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# Capricious, or tied to history's apron strings? Floristic regions in north-west European brambles (*Rubus* subgenus *Rubus*, Rosaceae)

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## ABSTRACT

**Aim** To classify and describe distributional patterns in apomictic *Rubus* subgenus *Rubus* in north-west Europe and to characterize the major regions by statistically derived character species.

**Location** North-western Europe, in particular Ireland, the United Kingdom, the Netherlands, Denmark and Germany.

**Methods** We used TWINSpan analysis to distinguish hierarchically ordered phytogeographical regions using grid-based distributional patterns of bramble species, Dufrenoy–Legendre indicator species analysis to define character species for the regions, and descriptive statistical analysis of broad-scale abiotic factors derived from the LANMAP landscape classification for each region.

**Results** Grid cells were classified into 114 initial groups and 12 regions (florulas), forming three major bramble territories. Up to 15 indicator species could be assigned to each florula. The florulas in the British Isles are geographically isolated, unlike those on the continent. The florulas differ in minimum temperature in January, mean precipitation in August, and elevation. Although a clear view of the relationship between the bramble flora in the British Isles and the continental flora is obscured by the lack of data from Belgium and France, the major biogeographical patterns coincide with the genetic structure of the genus as published by Sochor *et al.* (2015). Other factors forming the basis for the observed patterns are isolation (especially in the British Isles), and arguably also landscape history and landscape patterns.

**Main conclusions** Phytogeographical patterns in *Rubus* subg. *Rubus* are strongly influenced by historical factors and can be traced back to the hybridization of sexual *Rubus ulmifolius*, *Rubus canescens* and *Rubus* ser. *Glandulosi* especially. Geographical and ecological factors also play a role in the realization of large-scale patterns, but these factors seem to be closely tied to the history and genetic structure of the genus through inherited ecology from the ancestral species.

## Keywords

apomicts, hybridization, indicator species, inherited ecology, isolation, land use history, phylogeography, phytogeographical regionalization, polyploids, twinspan

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## INTRODUCTION

For a long time, recurrent patterns in the distributions of plants have attracted the attention of naturalists. Two ways to study these patterns are the identification of floristic

elements, groups of species with a similar distribution, and the description of floristic regions, areas characterized by a broadly similar flora (McLaughlin, 1994; Finnie *et al.*, 2007). These floristic phytogeographical approaches, essentially two sides of the same coin, provide spatially explicit frameworks

for many fields of research – for example, historical and ecological biogeography, systematics and evolutionary biology – but also for more applied questions, such as planning and conservation (Kreft & Jetz, 2010).

Floristic phylogeographical studies generally exclude apomictic groups in the genera *Rubus*, *Taraxacum* and *Hieracium*, often without explicit arguments (e.g. Andersson, 1988; Preston & Hill, 1997; Dahl, 1998). Reasons for their exclusion may include incomplete taxonomic knowledge, the absence of reliable distributional data or simply the opinion that ‘microspecies’ are not real species and that their large numbers would influence the analysis in an unacceptable way. Other authors emphasize scientific opportunities for the study of biogeographical patterns in apomictic genera (Tyler, 2000; Bijlsma & Haveman, 2007). Interestingly, the distributions of many apomictic species probably reflect different processes from those that operate in the ranges of amphimictic species. Many European vascular plant species remigrated from remote areas in the south or east during the Holocene, and their current ranges have no simple relationship with the areas where the species survived during the last glaciation (Dahl, 1998). On the contrary, most apomictic species have to be regarded as neospecies in the sense of Levin (2000) and are supposed to have their origin in their current distributional areas and to be still in the phase of range expansion.

In this paper, we focus on *Rubus* L. subgenus *Rubus* (bramble) in north-western Europe. This is one of the largest apomictic complexes in Europe, with only a few sexual diploids and probably over 1000 apomictic polyploids. Weber (1995) estimated there to be 300–400 sexual *Rubus* species world-wide, fewer than 10 of which are found in western Eurasia. The main centres of diversity in the genus are Southeast Asia, the Andes in South America, the coastal regions of North America, and the Atlantic and sub-Atlantic region of temperate Europe (Weber, 1995). The European blackberry flora is made up of a polyploid series ( $x = 7$ ), with ploidy levels from  $2x$  up to  $6x$  and perhaps  $7x$  (Grant, 1971). Diploids are found to be 100% amphimictic, whereas triploids are obligate apomicts; tetraploid *Rubus* plants have varying degrees of sexuality. *Rubus* ser. *Glandulosi*, comprising mainly glandular, mountain-dwelling polyploids of woodlands, is especially characterized by a high degree of retained sexuality (Šarhanová *et al.*, 2012).

Gustafsson (1943) hypothesized that apomixis in *Rubus* subg. *Rubus* originated as a result of hybridization events between (now extinct) ancestral species and subsequent polyploidization after the last glaciation, a hypothesis that was largely confirmed by a recent broad-scale molecular study of European brambles (Sochor *et al.*, 2015). In that study, it was shown that the European apomictic brambles probably originated from only six ancestral species, largely after the retreat of the Pleistocene ice sheets. It was argued, however, that the first large polyploidization events that generated the recent apomictic lineages (e.g. in *Rubus* ser. *Rubus*) must have occurred during a glaciation cycle earlier than the Last

Glacial Maximum. The findings are consistent with Stebbins' secondary-contact hypothesis (Stebbins, 1986), which explains the high proportion of polyploids from hybridization events in formerly glaciated areas after the rapid expansion of distributional ranges of remigrating species. Speciation and range expansion of most *Rubus* species are thought to have taken place in man-made landscapes, and still continue (Matzke-Hajek, 1997).

In this paper, we consider the biotypes stabilized by apomixis and with distributional ranges  $> 50$  km as species, in concordance with authors such as Weber (1995) and Kurtto *et al.* (2010). Each of these apomictic species probably consists of only one or a few clones with limited genetic variation (Kraft & Nybom, 1995; Nybom, 1998) and are morphologically well defined, as well as possessing distinct phylogeographical and ecological features (Haveman, 2013). Although there are reasons to consider even the stabilized apomictic biotypes with smaller distributional ranges as species (Haveman & de Ronde, 2013), they are omitted from this study because insufficient (distribution) data are available. Ecologically, the distributional ranges of the species within *Rubus* subg. *Rubus* in Europe are thought to be constrained by winter cold and summer drought (Weber, 1995; p. 296), which explains their scarcity or even absence in large parts of the Nordic countries, at lower elevations in eastern Europe, and in southern Europe (Kurtto *et al.*, 2010). In the Atlantic and sub-Atlantic zone, the highest diversity is found in the lowlands and lower hills, on loam and loamy sands (Matzke-Hajek, 1997).

In the *Atlas Flora Europaeae*, Kurtto *et al.* (2010) mapped about 750 *Rubus* species, but distributional data are very scarce over large areas, such as France and south-eastern Europe (Kurtto *et al.*, 2010, p. 31). Range size and structure differ considerably among bramble species; Kurtto *et al.* (2010) grouped the species into five categories, based only on range diameter: very widely distributed (W1, range diameter  $> 1500$  km), widely distributed (W2, 500–1500 km), supraregional (R1, 250–500 km), regional (R2, 50–500 km) and local (L,  $< 50$  km). This last category of locally distributed species is usually not treated taxonomically (Weber in Kurtto *et al.*, 2010, p. 29) and is not included in the *Atlas Flora Europaea*. Bijlsma & Haveman (2007) also discerned five categories, but they also took the internal structure of the distributional ranges into account.

Even between adjacent regions, the *Rubus* flora may differ significantly. The *Rubus* floras of two adjacent regions in Germany (Westphalia and Eifel/Niederrheinische Bucht) have only 64 species in common out of a total of 147 species, whereas 53 species are unique for Westphalia and 30 for the Eifel/Niederrheinische Bucht (Weber, 1985; Matzke-Hajek, 1993). In an attempt to summarize the distributional patterns of *Rubus* in Great Britain and Ireland, Newton (1980) and Newton & Randall (2004) proposed six main *Rubus* regions ('florulas', small floras), which were divided into many regional complexes. Newton (1980) noticed that the species diversity in *Rubus* subg. *Rubus* decreased northwards,

probably as a result of lower winter temperatures. Furthermore, some seemingly omnipresent species were unexpectedly absent from certain areas (e.g. *Rubus dasyphyllus*), probably caused by the vigorous development of regional and local taxa in these areas (Newton, 1980). Gustafsson (1943, p. 157) lamented over similar observations: 'There rests something capricious, sometimes even enigmatic, over the dispersal of the blackberries'.

No attempts have been made so far to analyse the distributional patterns of *Rubus* species in north-west Europe. The central objective of our study is to classify and describe the spatial patterns of *Rubus* species, based on grid data from the Republic of Ireland, the UK, the Netherlands, Denmark and Germany. These countries lie in the centre of species diversity of the subgenus (Matzke-Hajek, 1997; Kurtto *et al.*, 2010), and sufficient distributional data are available from these countries. We characterize the resulting phylogeographical regions by means of indicator species analysis. Furthermore, we examine the internal structure of the regions distinguished. We summarize broad-scale ecological factors (climate, soil and elevation) for each region, derived from the European landscape classification in LANMAP (Mücher *et al.*, 2010), and propose some preliminary explanations for the observed spatial patterns.

## MATERIALS AND METHODS

### Survey area

The area of this study comprises the national territories of Ireland, Great Britain, the Netherlands, Denmark and Germany, for which national grid-based distributional data for *Rubus* were available. Unfortunately, Belgium and France, both countries with high *Rubus* species diversity, could not be included because of a lack of data (Kurtto *et al.*, 2010). The study area thus extends from the westernmost part of Ireland to the border between Germany and Poland, and from the Germany's southern border to the Shetland Islands. Elevation ranges from 2800 m in the German Eastern Alps to 10 m below sea level in the Netherlands (Mücher *et al.*, 2010). The climate is North Atlantic (humid with rather low temperatures in summer and winter, but not extremely cold) in the northern part of the survey area, and Central Atlantic in the southern parts of Ireland, Great Britain, the Netherlands and adjacent Germany (moderate climate where the average winter temperature does not go far below 0 °C and the average summer temperatures are relatively low). The eastern and southern part of Germany is characterized by a relatively continental climate (warm summers and rather cold winters) (based on LANMAP; Mücher *et al.*, 2010).

### Distributional data

The operational geographical units (OGUs) in this study are grid cells with at least one *Rubus* occurrence. *Rubus* distributional data from Britain and Germany were obtained from

the Botanical Society of the British Isles and the Bundesamt für Naturschutz respectively (date December 2007). The basis for the distributional maps in the British database are the 10 km × 10 km grid of the Ordnance Survey and the similar Irish grid, which are based on the OSGB36 map datum. The basis for the distributional maps of German species was the degrees-based grid on the TK25 (the so-called 'Messtischblatt'). Its projection causes a slightly variable OGU area, varying from approximately 121 km<sup>2</sup> in the north to 136 km<sup>2</sup> in the south. Danish *Rubus* data were digitized from the atlas published by Martensen *et al.* (1983). The grid used in this publication is an extension of the German grid with cells of approximately 11 km × 11 km. For the Dutch data, we used the national database described by van de Beek *et al.* (2014). The Dutch grid has 5 km × 5 km cells based on the WSG84 map datum used for floristic inventories, which have been rescaled to 10 km × 10 km for this study. All grid cells in the border area of the Netherlands and Germany are included in the analysis, even if they are overlapping.

Species not belonging to *Rubus* subg. *Rubus* (e.g. *Rubus chamaemorus*, *Rubus saxatilis* and *Rubus idaeus*; nomenclature throughout this paper follows Kurtto *et al.*, 2010) were excluded from the data set. Distributional area categories for the *Rubus* species were derived from the distributional maps in *Atlas Flora Europaeae* (Kurtto *et al.*, 2010) and classified into four classes according to Table 1. OGUs with three or fewer species were omitted from the analysis, because testing of the method (see below) gave ambiguous results for such species-poor OGUs. The final data set consisted of 618 species, 2839 classified OGUs and 22,451 species occurrences.

### Floristic regionalization

Classification of the OGUs was carried out with a modified version of TWINSpan. The original version of the program (Hill, 1979) is strictly dichotomous: in each subsequent step, it divides every existing groups into two new groups, resulting in 1, 2, 4, 8, 16, etc. groups, unless the threshold for the minimum group size or for the number of groups is reached. In the modified version of TWINSpan (Roleček *et al.*, 2009), implemented in the classification program JUICE 7.0.45 (Tichý, 2002), only the most heterogeneous group is split in two new groups at each step, resulting in 1, 2, 3, 4, etc. groups, until a user-set threshold of group heterogeneity or a user-defined number of groups or minimum group size is

**Table 1** *Rubus* distributional categories used in this study (based on the categories given in Kurtto *et al.*, 2010, p. 29)

Code	Category	Diameter of distributional area (km)
W1	Very widely distributed	> 1500
W2	Widely distributed	500–1500
R1	Supraregional	250–500
R2	Regional	50–250

reached. These stopping rules tend to avoid imposed divisions of homogeneous groups at the higher levels. For our initial analysis, the minimum group size was set to 15. TWINSpan was forced to stop when the total inertia (the sum of all eigenvalues and a measure of heterogeneity) in the group reached a maximum of 4.0. This resulted in a total number of 114 'initial groups', which are more or less equivalent to the regional complexes defined by Newton & Randall (2004). To arrive at geographically coherent *Rubus* florulas, we analysed the TWINSpan dendrogram, after which we set the final minimum group size to 350 and the maximum number of groups/florulas to 13.

### Indicator species and distributional characteristics

JUICE was used to compute indicator species for each division step in the final analysis, following the method of Dufrêne & Legendre (1997), with a threshold of 20%. On the basis of the TWINSpan table, we computed the total number of species in each distributional area category for each region.

### Environmental characteristics

Descriptive statistics for the environmental factors were derived from LANMAP (Mücher *et al.*, 2010). Using the centroids of each grid cell in the analysis, corresponding data for soil features, elevation and climate were extracted from the LANMAP data set, using ArcGIS 10.1 (ESRI, 2011). We used the R package (R Development Core Team, 2011) for the construction of graphs of broad-scale ecological factors: minimum temperature of the coldest month (T\_MIN\_JAN in LANMAP), maximum temperature of the warmest month (T\_MAX\_AUG), mean precipitation of the warmest month (P\_MEAN\_AUG) and mean elevation (ALT\_MEAN), as well as geological parent material (Parent\_Mat).

## RESULTS

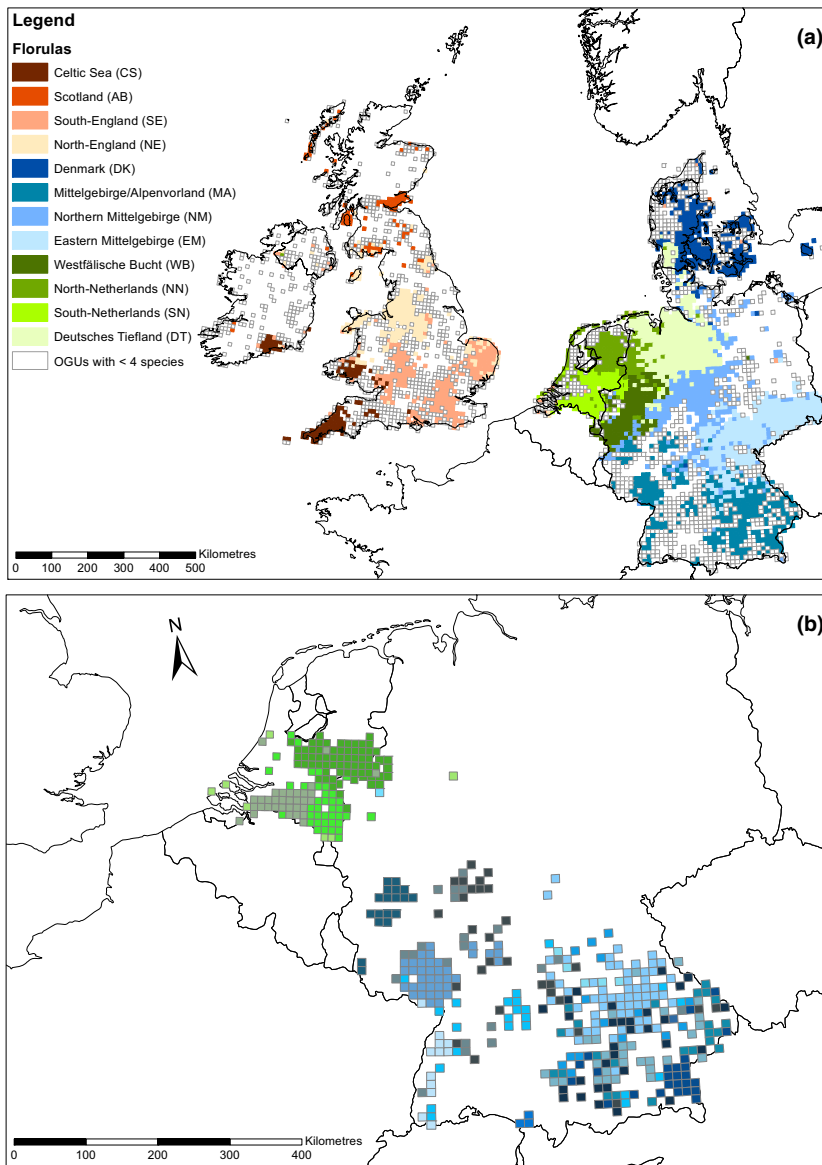
The TWINSpan analysis resulted in 12 florulas (Fig. 1a, Table 2). On the basis of the first and third divisions, three major bramble territories were distinguished (Fig. 2): the British Isles territory (BI, red in Fig. 2), the south-east continent territory (SEC, blue) and the north-west continent territory (NWC, green). It should be noted that the BI territory extends into the extreme south-western part of the Netherlands. The SEC territory comprises upland regions in the southern part of Germany (the Alpine foreland as well as most regions belonging to the central uplands and South German Scarplands on both sides of the Rhine valley), the eastern parts of the North German lowlands, as well as large parts of Denmark. The NWC territory is compact, comprising the western sand areas of the North German lowlands and the Netherlands, as well as the uplands of the Rhenish Massif. Each of these bramble territories is divided into four florulas. From the differences in geographical homogeneity

of the florulas (Fig. 1b), it is clear that the initial groups in the SN (South Netherlands) florula form relatively well-defined 'nuclei', whereas in the MA (Mittelgebirge and Alpenvorland), such nuclei appear next to scattered initial groups. Apart from the South England (SE), Denmark (DK) and MA florulas, all florulas are internally rather homogeneous, with groups in coherent nuclei (see Appendix S1).

There is a striking difference in the numbers of indicator species in the florulas (Fig. 3). Several florulas are characterized by only one or a few indicator species, like the South England florula (SE), the northern Mittelgebirge florula (NM), MA, and the North Netherlands florula (NN). Other florulas are very rich in indicator species, such as the Celtic Sea florula (CS), and the South Netherlands florula (SN), both with 10 or more indicator species. Another remarkable outcome of the indicator species analysis was the difference in structure of the indicator species groups between BI on one side, and SEC and NWC on the other side, going from higher to lower hierarchical levels. In the BI territory, every step in the TWINSpan division, except the 'England' intermediate region (see Fig. 3), consisted only of indicator species that did not appear at lower levels (shown in bold in Fig. 3), whereas in the SEC and NWC territory step several indicator species that reach higher indicator values at subordinate levels occurred in each intermediate division. In other words, the florulas and the intermediate steps in the SEC and NWC territories both shared indicator species on a higher level, whereas the florulas and the intermediate steps in the BI territory were more independent in terms of indicator species.

We found a considerable difference in total species numbers and proportion of species distributional area classes between the florulas (Fig. 4). The Scotland florula (AB) and DK both consist of fewer than 100 species, whereas the SE florula, the NM florula and the Westfälische Bucht florula (WB) are very rich in species, each with over 180 species. AB, DK and the Eastern Mittelgebirge florula (EM) have low numbers of regionally distributed species, with summarized percentages for the R1 and R2 categories below 30%. The remaining florulas (WB, NN, SN and the Deutsches Tiefland florula, DT) had a relatively high number of regionally distributed species ( $R1 + R2 > 40\%$ ).

Mean precipitation in August and minimum temperature in January were the two climatic characters that showed the largest differences between the florulas (Fig. 5). As expected, the florulas in BI had a minimum temperature above 0 °C in January, whereas in the SEC florulas the median of the temperature in January was below 0 °C; the NWC florulas were intermediate for this variable. Precipitation in the driest month showed the greatest variation between the two 'Atlantic' florulas in the BI territory at one extreme (with the median above 85 mm; CS and AB) and the southern florula in BI at the other (with the median just above 60 mm; the SE florulas). All other florulas showed intermediate values for the precipitation in August, with a large spread in the values in the large MA in the SEC territory. Mean elevation was highest in the florulas belonging to the SEC territory: well



**Figure 1** Map of the 12 distinguished florulas on the basis of the TWINSpan analysis of the OGU with four or more *Rubus* species in Ireland, Great Britain, the Netherlands, Denmark and Germany (a) and of the initial TWINSpan groups in SN and MA (all 114 groups in Fig. S1 in Appendix S1) on the basis of OGU with four or more species (b).

**Table 2** Levels of distinguished biogeographical regions based on the TWINSpan analysis of grid data of the occurrences of *Rubus* subg. *Rubus* in north-west Europe.

Territory	Florula	Initial groups
British Isles (BI)	Celtic Sea (CS)	1–5
	Scotland (AB)	6–9
	South England (SE)	10–37
	North England (NE)	38–52
South-east continent (SEC)	Denmark (DK)	53–60
	Mittelgebirge and Alpenvorland (MA)	61–73
	Northern Mittelgebirge (NM)	74–87
North-west continent (NWC)	Eastern Mittelgebirge (EM)	88–95
	Westfälische Bucht (WB)	96–98
	North Netherlands (NN)	99–105
	South Netherlands (SN)	106–109
	Deutsches Tiefland (DT)	110–114

over 250 m a.s.l. in the northern and eastern Mittelgebirge florulas (NM and EM respectively), and over 400 m a.s.l. in MA, although there was considerable variation in elevation in these florulas. Typical lowland florulas (well below 100 m a.s.l.) were DK, NN, SN and DT (Fig. 5).

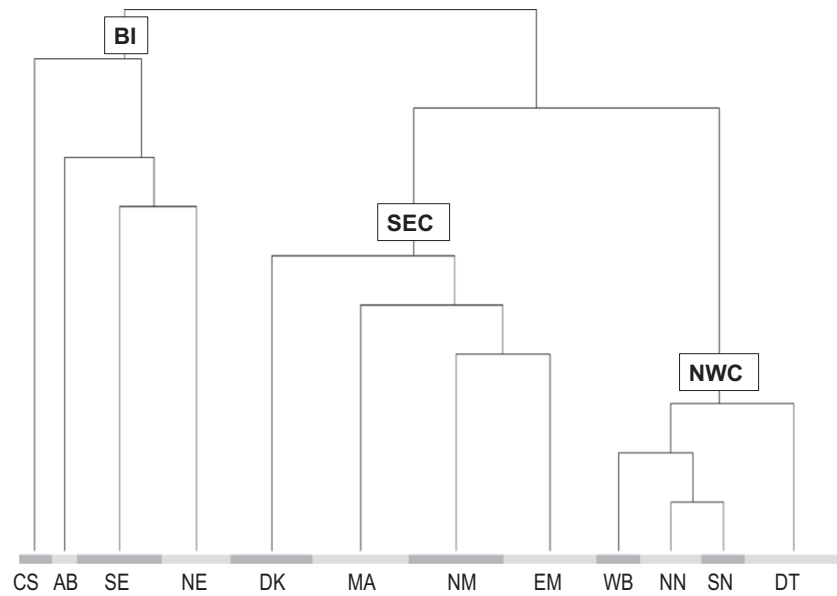
Parent material varied greatly within the florulas (Fig. 6), but in several florulas one type of parent material was dominant: crystalline rocks and migmatites in CS, glaciofluvial deposits in NE and DK, and sands in NN, SN and DT.

## DISCUSSION

### Quality and availability of data

The aim of this study was to classify and describe distributional patterns in *Rubus* subg. *Rubus* in north-western Europe on the basis of grid-based occurrences of bramble





**Figure 2** TWINSpan dendrogram of the classification of grid data of occurrences of *Rubus* subg. *Rubus* in north-western Europe with the codes of the distinguished territories and florulas.

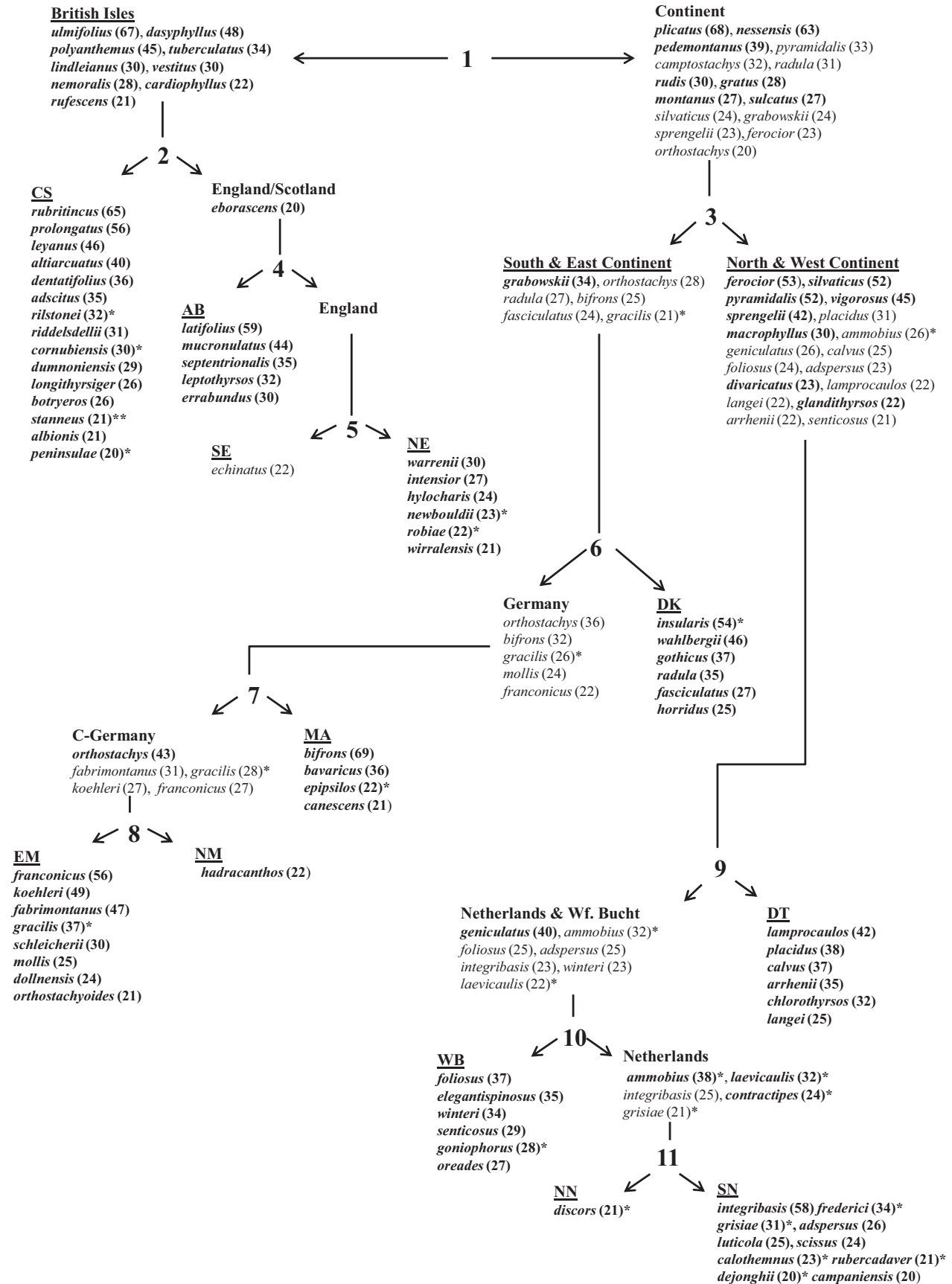
species. Using TWINSpan, we distinguished three bramble territories, divided into 12 florulas, all positively characterized by indicator species. Although the available data were collected over many years by different specialists, we believe that the results in this study largely reflect real patterns. Our florulas are consistent with the intuitive regionalizations by Newton (1980) and Newton & Randall (2004) of the bramble flora of the British Isles, and with our own experiences in the Netherlands. Another cause for concern could be the incompleteness of the data: several newly described species are missing from the data set, such as *Rubus wittigianus* (Weber, 2002), *Rubus uncimontanus* (van de Beek & Troelstra, 2013), and *Rubus paludosus* and *Rubus favillatus* (van de Beek, 2014). Most of these species have small distributional areas and are limited to only one florula, such that their absence from the database is likely to make little difference to the final results.

The empty (white) regions, especially in the BI territory, are not determined by a lack of data, but reflect the unsuitability of larger regions for brambles (Newton & Randall, 2004; Kurtto *et al.*, 2010). An exception and a more serious problem is the underrepresentation of data from Ireland, as already stated by Newton & Randall (2004), and the results for this island have to be interpreted with reservations. The lack of data from Belgium and France can also be considered a serious drawback of our analysis, as it obstructs the view of the connection between the flora in the south-westernmost part of the Netherlands and the flora of the BI territory. This can only be resolved by a systematic inventory of bramble species in both countries.

### The historical basis of the florulas

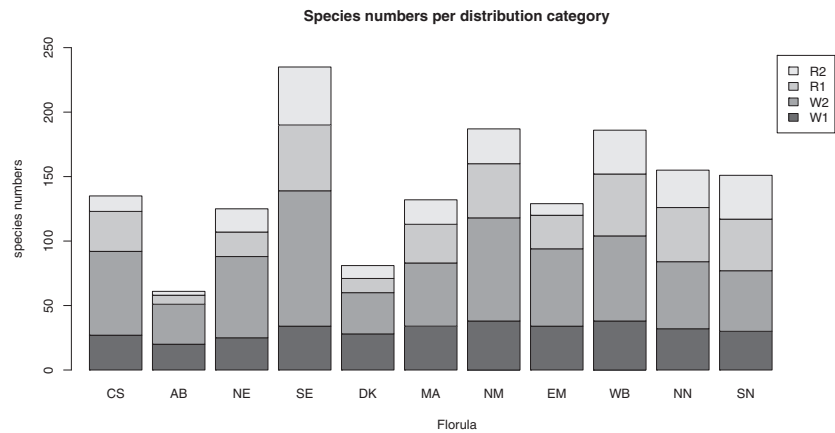
In a recent, rather provocative paper, Heads (2015) argued that species' present environment and biology (including

their means of dispersal) largely fail to explain their current distribution, and that the histories of clades often give better explanations of the patterns found. Heads illustrates this with many examples based on old taxa, but it can be argued that it is even more likely for young species such as those in *Rubus* subg. *Rubus*. Most *Rubus* species are neospecies (Levin, 2000) with unsaturated distributional areas, and at least the regional (R2) and supraregional (R1) species are thought to have broad ecological requirements, occurring in a variety of habitats on a wide range of soil types (Weber, 1981; Matzke-Hajek, 1997). This hypothesis is supported by the success of introductions outside species' natural ranges in areas with contrasting climates (Bijlsma & Haveman, 2007). It is tempting to attribute the range borders of more widely distributed species to ecological factors, but it appears that differences in climate are probably too small to directly explain differences in species composition between the florulas in SEW and NWC (Fig. 5), with the possible exception of the precipitation in August in MA in the SEW flora. On the contrary, the results of a broad-scale genetic analysis of *Rubus* in Europe by Sochor *et al.* (2015) suggest a historical background to the major patterns presented in this paper. A comparison of the maps with the distribution of haplotypes presented by Sochor *et al.* (2015) and our Fig. 1 shows a remarkable coincidence of the border between the NWC and SEC territory and dominance by 'ulmifolius' and 'canescens' haplotypes: the *Rubus* flora in NWC is an 'ulmifolius flora', whereas the *Rubus* flora in SEC can be defined as a 'canescens flora'. *Rubus ulmifolius* and *Rubus canescens* are among the six sexual ancestral species of the European apomictic *Rubus* flora. Based on the distribution of haplotypes, Sochor *et al.* (2015) hypothesized that after the retreat of the Pleistocene ice sheets, *R. ulmifolius* migrated from the Atlantic–Mediterranean area northwards, where it met and hybridized with (among others) *R. canescens* and sexual tetraploid

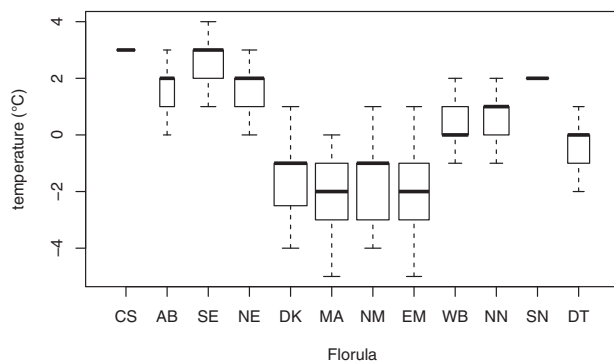


**Figure 3** Stepwise Dufrene–Legendre indicator species for the groups at each branch in the TWINSpan analysis (Dufrene & Legendre, 1997) with significant ( $P \leq 0.01$ ) indicator values  $\geq 20\%$  in parenthesis, until they have reached their maximum indicator value. Species are given in bold where their indicator value reaches a maximum value; species with an asterisk are regionally distributed species (R1 and R2; Table 1). The sequence of branching is given with numbers. Underlined groups are treated in the text.

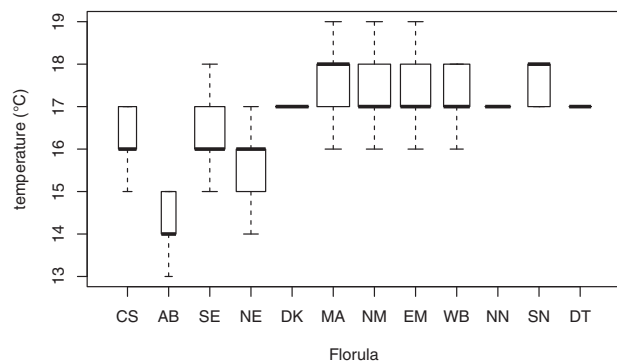
**Figure 4** Species numbers of *Rubus* subg. *Rubus* per distributional area category (Table 1) for each florula (based on distributional data in Kurtto *et al.*, 2010). See Table 2 for the used abbreviations for the florulas.



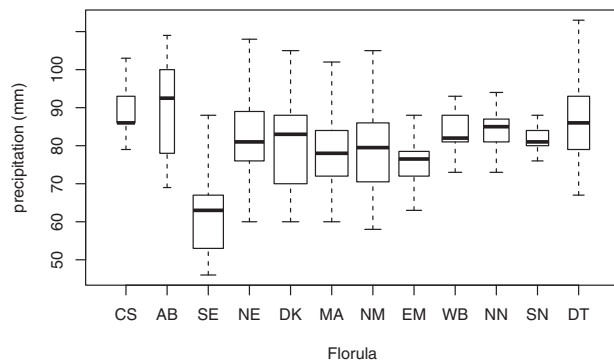
**Minimum temperature in January**



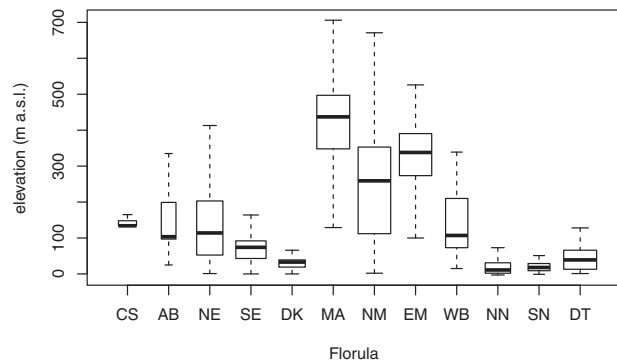
**Maximum temperature in August**



**Mean precipitation in August**



**Mean elevation**



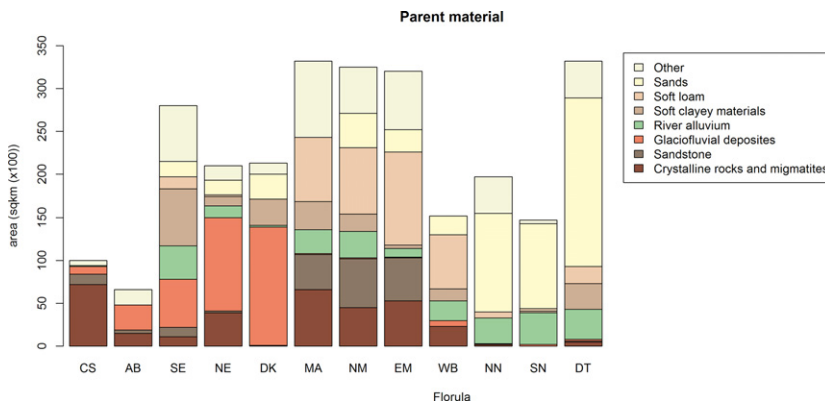
**Figure 5** Box-and-whisker plots of the minimum temperature in January, mean temperature in August, mean precipitation in August, and mean elevation for the OGU per florula (based on data from Muecher *et al.*, 2010). See Table 2 for the used abbreviations for the florulas.

representatives of *Rubus* ser. *Glandulosi* (such as *Rubus hirtus*), emerging from the Balkans. These two geographical descent lines are the basis for the present *Rubus* flora, reflected in the florulas distinguished here.

### Ecological patterns – or history after all?

At a small scale, ecological processes may play an important role in the distributional patterns of *Rubus* species (Heads,





**Figure 6** Parent material in the 12 *Rubus* florulas, as numbers of OGU (based on data from Múcher *et al.*, 2010). See Table 2 for the used abbreviations for the florulas.

2015), and thus in the observed patterns. To examine this, we will discuss some examples: the isolation and the existence of physical barriers, geology and landscape patchiness, and landscape and occupation history.

It is clear that the florulas in BI are physically isolated by large areas which are poor in brambles (Fig. 1a). Both the high splitting levels in the dendrogram (indicating relatively large differences in species composition, Fig. 2) and the lack of transgradient indicator species (i.e. species indicative for several different levels of the classification; Fig. 3) in BI imply that these florulas are effectively isolated. Apparently, the blank areas between the florulas in BI, consisting of larger upland regions, moorlands and agricultural landscapes on calcareous soils (Newton & Randall, 2004), are not only devoid of brambles, but also represent effective dispersal barriers which can be overcome only with great difficulty although bramble seeds are dispersed rather effectively even over large distances (Weber, 1987). Isolation is not only a function of the environment and dispersal capacity: it is also determined by the age of the species. Given the high dispersal capacity of at least most of the bramble species, the florulas represent young to very young species pools (probably < 6000 years; Matzke-Hajek, 1997), which makes the observed pattern at least partly an effect of the particular breeding system in *Rubus* subgenus *Rubus*.

On such a small scale, between the florulas and even more so within the florulas, the distribution of abiotic factors might have a pronounced influence. This is most clear from the difference in parent material between WB on the one hand and DT, SN and NN on the other (all in the NWC flora, Fig. 6); in other florulas, it is somewhat less clear. The scattering of initial groups in MA for instance (Fig. 1b) might be related to edaphic and mesoclimatic factors. This region is characterized by a relatively high mean elevation, and the range in elevation is large, a topography that will arguably result in a wide range of site conditions. It is tempting to also conclude this from the lack of a dominance of one of the types of parent material in MA (Fig. 6), but it could likewise be attributed to the vastness of the region. Another, more genus-specific explanation for the lack of coherent nuclei in parts of MA and SE could be the

distribution of woodland remnants in the landscape. Beijerinck & ter Pelkwijk (1952) observed a difference between *Rubus* species growing exclusively in old forest remnants and typical inhabitants of open agricultural landscapes, a difference that was confirmed by later ecological and phytogeographical studies (Matzke-Hajek, 1997; Bijlsma, 2002, 2004). We hypothesize that this gross difference in species ecology might influence the observed patterns, which is conceivable especially when it is related to the genetic background of the ancestral species and the 'inherited ecology' of the species groups that form the species pools in SEC and NWC respectively. Ecologically, the three ancestral species that gave birth to the *Rubus* species pools of these larger areas can be characterized as 'cool and humid' (*Rubus* ser. *Glandulosi*), 'warm and humid' (*R. ulmifolius*) and 'warm and dry' (*R. canescens*), and their descendants will have inherited these characteristics. As demonstrated by Sochor *et al.* (2015), the Central European flora, coinciding with our SEC territory, is characterized by the two extremes in this, the descendants of *Rubus* ser. *Glandulosi* and those of *R. canescens*, whereas north-west Europe (our NWC territory) has an ecologically more 'even' *Rubus* flora, derived particularly from *R. ulmifolius*. A landscape with cool, humid habitats as well as warm, dry habitats at a similar scale to our OGU could therefore cause the observed patterns, and this is imaginable in upland areas like MA. The hypothesized process might be reinforced by the relatively high percentage of retained sexuality in *Rubus* ser. *Glandulosi* which are typically ancient woodland inhabitants, resulting in high rates of speciation (Šarhanová *et al.*, 2012) and high numbers of young species with small distributional areas. Retained sexuality is regarded as a motor of diversity in apomictic genera through hybridization, as was reported for instance for the *Ranunculus auricomus* aggregate (Hörandl *et al.*, 2009), but also for *Rubus* ser. *Glandulosi*, especially in some montane areas (Šarhanová *et al.*, 2012; Haveman & de Ronde, 2013). A final examination of these hypotheses (through scaling of distributional patterns) is only possible if more species are tested on their provenance.

A third complex of factors influencing the differences in *Rubus* species composition at the scale of florulas might be

landscape history, including land use (Bijlsma & Haveman, 2007; Haveman *et al.*, 2012, 2014). Evidence for landscape history and occupation patterns as factors in the realization of the florulas and initial groups can be derived from the distribution of initial groups, from which we take the well-defined nuclei in SN as an example (Fig. 1b). The first of these is a well-established regional complex north of the Rhine flood-plain, suggesting that the river and flood-plains act as a barrier to the spread of *Rubus* species. South of these flood-plains, two initial groups form two nuclei, a western Brabant nucleus and an eastern Brabant–Limburg nucleus. As described by Haveman *et al.* (2014) in a study of the geographical variation in bramble scrub types, the relatively species-rich western nucleus consists of old agricultural landscapes, whereas the more species-poor eastern nucleus consists of relatively young heathland afforestations and former peat areas. The species in the species-rich areas might consist of vicariant species that originated in these areas, whereas the species in the poor areas are more likely to have migrated into these areas after the landscape became available. In the Netherlands, the species pools in such poor areas are often dominated by taxa from *Rubus* subsect. *Rubus* (Haveman *et al.*, 2014). This might be attributed to the general ecology of the species of this subsection, which prefer acidic soils, and their ability to grow in microclimatically less favourable, i.e. less humid, conditions (Bijlsma, 2004). This is likely to make them the early colonists of young landscapes. Many species in other groups avoid the harsh conditions in such young landscapes, preferring more humid microclimates and better soils.

## CONCLUSIONS

Although ecological factors certainly have their bearing on the observed patterns, as is clear from examples given, the influence of the history of *Rubus* subg. *Rubus* plays an important role through all these factors. This is most striking for the difference between the NWC and SEC territories, which seem to be genetically determined by the dominant influence of *R. ulmifolius* and *R. canescens*, respectively. Studying distributional patterns in the relatively early, expansive stages of a species complex like *Rubus* subg. *Rubus* (Matzke-Hajek, 1997) might prove to be valuable for understanding distributional patterns in older clades, for instance with regard to the expansion and stabilization of species or species groups. This paper is only a start, however, and many questions remain on the relationships between history and ecology in the realization of *Rubus* distributional ranges.

For a better understanding of the realization of the distributional patterns in *Rubus* subg. *Rubus*, more information on the provenance of the apomictic species will prove invaluable. Until now, the ancestral background is known for only a small fraction of the species (Sochor *et al.*, 2015), but the combination with the floristic *Rubus* regions and knowledge of the ecology of species has already provided new insights. Phyto-geographical studies at different scales could show the tenabil-

ity – or otherwise – of the hypothesized causes of the observed patterns in this paper. These patterns might appear to be less capricious than perceived by Gustafsson (1943, p. 157), having their background in the combined history and ecology of the genus after all. Once the species are known, and their provenance is clarified, their caprices might be understood.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Map of the initial TWINSpan groups of *Rubus* occurrences

**Figure S1** Map with the 114 initial twinspace groups based on presence–absence data of species of *Rubus* subgen. *Rubus* in the British Isles, the Netherlands, Germany and Denmark.

## BIOSKETCH

The main research interests of R.H. comprise the taxonomy and ecology (in a wide sense) of the agamic complexes *Rubus* subg. *Rubus* (Rosaceae) and *Hieracium* (Asteraceae), including the evolutionary backgrounds of apomictic species, as well as the phytosociological classification of the vegetation in which these species occur. As a trained phytosociologist, he coordinates the inventory and monitoring of nature conservation values for the Dutch Ministry of Defence.

Author contributions: R.J.B., R.H. and I.R. conceived the ideas; R.H. and I.R. analysed the data; the writing was led by R.H. and J.S.

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