Forest Research

Priorities for research on emerging species

An analysis based on species diversity in present and future environments

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Summary

This report summarises the variation in the diversity of forest tree species in different climatic regions of Britain. Progress on three areas is reported:

1. An analysis of species diversity in different climate regions to identify shortfalls.
2. The extent to which species can substitute for each other if one gets into trouble using estimates of species climate space.
3. The identification of novel future climates that may require additional species.

Measured species diversity, which takes account of relative abundance, in the wet climate regions of Britain that are dominated by Sitka spruce is low and is being further reduced in terms of useable species by the impacts of new pests and diseases. However, species richness (the total number of species present) is high in these regions so there appears to be an underlying diversity of currently low abundance species that require research to determine if they could be more widely planted in the future.

In addition, the potential impacts on species composition of shifts in climate zones caused by climate change are examined and gaps identified for future climates. In particular, the appearance of novel warmer climates for Britain requires research to determine impacts on existing species and to continue evaluation of new species and provenances.

The report concludes with a series of recommendations on directions for future research within the Emerging Species Work Area.

1. Introduction

1.1. Background

The trees used in British forestry are a mix of native and introduced species. The selection of species for forestry involves two broad considerations: biological suitability and the fulfilment of economic and other objectives (Anderson, 1961). The assemblage of species that are adapted to the climate and soils of an area provide a pool from which appropriate ones can be selected to meet objectives. Sufficient numbers (richness) of species have to be maintained in these pools to meet present and future needs.

Current choices and recommendations about species are based on decades of research and practical experience. However, increasing incidences of new pests and diseases are eroding species richness by partially or completely preventing continued use of important species. Furthermore, projected shifts in regional climates caused by climate change will require alterations to the composition of available species by, for example, increasing the number of species or provenances that can tolerate the warmer drier conditions that are projected to occur more frequently in southern Britain.

A principal aim of research on tree species is to ensure that a diverse range of species and provenances are available for use in the different climatic regions and soils of Britain, with sufficient interchangeability to allow substitution when a current species runs into difficulties. This requires maintaining knowledge on the positive and negative characteristics of a broad range of species.

A wide range of tree species can be grown in the temperate climate of the British Isles but knowledge of the potential of each species for forestry varies considerably. Species can be categorised into four groups according to the extent of current use in forestry and how much is known about their silvicultural characteristics (Kerr & Jinks, 2015):

1. **Principal tree species** are defined as species that are currently widely used for timber production and will continue to be dominant species unless affected by a new pest or disease or become adversely affected by climate change.

2. **Secondary tree species** are trees that have been planted on a much smaller scale than the principal species because they are restricted to particular climate zones or have been overshadowed by more popular principal species. The qualities of secondary species are reasonably well understood and they have demonstrated their suitability for forestry under current conditions and so have potential for wider use in future.

3. **Plot-stage species** are a group of species that have not been planted commercially on any significant scale, but have demonstrated positive silvicultural characteristics in trial plots and have qualities suitable for forestry objectives to justify further testing and development.

4. Specimen-stage species are species that have not been trialled for forest potential in experimental plots, but have demonstrated as specimens in tree collections positive traits of good form, growth rate and hardiness to warrant further testing in plots on a limited scale. Work on identifying these species is currently covered by a separate Arboreta project.

A broad aim for emerging species research is to provide sufficient knowledge to promote identified species from lower to higher categories, e.g. move a species from the experimental plot-stage to the commercial secondary or eventually principal categories, or from the tentative specimen stage to the plot stage for further study.

Within the principal and secondary categories are groups of species with similar environmental tolerances that can be used together in different ways for diversifying plantations and that can to some extent substitute for each other if the use of a principal species becomes restricted by, for example, a new disease.

The current composition of the primary and secondary categories is also focussed towards the climatic suitability and needs of the twentieth century, and is not necessarily fully compatible with the future climate of the British Isles. Consequently, both categories require to be extended with species that might be suited to the future climate of Britain.

Principal and secondary species can be further categorised into different groups according to their current use and tolerances of different climates and soils. Determination of the abundance and diversity of species within environmental groups can be used to identify potential shortfalls and to set priorities to ensure that resource is focussed on filling deficits in important species groups rather than adding new species to situations where there are already adequate pools of species. A previous report commissioned by CFS (Hubert, Jinks, Lee, & Mason, 2009) presented a comprehensive list of non-native species for consideration in Britain under anticipated climate change scenarios. Their list was compiled from several publications, supplemented with unpublished information from FR trials and expert opinion and supports current research on evaluating emerging species and revising provenance information. The aim of the work presented in this report is to extend species selection by analysing species diversity categorised by climate and soils and to determine the extent to which current species can substitute for each other within defined groups.

Such an assessment has to be carried in the context of climate and other environmental variables to ensure that all conditions for biological suitability are analysed; however, there are many environmental factors that affect tolerances of trees and they operate at different spatial scales. The number of tree species that can be grown in Britain is ultimately limited by the climate of the British Isles, within which there are the regional climatic differences caused by geography and topography that support different assortments of species. At local spatial scales, species suitability depends additionally on microclimates, geology, hydrology, soil physical and chemical properties, and biotic factors. Additionally, many local factors such as soil types are themselves correlated with climate. All these influences combine to create a mosaic of site types for trees, and decision support tools like Ecological Site Classification (ESC) (Pyatt, Ray, & Fletcher, 2001) provide a methodology for evaluating site suitability for different species based on levels and interactions of these multiple factors.

For analysing species diversity and potential substitutability, the number of factors and their interactions at the local scale can be too complex for the simple understanding of patterns, and so local-scale information needs to be simplified to include only key explanatory variables and aggregated to capture the broad patterns of variation in species composition at regional scales. This study considers temperature and moisture as the primary factors controlling species distribution, with soil types as secondary factors. But there is a trade-off between simplification and having greater explanatory ability obtained by including more factors, and it must be recognised that simple variables like average temperature are often proxy measurements for other related factors that may operate differently across a species range. The relationships summarised in this report are intended to capture elements of the autecology of species rather than provide all the information needed for species choice in particular planting situations; ESC is designed to incorporate the sophistication needed to meet this requirement at the site-scale.

1.2. Objectives

Work on the areas summarised in this report is still in progress and further development of topics and techniques is continuing under Programme 3. This report summarises progress on three related objectives:

1. To categorise the abundance of the 20 most common tree species by climate zone and soil groups to assess species diversity within climate zones, and to identify clusters of similar species and climate zones. This provides a basic foundation of information about the tolerance of species to climate factors and soils and is used to analyse current species diversity.
2. To measure the climate space occupied by species in Britain and to determine the extent of potential species substitution from overlaps in climate space and by shared soil groups. This measures the extent that species can substitute for each other in terms of climate and soils.
3. To analyse how the current species composition is suited to the future climate and identify potential species gaps for further research.

1.3. Approach

The approach used to measure the abundance of species in different climate regions is based on calculating the environmental conditions of their distributional areas. Two kinds of information are needed to do this: firstly, an accurate data set of the geographic locations of where species are growing, and secondly estimates of climate and soil at each of these locations. For the first requirement, the comprehensive data on species occurrence stored in the Forestry Commission subcompartment database is used; this also holds records of yield class which provides a measure of species growth in different environments. For environmental data, widely available gridded climate data and FC digital records of soil type were extracted for each occurrence location (see Methods for details).

It is important to understand the assumptions and potential limitations with this approach. The profiles of species abundance classified by environmental factors obtained can be interpreted as representing aspects of the environmental niche of a species, which is the combination of all variables in which a species can live and is often described as an n-dimensional hypervolume (Hutchinson (1957).

The region bounded by the environmental temperature and moisture limits of a species growing in Britain defines a climate space that represents features of its wider ecological niche. Two categories of niche: the fundamental and realised niches, are recognised that delineate the potential and actual environments where populations of a species can grow and perpetuate (see Table 1 for more details on niches), and Sax et al. (2013) introduced an additional concept, the tolerance niche, characterised by conditions that enable individuals of a species to survive but preclude a species from having self-sustaining populations (Table 1).

In the context of forestry, there are differences between the realised niches of native and introduced species. The realised niche of a 'wild' native woodland species is a subset of the fundamental niche that represents the environmental space where self-sustaining populations are maintained, i.e. are adapted in the Darwinian sense of fitness. Whereas the realised niches of an introduced exotic species planted in Britain may fall within either their fundamental or tolerance niches, or straddle both, because they are more likely to have been planted rather than to have regenerated from natural reproduction, and to have received interventions to control competing species at critical stages of development. The extent to which introduced species regenerate depends in part on whether their planted climate space (realised niche) occupies the fundamental or tolerance niche: the former increases the risk of invasiveness; the latter reduces the likelihood of natural regeneration.

As a resource for measuring realised niches of species, the size and extent of the public forest estate makes it a large practical experiment where poorly adapted species are more likely to reduce in scale or become eliminated over time and better adapted ones persist. However, interpreting the profiles in the abundance of species in different climate zones as measures of their true realised niche has to be qualified because, especially in planted forests, the abundance of a species growing in an area or region is the result of historic choices to meet objectives as much as perceived suitability to an area's climate and soils. Preference for planting a fashionable species can saturate the available planting sites to the exclusion of other species that are environmentally suitable. However, even in regions dominated by a few species, there are in many cases sufficient plantings of other species recorded to provide large enough sample sizes for analysis.

2. Methods

All summaries, statistical analyses and graphical presentations were carried out using the R statistical language (R Core Team, 2016).

2.1. Summaries of species abundance by climate and soil groups

2.1.1. Species abundance

The Forestry Commission subcompartment database (SCDB) was used as the source of data on species abundance across Britain. A working copy of the SCDB shape files and associated attribute information was made in 2016. For analysis, the location of each subcompartment was determined as the geographic coordinates of each polygon centroid. The main attribute information extracted for analysis was species identity, species area per subcompartment, and yield class. Primary, secondary and tertiary species in the SCDB were treated as equal categories. Records for mixed species categories were excluded from further analysis, and species areas were calculated from subcompartment area and percentage of species occupancy.

2.1.2. Species selection

Twenty species were selected ranked by number of records in the SCDB (Table 2). *Quercus* and *Betula* were recorded in the database either as individual species (*Quercus robur*, *Q. petraea*, *Betula pendula*, *B. pubescens*) or, more frequently, as combined generic categories of ‘oak’ and ‘birch’. For analysis, the individual species records were recategorised into the appropriate generic category. In all figures and tables, species are referred to by their Forestry Commission codes (Table 2).

2.1.3. Climate variables

Gridded average monthly temperature and precipitation for 1960-1990 were extracted from WorldClim.org (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) as gridded climate data files (geoTIFFs) for the whole of Britain at a resolution of 30 arc seconds (approximately 900m). Although the data are adjusted for the elevation at the grid coordinates, no resampling and cofactor adjustment was carried out to convert to a finer resolution and it must be remembered that microclimates can be poorly predicted by weather station interpolations unless factors such as aspect are considered.

Temperature and precipitation records for each subcompartment were extracted using R’s spatial libraries by overlaying climate rasters and extracting variables from raster layers for the nearest point to each subcompartment centroid. Gridded climate data and derived measures for climate analysis were stored as R raster layers.

The climate variables were used to calculate bioclimates that formed the basic categorical units within which species are distributed. The bioclimate classification system of Rivas-Martinez and Rivas-Saenz (1996) was adopted for this study because the classification is based on the correspondence between vegetation and climate and so is biologically relevant. It is a global system that enables direct comparison of present and future climate zones in Britain with regions elsewhere in the world.

Annual positive temperature (T_p), which is the annual sum of monthly positive temperatures, was calculated to provide a measure of climatic warmth, and the ombrothermic index (I_o), which is yearly positive precipitation (P_p) divided by T_p, and is considered to be a simple measure of wetness or aridity.

The labels for the different levels of T_p and I_o assigned by Rivas-Martinez and Rivas-Saenz (1996) are long and not particularly memorable, so shortened descriptions are used: T_p is called 'warmth' and is divided into cold, cool and warm levels; I_o is 'wetness' and split into dry, humid and wet levels; these categories are further subdivided by qualification with the adverbs of degree 'very' and 'extremely', e.g. "very wet" (See Figure 11c as an example of the conversion between the two systems). The shortened descriptors are used for convenience and words like 'warm' really describes how a Sitka spruce might feel if it was human rather than necessarily explains too much about its physiological responses.

T_p and I_o are combined to form **climate zones** that are the basic categorical units and are designated by the combination of the two level descriptors, which begin with capital letters, separated by a colon, for example Warm:VDry. In later sections, clusters of similar climate zones are combined into four broader **climate regions** that are described by dominant temperature and moisture regimes separated by a hyphen, e.g. warm-dry, and cold-wet. Finally, climate descriptors are applied to categories of species that share similar patterns of abundance across climate zones, for example, 'warm species' predominantly occur in Warm climate zones, humid-wet species occupy Humid to Wet climate zones.

Other variables such as elevation, ESC climate and soil responses, indices of oceanicity, and measures of seasonal temperature differences have also been included in other analyses that are not discussed further in this report.

2.1.4. Soil Type and Groups

Soil-type shapefiles, classified using the FC soil classification system (Kennedy, 2002) were copied in 2016 from the FC Spatial Database Repository as the primary data source for the most prevalent soil type in each subcompartment. Soil type in each subcompartment was extracted by overlaying subcompartment centroids over soil-type polygons in R. Because of the large number of different soil types in the dataset, soil types were aggregated into their appropriate FC soil groups for subsequent analysis (Kennedy, 2002).

2.1.5. Statistical summary and analysis

All relevant subcompartment attribute, climate and soil group information were combined into a single R spatial dataframe for use in subsequent analysis.

In a given area, species abundance can be expressed as either the total area of the subcompartments where a species is recorded, or as the number of subcompartments containing the species. In practice both measures are correlated because of the relatively finite range of individual subcompartment areas. The number of subcompartments containing a species within a zone rather than area occupied is used for most of the analyses of abundance because counts of subcompartments are more appropriate for the particular statistical techniques used such kernel density estimation.

To group species by climate and soils, abundance information was summarised as a series of contingency tables which are presented as graphical matrices classified by paired combinations of species, climate zones and soil groups. However, it is difficult to discern patterns of abundance in large tables and correspondence analysis (CA), which is an extension of Principal Component Analysis (PCA) suited to analysing frequencies formed by two categorical variables, was used to reduce the dimensions of the data without losing important information and to identify associations between species, climate and soil (Bendixen, 2003). CA was applied using the FactoMineR and factoextra packages of R and clusters of species with similar profiles were further delineated using hierarchical cluster analysis (HCA) after CA using functions in FactoMineR.

Measurement of the diversity of species in each climate zone was assessed by three indices:

Species richness (S), as the total number of species recorded in each zone

Species diversity, calculated as Shannon's diversity index (H) using

$$H = -\sum_{i=1}^{n} p_i \,.\, \ln p_i$$

where p_i is the proportion of species i relative to the total number of species (n). H takes the relative abundances of different species into account and typically ranges between 1.5 and 3.5 in ecological studies. H is highly non-linear but can be interpreted in terms of the effective number of equally abundant species as exp(H), thus an index of 1 is equivalent to 2.7 evenly distributed species, 2 = 7.4 species, etc.

Species evenness, using Shannon's equitability index (E_H), calculated as

$$E_H = H/\ln S$$

where S is the species richness. E_H ranges from 0 to 1, with 1 being complete evenness.

2.2. Species abundance and climate space

A species can be considered as occupying an area of climate space bounded by the temperature and moisture limits for growth or survival. The climate spaces of species are defined using two-dimensional kernel density estimation using T_p and I_o as variables. In one dimension, kernel density estimation produces a 'smoothed histogram' of the frequency distribution of subcompartments categorised by measures such as temperature and wetness (e.g. Figures 11a&b). Plots of kernel density estimates for single variables like temperature provide a simple visual display of the variation in abundance across the variable span, but they are analogous to visualising the silhouettes of a mountain along separate axes; the full topography cannot be constructed from amalgamating simple profiles, but requires contours of elevation. Two-dimensional kernel density estimation using the kernelsmooth package in R was used to create contours of conditional probability that displayed the relative abundance of subcompartments within the two-dimensional space bounded by temperature and wetness (see Figure 11c as an example).

For simple display of the climate space occupied by each species, 95% and 50% contours of probability mass were estimated and plotted as polygons (Figure 12). The 95% contour represents the maximum extent of occurrence of a species, while the region within the 50% probability contour is considered to represent regions of high abundance where there is a high density of subcompartments containing a particular species. Grouping species that occupy similar climate space is difficult because of the irregularity of the outlines of the contour polygons. Consequently, the outlines were simplified by fitting ellipses that enclosed 95% of all observations within the 50% contour polygons of species. Comparison of the shape and coverage of the ellipses was then used to group species into four climate categories.

To determine the extent to which two species overlap in climate space, the areas within the 50% contour polygons of paired species were overlaid and the area of overlap calculated as proportions of the total area of each species' area using methods outlined by Fieborg and Kochanny, (2005). Within the overlap range, the extent to which species occur on similar soil groups was initially assessed using chi-square test of independence on contingency tables of soil frequencies. In nearly all cases, the chi-squared statistic was highly significant because of the large sample sizes making weak relationships statistically significant. Consequently, Cramer's V was used as the measure of the degree of association in frequency of occurrence of the two species with soil groups; Cramer's V ranges for 0 to 1 with lower values representing higher degrees of association (note, this is the reverse order of the correlation coefficient where high values indicate high correlation). Overall results of climate and soil overlaps are summarised as a graphical matrix table.

2.3. Species abundance and future climates

To assess the extent to which current subcompartments shift climate zones in future climate change scenarios, climate data were used from climatic projections from the HadGEM2-ES Global Circulation Model (GCM) (Collins et al., 2011) created using the Delta method fro downscaling (Ramirez-Villegas & Jarvis, 2010). Gridded climate data were downloaded for four IPCC Special Report Emission Scenarios (IPCC SRES SPM, 2000) from http://www.ccafs-climate.org/data_spatial_downscaling/ These four simulations adopt representative concentration pathway (RCP) scenarios which were developed to represent the possible future climate scenarios under different levels of socio-economic growth and mitigation (Stocker et al., 2013). RCP scenarios RCP2.6, RCP4.5, RCP6.0, and RCP8.5 represent scenarios where the radiative forcing by the year 2100 reaches 2.6, 4.5, 6.0, and 8.5 Wm^{-2} (watts per sq. m.), respectively. Each scenario provides the atmospheric concentrations of various greenhouse gases and tropospheric and stratospheric aerosols that are used to drive coupled ocean–atmosphere climate models. The dataset used here are the projections for the 2050s and T_p and I_o were derived for each subcompartment using the projected temperature and precipitation grids. Numbers of subcompartments were counted within each future climate zone.

3. Results

3.1. Summaries of species abundance by climate and soil groups

Maps of T_p, I_o, derived climate zones, and locations of all subcompartments are shown in Figure 1. The classification of Rivas-Martinez & Rivas-Saenz (1996) produced 17 climate zones for Britain, 12 of which contained subcompartments. Abundance of species in each climate zone is summarised as total subcompartment area in Figure 2 and by number of subcompartments containing each species in Figure 3. These two measures of abundance are highly correlated because of the relatively small range of areas of individual subcompartments; consequently, patterns of species abundance are broadly similar in Figures 2 and 3. The marginal totals of area of each species in Figure 2 are the equivalent of stocked area summarised in Forestry Commission (2011), with Sitka spruce being the most abundant species. The highest abundance of subcompartments occurs in zones with Cool climates, and these are dominated by Sitka spruce, whereas zones with Warm climates are made up of a wider distribution of species.

Despite large variation in the abundance of subcompartments (Figure 3&4a), species richness was high across all climate zones except for the Extremely Wet region of the Cool and Cold thermal zones (Figure 4b), which is only represented by a relatively small number of subcompartments (Figure 4a). Richness was at the maximum value of 20 species in all wetness categories of the Warm zone and in the Humid to Wet range in the Cool zone and decreased slightly to 18-19 species in the Cool:VWet and Cold:VHumid to Cold:VWet ranges.

In contrast, species diversity and evenness (Figure 4c&d) varied much more between climate zones and showed little relationship with abundance of subcompartments (Figure 4a). Generally, both the Shannon Index (H) and equitability (E_H) followed similar patterns and were lower in Cool and Cold climates and decreased with increasing wetness (Figure 4c&d). Both indices were highest in the humid regions of both the Warm and Cool zones and in Warm:VHumid zone, where average H was 2.53, which is equivalent to 12.6 evenly distributed species. H was slightly lower in Warm:Dry at 2.23 (equivalent to 9.2 evenly distributed species). In the zone with the most abundant subcompartments, the Cool:Wet, H was 1.96 which is equivalent to 7 evenly distributed species. As with species richness, the lowest H indices occurred in the Extremely Wet zones of the Cool and Cold with an average of value of 1.18 (3.2 species equivalents). Variation in species evenness (E_H) was very similar to the pattern of H.

Correspondence analysis using the abundance data in Figure 3 showed that the first two dimensions (eigenvectors) accounted for 88.4% of the variance, and cluster analysis using both dimensions suggested 6 clusters of species with similar patterns of abundance across climate zones (Figure 5a). Five clusters ranged along Dimension 1 with a similar span across Dimension 2. Corsican pine and sweet chestnut were paired together at the most positive region of Dimension 1, followed by a cluster containing the majority of broadleaves (oaks, ash, beech, and sycamore), plus western red cedar and Lawson cypress. A third group had three conifers (Douglas-fir, grand fir, western hemlock) with birches, followed by a close group containing hybrid and Japanese larches plus Norway spruce, with Sitka spruce, noble fir, and lodgepole pine forming a fifth cluster at the most negative region of Dimension 1. European larch and Scots pine formed the sixth cluster which was located higher up Dimension 2 above the other five clusters.

Cluster analysis of climate zones in species-space revealed four climate clusters which could be interpreted as the fundamental climate zones of Britain affecting species abundance. Warm:Dry and Warm:Humid were paired as a single cluster, while Warm:VHumid was in the same cluster as Cool:Humid and Cool:VHumid. VWet and ExWet zones of Cool and Cold formed the largest cluster which also included Cool:Wet, while Cold:Wet and Cold:VHumid formed the final cluster.

Variation in average yield class between species and climate zones are summarised in Figure 6. Generally, mean yield class of most species decreases in colder and wetter climates. With the exception of the three pine species, mean yield class of conifers was lower in the Warm:Dry zone compared with Warm:Humid and Warm:VHumid, with less apparent difference amongst broadleaved species. Most conifers showed a positive relationship between yield class and temperature (Figure 7), most of the increase occurs over cold and cool temperature ranges, with less increase or even a decrease evident in the warm range. Growth of broadleaves appears to be less responsive to temperature. However, relationships between yield class and temperature require further analysis to understand these relationships. As well as a decrease at dry levels of I_o, mean yield class of conifers, and some broadleaves, tends to decrease with increasing wetness (Figure 8), but this might reflect a response to decreasing temperatures because wet regions are also cool or cold. Yield classes of several conifers that are not abundant in wet regions of the Cool and Cold zones, such as western hemlock and Douglas-fir, apparently do not decline excessively in these zones. Relationships between yield class and environmental variables can be explored further using multiple regression models.

Soils and climate are correlated and variations in soil preferences amongst species growing in the same climates are discussed below in the context of species overlaps. For completeness, abundance of soil groups associated with different species and found in different climate zones are summarised in Figures 9 & 10. Brown earths and gleys are the most frequent soil category.

3.2. Species abundance and climate space

The summaries of species abundance by climate zones in the preceding section are useful for providing a synopsis of their distributional area and for identifying broad affinities amongst species. But to understand the extent to which one species can be replaced by others requires more detailed delineation of abundance in climate space rather than just summarised by zonal categories.

The climate space occupied by all subcompartments is shown in Figure 11 using kernel density estimation to describe variation in abundance with annual positive temperature (T_p, Figure 11a), wetness (I_o, Figure 11b), and in the two-dimensional space described by both climatic variables (Figure 11c). Variation in abundance with temperature is bimodal with peaks of abundance at both the cool and warm levels (Figure 11a), whereas abundance against wetness is broadly skewed towards drier regions, with abundance decreasing at wetter levels (Figure 11b). One-dimensional kernel density estimates for each species are plotted in Appendices 1&2.

In the climate space described by both temperature and wetness, the upper and lower boundaries of abundance of subcompartments along the wetness scale are reasonably clearly defined and are in part due to cut-offs at coast lines (Figure 11c). The lower and upper temperature boundaries are more ragged reflecting in part effects of topography.

Subcompartments located in warm region have the highest abundance mainly because they are located across a wide geographic area that has a similar climate profile and so become condensed in climate space. In the cooler regions, abundance of subcompartments is more dispersed with regions of higher abundance interspersed with lower density regions; the highest density region occurs along the lower edge of the wetness scale. This lumpiness reflects the non-uniform geographic distribution of forests across Britain.

Species occupy different regions within the overall climate space of all subcompartments (Figure 12). Two probability contours are used to show overall extent of climate space occupied by species (95% contour) and high-abundance regions of the range (50% contour). The maximum extent of species abundance is wide for most species and is primarily defined by temperature rather than wetness. The maximum range of most species extends into the Warm region with the extent of spread into the Cool and Cold zones being the main cut off for species ranges. The majority of species occupy most of the available wetness zones within their thermal zones. The 95% extent region can be considered as defining the climate space for which a species is adapted, i.e. represents the tolerance niche within Britain, assuming that less-suited species have been eliminated or not chosen for planting. Within this tolerance niche, are subregions of higher abundance were a species grows well and has been selected for planting, and other regions of lower abundance where a species is still well-adapted, but has not been planted extensively for other reasons, such as being displaced by a more popular species. In the latter case, a species can be considered as being under-utilised.

The regions of high abundance (50% contours) vary much more between species than maximal extents and are defined by wetness as well as temperature. These can be considered as delineating the core climate regions of a species (Figure 12). By simplifying the outlines of the abundant regions using ellipses, four groups of species can be separated on the basis of their regions of high abundance (Figure 13), though some like sycamore and Japanese larch are on the border between two categories.

Eight species have narrow thermal amplitudes where their high abundance regions are confined to either warm or cooler temperature zones, and they are categorised by the temperature zone where they are most abundant, i.e. as either cool or warm species. The Three cool species, Lodgepole pine, Sitka spruce, and noble fir, are most abundant in the Cool and Cold zones (Figure 13a), whereas the other five species such as Corsican pine and many broadleaves peak in the Warm zones (Figure 13b).

The remaining 12 species have broad thermal amplitudes with abundance regions that cover both Cool/Cold and Warm zones, but differ in their amplitude for range of wetness zones and these are categorised by how far along the wetness gradient their ranges extend. The range of wetness zones for 8 of these species, such as Douglas-fir and Scots pine, is confined to the Dry to VHumid zones and only partially extends into the Wet zone; these 8 species are categorised as the dry-humid species (Figure 13c). Norway spruce, Japanese and hybrid larches, and birches have the broadest amplitudes for both temperature and wetness and are categorised as the humid-wet species because their high abundance range extends into the Very Wet (Figure 13d).

The extent to which species can potentially substitute for each other depends on climatic, soil, and silvicultural suitability. Climatic suitability can be approximately judged from the coincidences of ellipses in Figure 13; however, this does not account for potential differences between species in preferences for soils and more accurate measures of the extents of overlap was obtained using a two-stage process. First, the degree of climatic substitution between pairs of species was measured by overlaying their 50% probability polygons that outline the high abundance regions and calculating the extent of overlap. Second, soil substitution was determined by calculating the extent to which both species share the same abundance frequencies of the soil groups within the overlap region.

Overlapping all 20 species produces 190 paired comparisons and depictions of each paired polygon overlap are shown in Appendix 3, together with values for the proportions of each species abundance region that is occupied by the overlap region. Similarity between the pairs of species in the occurrence on different soil groups within the overlap regions are summarised in Appendix 4.

The overall extent of species substitution using both climate and soil overlap criteria is summarised in Figure 14. Species that occur predominantly in the Warm zone are predominantly mutually interchangeable, though some combinations differ in abundance on different soil groups. For example Corsican pine is climatically overlapped by 12 species, but two of these, ash and oaks, differ in soil abundance within their respective overlap regions (Appendices 3 & 4, graphs 58 & 63). In contrast, species occupying Cool and Cold zones are overlapped by fewer species, reflecting the lower diversity in these zones. For example, Sitka spruce is overlapped by 5 species which have similar patterns of abundance across soil groups; however three of these species (Japanese and hybrid larches, and lodgepole pine) have restrictions on use due to diseases.

3.3. Species abundance and future climates

Examples of changes in the frequency distribution of climate zones in projected future climates are shown in Figure 15a. Further work on potential shifts in climate zones is in progress and will apply outputs from other GCMs to estimate uncertainties in the extent of zone shifts. These initial results using HadGEM2-ES illustrate the approach being developed rather than being presented for firm conclusions.

The maps illustrate the well-understood projected shifts from colder and cooler to warmer climates across Britain in the framework of the climate and species categories developed in this study. In the climate zone system of Rivas-Martinez and Rivas-Saenz, (1996), the Mediterranean climate is a macroclimate that ranks alongside the temperate climate. Usefully, the system identifies a variant of the temperate climate region termed 'submediterranean', with summer drought indicated by monthly ombrothermic indices that are less than 2. Figure 15b illustrates potential regions with a submediterranean climate for the projected climates in Figure 15a. At present, no parts of Britain are classed as submediterranean, but the area is projected to appear in all emissions scenarios, though the extent varies. The low occurrence in the RCP6.0 is primarily because most of the projected changes in climate occur after the 2050s in this scenario.

Categorising the abundance of subcompartments by the current and projected climates for different scenarios shows the appearance of novel climates particularly with current Warm zones shifting to become Very Warm zones (Figure 16). The projections also show a disappearance of subcompartments in Cold zones and a huge shift of abundance from Cool to Warm zones with particular expansions into Warm:VHumid and Warm:Wet zones which although they occur already in the British Isles, do not currently contain a high abundance of subcompartments.

Defining climatic tolerances of species and geographic climate zones using the same variables enables these spaces to be mapped to other regions of the world. For example, regions of the world which currently have Very Warm:Dry climates are shown in Figure 17a, and with Warm:Humid to Warm:Very Wet in Figure 17b. These regions represent potential donor regions for candidate species for increasing species richness, and where current British forest species occur, can provide information about how these species might perform in future climates and the opportunities for provenance selection. Similarly, the climates within species niches can be mapped to global climates. Figure 17 shows that climate analogues occur in traditional donor regions such as N. America and Europe, but also maps to regions of Asia that have been relatively under examined for forest species, although a significant garden flora originates from these regions.

4. Discussion

The analysis carried out so far allows some general conclusions to be drawn about future needs and directions for research on emerging species. However, more detailed work is required for refinement in relation to soils (work not reported here suggests that soil types can be recategorised into more silviculturally relevant groups), exploring to see if NFI data can be used to improve niche estimation of certain species, and carrying out more detailed species overlap analyses within climate regions rather than just across the full climate range. Scope for incorporating the impacts of pests and pathogens in the context of climate space could also be investigated.

Table 3 summarises the interrelationships between the occurrence of species classified by climatic tolerance and the four climate regions identified from correspondence analysis, which are labelled as warm-dry, cool-humid, cool-wet and cold-wet regions. Both the warm-dry and cool-humid regions have the greatest species richness with dry-humid and humid-wet species occurring in both regions, but warm and cool species occupying their respective warm and cool regions. Although this region has high species richness and diversity, substantial areas are likely to become warmer and experience summer drought which suggests three requirements for ongoing and future research: 1) obtain more information on impacts of drought on survival and growth of existing species (work on this is underway in a different programme), 2) an assessment of provenances that might be better suited to this climate shift, and 3) testing and developing species whose tolerance niches encompass the future climate, e.g. pines and cedars.

The cool and cold regions have the greatest forest area. They have the same cool and humid-wet species found in the warm-dry, but the transit from cool-humid to cool-wet and cold-wet is marked by the reduction or elimination of dry-humid species, leading to a reduction of richness from 15 in the cool-humid region, to 9 and 7 species in the cool-wet and cold-wet regions. Subtracting species that are restricted by diseases reduces species numbers to 10, 5, and 3 respectively. The low diversity and richness in these regions is obviously caused by the saturation of forestry with Sitka spruce that creates a monoculture vulnerability that has to be a focus for diversification, though the vulnerability could be offset by genetic selection for resistance against pests and pathogens. The experience with Dothistroma Needle Blight on Corsican, lodgepole and other contingency pines, together with *Phytophthora ramorum* on larches, suggests a need to maintain generic as well as species diversity in forest regions.

However, the dominance of Sitka spruce masks an underlying species diversity amongst dry-humid species that are not abundant at present, but whose full ranges of occurrence extend into these regions and where yield class summaries suggest they can grow productively. This broad conclusion supports the advocacy for greater use of species like western hemlock and Douglas-fir (Cameron, 2015) as well making more use of Norway spruce (Wilson, 2011) and birches. However, generalisations about increasing use of existing species for diversifying these regions need considerable refining to take into account other climate factors such as wind, understand more about potential differences in soil tolerances, as well as non-environmental issues. A next step will be to analyse overlaps of climate space and soils between Sitka spruce and dry-humid species using wider probability contours than 50% used in the full-range analyses reported here. Analyses using ESC criteria should provide helpful insights on defining the limits of potential substitution by dry-humid species.

The shifts in climate zones towards warmer temperatures are, of course, well understood (Broadmeadow, Webber, Ray, & Berry, 2009). The potential shifts of cool and cold regions to warm moist climates to some extent relieves present climate limitations on species choice, but of course opens up many new questions about species silviculture and vulnerability to pests and pathogens. Future WarmV:Humid and Warm:Wet zones are uncommon in Britain's present forestry climate, but occur elsewhere in the world in both the traditional donor regions like Pacific NW America, and in less-researched regions of Asia. A systematic survey of potential species in these regions, matched with an assessment of their performance so far in experiments and tree collections should help build up a list of potential species that can be prioritised for further research.

5. Conclusions and Recommendations

Two situations are identified where increases in species diversity are needed. Firstly, in the present climate where impacts of pests and diseases are eroding the diversity of useable species, particularly in the wet climate regions of Britain that are dominated by Sitka spruce. Secondly for the future climate where model projections suggest significant shifts in climate zones that will encompass existing species and will require continued evaluation of new species and provenances.

Three work streams are proposed to address these issues.

1. Increasing diversity in the present climate

1.1. Assess the extent to which underutilised principal and secondary species can substitute for Sitka spruce using climate space overlaps within the Wet zones.

1.2. Assess and review the performance of principal, secondary species and plot-stage species (e.g. Pacific silver fir) with Sitka spruce in existing species trials in the Wet zones.

1.3. Continue investigations on increased use of secondary species, including:

- examining provenance recommendations by re-assessing surviving provenance trials in all climate zones,
- pest and disease susceptibilities and limitations,
- silvicultural deployment (establishment methods, mixtures, etc.

Priorities include secondary species such as western red cedar and western hemlock.

2. The suitability of current species in future climates

2.1. Assess the extent to which the existing warm species can grow in future warm climates of Britain by analysing the extent to which the full climate space of species overlaps future projected climate. This will involve constructing climate space models using data from the complete geographic range of species, including subdivisions for provenances if available.

3. Identifying species for future climates

3.1. Refining the demarcation of future climate zones using projected climate data from several GCMs.

3.2. Match future climate zones to current climates elsewhere in the world and carry out inventories of native and introduced species in the analogue regions and identify potential forestry species (candidate species). The focus will be on filling gaps from lesser known regions of the world and seeking drought tolerant species like pines, cedars, etc.

3.3. Review existing species trials and tree collections to summarise growth and performance of candidate species under current conditions.

3.4. Construct tolerance niches for candidate species to be used to assess tolerance within the full range of future climates in Britain.

3.5. Establish new comparative species and provenance trials of the most promising candidates in selected climate zones that are currently close to the future climate.

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I would like to thank the staff of the FC Inventory, Forecasting and Operational Support team for maintaining and providing the superb subcompartment database without which this work would not be possible. I also thank Gary Kerr, Matt Parratt and Ian Willoughby for helpful discussions during the evolution of the approaches used in this study.

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Table 1. Categories of ecological niches**.** (From Sax et al., (2013)).

Category	Niche	Distribution
Fundamental	The set of physical conditions and resources that enable a species to maintain self-sustaining populations, but which may not be fully occupied due to the presence of antagonistic species interactions, the absence of required positive species interactions, or dispersal limitation.	The geographical space that could be occupied as defined by the fundamental niche; some portions of this space could be identified by the presence of self-sustaining, naturalized populations.
Realized	The set of physical conditions, resources, and biotic interactions that correspond with the conditions in which species maintain self-sustaining populations.	The geographical space occupied by a species within its native range; the conditions occurring within that geographical space are normally equated with the realized niche; however, following changes in environmental conditions (e.g., climate change) it is possible for the realized distribution of a species (i.e., the places where it is located geographically) to have conditions that no longer match the realized niche.
Tolerance	The set of physical conditions and resources that enable individuals to live and grow, but preclude a species from establishing self- sustaining populations; just as the fundamental niche is unlikely to be entirely occupied by self-sustaining populations due to dispersal limitations, the presence of antagonistic species interactions, or the absence of required positive species interactions, these same factors will exclude individuals from living and growing in all parts of the tolerance niche.	The geographical space that could be occupied as defined by the tolerance niche; some portions of this space could be hypothesized to occur based on the presence of individuals, for example, planted through horticulture, that survive ambient conditions but do not establish self-sustaining populations.

Table 2. List of species analysed**.**

Species code	Common name	Latin name
SS	Sitka spruce	*Picea sitchensis*
SP	Scots pine	*Pinus sylvestris*
LP	Lodgepole pine	*Pinus contorta*
CP	Corsican pine	*Pinus nigra* ssp. *laricio*
JL	Japanese larch	*Larix kaempferi*
BI	Silver birch Downy birch	*Betula pendula* *Betula pubescens*
NS	Norway spruce	*Picea abies*
OK	Sessile oak Pedunculate oak	*Quercus petraea* *Quercus robur*
DF	Douglas-fir	*Pseudotsuga menziesii*
BE	Beech	*Fagus sylvatica*
HL	Hybrid larch	*Larix* × *eurolepis*
EL	European larch	*Larix decidua*
AH	Ash	*Fraxinus excelsior*
WH	Western hemlock	*Tsuga heterophylla*
SY	Sycamore	*Acer pseudoplatanus*
SC	Sweet chestnut	*Castanea sativa*
GF	Grand Fir	*Abies grandis*
RC	Western red cedar	*Thuja plicata*
NF	Noble fir	*Abies procera*
LC	Lawson cypress	*Chamaecyparis lawsoniana*

Table 3. Species richness in the main climate regions of Britain**.** Climate regions are aggregated from climate zones with similar patterns of species abundance; species categories have similar ecological amplitudes for temperature or wetness. Species coloured red currently have restricted use because of fungal diseases, and pink have an uncertain future because of developing disease situations.

Regional climates			Species categories			
Climate region	**Constituent climate zones**	**Percentage of PFE area occupied**	**Warm**	**Cool**	**Dry-Humid**	**Humid-Wet**
Warm-dry	Warm:Dry Warm:Humid	10	AH, BE, CP, OK, SC		DF, EL, GF, LC, RC, SP, SY, WH	BI, HL, JL, NS
Cool-humid	Warm:Humid Cool:Humid Cool:VHumid	46		LP, NF, SS	DF, EL, GF, LC, RC, SP, SY, WH	BI, HL, JL, NS
Cool-wet	Cool:Wet Cool:VWet Cool:ExWet Cold:VWet Cold:ExWet	38		LP, NF, SS	WH, GF	BI, HL, JL, NS
Cold-wet	Cold;VHumid Cold:Wet	6		LP, NF, SS		BI, HL, JL, NS

Figure 1. Climate zones based on the categories of Rivas-Martinez & Rivas-Saenz, (1996), and locations of subcompartments. a) warmth calculated as the annual positive temperature T_p, b) wetness calculated as the ombrothermic index I_o, c) zones defined as combinations of T_p and I_o, d) locations of NFE subcompartments.

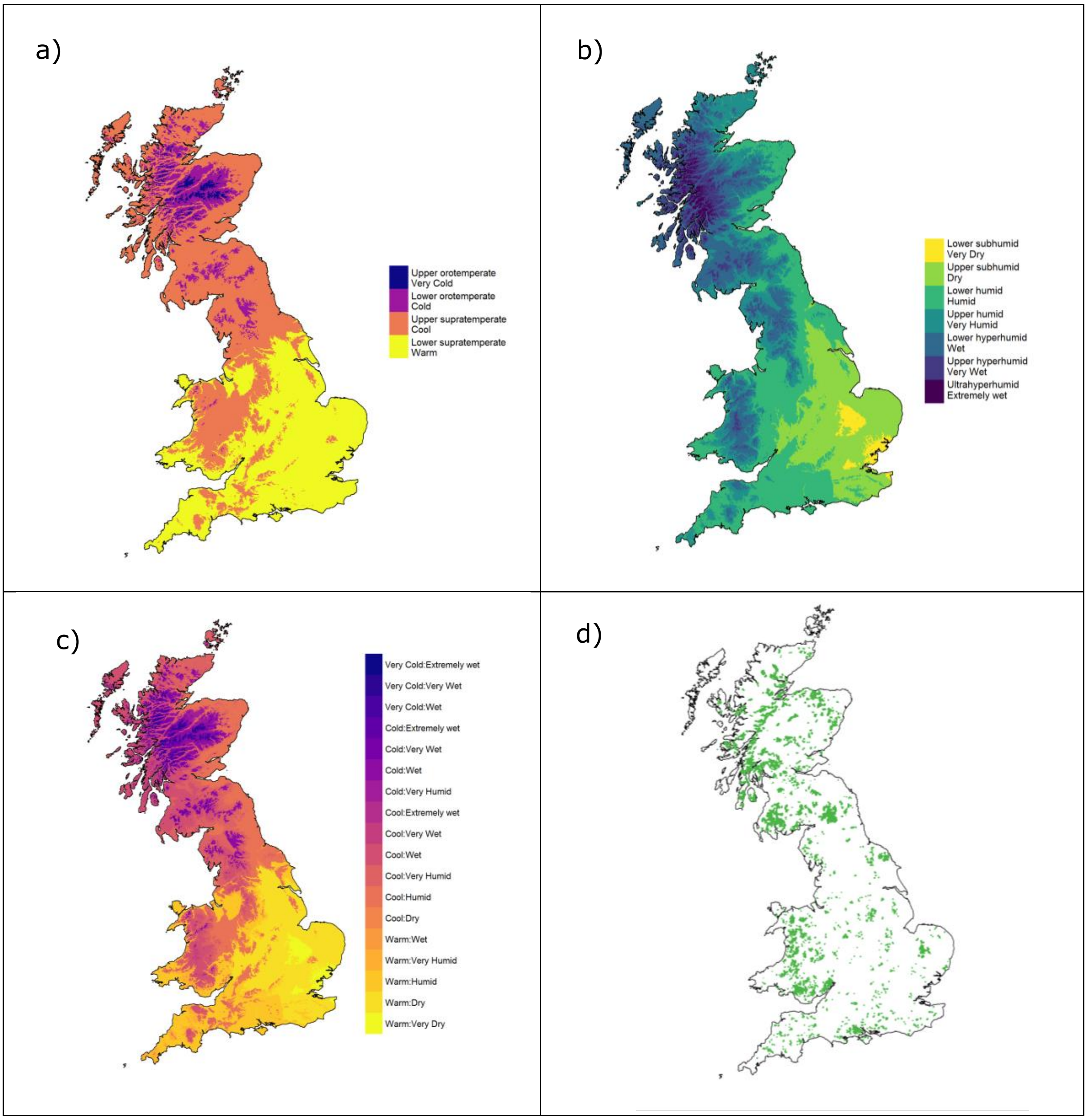


Figure 2. The area occupied by 20 species in different climate zones. Numbers show the area (thousands of ha) in each cell, dot-area shows the corresponding relative magnitude. Bars show the marginal totals of area for zones and species.

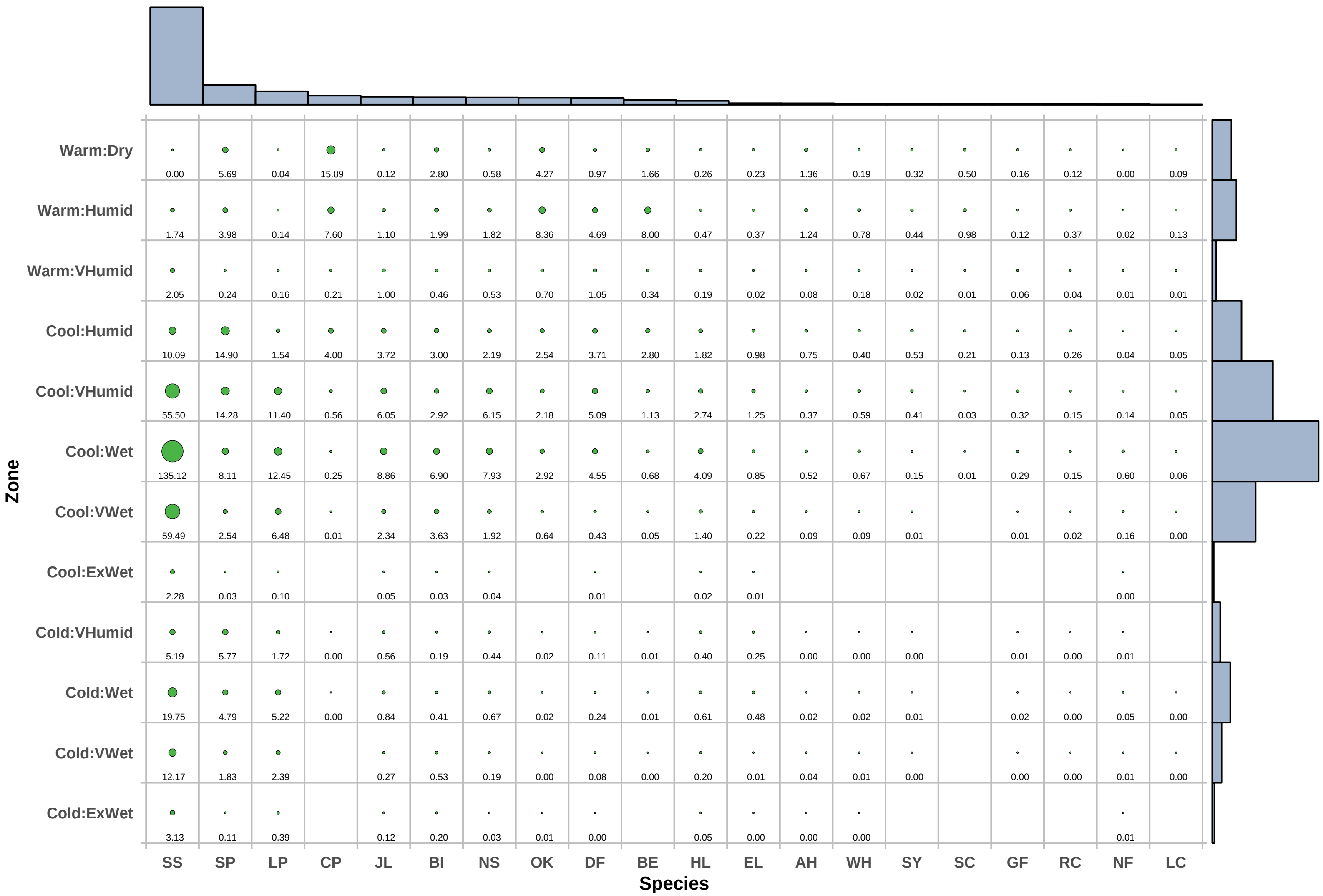


Figure 3. The number of subcompartments occupied by each species in different climate zones. Dot-area shows the relative number of subcompartments in cells. Bars show the marginal totals of subcompartments for species and zones.

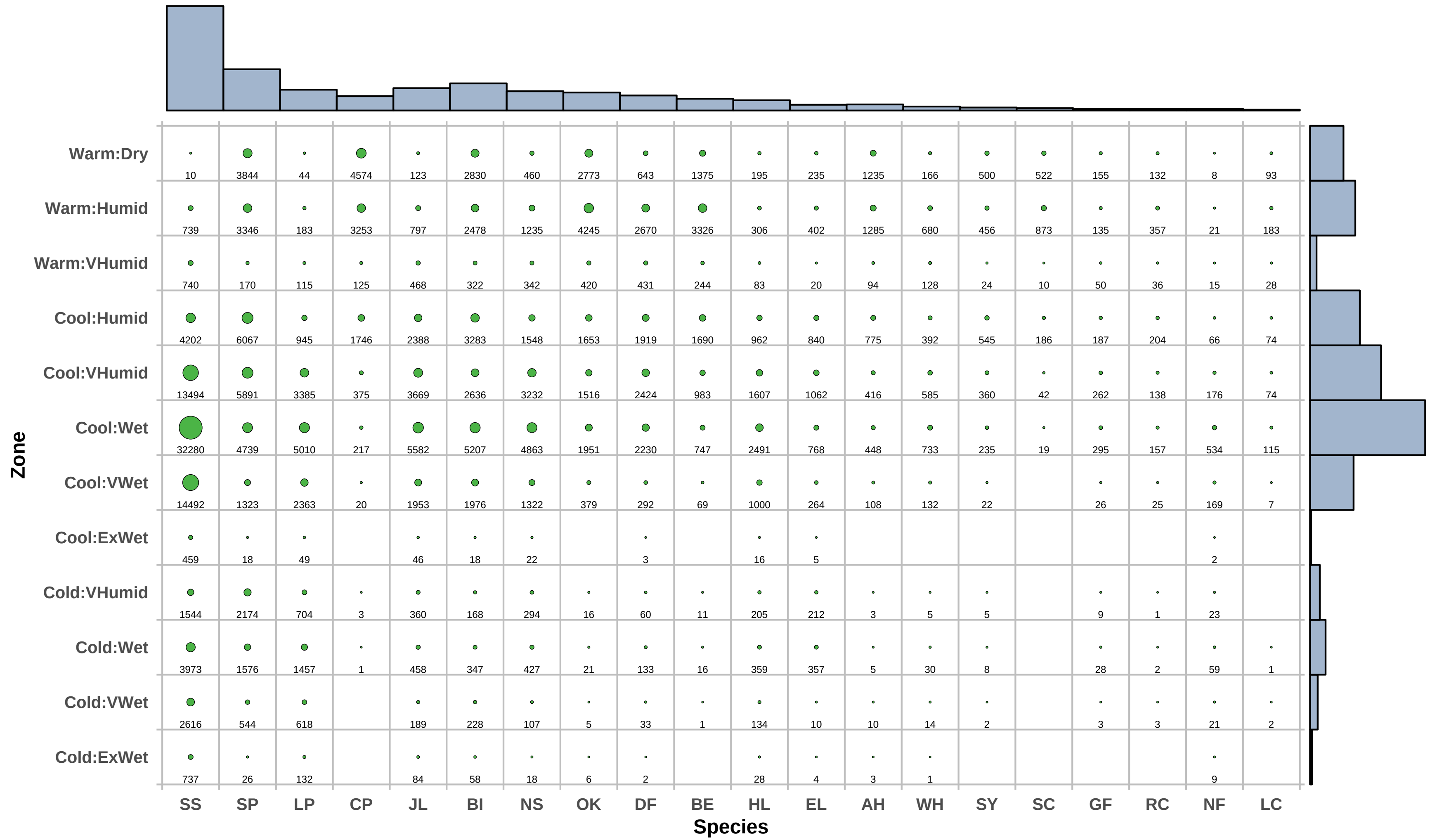


Figure 4. Variation in abundance of subcompartments and species diversity with climate zones. a) species abundance replotted from Figure 3, b) species richness (S, maximum=20), c) Shannon diversity index (H), d) species equitability (evenness, E_H). Measures are plotted against wetness (ombrothermic) zones and are grouped by thermal zone.

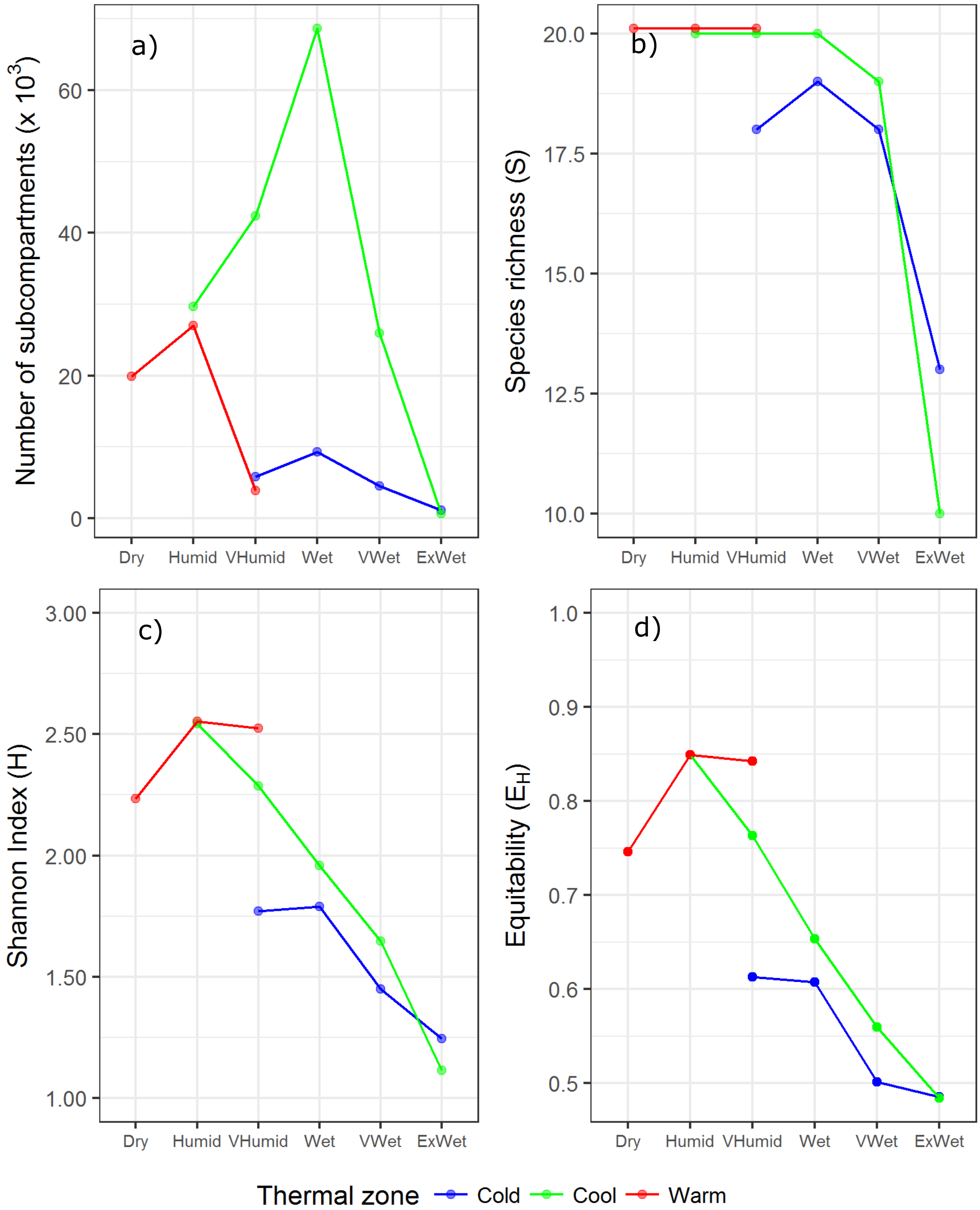


Figure 5. Clusters of similar species (a) and climate zones (b) derived from correspondence analysis and subsequent hierarchical cluster analysis of the contingency table of number of subcompartments shown in Figure 3. Axes are the first two dimensions from correspondence analysis. Species (a) or climate zones (b) sharing the same coloured points are members of the same cluster.

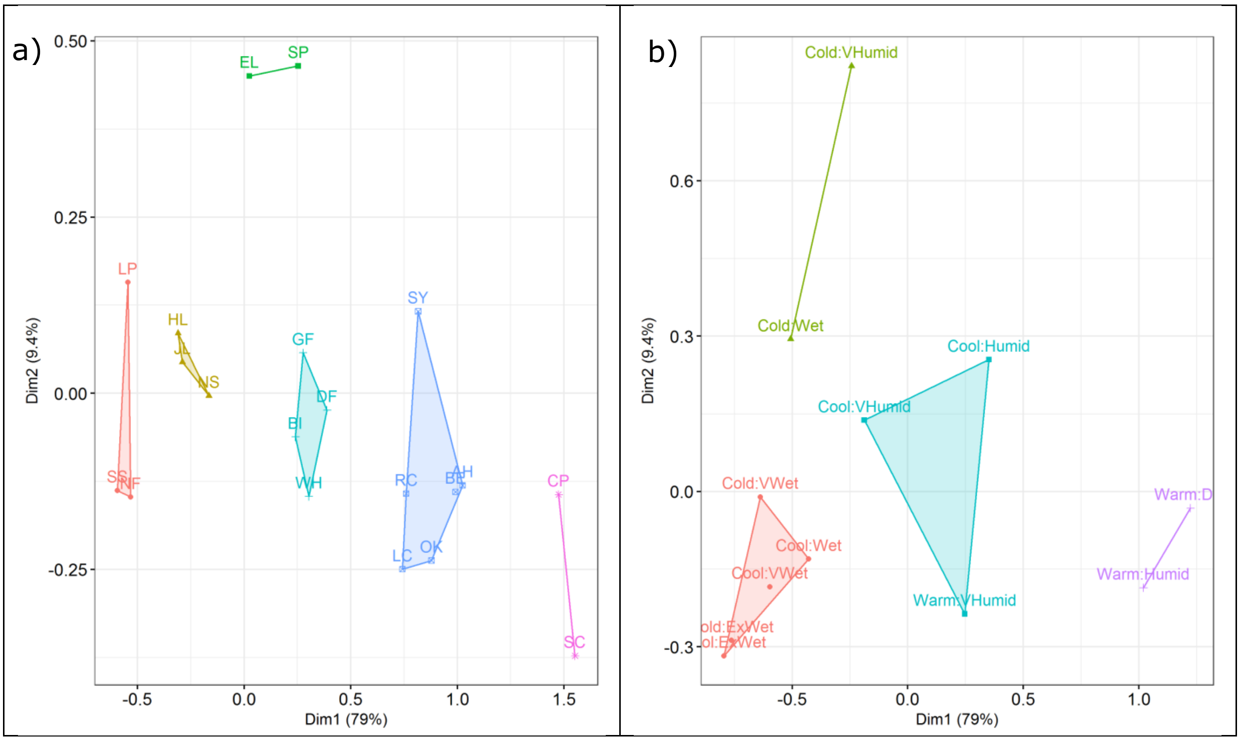


Figure 6. Average yield class of species in different climate zones. Dot-area shows the relative size of yield class in each cell.

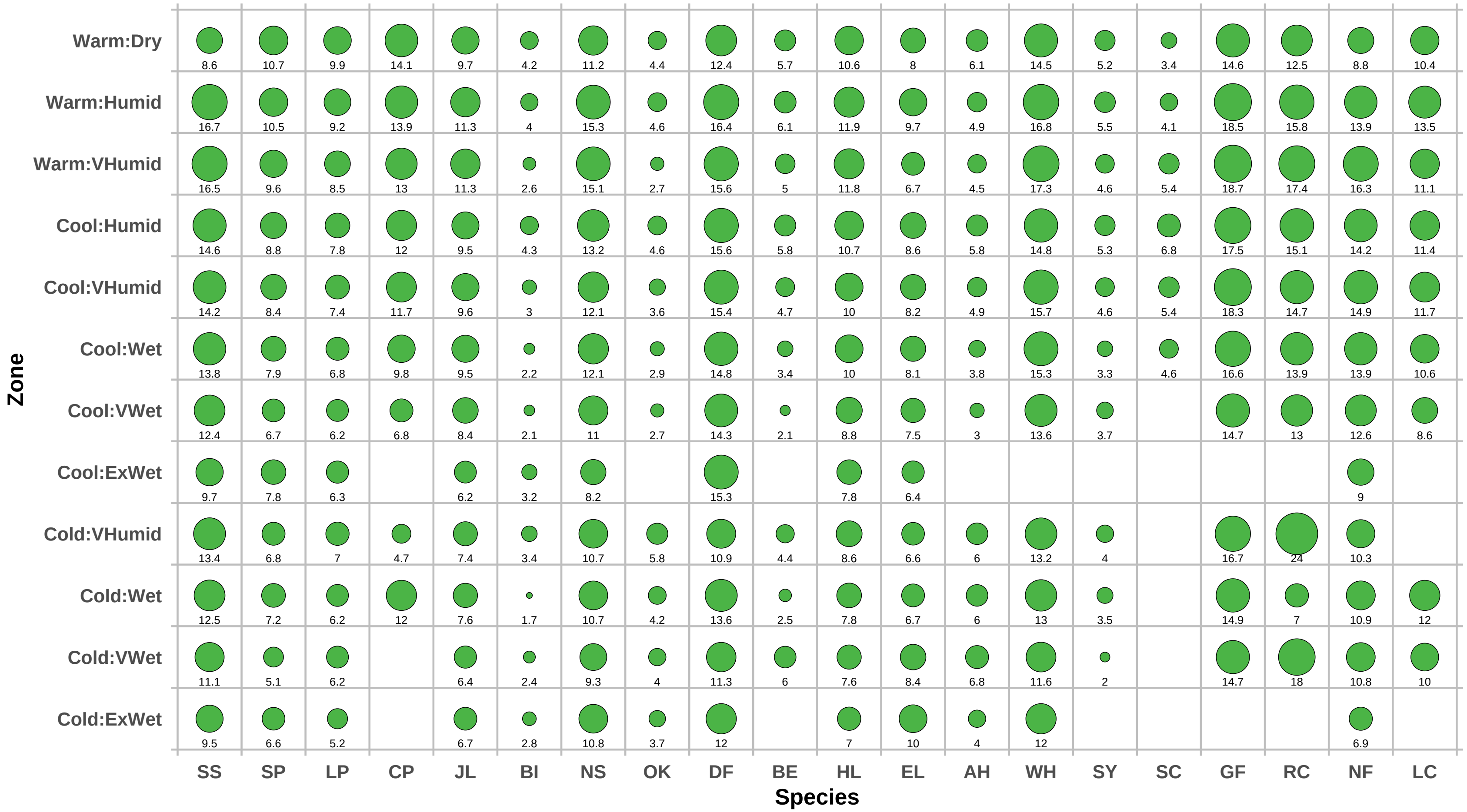


Figure 7. Variation in yield class with annual positive temperature (T_p). Mean yield class is calculated at binned intervals of T_p. Bars are standard errors and are plotted when larger than the diameter of points. Vertical lines show boundaries of warmth zones; for labels see Figure 11a.

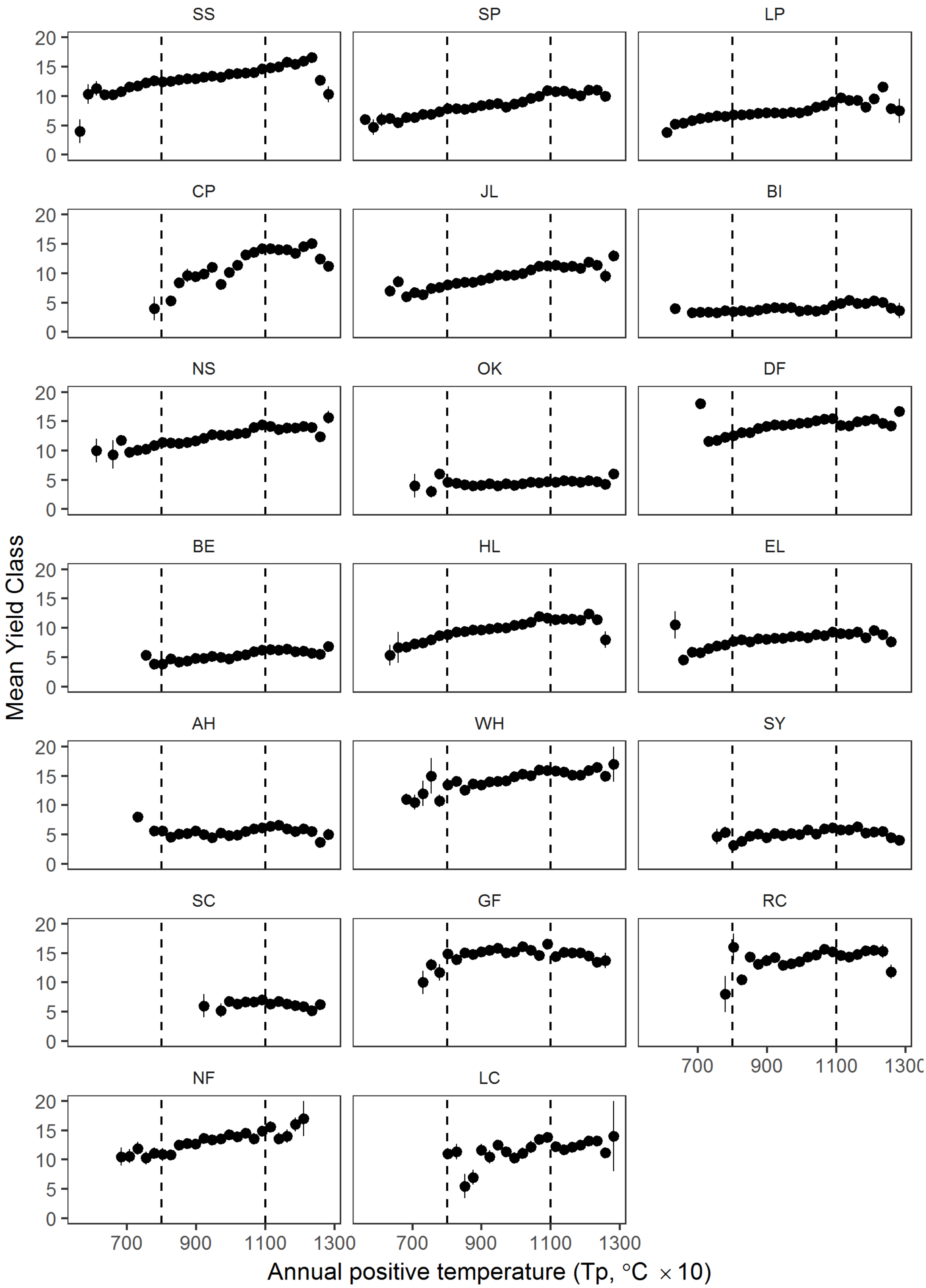


Figure 8. Variation in yield class with ombrothermic index (I_o). Mean yield class is calculated at binned intervals of I_o. Bars are standard errors and are plotted when larger than the diameter of points. Vertical lines show boundaries of wetness zones; for labels see Figure 11b.

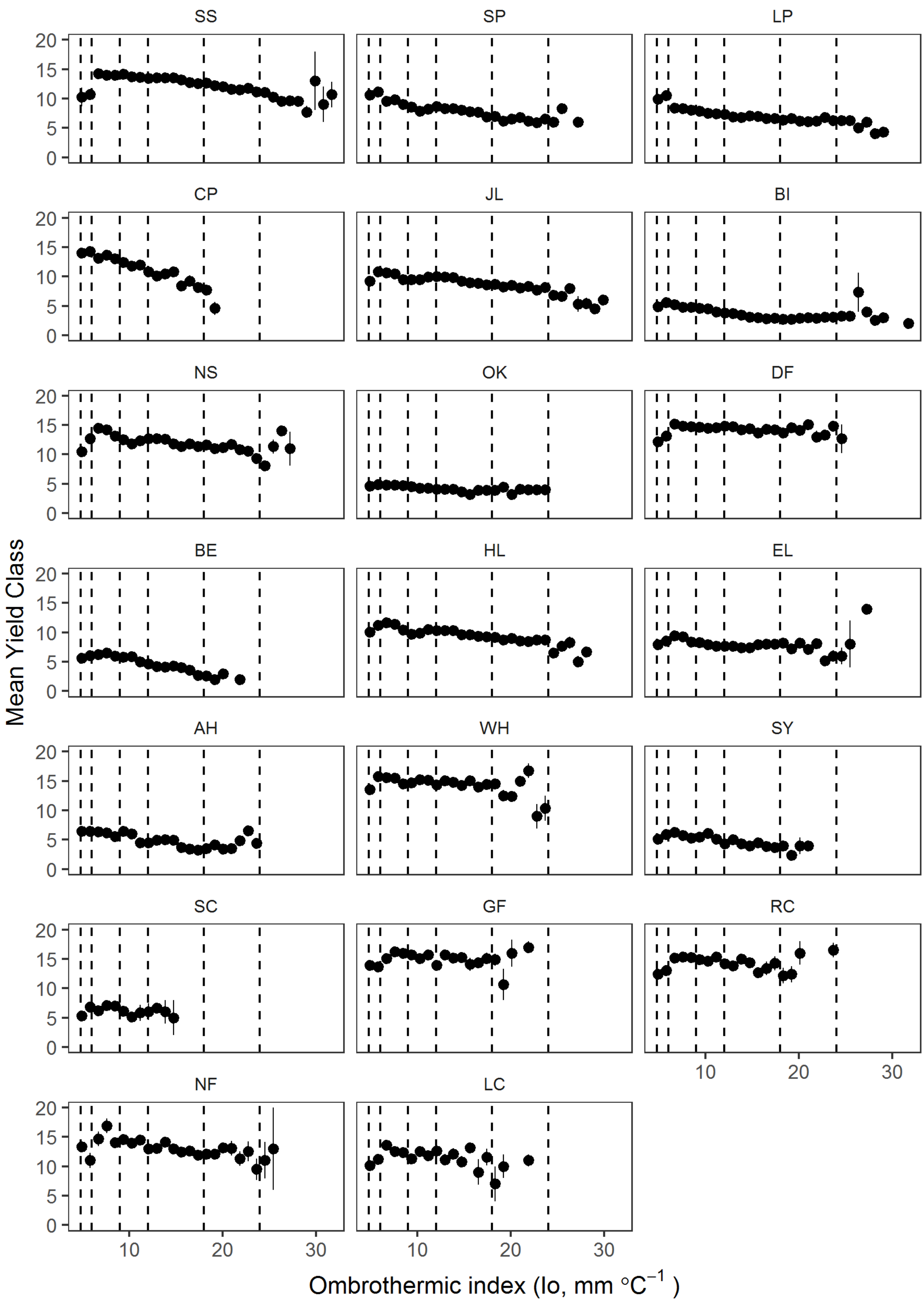


Figure 9. The number of subcompartments categorised by species and soil group. Dot-area shows the relative number of subcompartments per cell. Bars show the marginal totals of subcompartments for species and soil groups.

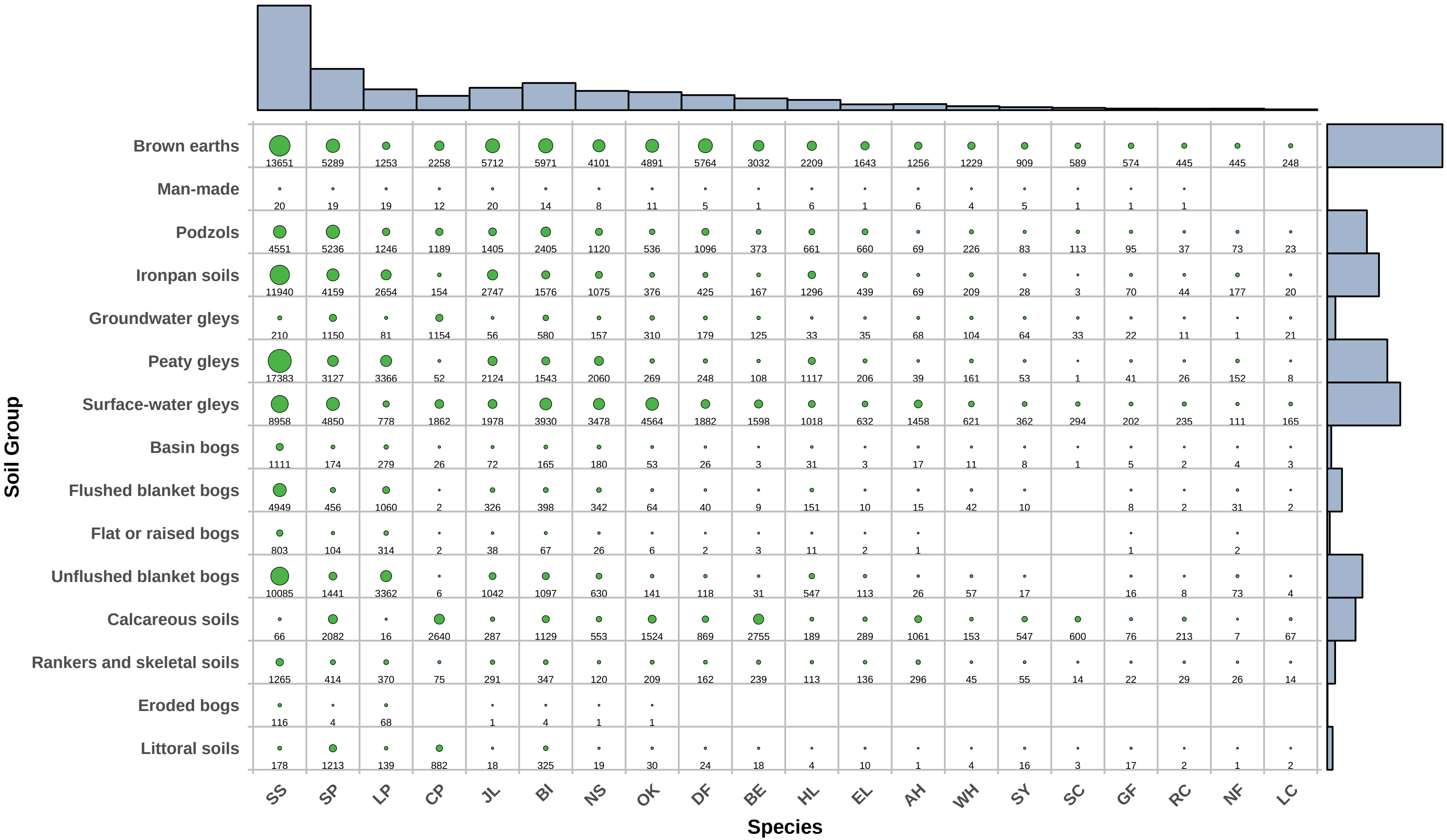


Figure 10. The number of subcompartments categorised by soil group and climate zone. Dot-area shows the relative number of subcompartments per cell. Bars show the marginal totals of subcompartments for soil groups and climate zone.

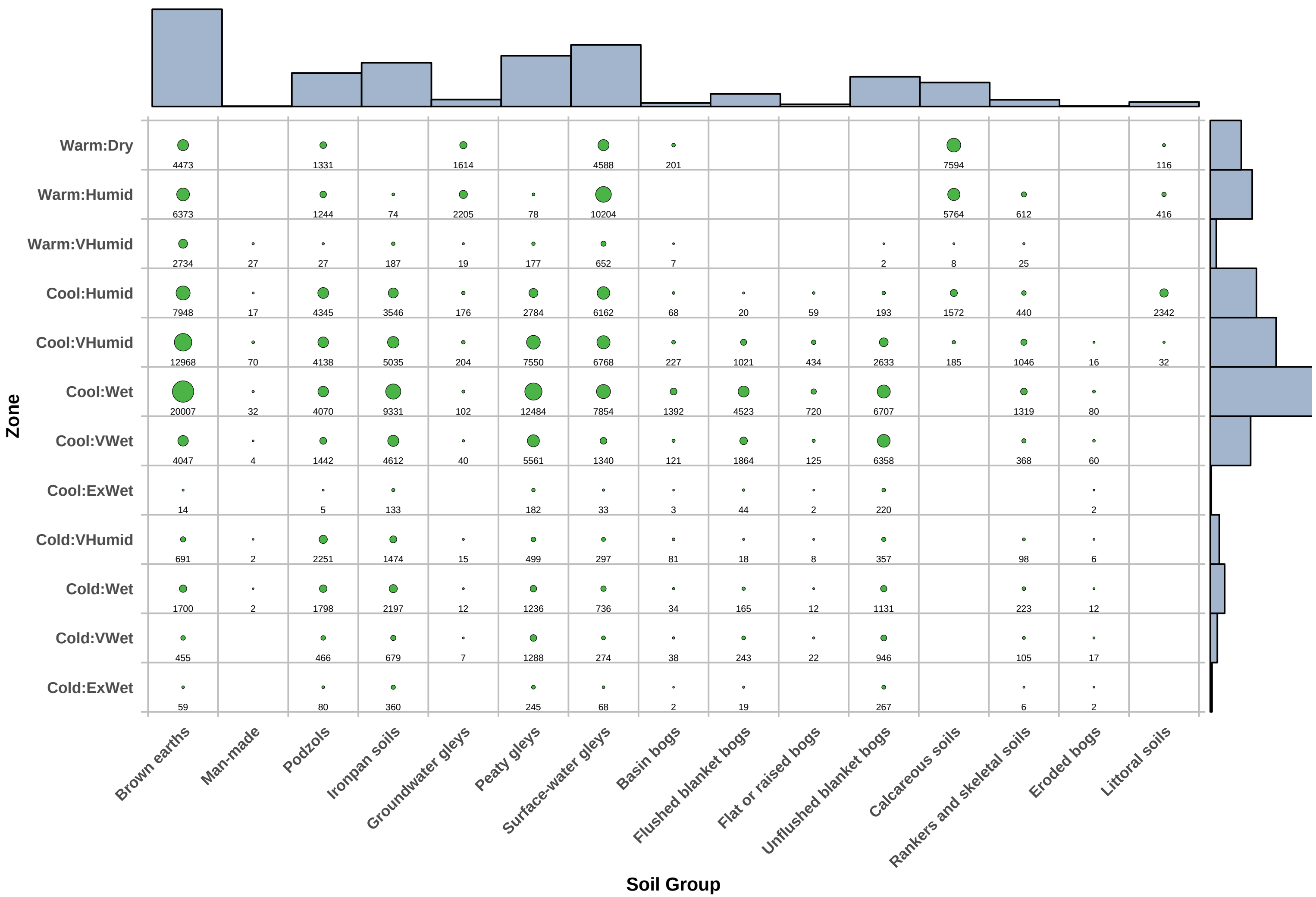


Figure 11. The distribution of subcompartments along gradients of a) annual positive temperature (T_p), b) ombrothermic index (I_o), and c) in two dimensions with T_p and I_o, in the climate space of Britain. Climate variables are calculated and classified according to the system of Rivas-Martinez and Rivas-Saenz (1996). Curves in a) and b) are kernel density estimates and show variation in the abundance of subcompartments with temperature and wetness. Points in c) show the locations of subcompartments in the space described by temperature and wetness. Filled contours that range from light green to red show areas containing increasing proportions of probability density, i.e. increasing abundance of subcompartments. The greatest abundance occurs in the warm-dry zone.

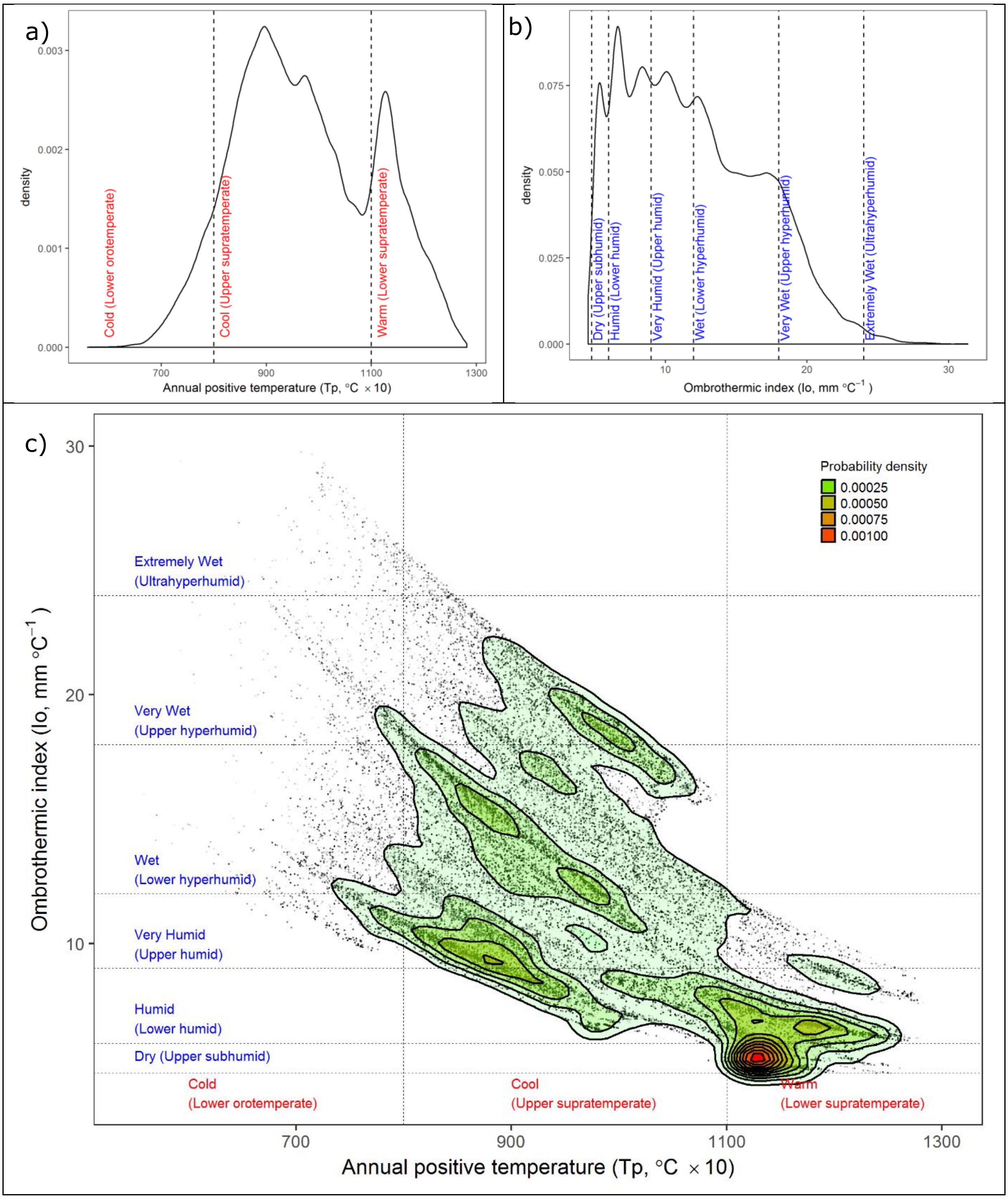
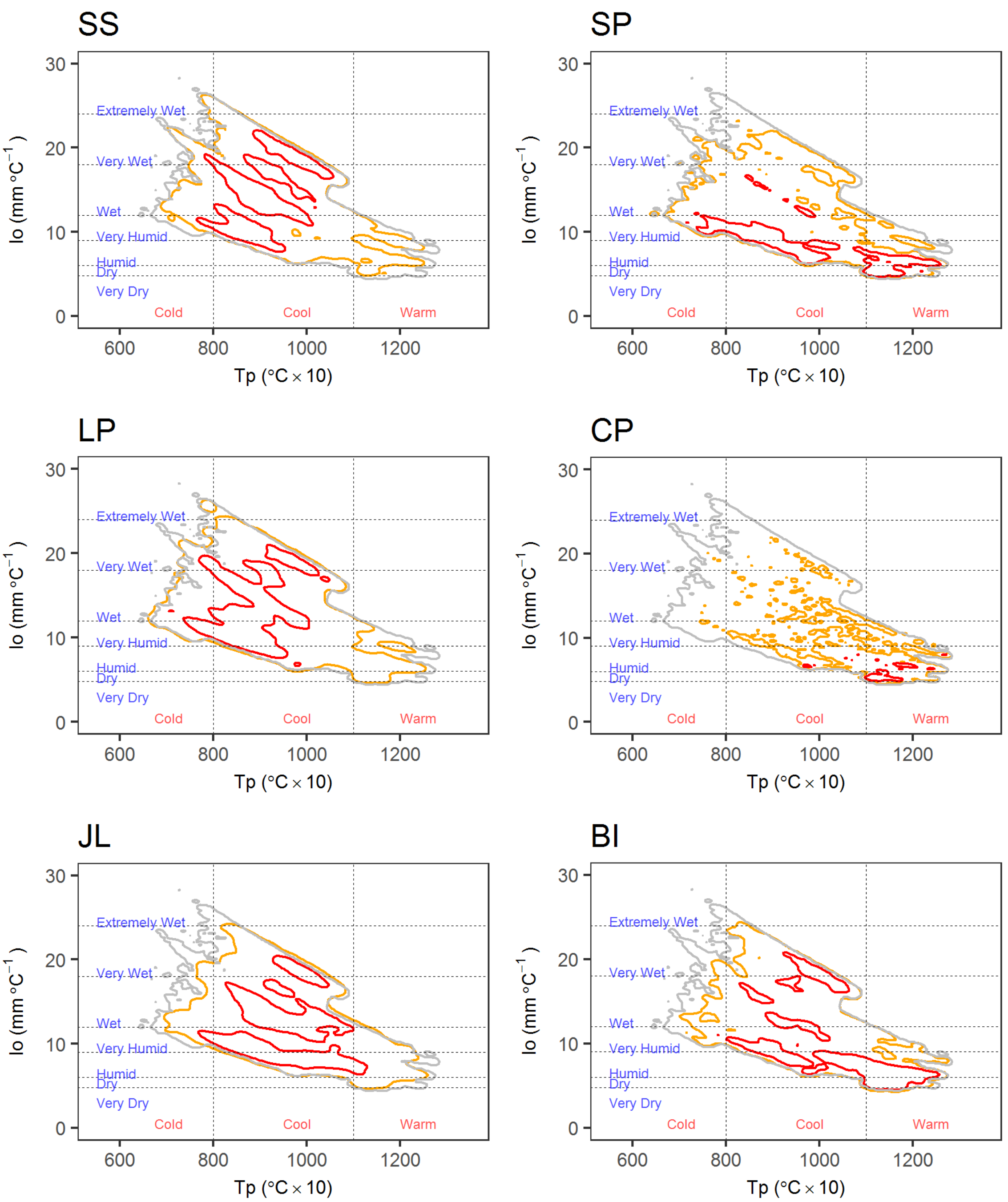
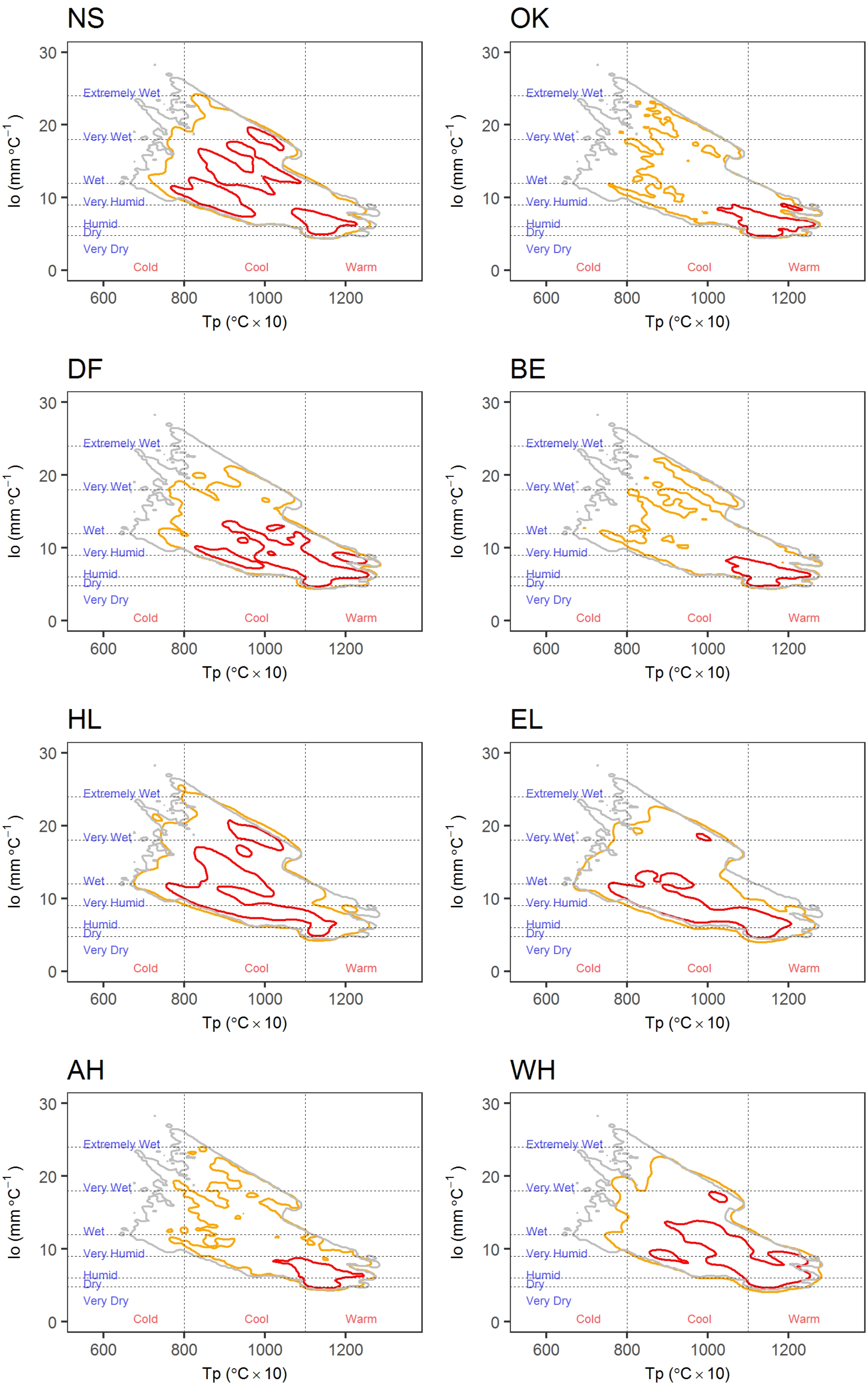


Figure 12. The climate space of 20 species growing on the Public Forest Estate in Britain. Climate space is defined by temperature (T_p) and wetness (I_o), and categorised using thresholds of Rivas-Martinez & Rivas-Saenz, (1996). Grey contours show the boundary of the full extent of all subcompartments. Orange and red contours represent 95 and 50% of the volume of probabilities, which indicate the major extent and high-abundance regions of species range.



Emerging species



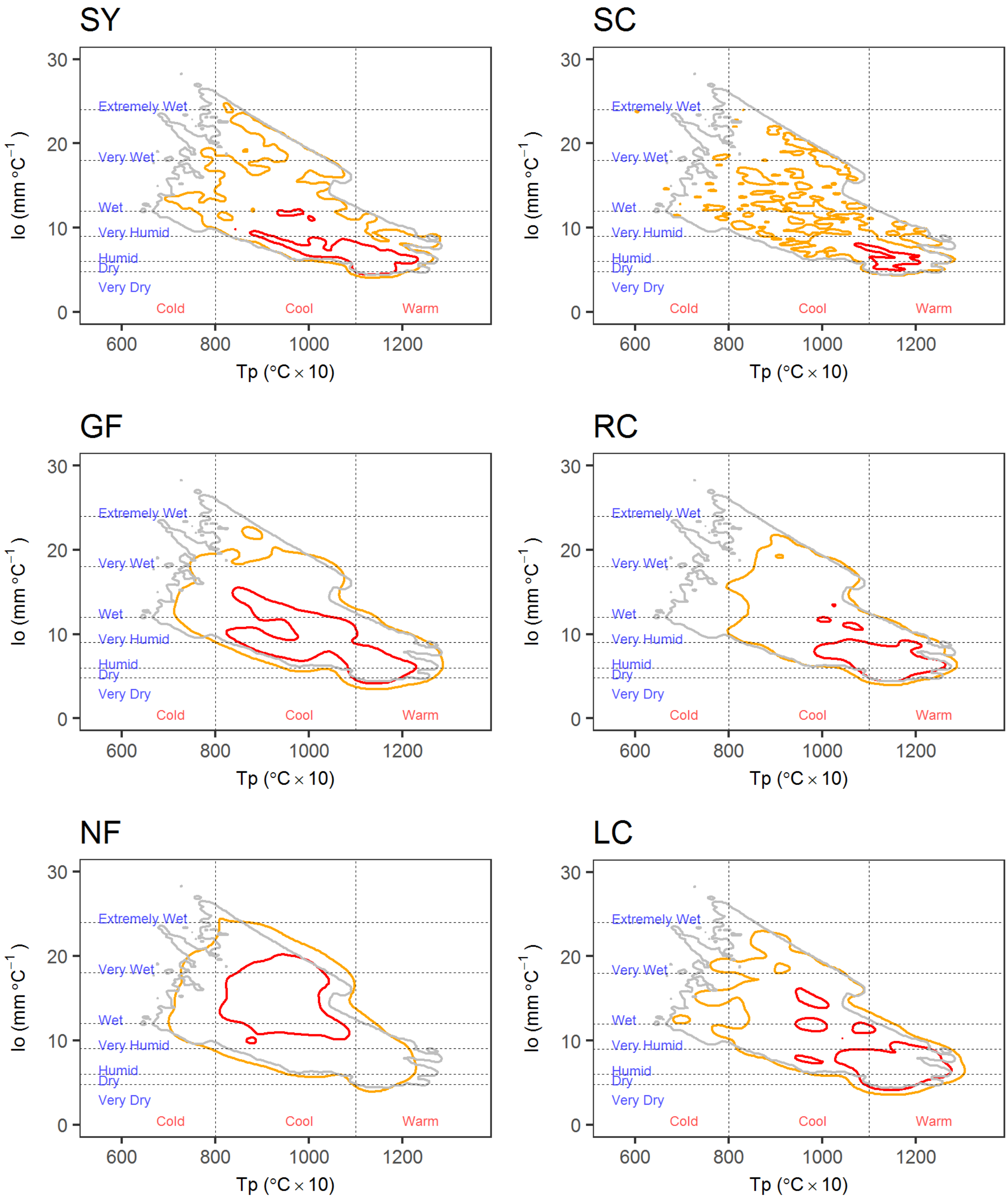

SY
SC
GF
RC
NF
LC
30
20
10
0
Io (mm °C^{-1})
Extremely Wet
Very Wet
Wet
Very Humid
Humid
Dry
Very Dry
Cold
Cool
Warm
600
800
1000
1200
Tp (°C × 10)

Figure 13. Climate space regions of 20 species drawn as ellipses fitted as 95% confidence intervals around the 50% probability contours shown in Figure 12. Species are grouped by region within climate space: a) Cool: species absent from warm zones, b) Warm: species predominantly found in warm zones, c) Dry-Humid: species that occupy all thermal zones and are most abundant in drier wetness zones, and d) Humid-Wet: species that extend into the Very Wet.

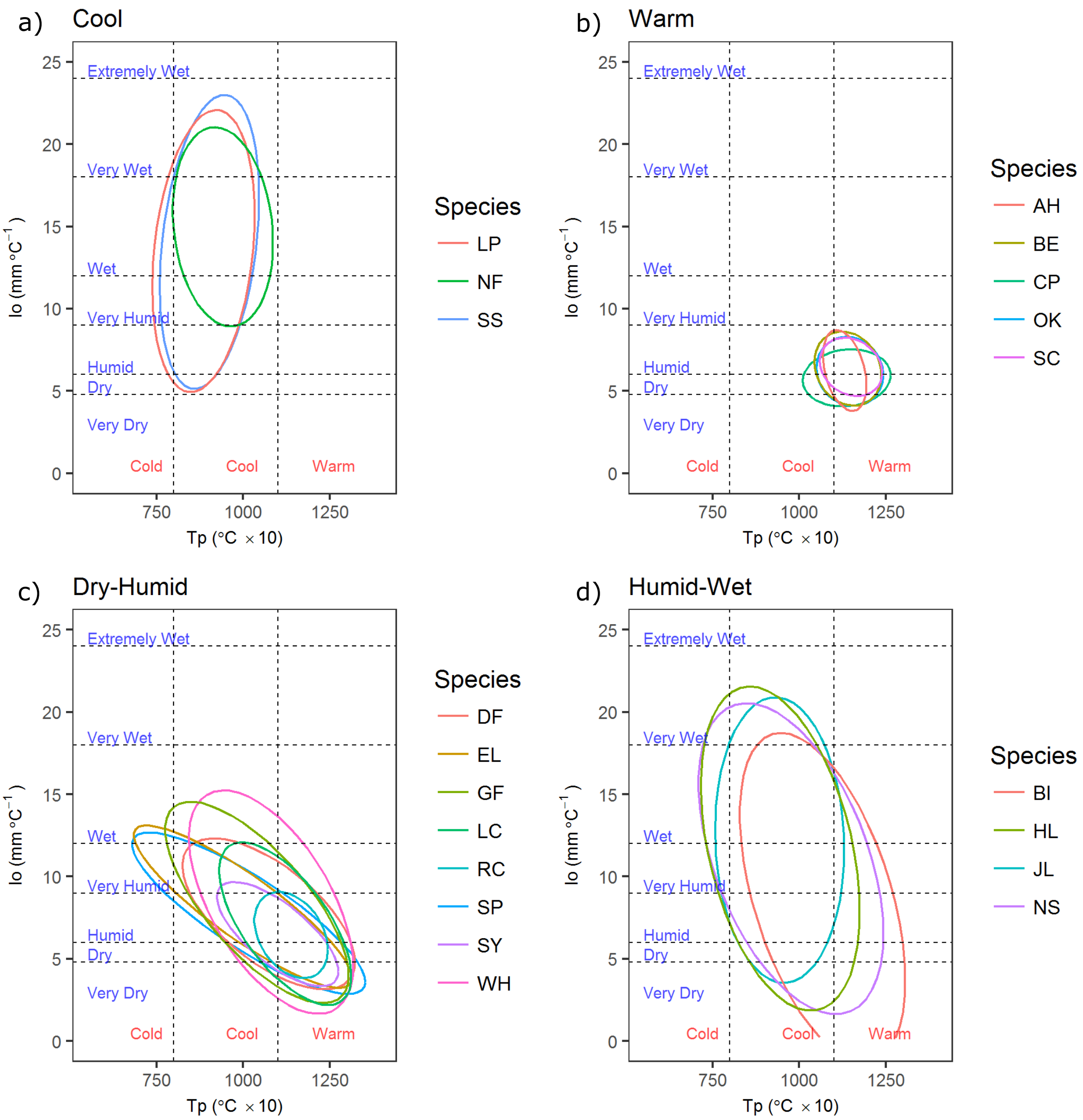


Figure 14. Graphical matrix summarising the proportions of climate space overlapped by pairs of species. The colour and size of a point indicates the proportion of the climate space of species listed at the head of the columns that is overlapped by the species listed in the rows; the darker and larger the point the greater the overlap. Cells with a cross show species pairs with dissimilar patterns of abundance by soil groups within the overlap regions which was assessed using Cramer's V value of 0.4 as the threshold.

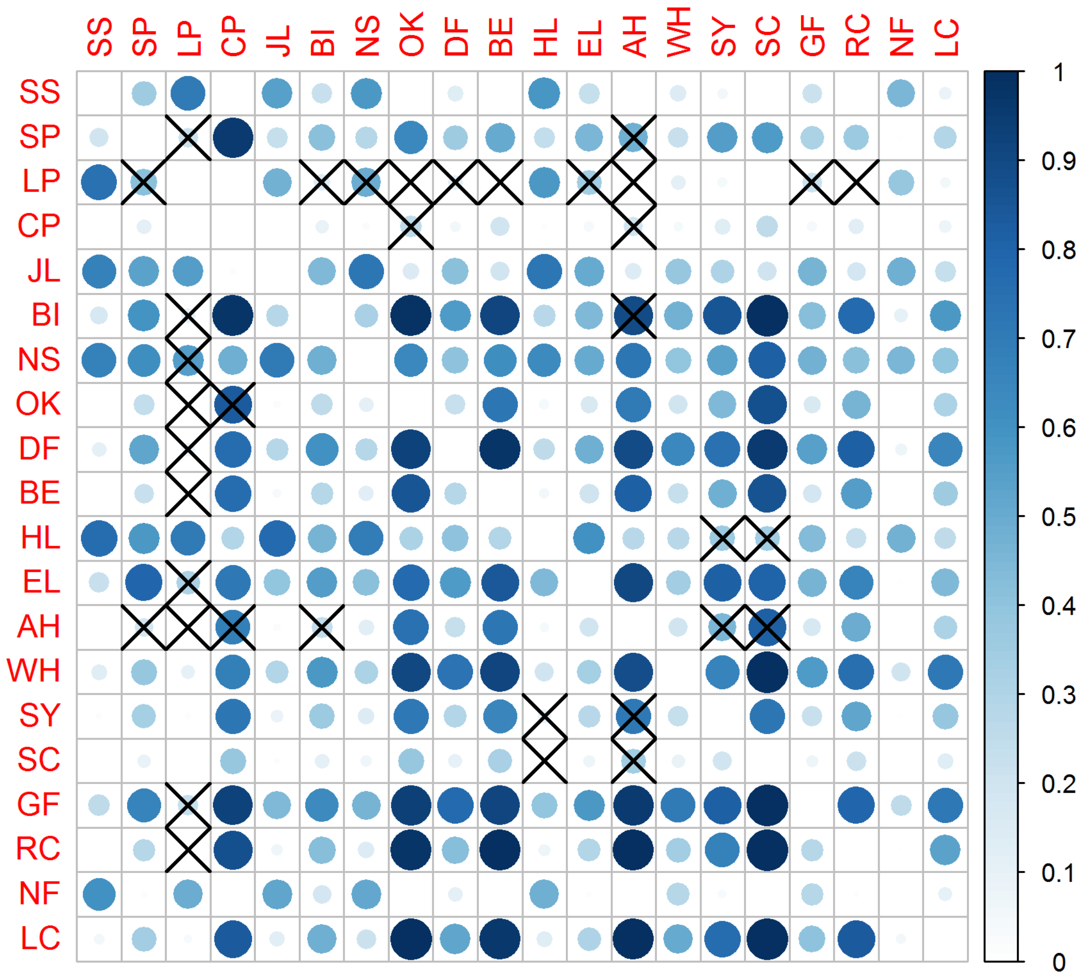


Figure 15. a) Projected changes in the distribution of climate zones, and b) prevalence of the submediterranean climate (red), for different Representative Concentration Pathways (RCPs) using gridded climate data derived from HadGEM2-ES GCM.

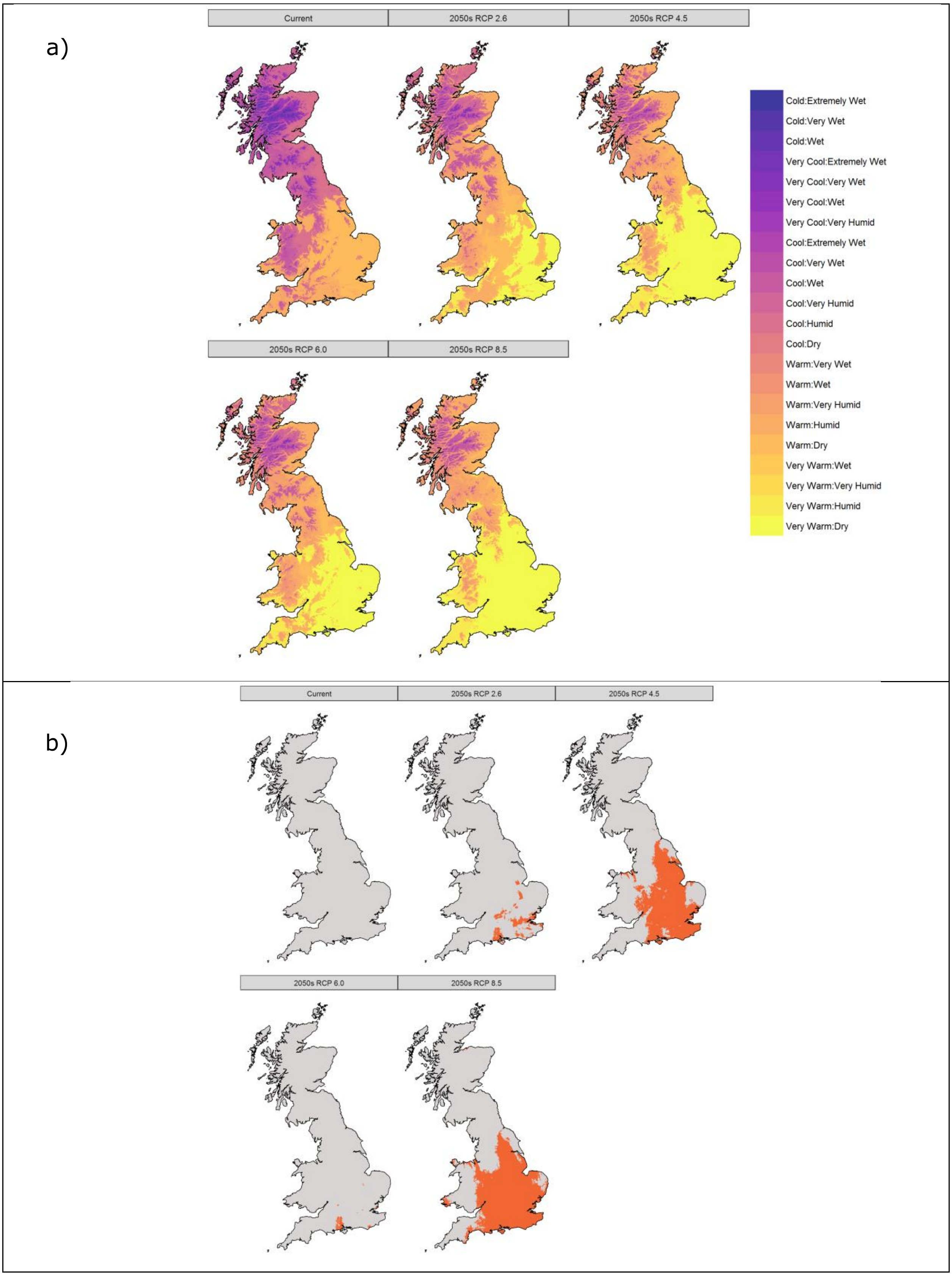
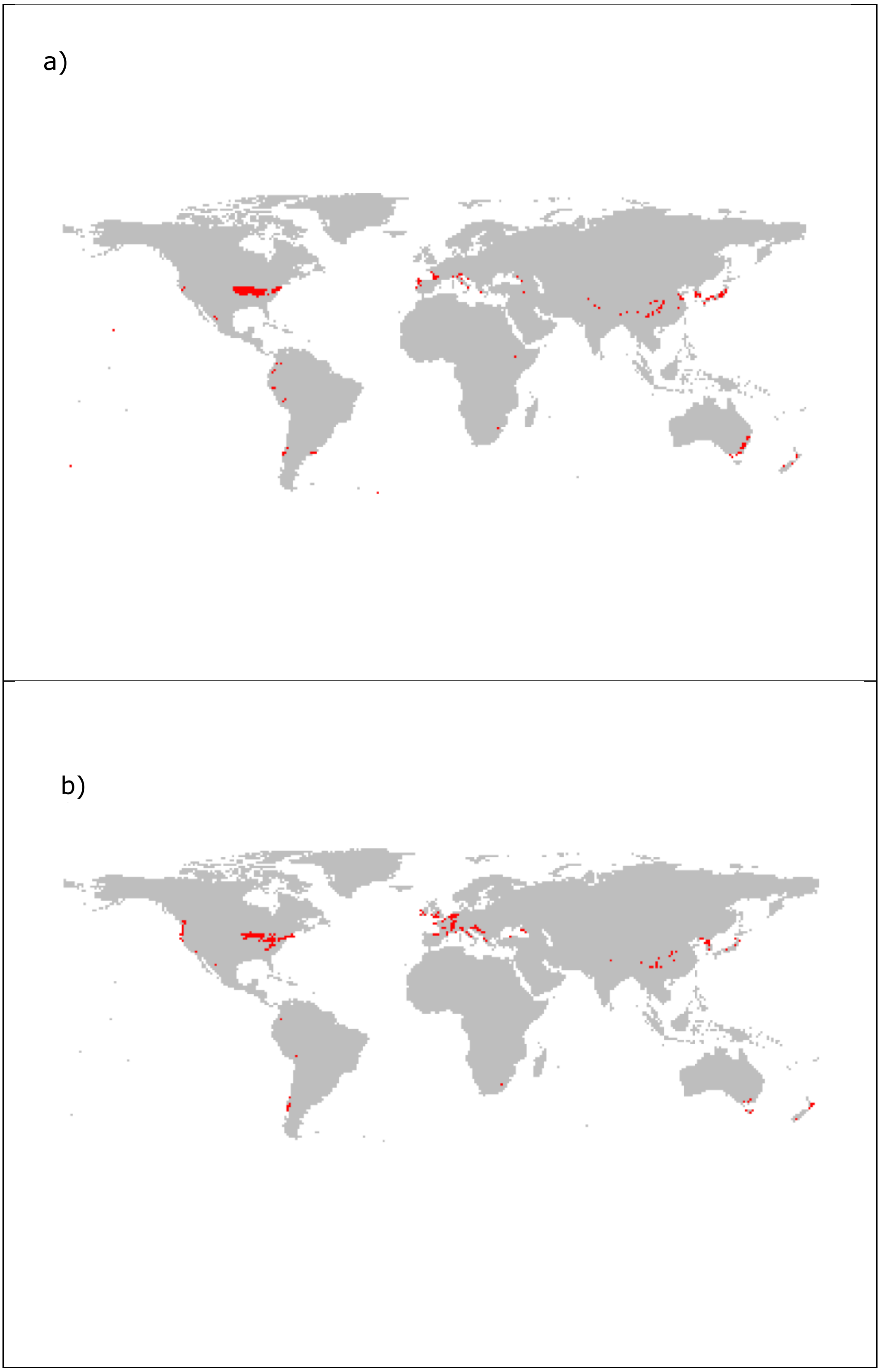


Figure 16. Changes in the distribution of abundance of subcompartments for different emissions scenarios using gridded climate data derived from HadGEM2-ES GCM.

Figure 17. Current regions of the world with a) Very Warm:Dry climate, and b) Warm:Humid, Warm:Very Humid, and Warm:Wet climates.



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