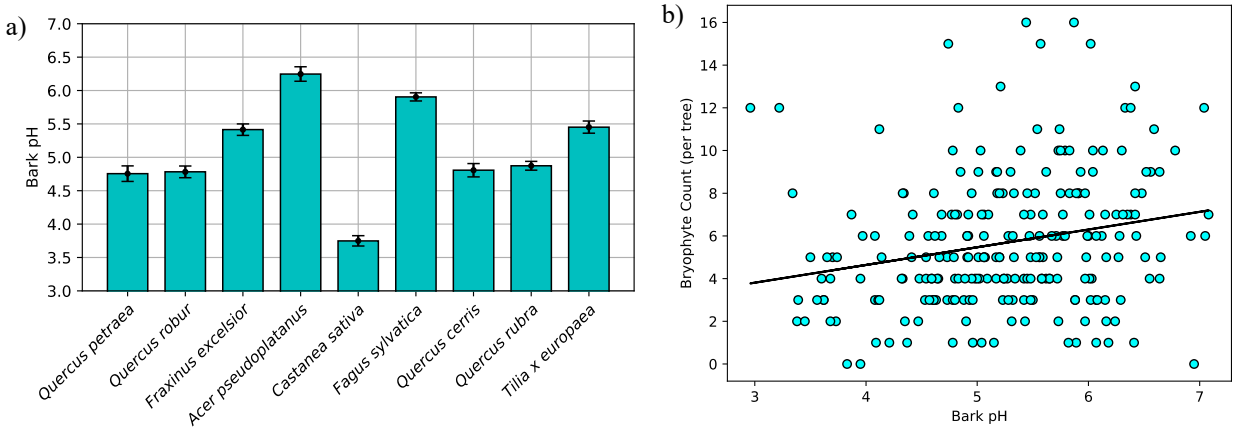

Figure 6. (a) Barplot representing mean bark pH for each of the nine tree species with standard error bars representing standard error of the mean. (b) Individual tree bryophyte count plotted against bark pH with a regression line (y = 0.83 + 1.32).

3.3.3.Bark Conductivity

Initially, an ANOVA and linear regression were performed between individual tree bryophyte count and bark conductivity. Once more, the ANOVA showed statistical significance between the groups (F(8, 222) = [6.16], $p < 0.001$) and the regression ($y = 0.0027x + 4.96$) suggested a fair relation between the two variables, which was confirmed by a Pearson's correlation test which showed a weak, but statistically significant, positive relationship between the variables (r = 0.212, p = 0.0011).

However, it became apparent that outliers may be skewing the dataset, as illustrated in Figure 7a. Using the three sigma rule (Zhao et al., 2013) – where data points that fall more than three standard deviations away from the mean are considered outliers – it was confirmed that the three data points were indeed outliers (> 712.34), and they were removed from subsequent analyses. The resulting linear regression ($y = 0.0032x + 4.86$) suggested a fair correlation between individual tree bryophyte abundance and conductivity (see Figure 7b). Although, Pearson's correlation showed that the positive relationship was not statistically significant ($r = 0.114$, $p = 0.08$). But since it was nearly significant, this suggests it might reach significance on a larger dataset.

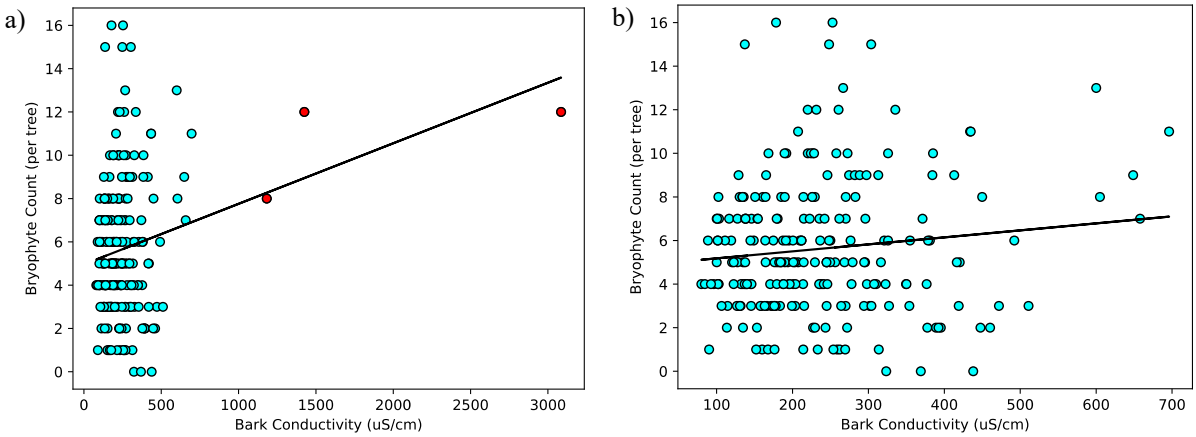

Figure 7. Scatterplot of individual tree bryophyte count VS bark conductivity (uS/cm) with (a) regression line (y = 0.0027x + 4.96) and outliers (shown in red), and (b) regression line (y = 0.0032 + 4.86) and outliers removed.

The outliers were also subsequently removed from the ANOVA and a barplot was produced for the new dataset (see Figure 8). The ANOVA on the cleaned-up data maintained significant differences in conductivity between the tree species ($F(8, 210) = [16.69]$, $p < 0.001$). Pairwise independent *t*-tests (with Bonferroni correction) then revealed the following: (1) *Q. petraea* and *Q. robur* were not significantly different, (2) neither *Q. petraea* nor *Q. robur* were significantly different from *Q. cerris, Q. rubra, T. europaea* and *F. sylvatica*; (3) *Q. robur* was not significantly different from *A. pseudoplatanus*; (4) *Q. petraea* was significantly different from *A. pseudoplatanus* and *C. sativa*; (5) *Q. robur* was only significantly different from *C. sativa*; and (6) *F. excelsior* was significantly different from all tree species excepting *C. sativa*.

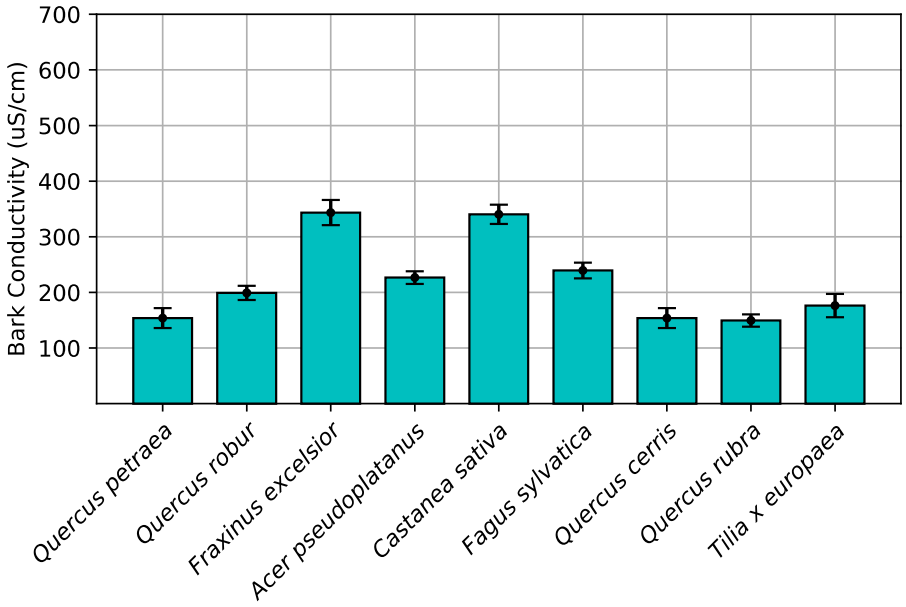

Figure 8. Barplot representing mean bark conductivity (uS/cm) for each of the nine tree species with standard error bars representing standard error of the mean.

4. Discussion

The main aims of this study were to (1) investigate bryophyte community variations between three native declining trees and six potential replacements, (2) compare methods for assessing the diversity of communities, (3) contrast a commonly used similarity metric with a novel proposed method, and (4) evaluate differences in bark chemistry and their relationship with bryophyte abundance. Four hypotheses were also tested and will be addressed in the following sections.

4.1. Assessing the Efficacy of Diversity Metrics

Estimating richness and diversity remains a persistent challenge in ecology, and while many metrics have been proposed, their applicability universally remains limited due to the complex nature of ecosystems and the varying scales at which biodiversity operates (Purvis and Hector, 2000; Chiarucci, Bacaro and Scheiner, 2011). One of the objectives of this study was to evaluate the effectiveness of three frequently employed diversity metrics (Simpson, Shannon, and Chao1) alongside relative diversity in understanding bryophyte community diversity across nine tree species.

After the calculations were performed, it became apparent that there was a significant lack of agreement between each of the diversity metrics, and their applicability in this context was diminished. That being said, across all metrics, *F. excelsior* exhibited the highest diversity. Due to this agreement, it is possible to say with some certainty that *F. excelsior* indeed hosts the largest diversity of bryophytes, and my hypothesis (that *F. excelsior* would be the most diverse tree species) is correct.

However, this agreement between metrics cannot be observed for any of the other tree species. The potential reasons for these discrepancies are discussed below.

While relative diversity can resolve some of the issues around sampling biases (e.g., unequal sampling sizes), it does not yield information about the evenness of the community, nor does it suggest where diversity may have been neglected (i.e., it does not capture the undetected species). Thus, it cannot be employed alone for assessing the diversity of a community.

Metrics such as Simpson and Shannon that do consider community evenness are helpful. However, both indices introduce their own biases: the former assigns more importance to species richness and the latter places more weight on species evenness (Kim et al., 2017). Even greater limitations can emerge when utilising these metrics related to lack of interpretability and non-linearity (see Daly et al. 2018 for detailed examples of these issues).

Given the purpose of this study, a metric, such as Chao1, that attempts to estimate true diversity (i.e., extrapolates the species accumulation curve) may be the most appropriate. However, while Chao1 does resolve some of the issues related to incomplete sampling, it too presents its own limitations. That is, it is strongly influenced by sample size, it estimates minimum richness, and it assumes homogeneity among the samples (i.e., the species present in a sample are assumed to be representative of the overall species diversity within that specific sample); (Cazzolla Gatti, Amoroso and Monaco, 2020). These limitations diminish Chao1's suitability in this scenario, as, in the present study, the sample sizes are not equal, and we cannot assume that our samples are homogeneous.

Taking into consideration the findings of this study – that none of the diversity metrics used were reliable methods for understanding diversity – it becomes clear that alternative methods for estimating diversity must be employed.

4.2. A Novel Method for Comparing Similarity

This study proposed a novel method for comparing similarity between two communities. The method was compared with the commonly used SSI. As mentioned in the methods, the main issues with SSI are that (1) it is highly sensitive to sample size and (2) it has limited ability to account for the rarity or dominance of species, given its incidence-based nature. The proposed method, NEDI, aimed to address these limitations by (1) incorporating relative abundances of species and (2) utilizing Euclidean distance, which efficiently captures differences in abundances of corresponding species.

Using NEDI, *Q. petraea* and *Q. robur* exhibit the same pattern of similarity. That is, they are both similar to *Q. cerris, F. sylvatica* and *Q. rubra* (in order of most to least similar). Conversely, the results from SSI suggest that *Q. petraea* and *Q. robur* differ in their similarities to other tree species. In other studies comparing bryophytic communities between tree species, *Q. petraea* and *Q. robur* are often combined to essentially represent one species (Mitchell et al., 2016; Mitchell et al., 2019; Gustafsson et al., 2023). This implies they do not differ enough in bryophyte diversity to demand separate consideration or management. The results from my metric agree with this perspective since the species do not differ in their similarity results, suggesting that my method is more effective in assessing similarity for *Q. petraea* and *Q. robur*.

Furthermore, the results of NEDI, indicating that *Q. cerris* and *F. sylvatica* exhibit the highest similarity to the two native *Quercus* species, corroborate the findings of Mitchell et al. (2021a), whose study also suggested that *F. sylvatica* and *Q. cerris* are close matches to *Q. petraea* and *Q. robur* in terms of their bryophyte communities. Additionally, their study found that *A. pseudoplatanus and C. sativa* were the least similar to the native *Quercus* species which again agrees precisely with the NEDI results. In contrast, SSI did not reach this conclusion for *A. pseudoplatanus*.

Finally, both SSI and NEDI show that *Q. rubra* is similar to the two native *Quercus* species (although to differing extents). This agrees with the findings of Gustafsson et al. (2023) who found no significant differences in the bryophyte communities of *Q. petraea*/*Q. robur* and *Q. rubra.* Again, this implies NEDI has been successful in evaluating similarity between *Q. petraea* and *Q. robur* and the six potential replacement species. Although, SSI was also a strong predictor in this case.

For *F. excelsior*, the results from SSI and NEDI show a high degree of agreement in relation to their similarity values. Both metrics suggest that *T. europaea*, *A. pseudoplatanus* and *F. sylvatica* are similar to *F. excelsior*. Although, they do differ in their order of similarity, with SSI ranking *A. pseudoplatanus* as the most similar, and NEDI ranking *T. europaea* as the most similar.

While Mitchell et al. (2014) found that *A. pseudoplatanus* was a good match for *F. excelsior* in terms of shared bryophyte diversity, no studies were found which directly compared the bryophyte similarities between *F. excelsior* and *T. europaea*. Therefore, the validity of the results from NEDI cannot be confirmed in this regard. Nevertheless, considering the successful calculations for *Q. petraea* and *Q. robur*, and the findings in agreement with Mitchell et al. (2014) and Mitchell et al. (2021a), we can reasonably maintain that the results from NEDI, suggesting similarity between *F. excelsior* and *T. europaea*, hold some value. Furthermore, NEDI indicates that *C. sativa* was the least similar to *F. excelsior*, a finding consistent with previous suggestions that *C. sativa* may be an

unsuitable replacement for F. *excelsior* in terms of biodiversity (Mitchell et al., 2014). This last observation is also consistent with SSI.

When comparing the results from SSI and NEDI, it becomes apparent that they each propose one tree species which is highly similar to all three native trees. For SSI, this tree is *T. europaea* and for NEDI it is *F. sylvatica*. The behaviour of these respective trees might be described as generalist, since they host bryophyte communities which are similar to many different trees, suggesting an ability to accommodate a wide variety of bryophyte species. Indeed, in accordance with NEDI, *F. sylvatica* has been found to share many bryophyte species with *Q. petraea*, *Q. robur* and *F. excelsior* (Mitchell et al., 2014; Mitchell et al., 2019; Mitchell et al., 2021a). Again, it is less clear whether this assumption holds true for *T. europaea*. However, since the predictions from NEDI appear relatively stronger than SSI, it seems reasonable to conclude that *F. sylvatica* may serve as a more reliable generalist host for bryophyte communities in this context.

Overall, while the two similarity metrics exhibit a relatively high degree of agreement relating to the most similar tree species, NEDI appears to align slightly better with the literature. That being said, few studies are available which directly compare the bryophytic communities between the three native species and six potential replacements investigated in this study. Thus, this research highlights a current gap and presents novel findings that may inform future studies of a similar nature.

4.3. Relating Bark Chemistry and Bryophyte Abundance

This study examined three bark chemistry properties which have been shown to influence epiphyte abundance (Becker, Dobson and Howard, 2019; Kubiak and Osyczka, 2020; Zarate-García et al., 2020; and references therein). The findings indicated significant variations among all bark properties across the nine tree species (which supports my first hypothesis), with both WHC and pH demonstrating a notable impact on bryophyte abundance. This partially supports my fourth hypothesis regarding the association between bark chemistry and bryophyte abundance. However, conductivity did not display a significant correlation with bryophyte abundance. These findings will be discussed in detail below.

4.3.1. Bark water holding capacity

Bark WHC has been shown to influence epiphyte abundance and preferences for host trees, with significant differences in WHC frequently observed between tree species (Callaway et al., 2002; Mistry and Berardi, 2005; Becker, Dobson and Howard, 2019; Kubiak and Osyczka, 2020; Zarate-García et al., 2020). Bryophytes, in particular, are “poikilohydric”, meaning they cannot regulate their own water and instead rely on their environment for hydration (J. Ellis et al., 2015). It has been

suggested that bark with high WHC improves the conditions needed for epiphytic growth by increasing the humidity surrounding the bark substrate (Callaway et al., 2002).

In accordance with previous studies, this study found a positive relationship between bark WHC and bryophyte abundance. Though significant, this relationship was relatively weak, whereas other studies have seen strong positive relationships between the same or similar variables (Callaway et al., 2002; Mistry and Berardi, 2005; Kubiak and Osyczka, 2020; Zarate-García et al., 2020). This discrepancy could be explained by climatic differences between study sites. This study area is characterised by a temperate climate with relatively high rainfall (see Mitchell et al. (2020) Metadata). Since epiphyte frequency has been linked to precipitation (Klinghardt and Zotz, 2021), it might suggest that in areas of high rainfall epiphytes are less dependent on – and consequentially less influenced by – the host tree's WHC, as they can obtain sufficient moisture from precipitation. Alternatively, the weak relationship could simply stem from a relatively small sample size, resulting in limited statistical power. A broader variation in WHC might have led to a more robust correlation.

This study also saw significant differences in WHC between multiple tree species. Given that this study is concerned with maintaining bryophyte communities, it is important to consider WHC consistency, since we know that bryophyte abundance and WHC are correlated. It could be argued that trees which are significantly different in WHC may not support similar, or enough, bryophyte species, thus may not be good replacements. The results showed that none of the three native trees were different from *A. pseudoplatanus* or *F. sylvatica*, and the two native *Quercus* species were not different from *Q. rubra*. These trees therefore emerge as potential candidates for substituting the three native trees in terms of WHC.

4.3.2. Bark pH

Bark pH has been shown to significantly influence epiphyte abundance (Mistry and Berardi, 2005; Fritz, Brunet and Caldiz, 2009; Tewari et al., 2009; Becker, Dobson and Howard, 2019; Kubiak and Osyczka, 2020; Shao et al., 2023). But while for WHC most studies reported a positive relationship with epiphyte abundance (see references above), findings regarding pH have been more variable (Mistry and Berardi, 2005; Fritz, Brunet and Caldiz, 2009; Becker, Dobson and Howard 2019).

This study observed a significant preference among bryophytes for more neutral bark pH. While the relationship appeared relatively weak, it's possible that a broader pH range among the tree species studied could have yielded a stronger correlation. For instance, none of the trees examined in the study displayed alkaline bark pH, making it unclear whether bryophyte abundance might have increased with higher pH levels. The differences between this study and other studies are likely due to the specific local adaptations of bryophyte taxa, enabling them to tolerate different pH levels. These

adaptations may be related to factors such as metal toxicity, mineral availability, or variations in enzymatic activity (Tessler et al., 2014; Tyler and Olsson, 2016).

This study also observed significant differences in pH between tree species. As discussed, particular bryophyte taxa are tolerant to specific pH conditions. Thus, one could argue that maintaining the same bark pH is important for preserving the same bryophyte community. The data analysis showed that *Q. petraea* and *Q. robur* were not different from *Q. cerris* or *Q. rubra*, and *F. excelsior* was not different from *T. europaea*. Therefore, these tree species can be considered viable substitutes in terms of pH for the three native species.

4.3.3. Bark conductivity

This study found no significant relationship between bark conductivity and bryophyte abundance. This is consistent with previous studies which have found no such association (Mistry and Berardi, 2005; Gosselin et al., 2017), though other studies have observed a relationship between conductivity and epiphyte abundance (Kapfer et al., 2012; Mitchell et al., 2021a).

On balance, it does not seem necessary to consider bark conductivity an essential shared feature between the native trees and their prospective substitutes, despite the fact that significant differences between tree species have been observed. This conclusion is supported by Kubiak and Osyczka (2020), who concluded that conductivity was not an important factor regulating the occurrence of epiphytes.

4.4. Bringing together diversity, similarity and bark chemistry: implications for conservation

This study assessed the efficacy of four metrics for quantifying diversity. Due to their inherent biases, limitations and the lack of consistency concerning their results (excepting *F. excelsior*), it appears prudent to disregard the majority of those results from the final assessment of tree species similarity. Conversely, both SSI and NEDI emerged as good metrics for similarity, with NEDI appearing slightly more accurate (based on findings from other studies). Thus, NEDI will be used to make some recommendations for conservation.

The results from NEDI found that *Q. petraea* and *Q. robur* exhibit the same pattern of similarity and the bark chemistry analyses found that there were no significant differences between the two species for WHC, pH or conductivity. Furthermore, other studies have shown that all bryophyte species associated with *Q. petraea* and *Q. robur* are cosmopolitan and not exclusively found on either tree

(Mitchell et al., 2019; Mitchell et al., 2021a). Thus, considering *Q. petraea* and *Q. robur* as one unit appears to be a reasonable approach for their conservation.

The three most similar species to the two native *Quercus* species were *Q. cerris, F. sylvatica* and *Q. rubra*. While *F. sylvatica* did not differ from *Q. petraea/robur* in bark WHC, it did exhibit differences in pH, whereas *Q. cerris* displayed the opposite pattern. Since *Q. cerris* displayed significantly lower WHC than *Q. petraea*/*robur*, it does not seem a good substitute, as it may not support enough bryophytes (i.e., as WHC and bryophyte abundance are positively correlated). However, since *F. sylvatica* displayed a more neutral pH than *Q. petraea*/*robur*, it is possible that it may actually increase the number of bryophytes (i.e., as pH and bryophyte abundance are positively correlated). Thus, *F. sylvatica* may be a good replacement for *Q. petraea*/*robur*. Additionally, *Q. petraea*/*robur* did not differ from *Q. rubra* in terms of bark WHC or pH, therefore *Q. rubra* would also appear to be a good replacement. However, it should be noted that the introduction of *Q. rubra* in Poland has been shown to adversely affect native bryophyte (and other plant) communities (Chmura, 2013; Woziwoda, Kopeć and Witkowski, 2014; Rola et al., 2021). Thus, this should be considered when making decisions about bryophyte conservation in the UK. These findings both confirm and contrast my initial hypothesis that *Quercus* species would be closely related in terms of bryophyte communities and bark chemistry. While it is true that *Q. rubra* emerged as a good match for *Q. petraea*/*robur*, *F. sylvatica* appears to be a better match than *Q. cerris* for the two native *Quercus* species.

The most similar tree species to *F. excelsior* were *T. europaea*, *A. pseudoplatanus* and *F. sylvatica*. In terms of bark WHC, *F. excelsior* did not differ from *A. pseudoplatanus* or *F. sylvatica*. Regarding pH, *F. excelsior* did not differ from *T. europaea*. Thus, no single species matches *F. excelsior* for both bark chemistry components considered. However, *T. europaea* has higher bark WHC than *F. excelsior,* suggesting that replacing the native species with *T. europaea* could increase bryophyte abundance. Similarly, *A. pseudoplatanus* and *F. sylvatica* exhibit more neutral pH than *F. excelsior*, suggesting that they too could increase bryophyte abundance.

However, one major issue persists. The only consistent finding across all diversity metrics was that *F. excelsior* exhibited the highest diversity. If we take this to be true, it becomes clear that replacing *F. excelsior* with just one of the tree species considered in this study will result in a loss of diversity. Replacing *F. excelsior* with more than one tree species could resolve this issue. The similarity values from NEDI suggest that *A. pseudoplatanus* and *T. europaea* are not very similar to one another. However, since they are the two most similar species to *F. excelsior*, this implies that they support different bryophyte communities which are shared with *F. excelsior*. Furthermore, *A. pseudoplatanus* has similar bark WHC to *F. excelsior*, while *T. europaea* shares similar pH. Therefore, a combination of the two substitute species could replicate both bark chemistry components of *F. excelsior*, and these

differences may well be the reason they support different *F. excelsior*-associated species. Thus, replacing *F. excelsior* with a combination of *A. pseudoplatanus* and *T. europaea* may be the solution to maintaining the bryophyte diversity associated with the declining tree species.

5. Conclusions

This study presents novel findings which can inform the management of three declining native species: *Q. petraea*, *Q. robur* and *F. excelsior*. While the study highlighted the limitations of four diversity metrics, it uncovered the utility of a proposed novel approach (NEDI) for quantifying similarity between communities. This method – combined with information regarding bark chemistry – revealed that: *Q. petraea* and *Q. robur* can be jointly managed for maintaining biodiversity; either *F. sylvatica* or *Q. rubra* could be a good replacement for *Q. petraea*/*robur*; and a combination of *A. pseudoplatanus* and *T. europaea* could support many *F. excelsior*-associated bryophytes.

To test these predictions, future studies should consider: (1) including more than one taxonomic group, (2) evaluating competitive interactions between native and novel organisms, (3) assessing functional differences between the native and novel trees, and (4) discerning the relative importance of various bark chemical properties. Should these observations corroborate my predictions, they could offer invaluable insights for conservation strategies aimed at safeguarding biodiversity in ecosystems threatened by the decline of native tree species.

Finally, taking into consideration the limitations of the diversity metrics employed in the present study, and the resulting lack of consistency between results, it becomes clear that future studies should avoid utilising those metrics for the purpose of comparing diversity between communities.

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Reference List

Andermann, T., Antonelli, A., Barrett, R.L. and Silvestro, D. (2022). Estimating Alpha, Beta, and Gamma Diversity Through Deep Learning. *Frontiers in Plant Science*, 13. doi:https://doi.org/10.3389/fpls.2022.839407.

Bahuguna, M.Y., Gairola, S., Semwal, D.P., Lal Uniyal, P. and Bhatt, A.B. (2014). Bryophytes and Ecosystem. In: *Diversity of Lower Plants*. New Delhi, India: I.K. International Publishing House.

Bates, J.W. (1992). Influence of Chemical and Physical Factors on Quercus and Fraxinus Epiphytes at Loch Sunart, Western Scotland: A Multivariate Analysis. *The Journal of Ecology*, 80(1), p.163. doi:https://doi.org/10.2307/2261073.

Bates, J.W. and Brown, D.H. (1981). Epiphyte differentiation between Quercus petraea and Fraxinus excelsior trees in a maritime area of South West England. *Vegetatio*, 48(1), pp.61–70. doi:https://doi.org/10.1007/bf00117362.

Becker, D., Dobson, A. and Howard, K. (2019). *Bark characteristics affect epiphytic bryophyte cover across tree species*. *California Ecology and Conservation Research*. Riverside: University of California. doi:https://doi.org/10.21973/N3H95Z.

Boyd, I.L., Freer-Smith, P.H., Gilligan, C.A. and Godfray, H.C.J. (2013). The Consequence of Tree Pests and Diseases for Ecosystem Services. *Science*, [online] 342(6160). doi:https://doi.org/10.1126/science.1235773.

Branco, M., Figueiras, F.G. and Cermeño, P. (2018). Assessing the efficiency of non-parametric estimators of species richness for marine microplankton. *Journal of Plankton Research*, 40(3), pp.230–243. doi:https://doi.org/10.1093/plankt/fby005.

Burgess, T.I., Scott, J.K., Mcdougall, K.L., Stukely, M.J.C., Crane, C., Dunstan, W.A., Brigg, F., Andjic, V., White, D., Rudman, T., Arentz, F., Ota, N. and Hardy, G.E.St.J. (2016). Current and projected global distribution of *Phytophthora cinnamomi* , one of the world's worst plant pathogens. *Global Change Biology*, [online] 23(4), pp.1661–1674. doi:https://doi.org/10.1111/gcb.13492.

Callaway, R.M., Reinhart, K.O., Moore, G.W., Moore, D.J. and Pennings, S.C. (2002). Epiphyte host preferences and host traits: mechanisms for species-specific interactions. *Oecologia*, 132(2), pp.221–230. doi:https://doi.org/10.1007/s00442-002-0943-3.

Champely, S. and Chessel, D. (2002). Measuring biological diversity using Euclidean metrics. *Environmental and Ecological Statistics*, 9(2), pp.167–177. doi:https://doi.org/10.1023/a:1015170104476.

Chao, A. (1984). Nonparametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics*, 11(4), pp.265–270.

Chao, A., Chazdon, R.L., Colwell, R.K. and Shen, T.-J. (2006). Abundance-Based Similarity Indices and Their Estimation When There Are Unseen Species in Samples. *Biometrics*, 62(2), pp.361–371. doi:https://doi.org/10.1111/j.1541-0420.2005.00489.x.

Chao, A. and Chiu, C.-H. (2016). Nonparametric Estimation and Comparison of Species Richness. *Biometrics*, 40(1), pp.1–11. doi:https://doi.org/10.1002/9780470015902.a0026329.

Chiarucci, A., Bacaro, G. and Scheiner, S.M. (2011). Old and new challenges in using species diversity for assessing biodiversity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, [online] 366(1576), pp.2426–2437. doi:https://doi.org/10.1098/rstb.2011.0065.

Chiu, C. (2023a). A species richness estimator for sample-based incidence data sampled without replacement. *Methods in ecology and evolution*, 14(9), pp.2482–2493. doi:https://doi.org/10.1111/2041-210x.14146.

Chiu, C. (2023b). Sample coverage estimation, rarefaction, and extrapolation based on sample-based abundance data. *Ecology*, 104(8). doi:https://doi.org/10.1002/ecy.4099.

Chmura, D. (2013). Impact of alien tree species Quercus rubra L. On understorey environment and flora: a study of the Silesian Upland (southern Poland). *Polish Journal of Ecology*, 61(3), pp.431–442.

Coleman, E.A., Schultz, B., Ramprasad, V., Fischer, H., Rana, P., Filippi, A.M., Güneralp, B., Ma, A., Rodriguez Solorzano, C., Guleria, V., Rana, R. and Fleischman, F. (2021). Limited effects of tree planting on forest canopy cover and rural livelihoods in Northern India. *Nature Sustainability*, 4(11), pp.997–1004. doi:https://doi.org/10.1038/s41893-021-00761-z.

Daly, A., Baetens, J. and De Baets, B. (2018). Ecological Diversity: Measuring the Unmeasurable. *Mathematics*, 6(7), p.119. doi:https://doi.org/10.3390/math6070119.

Denman, S., Doonan, J., Ransom-Jones, E., Broberg, M., Plummer, S., Kirk, S., Scarlett, K., Griffiths, A.R., Kaczmarek, M., Forster, J., Peace, A., Golyshin, P.N., Hassard, F., Brown, N., Kenny, J.G. and McDonald, J.E. (2017). Microbiome and infectivity studies reveal complex polyspecies tree disease in Acute Oak Decline. *The ISME Journal*, 12(2), pp.386–399. doi:https://doi.org/10.1038/ismej.2017.170.

Denman, S. and Webber, J. (2009). Oak declines: new definitions and new episodes in Britain. *Quarterly Journal of Forestry*, 103(4), pp.285–290.

Ennos, R., Cottrell, J., Hall, J. and O'Brien, D. (2019). Is the introduction of novel exotic forest tree species a rational response to rapid environmental change? – A British perspective. *Forest Ecology and Management*, [online] 432, pp.718–728. doi:https://doi.org/10.1016/j.foreco.2018.10.018.

Ford, C.R. and Vose, J.M. (2007). TSUGA CANADENSIS(L.) CARR. MORTALITY WILL IMPACT HYDROLOGIC PROCESSES IN SOUTHERN APPALACHIAN FOREST ECOSYSTEMS. *Ecological Applications*, 17(4), pp.1156–1167. doi:https://doi.org/10.1890/06-0027.

Fritz, Ö., Brunet, J. and Caldiz, M. (2009). Interacting effects of tree characteristics on the occurrence of rare epiphytes in a Swedish beech forest area. *The Bryologist*, 112(3), pp.488–505. doi:https://doi.org/10.1639/0007-2745-112.3.488.

Gatti, R.C., Amoroso, N. and Monaco, A. (2020). Estimating and comparing biodiversity with a single universal metric. *Ecological Modelling*, 424, p.109020. doi:https://doi.org/10.1016/j.ecolmodel.2020.109020.

George, J.-P., G. M. Sanders, T., Timmermann, V., Potočić, N. and Lang, M. (2022). European-wide forest monitoring substantiate the neccessity for a joint conservation strategy to rescue European ash species (Fraxinus spp.). *Scientific Reports*, 12(1). doi:https://doi.org/10.1038/s41598-022-08825-6.

Ghelardini, L., Pepori, A.L., Luchi, N., Capretti, P. and Santini, A. (2016). Drivers of emerging fungal diseases of forest trees. *Forest Ecology and Management*, [online] 381, pp.235–246. doi:https://doi.org/10.1016/j.foreco.2016.09.032.

Giordani, P., Brunialti, G., Bacaro, G. and Nascimbene, J. (2012). Functional traits of epiphytic lichens as potential indicators of environmental conditions in forest ecosystems. *Ecological Indicators*, 18, pp.413–420. doi:https://doi.org/10.1016/j.ecolind.2011.12.006.

Godefroid, M., Meurisse, N., Groenen, F., Kerdelhué, C. and Rossi, J.-P. . (2019). Current and future distribution of the invasive oak processionary moth. *Biological Invasions*, 22(2), pp.523–534. doi:https://doi.org/10.1007/s10530-019-02108-4.

Gosselin, M., Fourcin, D., Dumas, Y., Gosselin, F., Korboulewsky, N., Toïgo, M. and Vallet, P. (2017). Influence of forest tree species composition on bryophytic diversity in mixed and pure pine (Pinus sylvestris L.) and oak (Quercus petraea (Matt.) Liebl.) stands. *Forest Ecology and Management*, 406, pp.318–329. doi:https://doi.org/10.1016/j.foreco.2017.09.067.

Gustafsson, L., Franzén, M., Sunde, J. and Johansson, V. (2023). The non-native Quercus rubra does not substitute the native Quercus robur and Q. petraea as substrate for epiphytic lichens and bryophytes. *Forest Ecology and Management*, 549, pp.121482–121482. doi:https://doi.org/10.1016/j.foreco.2023.121482.

Hennon, P.E., Frankel, S.J., Woods, A.J., Worrall, J.J., Norlander, D., Zambino, P.J., Warwell, M.V. and Shaw, C.G. (2020). A framework to evaluate climate effects on forest tree diseases. *Forest Pathology*, 50(6). doi:https://doi.org/10.1111/efp.12649.

Hill, L., Hector, A., Hemery, G., Smart, S., Tanadini, M. and Brown, N. (2017). Abundance distributions for tree species in Great Britain: A two-stage approach to modeling abundance using species distribution modeling and random forest. *Ecology and Evolution*, 7(4), pp.1043–1056. doi:https://doi.org/10.1002/ece3.2661.

Hong, S., Yin, G., Piao, S., Dybzinski, R., Cong, N., Li, X., Wang, K., Peñuelas, J., Zeng, H. and Chen, A. (2020). Divergent responses of soil organic carbon to afforestation. *Nature Sustainability*, 3(9), pp.694–700. doi:https://doi.org/10.1038/s41893-020-0557-y.

J. Ellis, C., Eaton, S., Theodoropoulos, M. and Elliott, K. (2015). *Epiphyte Communities and Indicator Species* . An Ecological Guide for Scotland's Woodlands ed. Royal Botanic Garden, Edinburgh.

Jia, X., Shao, M., Zhu, Y. and Luo, Y. (2017). Soil moisture decline due to afforestation across the Loess Plateau, China. *Journal of Hydrology*, 546, pp.113–122. doi:https://doi.org/10.1016/j.jhydrol.2017.01.011.

Kakavas, K.V., Chavenetidou, M. and Birbilis, D. (2018). Chemical Properties of Greek Stump Chestnut (Castanea sativa Mill.). *Natural Products Chemistry & Research*, 06(04). doi:https://doi.org/10.4172/2329-6836.1000331.

Kapfer, J., Audorff, V., Beierkuhnlein, C. and Hertel, E. (2012). Do bryophytes show a stronger response than vascular plants to interannual changes in spring water quality? *Freshwater Science*, 31(2), pp.625–635. doi:https://doi.org/10.1899/11-037.1.

Kärvemo, S., Huo, L., Öhrn, P., Lindberg, E. and Persson, H.J. (2023). Different triggers, different stories: Bark-beetle infestation patterns after storm and drought-induced outbreaks. *Forest Ecology and Management*, 545, pp.121255–121255. doi:https://doi.org/10.1016/j.foreco.2023.121255.

Kim, B.-R., Shin, J., Guevarra, R.B., Lee, J.H., Kim, D.W., Seol, K.-H., Lee, J.-H., Kim, H.B. and Isaacson, R.E. (2017). Deciphering Diversity Indices for a Better Understanding of Microbial Communities. *Journal of Microbiology and Biotechnology*, 27(12), pp.2089–2093. doi:https://doi.org/10.4014/jmb.1709.09027.

Klinghardt, M. and Zotz, G. (2021). Abundance and seasonal growth of epiphytic ferns at three sites along a rainfall gradient in Western Europe. *Flora*, 274, p.151749. doi:https://doi.org/10.1016/j.flora.2020.151749.

Kubiak, D. and Osyczka, P. (2020). Non-forested vs forest environments: The effect of habitat conditions on host tree parameters and the occurrence of associated epiphytic lichens. *Fungal Ecology*, 47, p.100957. doi:https://doi.org/10.1016/j.funeco.2020.100957.

Legrand, I., Asta, J. and Goudard, Y. (1996). Variations in bark acidity and conductivity over the trunk length of silver fir and Norway spruce. *Trees*, 11(1), p.54. doi:https://doi.org/10.1007/s004680050058.

Löbel, S., Snäll, T. and Rydin, H. (2012). Epiphytic bryophytes near forest edges and on retention trees: reduced growth and reproduction especially in old-growth-forest indicator species. *Journal of Applied Ecology*, 49(6), pp.1334–1343. doi:https://doi.org/10.1111/j.1365-2664.2012.02201.x.

Magurran, A.E. (2013). *Measuring Biological Diversity*. John Wiley & Sons.

Mistry, J. and Berardi, A. (2005). Effects of phorophyte determinants on lichen abundance in the cerrado of central Brazil. *Plant Ecology*, 178(1), pp.61–76. doi:https://doi.org/10.1007/s11258-004-2493-8.

Mitchell, R.J., Beaton, J.K., Bellamy, P.E., Broome, A., Chetcuti, J., Eaton, S., Ellis, C.J., Gimona, A., Harmer, R., Hester, A.J., Hewison, R.L., Hodgetts, N.G., Iason, G.R., Kerr, G., Littlewood, N.A., Newey, S., Potts, J.M., Pozsgai, G., Ray, D. and Sim, D.A. (2014). Ash dieback in the UK: A review of the ecological and conservation

implications and potential management options. *Biological Conservation*, 175, pp.95–109. doi:https://doi.org/10.1016/j.biocon.2014.04.019.

Mitchell, R.J., Bellamy, P.E., Ellis, C.J., Hewison, R.L., Hodgetts, N.G., Iason, G.R., Littlewood, N.A., Newey, S., Stockan, J.A. and Taylor, A.F.S. (2019). Collapsing foundations: The ecology of the British oak, implications of its decline and mitigation options. *Biological Conservation*, 233, pp.316–327. doi:https://doi.org/10.1016/j.biocon.2019.03.040.

Mitchell, R.J., Chitanava, S., Dbar, R., Kramarets, V., Lehtijärvi, A., Matchutadze, I., Mamadashvili, G., Matsiakh, I., Nacambo, S., Papazova-Anakieva, I., Sathyapala, S., Tuniyev, B.S., Vétek, G., Zukhbaia, M. and Kenis, M. (2018). Identifying the ecological and societal consequences of a decline in Buxus forests in Europe and the Caucasus. *Biological Invasions*, 20(12), pp.3605–3620. doi:https://doi.org/10.1007/s10530-018-1799-8.

Mitchell, R.J., Hewison, R.L., Beaton, J. and Douglass, J.R. (2021a). Identifying substitute host tree species for epiphytes: The relative importance of tree size and species, bark and site characteristics. *Applied Vegetation Science*, 24(2). doi:https://doi.org/10.1111/avsc.12569.

Mitchell, R.J., Hewison, R.L., Beaton, J., Haghi, R.K., Robertson, A.H.J., Main, A.M., Owen, I.J. and Douglass, J. (2020). *Functional and epiphytic biodiversity differences between nine tree species in the UK*. NERC Environmental Information Data Centre. (Dataset). https://doi.org/10.5285/f539567f-a8cd-482e-89b8-64a951b52d93.

Mitchell, R.J., Hewison, R.L., Haghi, R.K., Robertson, A.H.J., Main, A.M. and Owen, I.J. (2021b). Functional and ecosystem service differences between tree species: implications for tree species replacement. *Trees*, 35(1), pp.307–317. doi:https://doi.org/10.1007/s00468-020-02035-1.

Mitchell, R.J., Pakeman, R.J., Broome, A., Beaton, J.K., Bellamy, P.E., Brooker, R.W., Ellis, C.J., Hester, A.J., Hodgetts, N.G., Iason, G.R., Littlewood, N.A., Pozsgai, G., Ramsay, S., Riach, D., Stockan, J.A., Taylor, A.F.S. and Woodward, S. (2016). How to Replicate the Functions and Biodiversity of a Threatened Tree Species? The Case of Fraxinus excelsior in Britain. *Ecosystems*, 19(4), pp.573–586. doi:https://doi.org/10.1007/s10021-015-9953-y.

Morris, E.K., Caruso, T., Buscot, F., Fischer, M., Hancock, C., Maier, T.S., Meiners, T., Müller, C., Obermaier, E., Prati, D., Socher, S.A., Sonnemann, I., Wäschke, N., Wubet, T., Wurst, S. and Rillig, M.C. (2014). Choosing and using diversity indices: insights for ecological applications from the German Biodiversity Exploratories. *Ecology and Evolution*, 4(18), pp.3514–3524. doi:https://doi.org/10.1002/ece3.1155.

Nagel, T.A., Iacopetti, G., Javornik, J., Rozman, A., De Frenne, P., Selvi, F. and Verheyen, K. (2019). Cascading effects of canopy mortality drive long-term changes in understorey diversity in temperate old-growth forests of Europe. *Journal of Vegetation Science*, 30(5), pp.905–916. doi:https://doi.org/10.1111/jvs.12767.

Purvis, A. and Hector, A. (2000). Getting the Measure of Biodiversity. *Nature*, 405(6783), pp.212–219. doi:https://doi.org/10.1038/35012221.

Ricotta, C. and Pavoine, S. (2022). A new parametric measure of functional dissimilarity: Bridging the gap between the Bray-Curtis dissimilarity and the Euclidean distance. *Ecological Modelling*, 466, p.109880. doi:https://doi.org/10.1016/j.ecolmodel.2022.109880.

Ricotta, C. and Podani, J. (2017). On some properties of the Bray-Curtis dissimilarity and their ecological meaning. *Ecological Complexity*, 31, pp.201–205. doi:https://doi.org/10.1016/j.ecocom.2017.07.003.

Rola, K., Plášek, V., Rożek, K. and Zubek, S. (2021). Effect of tree species identity and related habitat parameters on understorey bryophytes – interrelationships between bryophyte, soil and tree factors in a 50-year-old experimental forest. *Plant and Soil*, 466(1-2), pp.613–630. doi:https://doi.org/10.1007/s11104-021-05074-w.

Roswell, M., Dushoff, J. and Winfree, R. (2021). A conceptual guide to measuring species diversity. *Oikos*, 130(3), pp.321–338. doi:https://doi.org/10.1111/oik.07202.

Shannon, C.E. (1948). A Mathematical Theory of Communication. *Bell System Technical Journal*, 27(3), pp.379–423.

Shao, Y., Wang, S., Li, Y., Chen, Y., Zhao, H., Wang, J., Liu, F. and Yuan, Z. (2023). Importance of Bark Physicochemical Properties in an Epiphytic Bryophyte Community within a Temperate Deciduous Broadleaf Forest. *Diversity*, 15(5), pp.688–688. doi:https://doi.org/10.3390/d15050688.

Shi, X.-M., Song, L., Liu, W.-Y., Lu, H.-Z., Qi, J.-H., Li, S., Chen, X., Wu, J.-F., Liu, S. and Wu, C.-S. (2017). Epiphytic bryophytes as bio-indicators of atmospheric nitrogen deposition in a subtropical montane cloud forest: Response patterns, mechanism, and critical load. *Environmental Pollution*, 229, pp.932–941. doi:https://doi.org/10.1016/j.envpol.2017.07.077.

Simpson, E.H. (1949). Measurement of Diversity. *Nature*, 163(4148), pp.688–688. doi:https://doi.org/10.1038/163688a0.

Sørensen, T. (1948). A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analyses of the vegetation on Danish commons. *Biologiske skrifter*, 5, pp.1–34.

Spellerberg, I.F. and Fedor, P.J. (2003). A tribute to Claude Shannon (1916-2001) and a plea for more rigorous use of species richness, species diversity and the 'Shannon-Wiener' Index. *Global Ecology and Biogeography*, 12(3), pp.177–179. doi:https://doi.org/10.1046/j.1466-822x.2003.00015.x.

Sturrock, R.N., Frankel, S.J., Brown, A.V., Hennon, P.E., Kliejunas, J.T., Lewis, K.J., Worrall, J.J. and Woods, A.J. (2011). Climate change and forest diseases. *Plant Pathology*, 60(1), pp.133–149. doi:https://doi.org/10.1111/j.1365-3059.2010.02406.x.

Tessler, M., Truhn, K.M., Bliss-Moreau, M. and Wehr, J.D. (2014). Diversity and distribution of stream bryophytes: does pH matter? *Freshwater Science*, 33(3), pp.778–787. doi:https://doi.org/10.1086/676996.

Tewari, L.M., Tewari, G., Nailwal, T. and Pangtey, Y.P.S. (2009). Bark Factors Affecting the Distribution of Epiphytic Ferns Communities . *Nature and Science*, 7(5), pp.1545-0740.

Thomas, P.A. (2016). Biological Flora of the British Isles:Fraxinus excelsior. *Journal of Ecology*, [online] 104(4), pp.1158–1209. doi:https://doi.org/10.1111/1365-2745.12566.

Topalidou, E.T. and Shaw, M.W. (2015). Relationships between Oak powdery mildew incidence and severity and commensal fungi. *Forest Pathology*, 46(2), pp.104–115. doi:https://doi.org/10.1111/efp.12218.

Tyler, T. and Olsson, P.A. (2016). Substrate pH ranges of south Swedish bryophytes—Identifying critical pH values and richness patterns. *Flora*, 223, pp.74–82. doi:https://doi.org/10.1016/j.flora.2016.05.006.

Wolf, J.H.D. and Alejandro, F.-S. (2003). Patterns in species richness and distribution of vascular epiphytes in Chiapas, Mexico. *Journal of Biogeography*, 30(11), pp.1689–1707. doi:https://doi.org/10.1046/j.1365-2699.2003.00902.x.

Woziwoda, B., Kopeć, D. and Witkowski, J. (2014). The negative impact of intentionally introduced Quercus rubra L. on a forest community. *Acta Societatis Botanicorum Poloniae*, [online] 83(1), pp.39–49. doi:https://doi.org/10.5586/asbp.2013.035.

Yuan, Y., Buckland, S.T., Harrison, P.J., Foss, S. and Johnston, A. (2016). Using Species Proportions to Quantify Turnover in Biodiversity. *Journal of Agricultural, Biological, and Environmental Statistics*, 21(2), pp.363–381. doi:https://doi.org/10.1007/s13253-015-0243-0.

Zarate-García, A.M., Noguera-Savelli, E., Andrade-Canto, S.B., Zavaleta-Mancera, H.A., Gauthier, A. and Alatorre-Cobos, F. (2020). Bark water storage capacity influences epiphytic orchid preference for host trees. *American Journal of Botany*, 107(5), pp.726–734. doi:https://doi.org/10.1002/ajb2.1470.

Zhao, Y., Lehman, B., Ball, R., Mosesian, J. and de Palma, J.-F. (2013). Outlier detection rules for fault detection in solar photovoltaic arrays. In: *2013 twenty-eighth annual IEEE applied power electronics conference and exposition (APEC)*. IEEE, pp.2913–2920.

APPENDIX A: INFORMATION REGARDING BRYOPHYTE NAMES AND ABUNDANCES

Taxon	Authority	Taxon code
Amblystegium serpens	Amblystegium serpens (Hedw.) Bruch, Schimp. & W.Guembel	Amser
Atrichum undulatum	Atrichum undulatum (Hedw.) P.Beauv.	Atund
Bryum capillare	Bryum capillare Hedw.	Brcap
Brachythecium rutabulum	Brachythecium rutabulum (Hedw.) Bruch, Schimp. & W.Guembel	Brrut
Brachytheciastrum velutinum	Brachytheciastrum velutinum (Hedw.) Ignatov & Huttunen	Brvel
Campylopus introflexus	Campylopus introflexus (Hedw.) Brid.	Caint
Cirriphyllum crassinervium	Cirriphyllum crassinervium (Wils.) Loeske & Fleisch.	Cicra
Dicranum fuscescens	Dicranum fuscescens Sm.	Difus
Dicranella heteromalla	Dicranella heteromalla (Hedw.) Schimp.	Dihet
Didymodon insulanus	Didymodon insulanus (De Not.) M.O.Hill	Diins
Dicranum montanum	Dicranum montanum Hedw.	Dimon
Dicranum scoparium	Dicranum scoparium Hedw.	Disco
Dicranum tauricum	Dicranum tauricum Sapjegin	Ditau
Didymodon tophaceus	Didymodon tophaceus (Brid.) Lisa	Ditop
Frullania dilatata	Frullania dilatata (L.) Dumort.	Frdil
Frullania tamarisci	Frullania tamarisci (L.) Dumort.	Frtam
Hookeria lucens	Hookeria lucens (Hedw.) Sm.	Holuc
Homalothecium sericeum	Homalothecium sericeum (Hedw.) Bruch, Schimp. & W.Guembel	Hoser
Hypnum andoi	Hypnum andoi A.J.E. Sm.	Hyand
Hypnum cupressiforme	Hypnum cupressiforme Hedw.	Hycup
Hypnum cupressiforme var. resupinatum	Hypnum cupressiforme var. resupinatum (Taylor) Schimp.	Hycvr
Isothecium alopecuroides	Isothecium alopecuroides (Dubois) Isov.	Isalo
Isothecium myosuroides	Isothecium myosuroides Brid.	Ismyo
Kindbergia praelonga	Kindbergia praelonga (Hedw.) Ochyra	Kipra
Lepidozia reptans	Lepidozia reptans (L.) Dumort.	Lerep
Leucodon sciuroides	Leucodon sciuroides Schwaegr.	Lesci
Lophocolea bidentata	Lophocolea bidentata (L.) Dumort.	Lobid
Lophocolea heterophylla	Lophocolea heterophylla (Schrad.) Dumort.	Lohet
Lophocolea semiteres	Lophocolea semiteres (Lehm.) Mitt.	Losem
Metzgeria conjugata	Metzgeria conjugata Lindb.	Mecon
Metzgeria furcata	Metzgeria furcata (L.) Dumort.	Mefur
Mnium hornum	Mnium hornum Hedw.	Mnhor
Neckera complanata	Neckera complanata (Hedw.) Huebener	Necom

Neckera pumila	Neckera pumila Hedw.	Nepum
Orthotrichum affine	Orthotrichum affine Brid.	Oraff
Orthotrichum diaphanum	Orthotrichum diaphanum Brid.	Ordia
Orthodontium lineare	Orthodontium lineare Schwaegr.	Orlin
Orthotrichum lyellii	Orthotrichum lyellii Hook. & Taylor	Orlye
Orthotrichum pulchellum	Orthotrichum pulchellum Brunt.	Orpul
Orthotrichum stramineum	Orthotrichum stramineum Hornsch. ex Brid.	Orstm
Orthotrichum striatum	Orthotrichum striatum Hedw.	Orstr
Oxyrrhynchium hians	Oxyrrhynchium hians (Hedw.) Loeske	Oxhia
Plagiomnium affine	Plagiomnium affine (Blandow) T.J.Kop.	Plaff
Plagiothecium denticulatum	Plagiothecium denticulatum (Hedw.) Bruch, Schimp. & W.Guembel	Plden
Plagiothecium nemorale	Plagiothecium nemorale (Mitt.) A.Jaeger	Plnem
Plagiochila porelloides	Plagiochila porelloides (Torr. ex Nees) Lindenb.	Plpor
Plagiomnium rostratum	Plagiomnium rostratum (Schrad.) T.J.Kop.	Plros
Plagiothecium succulentum	Plagiothecium succulentum (Wilson) Lindb.	Plsuc
Plagiomnium undulatum	Plagiomnium undulatum (Hedw.) T.J.Kop.	Plund
Polytrichum formosum	Polytrichum formosum Hedw.	Pofor
Porella platyphylla	Porella platyphylla (L.) Pfeiff.	Popla
Radula complanata	Radula complanata (L.) Dumort.	Racom
Rhynchostegium confertum	Rhynchostegium confertum (Dicks.) Bruch, Schimp. & W.Guembel	Rhcon
Rhytidiadelphus loreus	Rhytidiadelphus loreus (Hedw.) Warnst.	Rhlor
Rhytidiadelphus squarrosus	Rhytidiadelphus squarrosus (Hedw.) Warnst.	Rhsqu
Rhytidiadelphus triquetrus	Rhytidiadelphus triquetrus (Hedw.) Warnst.	Rhtri
Scapania gracilis	Scapania gracilis Lindb.	Scgra
Scleropodium purum	Scleropodium purum (Hedw.) Limpr.	Scpur
Syntrichia laevipila	Syntrichia laevipila Brid.	Sylae
Syntrichia papillosa	Syntrichia papillosa (Wilson) Jur.	Sypap
Thamnobryum alopecurum	Thamnobryum alopecurum (Hedw.) Gangulee	Thalo
Thuidium tamariscinum	Thuidium tamariscinum (Hedw.) Bruch, Schimp. & W.Guembel	Thtam
Ulota bruchii	Ulota bruchii Hornsch. ex Brid.	Ulbru
Ulota crispa	Ulota crispa (Hedw.) Brid.	Ulcri
Zygodon conoideus	Zygodon conoideus (Dicks.) Hook. & Taylor	Zycon
Zygodon rupestris	Zygodon rupestris Schimp. ex Lor.	Zyrup
Zygodon viridissimus	Zygodon viridissimus (Dicks.) Brid.	Zyvir

Table A1: Information regarding taxon identity, authority and code. Taken from Mitchell et al. (2020) Metadata.

	Tree Species								
Taxon code	*Q. petraea*	*Q. robur*	*F. excelsior*	*A. pseudoplatanus*	*C. sativa*	*F. sylvatica*	*Q. cerris*	*Q. rubra*	*T. europaea*
Amser	0	1	2	3	0	2	0	0	0
Atund	0	0	0	0	0	0	0	1	0
Brcap	3	7	15	3	0	5	3	1	8
Brrut	2	5	27	14	2	16	5	2	19
Brvel	0	0	6	4	1	0	0	0	2
Caint	0	0	0	0	0	1	0	0	0
Cicra	0	0	1	0	0	0	0	0	0
Difus	0	0	0	0	2	0	1	0	0
Dihet	0	0	0	0	0	0	0	0	0
Diins	0	0	1	0	0	0	1	0	0
Dimon	0	0	0	0	1	0	0	0	0
Disco	3	4	4	0	6	8	5	2	2
Ditau	0	1	0	0	0	0	0	1	0
Ditop	0	0	0	0	0	0	0	0	0
Frdil	1	4	14	8	0	12	1	6	4
Frtam	1	0	3	1	0	0	0	0	0
Holuc	0	0	1	1	0	0	0	0	0
Hoser	1	5	15	20	0	7	0	0	8
Hyand	5	13	0	0	12	15	5	6	6
Hycup	8	22	21	10	17	26	10	13	21
Hycvr	8	21	24	24	4	15	6	4	24
Isalo	0	3	10	10	0	1	0	0	5
Ismyo	11	23	14	10	6	27	8	8	16
Kipra	1	7	11	8	1	13	3	5	11
Lerep	0	0	0	0	3	0	0	1	0
Lesci	0	0	1	2	0	0	0	0	0
Lobid	1	1	3	2	1	2	2	3	2
Lohet	0	0	1	0	3	0	1	0	1
Losem	0	0	0	0	0	0	0	1	0
Mecon	0	0	0	0	0	0	0	0	1
Mefur	5	16	25	22	1	25	4	4	26
Mnhor	3	7	1	0	13	11	5	3	5
Necom	0	0	2	6	0	0	0	0	1
Nepum	0	0	1	0	0	0	0	0	0
Oraff	0	0	4	5	0	5	1	0	2
Ordia	0	0	0	4	0	1	0	0	0
Orlin	0	0	0	0	7	0	0	0	0
Orlye	1	3	6	1	0	1	1	1	0

Orpul	0	0	1	0	0	2	0	0	0
Orstm	0	0	0	0	0	1	0	0	0
Orstr	0	0	0	0	0	0	0	0	1
Oxhia	0	1	0	0	0	0	0	1	0
Plaff	0	0	3	0	0	0	0	0	0
Plden	0	0	0	1	0	1	0	0	0
Plnem	0	2	1	0	0	0	1	0	1
Plpor	0	0	1	1	2	1	1	0	2
Plros	0	0	2	0	0	0	0	1	0
Plsuc	1	2	1	1	0	0	0	1	2
Plund	0	2	5	3	0	1	0	0	1
Pofor	0	1	0	0	3	2	2	0	1
Popla	0	0	0	0	0	1	0	0	0
Racom	0	0	3	2	0	0	0	0	1
Rhcon	0	2	2	1	0	0	0	0	0
Rhlor	0	3	0	1	2	3	1	2	3
Rhsqu	0	0	1	0	0	1	0	0	0
Rhtri	0	1	0	0	0	3	0	0	2
Scgra	0	0	0	0	1	0	0	0	0
Scpur	0	1	0	0	0	0	0	1	0
Sylae	1	0	3	4	0	0	0	0	1
Sypap	0	0	1	2	0	0	0	0	0
Thalo	0	0	1	0	0	0	0	0	0
Thtam	0	2	2	1	2	3	1	3	3
Ulbru	0	0	1	1	0	0	0	1	1
Ulcri	0	0	0	2	0	1	0	0	0
Zycon	0	0	3	0	0	0	1	0	0
Zyrup	0	2	2	2	0	2	0	0	0
Zyvir	0	4	5	15	0	5	1	1	11
Species Count	17	29	43	34	21	33	24	25	32
Total	56	166	251	195	90	220	70	73	194

Table A2: Information on incidence and abundance of bryophyte species across different the tree species.

APPENDIX B: PYTHON CODE

Richness/Diversity Barplot

```
import numpy as np
from matplotlib import pyplot as plt
import scipy

x=['$\\it{Quercus\ petraea}$','$\\it{Quercus\
robur}$','$\\it{Fraxinus\ excelsior}$',
   '$\\it{Acer\ pseudoplatanus}$','$\\it{Castanea\
sativa}$','$\\it{Fagus\ sylvatica}$',
'$\\it{Quercus\ cerris}$','$\\it{Quercus\ rubra}$','$\\it{Tilia\ x\
europaea}$' ]

Richness = [17, 29, 43, 34, 21, 33, 24, 25, 32]

Diversity = [46, 166, 251, 195, 90, 220, 70, 73,194]

width=0.4

values=np.arange(len(x))

plt.bar(values,Richness, width, label='Richness', color='g',
edgecolor='black')
plt.bar(values+width,Diversity, width, label='Diversity',
color='yellowgreen', edgecolor='black')
plt.ylim(0.1,275)
plt.xticks(values+0.2, x, rotation=45, ha='right',
rotation_mode='anchor')
plt.ylabel('Bryophyte Count')
plt.legend()
plt.gcf().subplots_adjust(bottom=0.4)
plt.gcf().subplots_adjust(top=0.9)
plt.grid(zorder=0)
plt.gca().set_axisbelow(True)
plt.show()
```

Bark Chemistry Barplot (e.g., pH)

```
import numpy as np
from matplotlib import pyplot as plt
import scipy

x=['$\\it{Quercus\ petraea}$','$\\it{Quercus\
robur}$','$\\it{Fraxinus\ excelsior}$',
   '$\\it{Acer\ pseudoplatanus}$','$\\it{Castanea\
sativa}$','$\\it{Fagus\ sylvatica}$',
'$\\it{Quercus\ cerris}$','$\\it{Quercus\ rubra}$','$\\it{Tilia\ x\
europaea}$' ]

y=[4.755384615, 4.782647059, 5.4146875, 6.2478125, 3.749583333,
5.905142857, 4.807142857, 4.874, 5.452580645]

SE=[0.116512437,  0.08711284,  0.085941166, 0.108126209,
0.077694308,
    0.060783915, 0.099969383, 0.065956696, 0.091625662]
```

```
plt.bar(x,y, width=0.70, color='c', edgecolor='black')
plt.ylim(3,7)
plt.xticks(rotation=45, ha='right', rotation_mode='anchor')
plt.ylabel('Bark pH)
plt.errorbar(x,y,yerr=SE,color='k', fmt='o', markersize=3,
capsize=4)
plt.gcf().subplots_adjust(bottom=0.4)
plt.gcf().subplots_adjust(top=0.9)
plt.show()
```

 # The method used was the same for conductivity and WHC.

Scatter Plot and Linear Regression (e.g., pH and bryophyte abundance)

```
import  numpy as np
from matplotlib import pyplot as plt
import scipy.stats
from scipy import stats
import os

import csv

file = open('……')
type(file)

data = np.loadtxt('…...',',usecols=[1,2])

ph = data[:,1]
bry = data[:,0]

m,c=np.polyfit(ph,bry,1)

plt.scatter(ph,bry,edgecolors = 'black', marker='o', color='cyan')
plt.plot(ph,m*ph+c, color='black')
plt.xlabel('Bark pH')
plt.ylabel('Bryophyte Count (per tree)')

stats.pearsonr(ph,bry)
```

 # The method used was the same for conductivity and WHC.

NEDI visualisation

```
!pip3 install networkx pandas
import numpy as np
import pandas as pd
import pylab as P

bc = pd.read_csv('…..)

tree_species = list(pd.unique(bc['Taxon_code']))

tree_features = {}
for species in tree_species:
    tree_features[species] = bc[bc['Taxon_code']==species]
```

```
for species in tree_species:
    tree_features[species] =
tree_features[species].drop(['Taxon_code'],axis=1)

for species in tree_species:
    tree_features[species] = tree_features[species].mean()

def sim_measure(a, b, method):
    if method == 'scalar':
        return a.dot(b)
    elif method == 'euclidean distance':
        return 1.0/(np.linalg.norm(a.values-b.values)+0.0001)

similarity = {}
for species1 in tree_species:
    similarity[species1] = {}
    for species2 in tree_species:
        similarity[species1][species2] =
sim_measure(tree_features[species1],tree_features[species2],
'euclidean distance')

gr = nx.Graph()
for species1 in tree_species:
    for species2 in tree_species:
        if tree_species.index(species1) <
tree_species.index(species2):
            gr.add_edge(species1, species2,
weight=100*similarity[species1][species2])

pos=nx.spring_layout(gr, iterations=10000, seed = 2) #i like seed (0

P.figure(figsize=(15,15))
P.title('Euclidean Distance Similarity')
P.gca().axis('off')
nx.draw_networkx_edges(gr,pos,edge_color='lightgray')
nx.draw_networkx_nodes(gr,pos,node_color='c', edgecolors ='black',
node_size=13)
nx.draw_networkx_labels(gr,pos, {label:r'$\it{'+label.replace('
',r'\ ')+'}$' for label in tree_species}, font_color='black',
verticalalignment='bottom')
P.show()
```

 # The method used was the same for SSI