Salix transect of Europe: latitudinal patterns in willow diversity from Greece to arctic Norway

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Abstract

Background

Willows (Salix spp.) are ecosystem "foundation species" that are hosts to large numbers of associated insects. Determining their patterns of distribution across Europe is therefore of interest for understanding the spatial distribution of associated fauna. The aim of this study was to record species composition at multiple sites on a long latitudinal gradient (megatransect) across Europe as a baseline for the future detailed analysis of insect fauna at these sites. In this way we used willow stands as comparable mesocosms in which to study floristic and faunistic changes with latitude across Europe.

New information

To determine spatial patterning of an ecologically important group on a latitudinal gradient across Europe, we sampled willows at the stand level in 42 sites, approximately 100 km apart, from the Aegean (38.8°N) to the Arctic Ocean (70.6°N), but at a similar longitude (21.2 to 26.1 °E). The sites were predominantly lowland (elevations 1 to 556 metres amsl, median = 95 m) and wet (associated with rivers, lakes, drainage ditches or wet meadows).
The median number of willow taxa (species and hybrids) per stand was four, and varied from one to nine. There is a progressive increase in willow diversity from south to north with the median number of taxa per stand in southern Europe being three, and in northern Europe six. A total of 20 willow species were recorded, along with 12 hybrids. The most widespread willow in the transect was *Salix alba* L. (occurring in 20 sites out of 42) followed by *S. triandra* L. (15 sites), *S. caprea* L., *S. phylicifolia* L. (14 sites) and *S. myrsinifolia* Salisb., *Salix ×fragilis* L. (13 sites). Voucher specimens from this study are deposited in the herbaria of the Natural History Museum (BM) and the Royal Botanic Gardens Kew (K). These samples provide a "snapshot" of willow diversity along a latitudinal gradient and an indication of the geographically changing taxonomic diversity that is presented to willow-feeding herbivores across Europe. It is anticipated that further papers will examine the insect fauna collected from these sites as part of this study.

**Keywords**

Biogeography, Bulgaria, ecospace, Estonia, Finland, Greece, Hungary, latitudinal gradient, Latvia, Lithuania, megatranssect, Norway, Poland, Romania, Salicaceae, salicophagy, spatial analysis, willow-feeding insects

**Introduction**

**The ecological significance of the genus *Salix***

Willows (the genus *Salix* L.) are "foundation species" (Ellison et al. 2005) in many wet habitats in the north temperate region. By providing an abundant food-source for many willow-feeding animals (generalists and specialists) they provide the basis for characteristic ecosystems (Brändle and Brandl 2001, Nyman et al. 2007). Willow leaves frequently show signs of leaf damage resulting from herbivore feeding. Herbivores include mammals: rodents (Tahvanainen et al. 1985b), deer, elk and, in the arctic, reindeer (den Herder and Niemelä 2003) and also phytophagous insects, notably Lepidoptera, Coleoptera and Symphyta Hymenoptera (sawflies) (Volf et al. 2015).

Phytophagous Coleoptera have, in addition to generalists that may potentially or sporadically feed on willow, several *Salix* specialists (Häggström and Larsson 1995, Volf et al. 2015) that will cue in on willow phytochemistry (Kolehmainen et al. 1995, Rowell-Rahier 1984a, Rowell-Rahier 1984b, Tahvanainen et al. 1985a). The suborder Symphyta contains a number of highly specialised willow-feeders (Leppänen et al. 2014, Roininen and Tahvanainen 1989) and are particularly abundant in Northern Europe, a fact which has been attributed to the greater number of willows in the north (Kouki et al. 1994). Willows are also host to numerous sap-sucking insects in the Hemiptera, especially aphids (Aphididae) (Blackman and Eastop 2014), psyllids (Psyllidae and Triozidae: Hill and Hodkinson 1995, Hill et al. 1998, Hodkinson et al. 2001, Serbina et al. 2015), leaf-hoppers (Cicadellidae) and spittle-bugs (Cercopidae).
The abundant herbivores further support a predator trophic level, from birds (Sipura 1999), ants and predatory beetles, as well as large numbers of parasitic wasps (Callan 1940). The diversity of willow-feeding herbivores suggests that willows can be considered a "superhost". The concept of superhost is usually applied to hosts of galling insects (de Araújo et al. 2013). Willows do indeed host many galling insects, but also act as a superhost more generally for many guilds of herbivorous insects. In a survey of 25 European tree species, willows had both the greatest number of phytophages and the greatest number of specialist herbivores (Brändle and Brandl 2001).

**Taxonomy of willow**

The genus *Salix* in Europe is usually considered to be a difficult and confusing group for classification and identification (Karrenberg et al. 2002, Meikle 1992, Rechinger 1992, Skvortsov 1999). The main reasons for this are: (1) genetically-based morphological polymorphism, (2) phenotypic plasticity (3) the prevalence of hybridization (4) differences in taxonomic opinion. Although some willows (such as *S. pentandra* L.) are rather uniform, other species are highly variable. *Salix myrsinifolia* is a good example of a species that shows extensive polymorphism: notably in leaf indumentum (hairy to glabrous) and leaf shape (narrowly to broadly elliptical). Although willow polymorphism is rarely formally tested in common garden experiments it is likely that much of this polymorphism is genetically based as different morphs can be found mixed in populations, having developed under the same environmental conditions.

Willows also exhibit phenotypic plasticity, such that even different plants of the same clone can look quite different, particularly if coppiced. Coppice shoots and their leaves can be very different from those of normal branches. However, probably the most remarkable and problematic aspect of willow taxonomy is the great ability for willows to hybridize. Crosses between quite unrelated species occur and many hybrids have a high degree of fertility. A recent study has shown that widespread hybridization is sufficient for chloroplast capture to occur even when species boundaries are maintained (Percy et al. 2014).

Coupled with this is the fact that many hybrids are of economic importance, due to their fast growth, and are widely planted. An example is the widespread hybrid *Salix ×rubra* Huds. (*S. purpurea* L. × *S. viminalis* L.). Another case is *S. ×meyeri* Rostk. ex Willd. (*S. euxina* I.V.Belyaeva × *S. pentandra*) frequently planted as a more easily propagatable alternative to *S. pentandra* (Zinovjev 2011). Sometimes hybrids are so widespread they behave effectively as homoploid hybrid species. An example is the crack willow (*S. ×fragilis*) which is a hybrid between *S. alba* and *S. euxina* (Belyaeva 2009) but which constitutes a characteristic landscape feature over much of Europe and which authors have in the past considered a species (Meikle 1984). Another case where taxonomic treatment varies is *S. bebbiana* Sarg. Here, we follow Skvortsov (Skvortsov 1999) in recognizing *S. bebbiana* as an Eurasian as well as a North American species, despite considerable variation across the range. However, many European authors (e.g. Bennett et al. 1991, Rechinger and Akeroyd 1993) consider the European *S. bebbiana* to represent a separate species, *S. xerophila* Flod. *Salix bebbiana* (=*S. xerophila*) is closely related to the
glabrescent Pale Willow (*S. starkeana* Willd.). However, *S. starkeana* is a comparatively rare willow.

**Geography of willow and stand level sampling**

Species of the genus *Salix* have a long history of being mapped in Europe starting with the monumental *Atlas Florae Europaeae* project (Jalas and Suominen 1976). In turn, these data have been used for detailed analyses of geographic distribution using numerical methods at a continent-wide (Myklestad and Birks 1993) and regional (Myklestad 1993) scale. A more recent resource at the country level (with more up-to-date taxonomy) is that of the Euro+Med Plantbase (Uotila 2011). However, stand composition cannot be easily predicted from occurrences in large grid squares or whole countries. Willows in natural stands across Europe provide a distinctive ecospace for the willow-feeding organisms and understanding the changing stand-level taxonomic composition of the *Salix* species is important for understanding the host choice and distribution of willow herbivores. It is the stand that provides the landscape unit and the ecospace within which host choice operates. Also large-scale mapping projects often exclude hybrids, which may be an important part of natural stands and particularly important as they may possibly form "hybrid bridges" (Floate and Whitham 1993) for herbivorous insects to move between hosts. Furthermore, direct observation of natural willow stands, as in this study, allows the co-collection of herbivores with the collection of voucher herbarium specimens.

The collection of data over a long geographical distance falls into the category of studies now dubbed 'megatransects'. The power and utility of this technique has been amply demonstrated by numerous recent studies. Some recent examples include: Anstett et al. 2014, Baltensperger and Huettkmann 2015, Baltensperger et al. 2015, Barrios-Garcia et al. 2014, Hernández et al. 2007, Huber 2015, Senterre et al. 2004.

**Material and methods**

**Stand selection**

Willow stands were examined during two journeys by road across Europe: Greece to Poland in April 2015 and Poland to Norway in June 2015 (Fig. 1). Sites were selected by driving approximately 100 km north of the previous site and opportunistically locating a suitable habitat in which to find willows, generally a river or low-lying ground. The spacing of sites varied according to logistic and travel constraints. In southern Europe, willows are largely restricted to riparian habitats, but northwards they become commoner in many more habitats. The sampling unit was the willow stand (willow dominated local area). The requirement for a site was that it had a stand of willows that met certain minimum size requirements (at least 100 m in longest linear dimension). A stand of willows is defined as a contiguous area where willows are the dominant vegetation for at least 100 m in linear dimension (as for instance along a river bank). Some stands are very extensive, in which case our sampling was limited to approximately 200 m in largest linear dimension.
Because willow stands differ so much in size, shape and density, it was not practical to impose equal area or grid sampling. Time constraints limited entomological and botanical sampling to 1-2 hours per site. A total of 42 sites were sampled across Europe from south to north (38.8 to 70.6°N) while minimising east-west deviation to between approximately 21.2 and 26.1°E. In addition to the 42 sites, a series of "Supplemental sites" are recorded at which additional insect collections were made but the full site recording process was not carried out.

Data collection

At each site latitude, longitude and altitude data were collected using a hand held Garmin Etrex global positioning system, accurate to within 3 m. Basic notes on the immediate environment were taken to provide a habitat profile of the sites. At each site, the willow diversity was determined and voucher specimens were made in order to validate the species present and to capture variation in species that exhibited considerable phenotypic variation. If the willows were flowering, an attempt was made to collect both male and female individuals. Willow abundance relative to abundance of other woody plants was estimated on a four-point scale: 1) abundant - 30% of individuals or more; 2) common - 10-30%; 3) occasional <10%; 4) rare - one or two individuals only were detected. Samples were processed using standard herbarium techniques and specimens are deposited at the Natural History Museum, London (BM) or at the Royal Botanic Gardens Kew (K). Field identifications were made by QC and DMP. Confirmation, and critical determination of all vouchers, including hybrids, was done by IB. In addition to herbarium samples, samples of leaf tissue were dried using silica gel to permit future DNA-based studies and retained at NHM.
Climate data

As background information, climate data for three contrasting individual sites is given from publically available data sources (Table 2). These use a dataset of mean historical monthly temperature (°Celsius) and rainfall (mm), computed globally for the period 1990-2009 by the Climatic Research Unit (CRU) of University of East Anglia (UEA) and available through the World Bank Climate Portal (World Bank Group 2015).

Table 1.
Latitude, longitude and general details of collecting sites, Salix transect across Europe, April-June 2015.

| SITE | Lat °N | Long °E | Alt (m asl) | date        | country         | river/site                          | habitat                                                                 |
|------|--------|---------|-------------|-------------|----------------|-------------------------------------|------------------------------------------------------------------------|
| 1    | 38.80007 | 22.462900 | 37 | 21-iv-2015 | Greece          | River (R.) Asopos, west of Thermopylae | Bank of fast-flowing rocky river partly shaded by Platanus and with Arundo and Tamarix along the stream bank |
| 2    | 38.902000 | 22.310150 | 33 | 21-iv-2015 | Greece          | R. Sperchios, near Leianokladi, east of Lamia | Bank of wide and rocky river bed in wide floodplain with Tamarix and Rubus etc. |
| 3    | 39.306694 | 22.528323 | 177 | 22-iv-2015 | Greece          | R. Enipeas east of Farsala | By irrigation pumping station, bank of river flowing through agricultural area (fields of wheat). With Cercis, Populus, Rubus etc. |
| 4    | 40.032685 | 22.175437 | 534 | 22-iv-2015 | Greece          | Stream near Kokkinogeia, Thrace | Damp drainage in foothills of the Olympus range with rapidly flowing stream meandering through. Rough grassy terrain with poplar and willow trees. |
| 5    | 41.113317 | 23.273893 | 31 | 23-iv-2015 | Greece          | At R. Struma, near Lithotopos | In mud and shallow water at the edge of a broad and muddy irrigation canal through agricultural land with willows, poplar and Rubus etc. |
| 6    | 41.412468 | 23.318609 | 90 | 23-iv-2015 | Bulgaria      | R. Struma, near Topolinitsa | Bank of river in narrow sandy grazed floodplain between the river and hills. |
| 7    | 42.165622 | 22.998141 | 392 | 24-iv-2015 | Bulgaria      | R. Struma, north of Boboshevo | Sandy riverbank with poplar, ash, willow and elm between rocky side of gorge and sandy flat with small church/shrine. |
| 8    | 42.923989 | 23.810563 | 339 | 24-iv-2015 | Bulgaria      | R. Kalnitza, near Botevgrad | Sandy banks of small polluted river in construction area with Rubus, Urtica, Prunus spinosa etc. |
| 9    | 43.739343 | 23.966755 | 35 | 24-iv-2015 | Bulgaria      | R. Danube, at Oryahovo | River bank by light industrial area at ferry port on the Danube with poplars, tree willows, Phragmites etc. |
| No. | Latitude  | Longitude  | Date | Location | Description |
|-----|-----------|------------|------|----------|-------------|
| 10  | 44.260343 | 23.786781  | 25-iv-2015 | Romania R. Jiu, at Podari, near Craiova | Clayey/sandy bank of river with white mulberry, poplar etc. |
| 11  | 44.961981 | 23.190337  | 25-iv-2015 | Romania R. Jiu, north of Rovinari | Along ditches in middle of ploughed fields with poplars and Phragmites etc. |
| 12  | 45.510676 | 22.737225  | 26-iv-2015 | Romania Meadow near Paucinesti, Carpathian region | Along ditches and in fields in grazed sedgy meadows in agricultural valley. Many plum trees in blossom. |
| 13  | 46.518504 | 21.512839  | 26-iv-2015 | Romania R. Crișul Alb, at Chișineu-Criș | Embanked river through town, grassy slope with thick willow patches. |
| 14  | 46.700744 | 21.312680  | 27-iv-2015 | Hungary R. Fekete-Körös, near Gyula | Bank of 20m wide river, grassy bank with willows and nettles etc. |
| 15  | 47.665648 | 21.261768  | 27-iv-2015 | Hungary Drainage ditches near R. Hortobagy, north-east of Balmazújváros | Broad drainage ditch between road and ploughed field with Phragmites etc. |
| 16  | 48.374291 | 21.725264  | 28-iv-2015 | Hungary R. Bodva, south of Szendrő | Bank of small river running through landscape of forest and agricultural fields. With poplars, Euonymus europaeus and Prunus spinosa etc. |
| 17  | 49.463447 | 21.697255  | 28-iv-2015 | Poland R. Panna, at Tylawa | Bank of small river (7-8 m wide) with stony to muddy bottom and alders, birches and blackthorns etc. |
| 18  | 50.470234 | 22.238372  | 29-iv-2015 | Poland Fields north of Rudnik nad Sanem | Agricultural land by E77 highway with old and young Salix viminalis plantations. Birch, alder and blackthorn common. |
| 19  | 50.673994 | 21.823391  | 29-iv-2015 | Poland R. Łęg, near Gorzyce | Wet meadow near embanked river with Phragmites etc. |
| 20  | 51.775039 | 21.197100  | 30-iv-2015 | Poland R. Pilica, at Warka | Sandy banks of large river (30m wide), banks managed for angling. |
| 20a | 51.775039 | 21.197100  | 11-vi-2015 | Poland R. Pilica, at Warka | Sandy banks of large river (30m wide), banks managed for angling. |
| 21  | 52.693980 | 21.852900  | 12-vi-2015 | Poland R. Bug, near Brok | Rough banks of wide muddy river used for angling with nettle, Rubus, Symphytum etc. |
| 22  | 53.554830 | 22.302990  | 12-vi-2015 | Poland Meadow near R. Biebrza at Wasocz, near Szczuczyn | Wet meadow with Typha, Menyanthes, Comarum etc. |
| 23  | 54.069430 | 23.117450  | 13-vi-2015 | Poland R. Czarna Hańcza, near Sejny on road from Suwalki | Sluggish 12m wide river with waterlilies and lined with Phragmites and Alnus, and adjacent meadow with Cirsium, Dactylorhiza etc. |
| 24  | 54.925830 | 23.774200  | 13-vi-2015 | Lithuania Embankment of River at Kaunas | Dry sandy ridge overlooking wide muddy river |
| No. | Latitude  | Longitude  | Date  | Country | Location Description                                                                 | Notes |
|-----|-----------|------------|-------|---------|-------------------------------------------------------------------------------------|-------|
| 25  | 55.795570 | 24.566780  | 13-vi-2015 | Lithuania | R. Levuo at Karsakiškis near to Panevėžys | Banks of river with birch and willow thicket |
| 26  | 56.711410 | 24.251620  | 14-vi-2015 | Latvia   | Near R. Misa, between Iecava and Kekana | Scrubby meadow beside farm track |
| 27  | 57.749630 | 24.402300  | 14-vi-2015 | Latvia   | R. Salaca short distance inland from Salacgriva | Rough meadow beside river with Alnus, Acer, Prunus etc |
| 28  | 58.422570 | 24.440630  | 15-vi-2015 | Estonia  | Field near Parnu | Rough pasture beside road, invaded by willows |
| 29  | 59.402890 | 24.935770  | 15-vi-2015 | Estonia  | R. Pirita at Lagedi near Tallinn | Banks of small shallow river with abundant aquatic macrophytes, by suspension footbridge |
| 30  | 60.272990 | 24.658430  | 16-vi-2015 | Finland  | Near Lake Bodom, Espoo, Finland | Along ditches near lake, in agricultural landscape of cereal fields and meadows, and aspen/birch groves |
| 31  | 61.099650 | 25.628200  | 16-vi-2015 | Finland  | Drainage flowing into lake Vesijärvi at Paimela near Lahti | Banks of small muddy river 6-7 m wide, in agricultural landscape with abundant aspen and birch |
| 32  | 62.049620 | 26.123690  | 17-vi-2015 | Finland  | Lake near Toivakkia | Forest and lake margin where road crosses end of lake in birch, aspen, pine and spruce forest |
| 33  | 63.015890 | 25.804570  | 17-vi-2015 | Finland  | Near Viitasaari | Along ditches beside forest track at margin of Pinus, Betula forest |
| 34  | 64.050740 | 25.526640  | 17-vi-2015 | Finland  | R. Pyhäjoki, at Joutenniva, south of Haapavesi | Banks of fast flowing rocky river through agricultural landscape with aspens, birches, alders and willows along banks |
| 35  | 64.612870 | 25.538050  | 18-vi-2015 | Finland  | Tributary of the R. Siikajoki near Mankila | Banks of small river (6m wide) and ditches, in agricultural area, with aspen and birch common |
| 36  | 65.328350 | 25.291750  | 18-vi-2015 | Finland  | R. lijoki at mouth, near Kestilä, north of Oulu | Banks of very wide river |
| 37  | 66.249470 | 23.89450   | 19-vi-2015 | Finland  | Small river between Kainuunkylä and Väystäjä | Wet scrub and woodland edge (birch and spruce) with abundant Trollius and other northern herbs |
| 38  | 67.212530 | 24.126290  | 19-vi-2015 | Finland  | Near Vaattojärvi | Between two small rivers flowing into lake with wet areas and ditches around birch, pine forest |
| 39  | 67.911830 | 23.634110  | 19-vi-2015 | Finland  | R. Muonion (Muonionjoki) just south of Muonio | Banks of wide (100-200m), rocky, fast-flowing river |
| No. | Lat. | Long. | Code | Date  | Country | Location | Notes |
|-----|------|-------|------|-------|---------|----------|-------|
| 40  | 68.813800 | 23.266580 | 374 | 20-vi-2015 | Norway | South of Siebe | In birch scrub on heathy ridge above lakeshore in reindeer management area |
| 41  | 69.724870 | 23.405810 | 289 | 20-vi-2015 | Norway | Shores of Lake Trangdalsvatn | Rocky slope down to clear, gravel bottomed lake, surrounded by birch and willow scrub |
| 42  | 70.652340 | 23.665830 | 67  | 21-vi-2015 | Norway | Jansvannet Lake, Hammerfest | Wet areas and margins of birch wood around lake |
| SUPPLEMENTARY SITES | SUPPLEMENTARY SITES | SUPPLEMENTARY SITES | SUPPLEMENTARY SITES | SUPPLEMENTARY SITES | SUPPLEMENTARY SITES | SUPPLEMENTARY SITES |
| i-A | 46.847908 | 8.631778 | 455 | 17-iv-2015 | Switzerland | R. Reuss, near Erstfeld | Gravel-bottomed river near motorway |
| i-C | 39.235768 | 20.523075 | -3  | 19-iv-2015 | Greece | R. Acheron, at Mesopotamo | Drained cultivated fields surrounded by drainage ditches in river delta |
| i-J | 45.447181 | 22.228965 | 236 | 26-iv-2015 | Romania | Near Caransebes | Wet area near highway interchange [no willows collected] |
| i-K | 52.302400 | 5.525235 | 11  | 1-v-2015 | Netherlands | Dyke in Flevoland | Near abundant drainage dykes by sea on reclaimed land. |
| ii-A | 56.411000 | 24.167880 | 33  | 13-vi-2015 | Lithuania | Near Bavska | Planted *S. alba* |
| ii-B | 56.715700 | 24.249580 | 12  | 14-vi-2015 | Latvia | R. Misa | Banks of river |
| ii-C | 59.403880 | 24.932620 | 43  | 15-vi-2015 | Estonia | Lagedi | Rough grassland invaded by shrubs near houses |
| ii-D | 65.324430 | 25.315300 | 6   | 18-vi-2015 | Finland | Kestilä | Margins of birch wood by road |
| ii-E | 66.229570 | 23.785480 | 87  | 19-vi-2015 | Finland | Near Kainuunkylä | Wet ditches by road at edge of birch wood |
| ii-F | 67.934880 | 23.656410 | 238 | 20-vi-2015 | Finland | Muonio | By river |
| ii-G | 68.458680 | 23.425840 | 346 | 20-vi-2015 | Finland | North of Hetta | Rocky area of birch and pine scrub |
| ii-H | 69.343310 | 23.601290 | 317 | 20-vi-2015 | Norway | South of Masi | Birch scrub with juniper |
| ii-I | 69.881290 | 21.731950 | 7   | 22-vi-2015 | Norway | West of Badderen | Rocky scrub by fjord |
| ii-J | 69.512520 | 20.703190 | 13  | 22-vi-2015 | Norway | Near Birtavarre | Rocky scrub by fjord |
Table 2.
Summary climate variables taken from publically available resources (see Methods) for three contrasting sites on the transect: 1 and 42, the most southerly and most northerly sites on map (Fig. 1) together with a middle site, 20, indicated by an arrow on map. Mean monthly temperature (°C) and mean monthly precipitation (mm) are given here. This table is provided as background information on the climatic gradient represented by the megatransect.

|                  | SITE 1 (nr. Thermopylae: 38.80, 22.46) | SITE 20 (Warka: 51.78, 21.20) | SITE 42 (Hammerfest: 70.65, 23.67) |
|------------------|---------------------------------------|-------------------------------|-----------------------------------|
| **Temperature, °C** |                                       |                               |                                   |
| Jan              | 5.31                                  | -0.53                         | -12.51                            |
| Feb              | 7.01                                  | 1.02                          | -12.58                            |
| Mar              | 9.9                                   | 3.58                          | -10.92                            |
| Apr              | 12.41                                 | 8.39                          | -6.08                             |
| May              | 17.8                                  | 14.15                         | 0.21                              |
| Jun              | 22.65                                 | 16.25                         | 6.96                              |
| Jul              | 24.99                                 | 19.4                          | 10.14                             |
| Aug              | 24.76                                 | 18.88                         | 8.73                              |
| Sep              | 20.53                                 | 13.02                         | 3.99                              |
| Oct              | 16.32                                 | 8.65                          | -3.07                             |
| Nov              | 10.76                                 | 2.82                          | -9.08                             |
| Dec              | 5.28                                  | -3.33                         | -11.62                            |
| **Precipitation, mm** |                                       |                               |                                   |
| Jan              | 49.06                                 | 25.28                         | 79.46                             |
| Feb              | 28.5                                  | 29.7                          | 76.35                             |
| Mar              | 43.45                                 | 29.48                         | 73.6                              |
| Apr              | 52.78                                 | 34.13                         | 54.42                             |
| May              | 44.53                                 | 40.14                         | 33.99                             |
| Jun              | 15.56                                 | 65.88                         | 42.68                             |
| Jul              | 24.76                                 | 79.65                         | 53.09                             |
| Aug              | 15.41                                 | 55.42                         | 55.79                             |
| Sep              | 34.78                                 | 53.66                         | 51.47                             |
| Oct              | 42.38                                 | 42.62                         | 82.58                             |
| Nov              | 66.34                                 | 42.03                         | 75.12                             |
| Dec              | 91.11                                 | 27.17                         | 87.93                             |
Results

Sites

Table 1 shows the 42 sites recorded in this study as well as details of further "supplemental sites" where insect collections were made but without the level of sampling accorded to the main sites. The geographical distribution of sites is shown in Fig. 1. The supplemental sites will not be discussed here but their basic details are given, as subsequent papers on the insects sampled along the transect may refer to them. The latitudinal variation provides an enormous variation in climate. Table 2 shows summary climatic statistics for three sites: the most southerly, the most northerly and a central site (Poland).

As can be seen from Table 1, site elevations varied from 1 m to 556 m above mean sea level (amsl), with a median of 95 m. Because the sampling was predominantly in lowlands, the diversity of mountain or upland willows was not captured in this study, nor was it intended to be. Instead we capture the diversity of large stands of willow found in wet low-lying areas, which from an "insect eye view" or "insect chemosensory perspective" represent the largest areas of willow resource in the landscape, generally associated with landscape features such as rivers, lakes, drainage ditches or poorly drained meadows.

Willows

Table 3 lists the total of 20 willow species that were recorded, together with the 12 hybrids. For each taxon the total number of sites (out of 42) is given. In this transect, the most widespread willow is Salix alba, which occurs in 20 sites (out of 42). This species is followed by S. triandra (with 15 sites), S. caprea, S. phylicifolia (with 14 sites each) and by S. myrsinifolia, S. ×fragilis (with 13 sites).

| Taxon                          | Number of sites on transect | Species or hybrid | Hybrid binomial (if available) |
|-------------------------------|-----------------------------|-------------------|--------------------------------|
| S. alba L.                    | 20                          | sp                | -                              |
| S. amplexicaulis Bory & Chaub.| 4                           | sp                | -                              |
| S. aurita L.                  | 6                           | sp                | -                              |
| S. bebbiana Sarg.             | 7                           | sp                | -                              |
| S. caprea L.                  | 14                          | sp                | -                              |
| S. cinerea L.                 | 9                           | sp                | -                              |
| S. eleagnos Scop.             | 1                           | sp                | -                              |
| S. euxina I.V.Belyaeva         | 4                           | sp                | -                              |
| S. glauca L.                  | 5                           | sp                | -                              |
| Species                        | Count | Type | Hybrid                                      |
|-------------------------------|-------|------|---------------------------------------------|
| S. gmelinii Pall.             | 1     | sp   | -                                           |
| S. hastata L.                 | 5     | sp   | -                                           |
| S. lanata L.                  | 1     | sp   | -                                           |
| S. lapponum L.                | 4     | sp   | -                                           |
| S. myrsinifolia Salisb.       | 13    | sp   | -                                           |
| S. pentandra L.               | 7     | sp   | -                                           |
| S. phylicifolia L.            | 14    | sp   | -                                           |
| S. purpurea L.                | 8     | sp   | -                                           |
| S. silesiaca Willd.           | 1     | sp   | -                                           |
| S. triandra L.                | 15    | sp   | -                                           |
| S. viminalis L.               | 9     | sp   | -                                           |
| S. alba × S. pentandra        | 1     | h    | S. ×ehrhartiana G.Mey                       |
| S. aurita × S. myrsinifolia   | 1     | h    | S. ×coriacea J.Forbes                       |
| S. cinerea × S. aurita        | 1     | h    | S. ×multinervis Döll                        |
| S. cinerea × S. triandra      | 1     | h    | S. ×krausei Andersson                      |
| S. euxina × S. pentandra      | 1     | h    | S. ×meyeriana Rostk. ex Willd.              |
| S. myrtilloides × S. glauca   | 1     | h    | -                                           |
| S. phylicifolia × S. myrsinifolia | 2   | h    | S. ×tetrapla Walk.                         |
| S. purpurea × S. viminalis    | 8     | h    | S. ×rubra Huds.                             |
| S. triandra × S. viminalis    | 3     | h    | S. ×mollissima Sm.                          |
| S. viminalis × S. cinerea     | 1     | h    | S. ×smithiana Willd.                       |
| S. alba × S. euxina           | 13    | h    | S. ×fragilis L.                             |
| S. ×fragilis × S. triandra    | 1     | h    | S. ×alopecuroides Tausch                   |

Site diversity (Table 4) was modest with the overall median number of willow taxa (species and hybrids) per stand being four. However, the stands showed a progressive increase in diversity from south to north with the median number of willow taxa per stand in southern Europe (Greece, Bulgaria, Romania) being three; the median number in central Europe (Hungary, Poland) being five; and the median number in northern Europe (Lithuania, Latvia, Estonia, Finland and Norway) being six.
Table 4.
Salix collections per site, trans-Europe transect, April-June 2015. Frequency in stands is given in brackets as: A=abundant, C=common, O=occasional, R=rare (see Methods under Data Collection).

| Site | Country | No. of taxa | Willow species and hybrids |
|------|---------|-------------|-----------------------------|
| 1    | Greece  | 3           | S. alba (O), S. eleagnos (O), S. purpurea (C) |
| 2    | Greece  | 3           | S. alba (C), S. amplexicaulis (C), S. triandra (O) |
| 3    | Greece  | 1           | S. alba (C) |
| 4    | Greece  | 3           | S. alba (C), S. amplexicaulis (C), S. triandra (O) |
| 5    | Greece  | 2           | S. alba (C), S. triandra (O) |
| 6    | Bulgaria| 4           | S. alba (C), S. amplexicaulis (C), S. purpurea × S. viminalis (O), S. ×fragilis (C) |
| 7    | Bulgaria| 4           | S. alba (C), S. amplexicaulis (C), S. euxina (O), S. triandra (O) |
| 8    | Bulgaria| 2           | S. alba (O), S. euxina (C) |
| 9    | Bulgaria| 1           | S. alba (A) |
| 10   | Romania | 1           | S. alba (A) |
| 11   | Romania | 3           | S. alba (C), S. purpurea × S. viminalis (C), S. triandra × S. viminalis (O) |
| 12   | Romania | 3           | S. cinerea (C), S. silesiaca (C), S. ×fragilis (O) |
| 13   | Romania | 4           | S. alba × S. pentandra (O), S. purpurea (O), S. triandra (O), S. ×fragilis (A) |
| 14   | Hungary | 7           | S. alba (O), S. euxina (O), S. purpurea × S. viminalis (O), S. triandra (C), S. triandra × S. viminalis (C), S. viminalis (O), S. ×fragilis (O) |
| 15   | Hungary | 4           | S. alba (O), S. cinerea (C), S. purpurea × S. viminalis (C), S. ×fragilis (C) |
| 16   | Hungary | 5           | S. alba (C), S. aurita (O), S. purpurea (C), S. triandra (C), S. viminalis (O) |
| 17   | Poland  | 3           | S. caprea (R), S. euxina (C), S. purpurea (C) |
| 18   | Poland  | 5           | S. aurita (O), S. cinerea (C), S. purpurea × S. viminalis (O), S. triandra (O), S. viminalis (C) |
| 19   | Poland  | 6           | S. alba (O), S. cinerea (C), S. purpurea × S. viminalis (C), S. triandra × S. viminalis (C), S. ×fragilis (C) |
| 20   | Poland  | 6           | S. alba (R), S. gmelinii (O), S. purpurea (C), S. triandra (C), S. viminalis (O), S. ×fragilis (A) |
| 21   | Poland  | 7           | S. alba (O), S. cinerea (R), S. cinerea × triandra (R), S. purpurea (C), S. triandra (A), S. viminalis (C), S. ×fragilis (C) |
| 22   | Poland  | 2           | S. bebbiana (A), S. ×fragilis (C) |
| Country  | Region | S. species combinations |
|----------|--------|-------------------------|
| Poland   | 3      | S. bebbiana (A), S. myrsinifolia (R), S. pentandra (O) |
| Lithuania| 7      | S. alba (R), S. caprea (A), S. purpurea (C), S. triandra (C), S. viminalis (O), S. viminalis × S. cinerea (O), S. ×fragilis (O) |
| Lithuania| 7      | S. alba (O), S. cinerea (O), S. myrsinifolia (A), S. pentandra (C), S. purpurea (C), S. triandra (O), S. ×fragilis (C) |
| Latvia   | 9      | S. alba (O), S. bebbiana (O), S. caprea (O), S. cinerea (A), S. myrsinifolia (O), S. pentandra (C), S. purpurea × S. viminalis (O), S. triandra (O), S. viminalis (O) |
| Latvia   | 5      | S. bebbiana (O), S. myrsinifolia (A), S. triandra (O), S. viminalis (C), S. ×fragilis (C) |
| Estonia  | 6      | S. caprea (C), S. cinerea × aurita (R), S. myrsinifolia (A), S. phylicifolia (C), S. triandra (O), S. ×fragilis (O) |
| Estonia  | 4      | S. myrsinifolia (A), S. phylicifolia × S. myrsinifolia (R), S. purpurea × S. viminalis (C), S. ×fragilis × S. triandra (R) |
| Finland  | 5      | S. aurita (R), S. caprea (R), S. cinerea (R), S. pentandra (R), S. phylicifolia (A) |
| Finland  | 6      | S. cinerea (O), S. euxina × S. pentandra (O), S. myrsinifolia (A), S. pentandra (O), S. phylicifolia (O), S. phylicifolia × S. myrsinifolia (C) |
| Finland  | 6      | S. aurita (C), S. bebbiana (O), S. caprea (O), S. myrsinifolia (A), S. pentandra (C), S. phylicifolia (C) |
| Finland  | 4      | S. aurita (O), S. caprea (C), S. myrsinifolia (C), S. phylicifolia (A) |
| Finland  | 3      | S. caprea (O), S. pentandra (R), S. phylicifolia (A) |
| Finland  | 4      | S. aurita (R), S. caprea (O), S. aurita × myrsinifolia (R), S. phylicifolia (A) |
| Finland  | 2      | S. myrsinifolia (O), S. phylicifolia (A) |
| Finland  | 4      | S. caprea (O), S. hastata (O), S. myrsinifolia (O), S. phylicifolia (A) |
| Finland  | 6      | S. caprea (R), S. glauca (A), S. hastata (O), S. lapponum (R), S. myrtilloides × S. glauca (R), S. phylicifolia (A) |
| Finland  | 6      | S. bebbiana (R), S. caprea (C), S. glauca (O), S. hastata (O), S. lapponum (A), S. phylicifolia (A) |
| Norway   | 2      | S. glauca (O), S. phylicifolia (A) |
| Norway   | 7      | S. bebbiana (O), S. caprea (C), S. glauca (C), S. hastata (O), S. lapponum (C), S. myrsinifolia (C), S. phylicifolia (C) |
| Norway   | 7      | S. caprea (O), S. glauca (C), S. hastata (C), S. lanata (R), S. lapponum (C), S. myrsinifolia (C), S. phylicifolia (C) |

SUPPLEMENTAL SITES
Three stands (in Greece and Bulgaria) had just one willow taxon and in all cases this was *S. alba*. One stand (site 26 in Latvia) had the maximum recorded number of taxa, nine per stand, while six sites (in Hungary, Poland, Lithuania and Norway) had seven taxa. Finally, Table 5 lists the voucher specimens collected.

### Table 5.
*Salix* collections (collectors: Quentin Cronk and Diana Percy), trans-Europe transect, April-June 2015. Accession number is collector-site-number (e.g. QCDP-A-1; QCDP-19-2). Sex is recorded as m=male, f=female, v=vegetative, b=in bud.

| Site | No. | Country  | Sex | Name                      | Notes                                      |
|------|-----|----------|-----|---------------------------|--------------------------------------------|
| A-i  | 2   | Switzerland |    | *S. eleagnos, S. purpurea × S. viminalis* |                                            |
| C-i  | 1   | Greece    |     | *S. alba*                 |                                            |
| J-i  | 2   | Romania   |     | *S. cinerea [not collected], S. ×fragilis [not collected]* |                                            |
| K-i  | 1   | Netherlands |   | *S. caprea*               |                                            |
| C-ii | 7   | Estonia   |     | *S. bebbiana, S. cinerea, S. euxina × S. pentandra, S. myrsinifolia, S. phylicifolia, S. ×fragilis, S. ×fragilis × S. triandra* |                                            |
| D-ii | 3   | Finland   |     | *S. aurita × S. cinerea, S. caprea, S. myrsinifolia × S. phylicifolia* |                                            |
| E-ii | 2   | Finland   |     | *S. bebbiana, S. lapponum* |                                            |
| H-ii | 5   | Norway    |     | *S. glauca, S. hastata, S. lapponum, S. myrsinifolia, S. phylicifolia* |                                            |
| I-ii | 3   | Norway    |     | *S. caprea, S. hastata, S. myrsinifolia* |                                            |
|   | Country     | Sex | Species               | Description                                                  |
|---|-------------|-----|-----------------------|--------------------------------------------------------------|
| 4 | 2b Greece   | f   | *S. amplexicaulis*    | Shrub to 4m                                                  |
| 4 | 3 Greece    | m   | *S. triandra* (var.) | Shrub to 4m                                                  |
| 5 | 1a Greece   | m   | *S. alba*             | Grey-barked tree to 10m                                      |
| 5 | 1b Greece   | f   | *S. alba*             | Grey-barked tree to 10m                                      |
| 5 | 2a Greece   | m   | *S. triandra* (var.) | Small shrub to 4m                                           |
| 5 | 2b Greece   | f   | *S. triandra*         | Small shrub to 4m                                           |
| 6 | 1a Bulgaria | m   | *S. alba*             | Tall grey barked tree to 15m                                 |
| 6 | 1b Bulgaria | f   | *S. alba*             | Tall grey barked tree to 15m                                 |
| 6 | 2 Bulgaria  | f   | *S. ×fragilis*        | Small tree to 6m                                            |
| 6 | 3 Bulgaria  | m   | *S. purpurea × S. viminalis* | Small shrub with reddish twigs, 2m |
| 6 | 4 Bulgaria  | f   | *S. amplexicaulis*    | Small shrub 2m                                               |
| 7 | 1a Bulgaria | m   | *S. amplexicaulis*    |                                                            |
| 7 | 1b Bulgaria | f   | *S. amplexicaulis*    |                                                            |
| 7 | 2a Bulgaria | m   | *S. triandra*         |                                                            |
| 7 | 2b Bulgaria | f   | *S. triandra*         |                                                            |
| 7 | 3a Bulgaria | m   | *S. alba*             |                                                            |
| 7 | 3b Bulgaria | f   | *S. triandra*         |                                                            |
| 7 | 4a Bulgaria | m   | *S. euxina*           |                                                            |
| 7 | 4b Bulgaria | f   | *S. euxina*           |                                                            |
| 8 | 1a Bulgaria | m   | *S. euxina*           |                                                            |
| 8 | 1b Bulgaria | f   | *S. euxina*           |                                                            |
| 8 | 2 Bulgaria  | m   | *S. alba*             |                                                            |
| 9 | 1a Bulgaria | m   | *S. alba*             | Tall trees to 30m and possibly planted. Similar trees are very common along the banks of the Danube. |
| 9 | 1b Bulgaria | f   | *S. alba*             | Tall trees to 30m and possibly planted. Similar trees are very common along the banks of the Danube. |
| 10| 1a Romania  | m   | *S. alba*             | Large tree to 20m                                           |
| 10| 1b Romania  | f   | *S. alba*             | Large tree to 20m                                           |
| 11| 1 Romania   | m   | *S. alba*             |                                                            |
| 11| 2 Romania   | f   | *S. purpurea × S. viminalis* |                                                            |
| 11| 3 Romania   | f   | *S. triandra × S. viminalis* |                                                            |
| 12| 1a Romania  | m   | *S. silesiaca*        | Shrub, twigs ridged under bark                               |
| 12| 1b Romania  | f   | *S. cinerea*          | Tree to 10m, twigs ridged under bark                         |
| 12| 2 Romania   | m   | *S. ×fragilis* (towards *S. euxina*?) | Glabrous tree to 10m                                        |
| 13| 1a Romania  | m   | *S. ×fragilis*        | Small coppiced growth by river                               |
| No. | Area    | Gender | Species               | Description                        |
|-----|---------|--------|-----------------------|-----------------------------------|
| 13  | Romania | f      | S. alba × S. pentandra| Small coppiced growth by river    |
| 13  | Romania | f      | S. triandra           |                                   |
| 13  | Romania | f      | S. purpurea           |                                   |
| 14  | Hungary | m      | S. triandra × S. viminalis | To 5m                          |
| 14  | Hungary | f      | S. triandra           | To 5m                            |
| 14  | Hungary | m      | S. euxina             | To 8m                            |
| 14  | Hungary | f      | S. ×fragilis          | To 8m                            |
| 14  | Hungary | f      | S. viminalis          | To 6m                            |
| 14  | Hungary | f      | S. purpurea × S. viminalis | To 2m                        |
| 14  | Hungary | f      | S. alba               | To 10m                           |
| 15  | Hungary | m      | S. cinerea            | Shrub to 4m with striae          |
| 15  | Hungary | f      | S. cinerea            | Shrub to 4m with striae          |
| 15  | Hungary | m      | S. purpurea × S. viminalis |                   |
| 15  | Hungary | f      | S. ×fragilis          |                                   |
| 15  | Hungary | m      | S. alba               | Small tree                       |
| 15  | Hungary | f      | S. alba               | Large tree, branches weeping     |
| 16  | Hungary | m      | S. alba               |                                   |
| 16  | Hungary | m      | S. triandra           |                                   |
| 16  | Hungary | f      | S. purpurea           |                                   |
| 16  | Hungary | v      | S. viminalis          |                                   |
| 16  | Hungary | f      | S. aurita             |                                   |
| 16  | Hungary | m      | S. alba               |                                   |
| 17  | Poland  | m      | S. euxina             |                                   |
| 17  | Poland  | f      | S. euxina             |                                   |
| 17  | Poland  | f      | S. purpurea           |                                   |
| 17  | Poland  | f      | S. caprea             |                                   |
| 18  | Poland  | f      | S. viminalis          | Young coppice plantation         |
| 18  | Poland  | m      | S. aurita             | Shrub to 4m weakly striate       |
| 18  | Poland  | f      | S. viminalis          | Shrub to 4m                      |
| 18  | Poland  | f      | S. purpurea × S. viminalis |                   |
| 18  | Poland  | f      | S. triandra           |                                   |
| 18  | Poland  | f      | S. purpurea × S. viminalis |                   |
| 19  | Poland  | m      | S. ×fragilis          | Abundant at this site            |
| 19  | Poland  | f      | S. purpurea × S. viminalis |                   |
| No. | Location | Sex | Species | Description
|-----|----------|------|---------|-------------
| 19  | Poland   | f    | S. viminalis |  
| 19  | Poland   | f    | S. triandra × S. viminalis |  
| 19  | Poland   | m    | S. alba | Occasional at this site  
| 19  | Poland   | f    | S. cinerea |  
| 20  | Poland   | m    | S. ×fragilis |  
| 20  | Poland   | f    | S. purpurea |  
| 20  | Poland   | m    | S. triandra |  
| 20  | Poland   | f    | S. triandra |  
| 20  | Poland   | f    | S. viminalis |  
| 20  | Poland   | f    | S. gmelinii |  
| 20a | Poland   | f    | S. triandra | small tree/shrub to 4m  
| 20a | Poland   | f    | S. triandra | small tree/shrub to 4m  
| 20a | Poland   | f    | S. ×fragilis | to 40m  
| 20a | Poland   | f    | S. alba | to 30m  
| 20a | Poland   | f    | S. ×fragilis |  
| 20a | Poland   | v    | S. gmelinii | large open sprawling shrubs to 5m  
| 20a | Poland   | v    | S. viminalis | shrub to 5m  
| 20a | Poland   | v    | S. purpurea | shrub to 4m  
| 20a | Poland   | v    | S. triandra |  
| 20a | Poland   | v    | S. ×fragilis | very glossy green upper sides to leaves  
| 21  | Poland   | m    | S. triandra | small trees or multi-stemmed shrubs to 10m high ×20m across  
| 21  | Poland   | f    | S. triandra |  
| 21  | Poland   | f    | S. ×fragilis | small bush to large tree to 20m  
| 21  | Poland   | v    | S. ×fragilis |  
| 21  | Poland   | f    | S. purpurea | shrub to 4m  
| 21  | Poland   | f    | S. cinerea |  
| 21  | Poland   | f    | S. cinerea × S. triandra | shrub to 3m  
| 21  | Poland   | v    | S. ×fragilis |  
| 21  | Poland   | f    | S. viminalis | bush to 6m  
| 21  | Poland   | f    | S. alba | tree to 30m  
| 21  | Poland   | f    | S. ×fragilis |  
| 21  | Poland   | f    | S. triandra |  
| 21  | Poland   | v    | S. purpurea |  
| 22  | Poland   | f    | S. ×fragilis | 15m medium tree  
| 22  | Poland   | v    | S. bebbiana | low bushes 2-3m with abundant cercopid spittle bugs and willow feeding scaraboid beetle  
| 22  | Poland   | v    | S. ×fragilis | shrub to 3m  

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| Page | Country | Type | Species | Description |
|------|---------|------|---------|-------------|
| 22 4 | Poland  | v    | S. ×fragilis | sapling 1.5m |
| 22 5 | Poland  | v    | S. bebbiana  | |
| 23 1 | Poland  | v    | S. bebbiana  | blue/grey-green foliage, 2-5m high |
| 23 2 | Poland  | f    | S. pentandra | trees all multistemmed (c. 4), to 15m, rugged bark, foliage with somewhat weeping habit |
| 23 3 | Poland  | v    | S. myrsinifolia | a few low bushes in the meadow with yellow-green foliage and some red pigmentation on stems, 1-1.5m |
| 23 4 | Poland  | v    | S. bebbiana  | |
| 23 5 | Poland  | v    | S. bebbiana  | |
| 24 1 | Lithuania| v    | S. caprea    | large shrub to 10m, planted? |
| 24 2 | Lithuania| v    | S. purpurea  | bushes to 2m |
| 24 3 | Lithuania| v    | S. viminalis × S. cinerea | small sapling, no striae |
| 24 4 | Lithuania| f    | S. ×fragilis | medium tree to 20m |
| 24 5 | Lithuania| v    | S. viminalis  | |
| 24 6 | Lithuania| v    | S. purpurea  | |
| 24 7 | Lithuania| m    | S. triandra  | |
| 24 8 | Lithuania| f    | S. triandra  | |
| 24 9 | Lithuania| f    | S. ×fragilis | |
| 24 12 | Lithuania| f    | S. alba      | |
| 25 1 | Lithuania| v    | S. purpurea  | |
| 25 2 | Lithuania| f    | S. alba      | |
| 25 3a | Lithuania| m    | S. pentandra | |
| 25 3b | Lithuania| f    | S. pentandra | |
| 25 4 | Lithuania| f    | S. triandra  | |
| 25 5 | Lithuania| v    | S. myrsinifolia | |
| 25 6 | Lithuania| v    | S. myrsinifolia | |
| 25 7 | Lithuania| v    | S. myrsinifolia | |
| 25 8 | Lithuania| v    | S. myrsinifolia | |
| 25 9 | Lithuania| f    | S. cinerea   | |
| 25 10 | Lithuania| v    | S. triandra  | |
| 25 11 | Lithuania| v    | S. ×fragilis | 5m h ×6m w |
| 26 1 | Latvia   | v    | S. cinerea   | small trees to 8m |
| 26 2 | Latvia   | m    | S. triandra  | |
| 26 3 | Latvia   | m    | S. pentandra | |
| 26 4 | Latvia   | v    | S. bebbiana  | |
| 26 5 | Latvia   | v    | S. purpurea × viminalis | |
| 26 6 | Latvia   | v    | S. bebbiana  | |
|   |   | Country | Sex | Species         |
|---|---|---------|-----|-----------------|
| 26 7 | Latvia | v | S. *viminalis* |
| 26 8 | Latvia | v | S. *myrsinifolia* |
| 26 9 | Latvia | f | S. *myrsinifolia* |
| 26 10 | Latvia | v | S. *caprea* |
| 26 11 | Latvia | v | S. *alba* |
| 26 12 | Latvia | v | S. *purpurea* × S. *viminalis* |
| 26 13 | Latvia | f | S. *triandra* |
| 26 14 | Latvia | f | S. *triandra* |
| 27 1 | Latvia | f | S. *myrsinifolia* | subglaubrous shrubs to 5m |
| 27 2 | Latvia | v | S. *bebbiana* | small bush with striae |
| 27 3 | Latvia | v | S. *viminalis* |
| 27 4 | Latvia | f | S. *triandra* |
| 27 5 | Latvia | v | S. *×fragilis* |
| 28 1a | Estonia | m | S. *triandra* | wide bush, 3m h ×4m w |
| 28 1b | Estonia | f | S. *triandra* |
| 28 2 | Estonia | v | S. *×fragilis* | young plants to 4m |
| 28 3 | Estonia | v | S. *×fragilis* |
| 28 4 | Estonia | f | S. *cinerea* × S. *aurita* | bush 3 ×4m, with striae |
| 28 5 | Estonia | v | S. *caprea* | vigorous bush to 4m, no striae |
| 28 6 | Estonia | f | S. *myrsinifolia* | bush to 2m |
| 28 7 | Estonia | f | S. *myrsinifolia* |
| 28 8 | Estonia | v | S. *phylicifolia* |
| 28 9 | Estonia | v | S. *myrsinifolia* |
| 29 1 | Estonia | v | S. *purpurea* × S. *viminalis* |
| 29 2 | Estonia | v | S. *×fragilis* × S. *triandra* |
| 29 3 | Estonia | f | S. *myrsinifolia* |
| 29 4 | Estonia | v | S. *myrsinifolia* |
| 29 5 | Estonia | v | S. *phylicifolia* × S. *myrsinifolia* |
| 29 6 | Estonia | f | S. *myrsinifolia* |
| 30 1a | Finland | b | S. *phylicifolia* | shrub to 4m |
| 30 1b | Finland | f | S. *phylicifolia* |
| 30 2 | Finland | f | S. *pentandra* |
| 30 3 | Finland | v | S. *aurita* | shrub to 4m, weakly striate |
| 30 4 | Finland | v | S. *caprea* | tree straight-trunked to 15m |
| 30 5a | Finland | b | S. *phylicifolia* |
| 30 5b Finland | f | S. phylicifolia |
| 30 6 Finland | v | S. cinerea | large shrub, no striae |
| 30 7a Finland | b | S. phylicifolia |
| 30 7b Finland | v | S. phylicifolia |
| 31 1 Finland | f | S. myrsinifolia | small shrub to 2m |
| 31 2 Finland | v | S. phylicifolia × S. myrsinifolia |
| 31 3 Finland | f | S. myrsinifolia |
| 31 4 Finland | v | S. phylicifolia |
| 31 5 Finland | v | S. euxina × S. pentandra | very small plants 1-2m |
| 31 6 Finland | v | S. myrsinifolia |
| 31 7 Finland | f | S. cinerea |
| 31 8 Finland | f | S. myrsinifolia | small plants 1-2m |
| 31 9 Finland | f | S. myrsinifolia |
| 31 10 Finland | f | S. myrsinifolia |
| 31 11 Finland | m | S. pentandra |
| 32 1 Finland | f | S. pentandra | to 4m |
| 32 2 Finland | v | S. aurita | to 2m |
| 32 3 Finland | f | S. myrsinifolia | to 2m |
| 32 4 Finland | f | S. phylicifolia | to 2m |
| 32 5 Finland | f | S. myrsinifolia | to 4m |
| 32 6 Finland | f | S. phylicifolia | to 3m |
| 32 7 Finland | f | S. myrsinifolia |
| 32 8 Finland | f | S. myrsinifolia |
| 32 9 Finland | v | S. bebbiana |
| 32 10 Finland | v | S. caprea |
| 33 1 Finland | v | S. caprea | small shrubs to 3m |
| 33 2 Finland | f | S. aurita | to 2m |
| 33 3 Finland | f | S. myrsinifolia | to 4m |
| 33 4 Finland | f | S. phylicifolia | to 3m |
| 34 1 Finland | f | S. phylicifolia | to 3m |
| 34 2 Finland | v | S. caprea | to 3m |
| 34 3 Finland | m | S. pentandra | c. 4m |
| 34 4 Finland | f | S. phylicifolia |
| 34 5 Finland | f | S. phylicifolia |
| 35 1 Finland | v | S. caprea | small tree to 4m |
| 35 2 Finland | v | S. aurita × S. myrsinifolia | shrub to 1.5m |
| Page | Country | Sex | Species                  | Description          |
|------|---------|-----|--------------------------|----------------------|
| 35   | Finland | f   | *S. aurita*              | old tree, 8m high    |
| 35   | Finland | f   | *S. phylicifolia*        | bushes to 6m         |
| 35   | Finland | f   | *S. phylicifolia*        |                      |
| 35   | Finland | f   | *S. phylicifolia*        |                      |
| 35   | Finland | f   | *S. phylicifolia*        |                      |
| 36   | Finland | f   | *S. phylicifolia*        | to 4m                |
| 36   | Finland | f   | *S. myrsinifolia*        | to 6m                |
| 36   | Finland | f   | *S. phylicifolia*        |                      |
| 37   | Finland | f   | *S. phylicifolia*        | shrub 1-3m           |
| 37   | Finland | m   | *S. hastata*             | 5m high spindly tree |
| 37   | Finland | v   | *S. caprea*              | 3-4m high            |
| 37   | Finland | m   | *S. hastata*             | in wet heathy scrub, less than 75cm |
| 37   | Finland | f   | *S. hastata*             |                      |
| 37   | Finland | f   | *S. myrsinifolia*        |                      |
| 38   | Finland | f   | *S. phylicifolia*        | to 3m                |
| 38   | Finland | f   | *S. glauca*              | to 1.5m              |
| 38   | Finland | f   | *S. glauca*              |                      |
| 38   | Finland | f   | *S. hastata*             | 1-1.5m               |
| 38   | Finland | m   | *S. phylicifolia*        |                      |
| 38   | Finland | v   | *S. caprea*              |                      |
| 38   | Finland | f   | *S. hastata*             |                      |
| 38   | Finland | f   | *S. myrtilloides × S. glauca* |              |
| 38   | Finland | v   | *S. caprea*              |                      |
| 38   | Finland | f   | *S. lapponum*            |                      |
| 39   | Finland | f   | *S. phylicifolia*        | bushes to 2m         |
| 39   | Finland | f   | *S. hastata*             | shrub to 1.5m        |
| 39   | Finland | f   | *S. hastata*             |                      |
| 39   | Finland | f   | *S. phylicifolia*        |                      |
| 39   | Finland | f   | *S. bebbiana*            |                      |
| 39   | Finland | f   | *S. hastata*             |                      |
| 39   | Finland | m   | *S. phylicifolia*        |                      |
| 39   | Finland | m   | *S. hastata*             |                      |
| 39   | Finland | m   | *S. hastata*             |                      |
| 39   | Finland | v   | *S. caprea*              |                      |
| 39   | Finland | v   | *S. caprea*              |                      |
| 39   | Finland | f   | *S. glauca*              |                      |
|   |   |   |   |
|---|---|---|---|
| 39 | 13a | Finland | m | S. glauca |
| 39 | 13b | Finland | f | S. glauca |
| 39 | 14 | Finland | f | S. lapponum |
| 39 | 15 | Finland | f | S. lapponum |
| 40 | 1a | Norway | m | S. phylicifolia |
| 40 | 1b | Norway | f | S. phylicifolia |
| 40 | 2 | Norway | b | S. glauca |
| 40 | 4 | Norway | m/f | S. phylicifolia | catkins bisexual |
| 40 | 5 | Norway | f | S. phylicifolia |
| 40 | 6 | Norway | f | S. phylicifolia |
| 41 | 1 | Norway | f | S. lapponum | grey bush willow 1-1.5m |
| 41 | 2 | Norway | b | S. glauca |
| 41 | 3 | Norway | f | S. glauca |
| 41 | 4 | Norway | f | S. phylicifolia | green bush willow 1-2m |
| 41 | 5 | Norway | f | S. phylicifolia |
| 41 | 6 | Norway | v | S. hastata | dwarf willow |
| 41 | 7 | Norway | v | S. glauca |
| 41 | 8 | Norway | f | S. myrsinifolia |
| 41 | 9 | Norway | f | S. myrsinifolia | 5m high with slender dark grey stems |
| 41 | 10 | Norway | m | S. myrsinifolia |
| 41 | 11 | Norway | f | S. bebbiana |
| 41 | 12 | Norway | v | S. caprea | 5m high with slender pale grey stems |
| 42 | 1a | Norway | v | S. lapponum |
| 42 | 1b | Norway | f | S. lapponum | shrub 1-1.5m |
| 42 | 2 | Norway | m | S. glauca | shrub c. 1m |
| 42 | 3a | Norway | m | S. glauca | dwarf shrub |
| 42 | 3b | Norway | f | S. lanata | dwarf shrub |
| 42 | 4 | Norway | v | S. caprea | to 5m |
| 42 | 5 | Norway | f | S. lanata | shrub less than 75cm |
| 42 | 6a | Norway | m | S. myrsinifolia | shrub to 4m |
| 42 | 6b | Norway | f | S. phylicifolia |
| 42 | 7 | Norway | f | S. myrsinifolia | shrub 5m |
| 42 | 9a | Norway | m | S. myrsinifolia |
| 42 | 9b | Norway | f | S. myrsinifolia |
| 42 | 10 | Norway | f | S. hastata |
| 42 | 11 | Norway | f | S. hastata |
| 42 | 13 | Norway | f | S. lapponum |
| Code | Country | Sex | Species 1 | Species 2 |
|------|---------|-----|-----------|-----------|
| 42 14 | Norway  | f   | S. glauca |           |
| 42 15 | Norway  | f   | S. glauca |           |
| A-i 1 | Switzerland | f    | S. eleagnos |       |
| A-i 2 | Switzerland | m    | S. eleagnos |       |
| A-i 3 | Switzerland | f    | S. purpurea × S. viminalis |       |
| A-i 4 | Switzerland | m    | S. purpurea × S. viminalis |       |
| C-i 1 | Greece    | m   | S. alba |           |
| J-i 1 | Romania   | -   | S. cinerea [Not collected] |       |
| J-i 2 | Romania   | -   | S. fragilis [Not collected] |       |
| K-i 1 | Holland   | f   | S. caprea |           |
| C-ii 1 | Estonia   | f   | S. euxina × S. pentandra |       |
| C-ii 2 | Estonia   | v   | S. ×fragilis |       |
| C-ii 3 | Estonia   | v   | S. ×fragilis × S. triandra |       |
| C-ii 4 | Estonia   | b   | S. phylicifolia |       |
| C-ii 5 | Estonia   | v   | S. myrsinifolia |       |
| C-ii 6 | Estonia   | f   | S. cinerea |           |
| C-ii 7 | Estonia   | f   | S. cinerea |           |
| C-ii 8 | Estonia   | v   | S. bebbiana |       |
| C-ii 9 | Estonia   | f   | S. bebbiana |       |
| C-ii 10 | Estonia | f   | S. phylicifolia |       |
| C-ii 11 | Estonia | f   | S. myrsinifolia |       |
| C-ii 12 | Estonia | f   | S. myrsinifolia |       |
| D 1 | Finland  | f   | S. aurita × S. cinerea |       |
| D 2 | Finland  | v   | S. caprea |           |
| D 3 | Finland  | f   | S. myrsinifolia × S. phylicifolia |       |
| E 1a | Finland  | m   | S. lapponum |       |
| E 1b | Finland  | f   | S. lapponum |       |
| E 2a | Finland  | m   | S. bebbiana |       |
| E 2b | Finland  | f   | S. bebbiana |       |
| H 1 | Norway   | m   | S. hastata |           |
| H 2 | Norway   | m   | S. hastata |           |
| H 3 | Norway   | m   | S. hastata |           |
| H 4 | Norway   | f   | S. phylicifolia |       |
| H 5 | Norway   | f   | S. phylicifolia |       |
Discussion

These samples provide a "snapshot" of willow diversity along a latitudinal gradient and an indication of the geographically changing taxonomic diversity that is presented to willow-feeding herbivores across Europe. What is particularly noticeable is the role in taxic diversity of hybrids. One third (10 out of 30) of the total taxa recorded were hybrids. This highlights the importance of recording hybrids, which are often inadequately reported in surveys. *Salix* hybrids are notable for their frequency in nature but comparative rarity in the literature on willows.

Also worthy of comment is the general increase in willow diversity from south to north (Table 4). This is the opposite of a common biogeographical pattern that species diversity is higher in warmer regions nearer the tropics, and lower nearer the poles. The genus *Salix*
has undergone a major radiation in boreal regions which may go some way towards explaining this inversion of the norm.

Finally, it should be noted that these willows formed the background for a major sampling of insects and it is anticipated that further papers forming part of this study will examine the insect fauna collected.

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Author contributions

QCC collected the willows, made preliminary identifications of the willow specimens and wrote the paper; ER assisted in the collection of willows and contributed to the writing; IB identified the willow specimens and contributed to the writing of the paper; DMP conceived and planned the study, jointly collected the willows and co-wrote the paper.

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