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Were the five rare heathers of the west of Ireland introduced through human activity? An ecological, genetic, biogeographical and historical assessment

Micheline Sheehy Skeffington[1,2]*, Nick Scott[2]
[1]Botany & Plant Science, NUI Galway, Ireland; [2] Clarinbridge, Co. Galway, Ireland

***Correspondence:** Micheline Sheehy Skeffington: michelinesheehy@gmail.com

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Abstract
Five rare Irish heather species have different disjunct 'Lusitanian' type distributions in Europe. They are confined in Ireland to the western coastal region and found elsewhere only, or principally, in the Iberian Peninsula. Two also occur in Britain, but only in the extreme southwest. None could have survived the last ice age in Ireland, and migration northwards, leaving hundreds of kilometre gaps *en route,* appears impossible. We assemble here the growing evidence that *Erica ciliaris* L. (Dorset Heath), *E. erigena* R. Ross (Irish Heath), *E. mackayana* Bab. (Mackay's Heath)*, E. vagans* L. (Cornish Heath) and *Daboecia cantabrica* (Huds.) K. Koch (St Dabeoc's Heath) have been introduced inadvertently through human activity, along with another heathland Lusitanian species *Simethis mattiazzii* (Kerry Lily), if over a long period. We suggest that the proximity to the coast of extensive heathland habitats in northern Spain and western Ireland along with the cutting of heathland for bedding and packing in Spain is a probable cause of their inadvertent carriage on a direct maritime trade route which dates from prehistorical times. By considering them together, we suggest that until a precise date for the earliest arrival in Ireland of each species is established, they should all now be considered as naturalised archaeophytes.

Keywords: *Erica*; *Daboecia*; Lusitanian; maritime trade route; prehistory

Introduction

Three heather species of the west coast of Ireland have classic disjunct Lusitanian distributions: they do not occur in the rest of Ireland or Britain, and they are found elsewhere principally, or only, in the Iberian Peninsula. Two further Irish heather species have disjunct Lusitanian type distributions, but also occur in southwest England; one also in northwest France. All five species display several characteristics associated with non-native species (Webb, 1985): they do not occur throughout the habitat that they would appear able to grow in; three are actively invading new territory in Ireland and while the other two are each limited to one small colony in Ireland, there are larger colonies in southwest England which are spreading. Most occur principally in disturbed habitat; three of them do not set seed in Ireland but do in north Spain; two are known to have reduced genetic diversity; and one hybridises

extensively with another more widespread species, which is not the case in north Spain.

It has already been proposed that two of these species were introduced from north Spain through human activity: *Erica erigena* R. Ross (Irish Heath), by pilgrims (Foss & Doyle 1988, 1990) and *E. mackayana* Bab. (Mackay's Heath), through smuggling (Sheehy Skeffington & Van Doorslaer, 2015). The results of a recent genetic study of the latter species (Fagúndez & Díaz-Tapia, 2023) are consistent with the theory of an introduction through human activity, principally through smuggling, but for one population the introduction was probably much earlier. Evidence has also been presented for the introduction of another Lusitanian heathland species, *Simethis mattiazzii* (Vand.) Sacc. (Kerry Lily), again possibly through smuggling (Lupton & Sheehy Skeffington, 2020).

Of the three other rare Irish heathers, two, *Erica ciliaris* L. (Dorset Heath) and *E. vagans* L. (Cornish Heath), occur as single very small populations. The fifth, *Daboecia cantabrica* (Huds.) K. Koch (St Dabeoc's Heath), is much more widespread than the others in the one locality where it occurs in Ireland. It is found in natural heathland often some distance from any human disturbance but is still actively expanding its territory.

In this paper we consider the ecological, genetic, biogeographical, and historical evidence for an introduced origin in Ireland for each of these five heather species and what this might allow us to conclude about possible trade routes and over what possible time span these may have existed. We do this by reviewing and interpreting what has already been established for each of the five species. We include *E. erigena* and *E. mackayana* both as an illustration of what we might be seeking with the three other heather species and so that we can then consider them together to see what this may reveal.

Method

The maps accompanying each species account show the current natural distribution as derived from national botanical websites: http://www.anthos.es (Spain); https://flora-on.pt (Portugal); https://inpn.mnhn.fr & https://www.tela-botanica.org (France); https://database.bsbi.org (Britain and Ireland). Only the BSBI Database (DDb) distinguishes records considered non-native or extinct. For the other sources we have used local floras (particularly Dupont, 2015), plus Fagúndez (2006) for *E. mackayana,* to attempt to eliminate any doubtful records, but many isolated ones are still likely to be introductions.

Erica mackayana (Mackay's Heath)

Erica mackayana was first discovered, and named, in Ireland in 1835, then described later the same year from northern Spain (Nelson, 2011). In Ireland it occurs as five small populations and one larger population, widely dispersed along the west coast, while outside of Ireland, it only occurs in the north of the Iberian Peninsula where it is common on heathlands in the Galician and Cantabrian mountains (Nelson & Fraga, 1983) (Fig. 1).

Erica mackayana does not set seed in Ireland, but spreads vegetatively on banks cut for turf, or around lakes in the bogs where it has become established (Webb, 1955; Nelson, 1989; Sheehy Skeffington & Van Doorslaer, 2015). It hybridises extensively in Ireland with the transfer of *E. mackayana* pollen to the

flowers of *E. tetralix* L. (and not the reverse) (Webb, 1955; Mugrabi de Kuppler *et al.,* 2015). The hybrid, which is common in Ireland, *E.* x *stuartii* (Macfarl.) Mast.*,* is very rare in Spain, even where *E. tetralix,* does occur with *E. mackayana*, which is not often (Fagúndez, 2006). *E. mackayana* establishes easily from cuttings, something not shared with the native *E. tetralix* (Sheehy Skeffington & Van Doorslaer, 2015).

Evidence has been put forward to show that *E. mackayana* is native to Ireland but none of it has been conclusive. Jessen (1949) claimed to have found fossil leaves from the Boreal age in a peat core near to its occurrence today on Roundstone Bog, but subsequently shed doubt on the certain identification of *E. mackayana* in the absence of seed (Jessen *et al.,* 1959).

A genetic study by Kingston & Waldren (2006) comparing Irish plants sampled from two populations with plants from four in north Spain demonstrated two broad clusters, each with Irish and Spanish samples. Though this suggests that the Irish populations came separately and from different parts of Spain, the authors concluded instead that the samples from Donegal must have mistakenly included plants of hybrid origin. The results for the other population, on Roundstone Bog, showed a constriction of the genetic diversity which they suggest indicates a founder effect and, unlike the Donegal population, they also found a clear differentiation from the Spanish populations indicating this species had been there for a long time. They ultimately concluded that the species was native to Ireland. Pene Eftonga (2013) in an unpublished PhD thesis provides results consistent with different origins for Irish populations, as well as also finding much lower genetic variation in Irish plants compared to Spanish plants, which is consistent with an introduction.

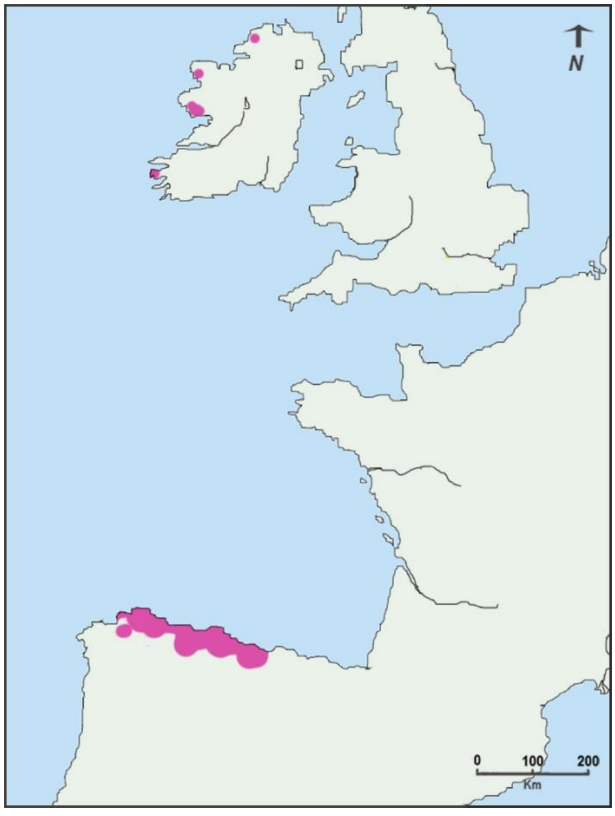

Figure 1. Distribution of *Erica mackayana*

Sheehy Skeffington & Van Doorslaer (2015) suggested that the species was introduced based on its occurrence in relation to *E.* x *stuartii,* the hybrid between it and *Erica tetralix,* particularly on Roundstone Bog in west Connemara. This is the largest population of *E. mackayana* in Ireland and is where it was first found in 1835 (Nelson, 2011). The occurrence of the species no more than 1 km from the small bog road crossing this large peatland complex, while the hybrid, *E. x stuartii*, extends much further from the road, suggests that it originated from an introduction near the road (Fig. 2) (Sheehy Skeffington & Van Doorslaer, 2015). Those authors also suggest that this location and that of the other, smaller, populations of *E. mackayana* in Ireland indicate that they had originally been introduced through trade, most likely smuggling. All are adjacent to a minor road or track leading from the coast through less inhabited areas and, other than the two populations in Connemara, are approximately 15 km inland.

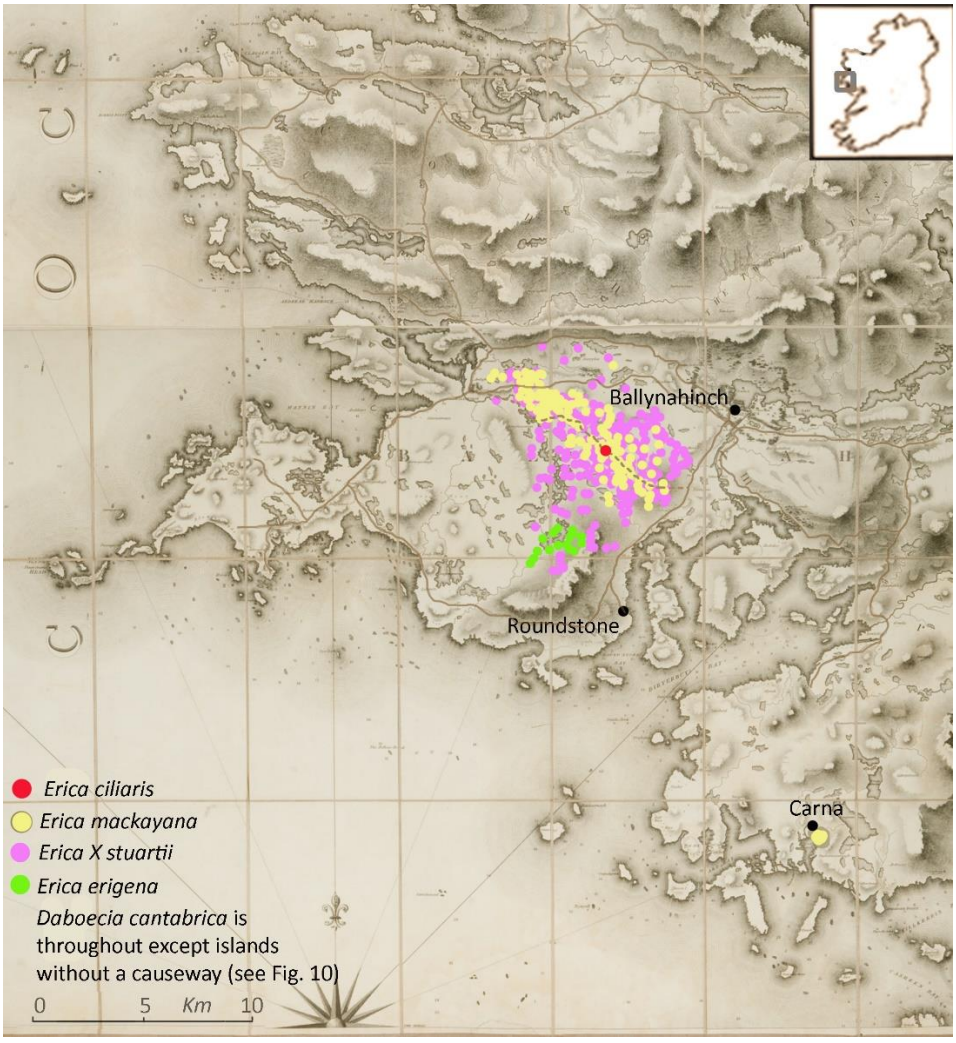

Figure 2. The distribution of four heathers in southwest Connemara placed on Larkin's 1819 map of Co. Galway, approximately contemporary with their first discovery. Tracks on the map have been enhanced (— [continuous line]) and the track across Roundstone Bog added (- - - [dashed line]). Species records overlay others in the order *E. ciliaris* > *E. mackayana* > *E. x stuartii*. The Distribution of *E. mackayana* and *E.* x *stuartii* from Sheehy Skeffington & Van Doorslaer (2015); distribution of other species from BSBI Distribution Database (database.bsbi.org)

The population on Roundstone Bog is far larger in extent than any of the others, so while it is bisected by a track, it is less clear where on the track it may have been introduced. This population is also accompanied by many more hybrid plants, indicating it has probably been there much longer. The other Connemara population, consisting of just a few plants at Carna, to the east of Roundstone Bay, is near the sea, at the head of a small bay (Fig. 2).

Fagúndez & Díaz-Tapia (2023) compared the genetic population structure of *E. mackayana* from five of the six populations in Ireland and six populations in northern Spain, along with plants of *E. tetralix,* sampled if it grew at the same site. The results for *E. tetralix* show the expected genetic relationships of a species which has recolonised northwards after the last ice age: each Irish population sampled is a subset of the populations to the south of it in Ireland and of those in Spain; the Spanish populations all have higher genetic diversity; and all the populations show an increasing difference in the relative proportion of genes with distance north.

The results for *E. mackayana* proved strikingly different from those for *E. tetralix*. While all the Irish populations were within the overall genetic variation of the Spanish plants, indicating they were originally derived from them, each Irish population proved to be most closely related to a different grouping of Spanish plants, rather than to each other. Plants from Kerry, Galway and Donegal were each genetically similar to different groups of plants sampled in Galicia and plants from Mayo were similar to plants sampled from populations in Asturias. There was also no increasing difference in the relative proportion of genes with distance north, instead all but one of the Irish populations were not substantially different genetically from the Spanish ones. The genetic diversity of the Irish populations was again lower than that of the Spanish populations and much less than it was for *E. tetralix* samples.

Fagúndez & Díaz-Tapia (2023) conclude that their results demonstrate with a high level of confidence that the Irish *E. mackayana* populations originated from North Spain through different dispersal events. We would suggest that their results are consistent with the introduction through smuggling in the 17th and 18th centuries for all but one of the populations. The exception is the population on Roundstone Bog. Although still within the genetic variability of the Spanish populations, the relative proportion of genes is strikingly different. The authors suggest that this could be accounted for by this population having been either derived from an unsampled population in northern Spain or that it was introduced to Ireland from there considerably earlier than the other populations. As the Roundstone population does not reproduce sexually and appears nearly uniform, these could not have changed, but if the time scale was sufficiently long, then the relative occurrence of the genes in the Spanish populations could have changed sufficiently. Alternatively, the Spanish population from which the Roundstone one was derived may have become extinct over time. A much earlier introduction would also explain why the Roundstone Bog population is so much larger and has a higher proportion of hybrids than the other Irish populations.

The small population on the coast at Carna proved not to be derived from the nearby one on Roundstone Bog, instead it was similar genetically to plants sampled in a different part of Galicia.

***Erica erigena* (Irish Heath)**

The first description anywhere of *E. erigena* was from Portugal published in 1576 (Nelson, 2011). For Ireland, there are herbarium specimens collected from 1700 onwards and later identified as this species (Nelson, 1989), but the first published account was not until 1830 describing a small population growing by a stream at Roundstone, Co Galway (Mackay, 1830) (Fig. 1). It was then reported on the coast of Co. Mayo in 1835 (Foss *et al.*, 1987). Outside of Ireland, *E. erigena* is found principally in southern and western Iberia, mostly near the coast. In France only a few populations occur on the Médoc Peninsula near Bordeaux (Foss and Doyle, 1988) (Fig. 3).

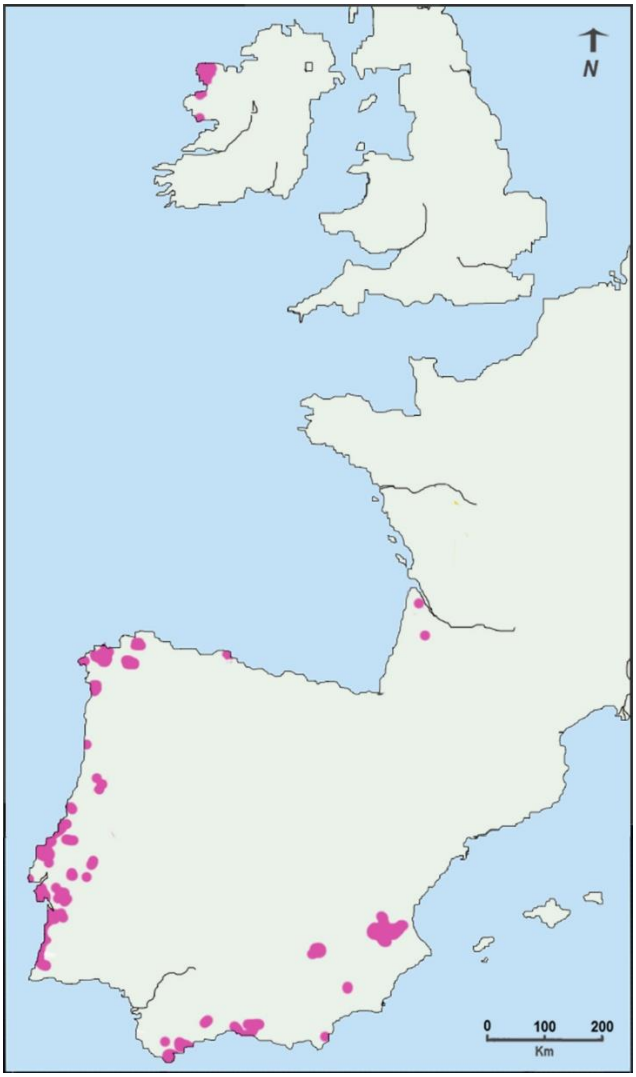

Figure 3. Distribution of *Erica erigena*

Foss *et al.* (1987) mapped all the known occurrences and detailed every previous published record for *E. erigena* in Ireland. Today it occurs as many separate colonies, making up a large broken population along much of the Mayo coast, extending just into Co. Galway on the north shore of Connemara. Some of these colonies extend inland along rivers and lakeshores, and it also occurs beside several lakes further inland (Foss *et al.*, 1987) (Fig 4).

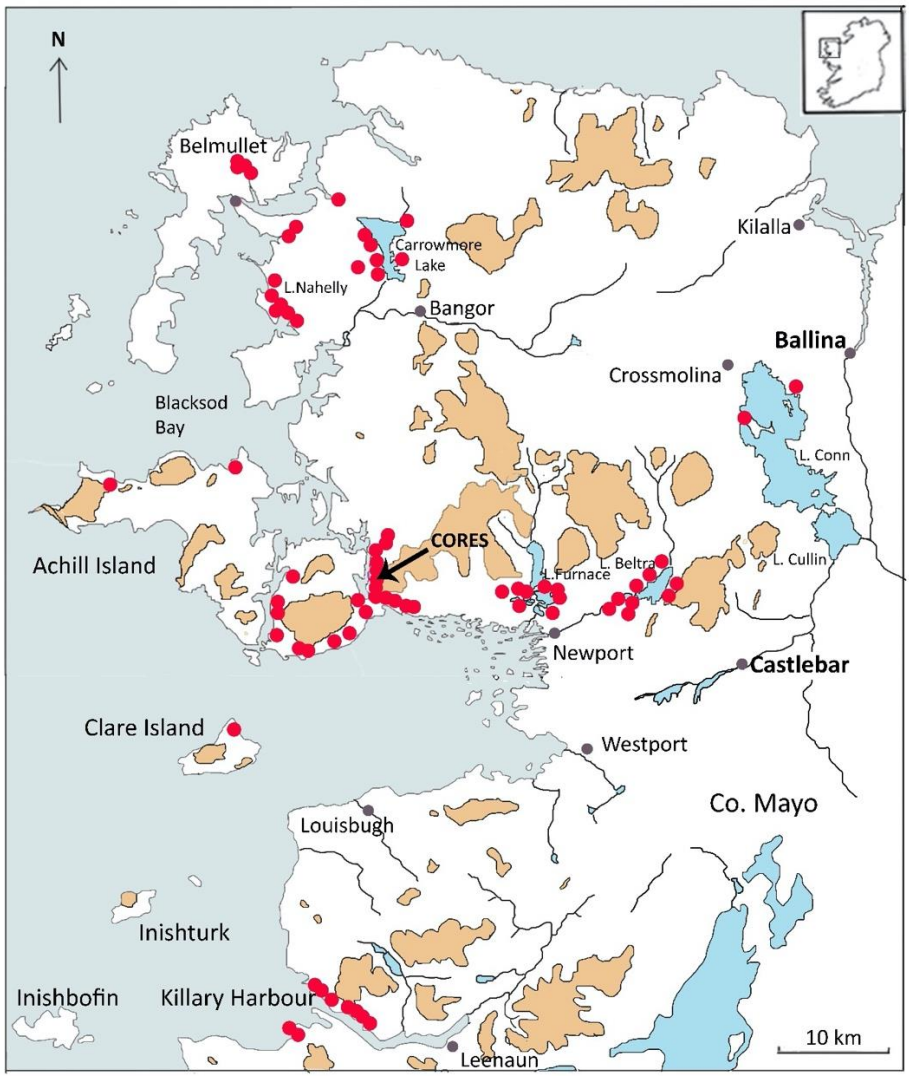

Figure 4. Entire Irish population of *Erica erigena* except for plants at Roundstone (Fig. 2) with site of pollen cores, on the slopes of Claggan Mountain. After Foss *et al*. (1987) and BSBI database (database.bsbi.org)

Foss *et al*. (1987) considered the largest and most extensive colony to be that beside Bellacragher Bay, where it is continuous for over 7 km along the coast and extends up the side of Claggan Mountain beside streams. This colony appears to be at the centre of the main population (Fig. 4). Most of the colonies that Foss *et al*. (1987) detail appeared to be expanding, with more recent reports tending to extend the species distribution. While this could be due to increased observations, it seems unlikely, as the botanists of the late 19th and early 20th century were thorough.

The small population at Roundstone in Co. Galway does not appear to be part of the extensive population in Mayo which just extends into Co. Galway near Killary Harbour, as it is separated from that site by *c.*20 km across Connemara. At Roundstone, it occurs about 2 km inland from the coast by streams and two small lakes on the far side of Errisbeg hill from Roundstone.

In Ireland *E. erigena* is associated with coastal and lake shores, stream sides, cut-over peatlands and other disturbed sites (Foss *et al*., 1987; Foss & Doyle, 1988).

On lake shores it tends to occur only within the zone of winter flooding, while on the coast, where it also occurs as a distinct fringe, it is just above shores associated with the disturbance of winter storms (Foss & Doyle, 1988). Though it is known to set seed (Webb & Scannell, 1983), it can also reproduce through branches, trodden into the wet peat by domestic animals, taking root and then breaking from the parent plant (Foss & Doyle, 1988).

On the Iberian Peninsula *E. erigena* rarely occurs far from the coast, and always at low altitude, except in the south where it is found up to 100 km inland and as high as 1000 m (Foss & Doyle, 1988). It occurs in heathland communities, including Mediterranean heathland in the far south of its range, but it also has an affinity with disturbed sites (Foss & Doyle, 1988).

Foss and Doyle (1988, 1990) provide a cogent argument for *E. erigena* having been introduced to Ireland by human activity: it is associated with disturbed habitat; appears to be actively invading new territory; is not frost tolerant (so would not have survived in Ireland or nearby refugia during the last ice age); its seeds and fruit are too heavy to be dispersed by wind and do not float; and the only migratory birds following the European coast are passerines too small to be able to carry the seed a long way. Those authors took two peat cores from within the largest population, on the side of Claggan Mountain. Using scanning electron microscopy to identify the ericaceous pollen to species, the first occurrence of *E. erigena* was dated 477 and 368 radiocarbon years BP respectively (i.e., the pollen occurred in the cores no earlier than *c.*1431 AD), coinciding with a decrease in woody species and increase in heathland and grassland pollen, indicating human activity. Foss and Doyle (1988) propose that the heather had expanded in the area with the woodland clearance, and that it may have originated from a first introduction nearby. They suggest the religious pilgrimage to Santiago de Compostela in northwest Spain as a possible means of introduction, noting that the Dominican Abbey at Borrishoole is only 14 km east of Claggan mountain and that it had known links with Spain. They point out that *E. erigena* is a particularly elegant heather that pilgrims may have brought home, but also that cut heathland vegetation is used in northern Spain for animal bedding and for packing in boats, and thus the seed could have inadvertently got onto goods taken home (Foss & Doyle, 1988). From the 14th century, Irish pilgrims sailed directly from various places on the west coast to A Coruña in Galicia on this pilgrimage, which was popular in Gaelic Ireland (Cunningham, 2018).

A subsequent genetic investigation of *E. erigena* found that samples taken from four sites in Co. Mayo were not genetically distinct from and slightly less diverse than Spanish samples taken from A Coruña, Galicia, suggesting a recent separation of the Irish populations from the Spanish (Kingston & Waldren, 2006).

Erica vagans **(Cornish Heath)**

Erica vagans was first recorded in Britain by John Ray in 1670, who found it growing "*by the wayside going from Helston to the Lizard-point in Cornwall, plentifully*" (Translation from Ray, 1670 in Nelson, 2011). The Lizard peninsula is now considered the only place where it grows naturally in Britain (Fig. 5), where it is confined to heathland communities associated with the serpentine rock that underlies much of the peninsula, on soils with an increased level of exchangeable ions, particularly potassium, calcium and magnesium, and not on heathland with more acidic soils (Marrs & Proctor, 1978).

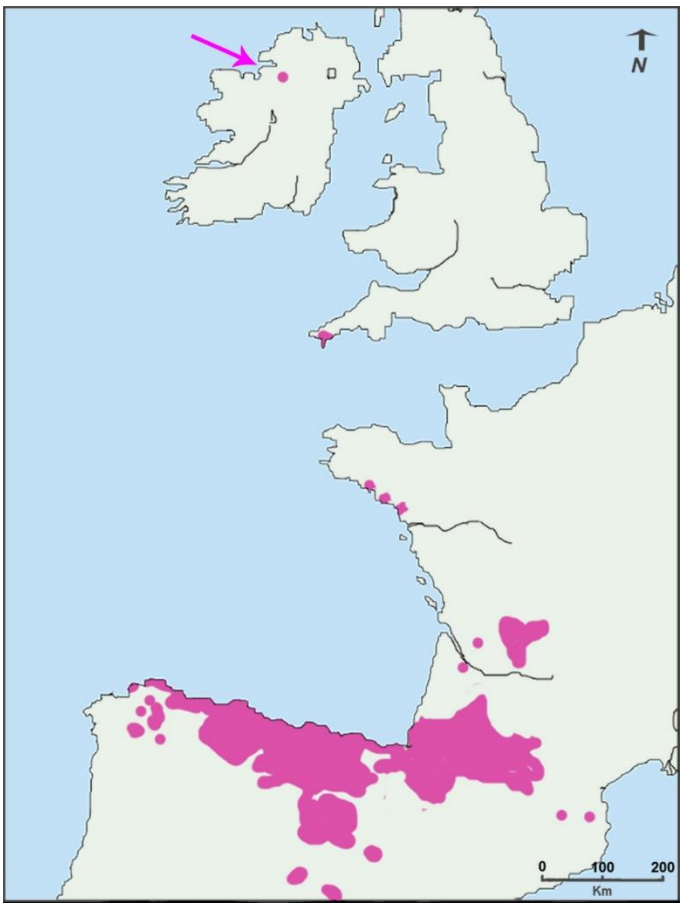

Figure 5. Distribution of *Erica vagans*

Erica vagans occurs as a single population in County Fermanagh, in Northern Ireland, where it first came to the notice of botanists in the 1930s (Praeger, 1938). All the plants are white-flowered and this distinctive 'white heather' was well-known by local people since, at least, the end of the previous century (Nelson & Coker, 1974). The plant grows in a remote area in a small alkaline flush in otherwise acidic bog (Forbes & Northridge, 2012). In Spain and Cornwall, the colour of the flowers varies from pure white through to rich pink, with the majority a shade of pale pink (Nelson & Coker, 1974).

Erica vagans was first collected in the early 17th century from the western Pyrenees (Nelson, 2011). Its main area of occurrence extends from there into and across Northern Spain where it grows on calcium-poor, or leached limestones, sometimes on ultrabasic soils, occasionally up to as high as 1,900 metres (Bayer, 1993) (Fig. 5). This heather has proved adept at establishing in the wild, frequently escaping from gardens in Britain, Ireland and the US (Nelson, 2011) so that the scattered small colonies recorded in northern France on our distribution map need to be treated with caution.

Erica vagans is listed as Critically Endangered in the Irish red data list (Wyse Jackson *et al.*, 2016) and is protected under the Wildlife (Northern Ireland) Order 1985, as amended by the Wildlife and Natural Environment Act (Northern Ireland) 2011. Because of this, the Northern Ireland Environment Agency monitors the Fermanagh site.

When Praeger first reported the Irish population he concluded that this new addition to the Irish flora must be native as he could think of no way it might have been introduced, *"…the district is a remote one, sparsely inhabited, the houses very scattered, poor, and without gardens. The station is not even near a highway. To reach it you take the old road from Belcoo to Garrison. You leave this for a rough track running up the hill through heather and stones, and the Cornish Heath occurs at a short distance from a branch of this track, on heathery ground sloping to a stream*" (Praeger, 1938). If you continue west on the old road, you will come, after only 20 km, to Donegal Bay, in the Republic, and once known for smuggling (Platt, 2011). The quiet old road is the ideal discrete route for carrying smuggled goods inland from the bay, while the main road to Enniskillen follows the shore of Lough Erne on the other side of the hill. The hillside, with the heather, is where the road first climbs into wild country, providing suitable hiding places for smuggled goods (Fig. 6).

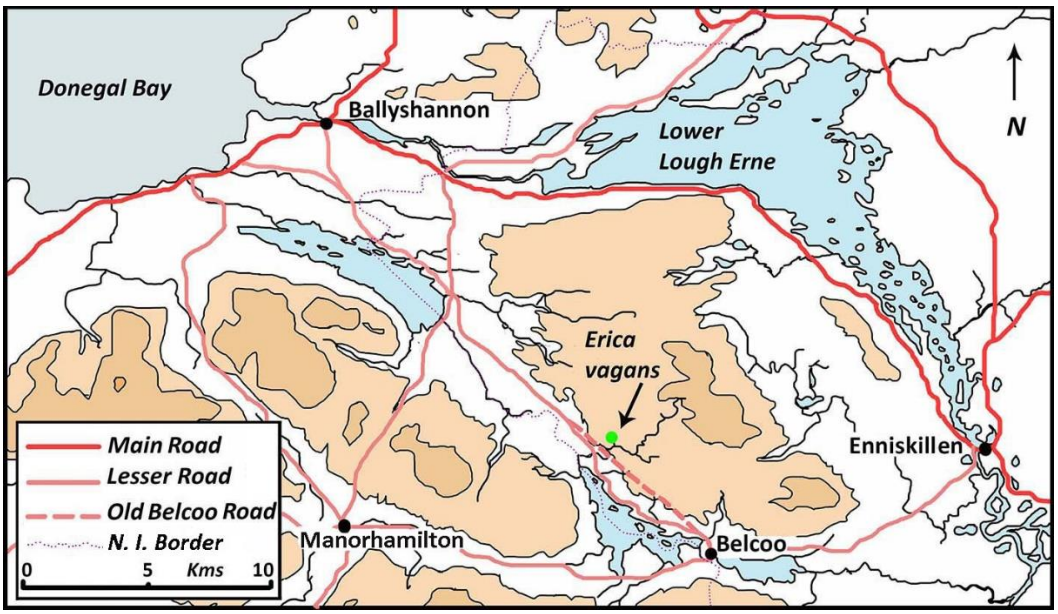

Figure 6. Location of the population of *Erica vagans* in Fermanagh, N. Ireland relative to the coast

The present authors visited this small population in early September 2019, when the heather was in full flower and found that Praeger's site description is still true: the hillside is '*remote*' with *'heather and stones'* and cattle grazing the open moorland. But some of the 'stones' are in fact large boulders, which in places are piled on top of each other against rocky outcrops.

Nelson and Coker (1974) provide a detailed description of the population forty years after Praeger: *"the ground slopes gently for the first ten meters of the study area and then there is an area where there are rocky outcrops and where the slope is greater. Beneath this there is a line of springs extending for a few meters across the top of the colony. This results in the ground here being very wet and the water from the springs seeps down the hillside"*. This, they explain, creates a *"flush area no more extensive than the colony"*. We found *E. vagans* just as Nelson and Coker describe, except we also noted how the rocky outcrops at the top of the flush

provided excellent cover for hiding large objects from the small track crossing the flatter ground above. This track is the one mentioned by Praeger, a minor branch of the main track which carries on up the hillside.

Nelson and Coker (1974) also report that seedlings *"appeared to be attached to adjacent plants by tough woody tissue and they must have been derived from the shoots, probably trampled into the ground by cattle"*. This is exactly what Foss & Doyle (1988) later describe for *E. erigena* in Co. Mayo and propose as a means for heather spreading after introduction. Nelson (2011) later confirms that *E. vagans* establishes easily from cuttings.

The soils in which the plants grew had a relatively high pH compared to the bog around the flush and plants were often growing near surface boulders within the flush (Nelson & Coker, 1974). All the plants were the unusual white-flowered form, suggesting that they were derived from 'one homozygous plant'; seed collected failed to germinate in an experiment, while seed from the Cornish population germinated well (Nelson & Coker, 1974). Surprisingly, considering their observations and results, those authors dismiss past proposals that this population of *E. vagans* had been introduced and conclude that it is a remnant of a once more widespread population, either native or one which was introduced in prehistory. As with Praeger, the two principal justifications given are the improbability of the plant having been introduced to this location, plus the fact that other Lusitanian species have similar odd distributions. To us, however, everything they report points instead to *E. vagans* having been inadvertently introduced to this site within historical times. Consistent with this is the fact that the population does not appear to have changed in extent in the fifty years since Nelson and Coker (1974) mapped it.

On a visit to the site in September 2022, we re-measured the maximum north-south axis which proved to be roughly the same length (60 m) as recorded by Nelson and Coker 50 years earlier. We also recorded the position of each plant (easier to spot in early September when in flower) using Google maps, working systematically around the outside of the population and then recording those in the middle less systematically. Three outlying plants recorded by Nelson and Coker (1974) by the streamside, of which we had re-found two on a previous visit in 2019, were not found, probably because the stream, with its steep bank, has been fenced. As a result, the vegetation there is no longer grazed or trampled and is much taller and denser. But the main population appears virtually the same size and shape, taking account of the slight skewing of their survey following the contours of the unevenly sloping land, while our recording method did not (Fig. 7).

We therefore suggest that the original introduction of *E. vagans* was by means of a seed or cutting, carried inadvertently on smuggled goods that were hidden behind the rocky outcrops at the top of the site. The resulting individual plant was unable to set viable seed but could then spread vegetatively down the slope by cattle trampling branches into the wet soils until it has reached the edge of the suitable habitat.

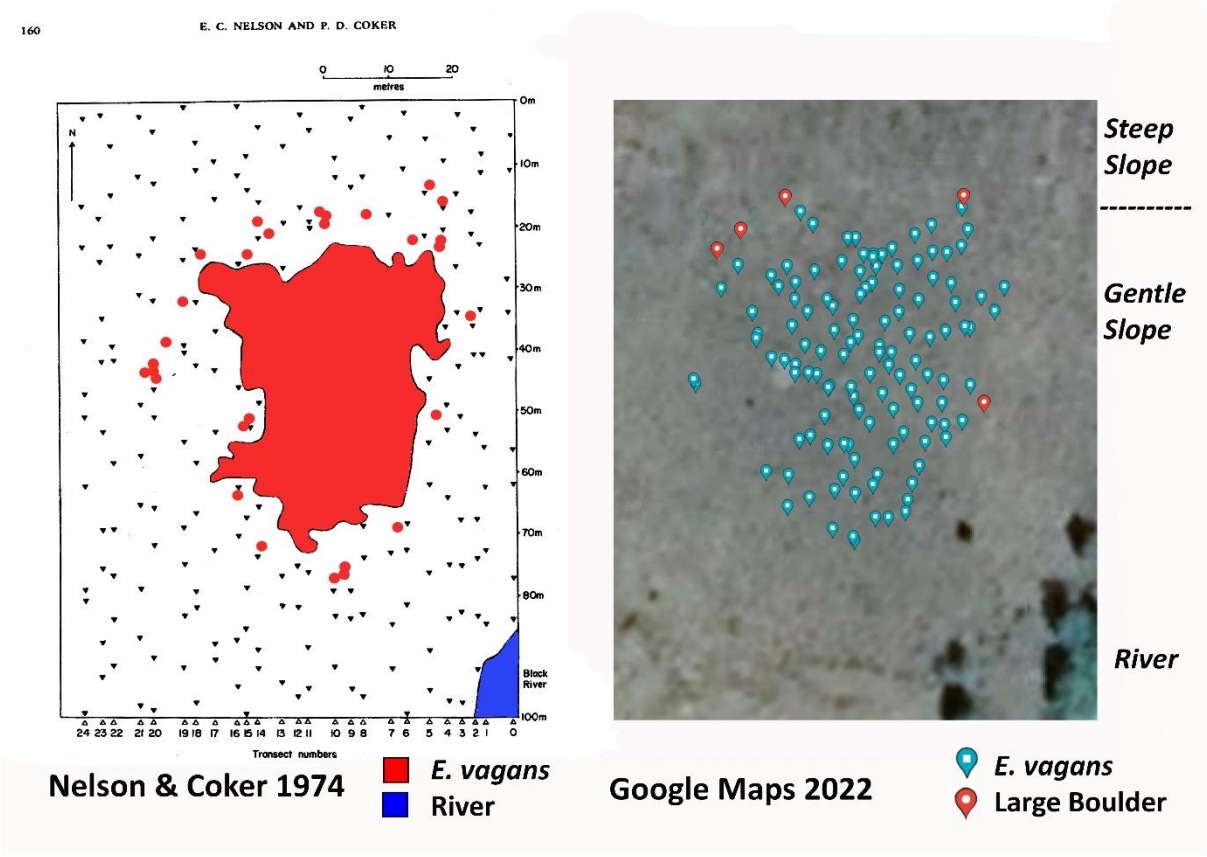

Figure 7. Population map of *Erica vagans*, Fermanagh, N. Ireland, copied from Nelson and Coker (1974); triangles represent quadrats without *E. vagans* (left); and as recorded in 2022 using Google Maps (right)

If *Erica vagans* is self-incompatible then a population derived vegetatively from only one individual would not set seed and would be uniform for any characteristic, such as flower colour, without needing to be homozygous. The Cornish population, which does set seed, is much more extensive and, in 2019, appeared to us to be still expanding. For instance, it was only halfway through a softwood plantation, where it was associated with the tracks.

Of note is that, according to the landowner (J. Broyan, pers. comm.), the same Fermanagh hillside was regularly used for hiding goods smuggled across the nearby Irish border. The border (Fig. 6) was created with the partition of Ireland in 1921. However, although this *E. vagans* population was reported later, this smuggling could not have been responsible for the introduction, since the 'white heather' was known locally in the previous century.

There are three other early records for *E. vagans* in Ireland, now extinct. All were on the coast and at places which may have been used for smuggling but are also not as remote, so that they could also have been introduced from gardens. There is an 1836 record for it on sea cliffs at Islandicane, Tramore, Co. Waterford (Moore & More, 1866), not re-found (Praeger, 1934). In 1899 it was found on coastal sandhills at Murlough, Co. Down and in 1928 at Carrablagh on the west shore of Lough Swilly in Co. Donegal (Nelson & Coker, 1974; BSBI Distribution Database). Re-found at Murlough in 1978 by Charles Nelson (Hackney, 1992), this population was amongst sand dunes at the end of a peninsula at the entrance to Dundrum Bay, an ideal temporary hiding place for smuggled goods. Furthermore, an

old path leads from Dundrum into the Mourne Mountains which is still known as the Smuggler's Trail. This population has since been eradicated as an alien species by the National Trust from what is now the Murlough National Nature Reserve (Graham Day pers. comm.).

Erica ciliaris (Dorset Heath)

Erica ciliaris was first described from northern Spain and Portugal in 1576, and first reported as occurring in England in 1770 (Nelson, 2011). In Ireland it occurs as a single population on Roundstone Bog in Connemara where about a dozen plants grow beside a small road; *E. mackayana* and *D. cantabrica* grow nearby (Webb & Scannell, 1983) (Fig. 2). This small population was first discovered in 1846, then lost between 1852 and 1965 (Nelson, 2011). *E. ciliaris* does not appear to set seed in Ireland (Webb & Scannell, 1983) and the individuals are morphologically similar, indicating they are probably one clone (Nelson, 2011). It was previously a protected species (Curtis & McGough, 1988) but was later removed from the list (Curtis, 2000). *E. ciliaris* is more widespread in southwest England, where it occurs as four main populations (Rose *et al*., 1996). The principal population is in Dorset, where it grows through much of the heathland around Poole Harbour. Chapman (1975) demonstrated that this population is expanding, by comparing the relative amount of the species with that of the hybrid at multiple points within its distribution. Unlike the other rare heathers of Britain and Ireland, *E. ciliaris* is regarded as native to northern France, having an extensive population in Brittany. It also occurs more sparsely further north into Normandy and along the coast south to a large population in the Landes in southwest France (Fig. 8).

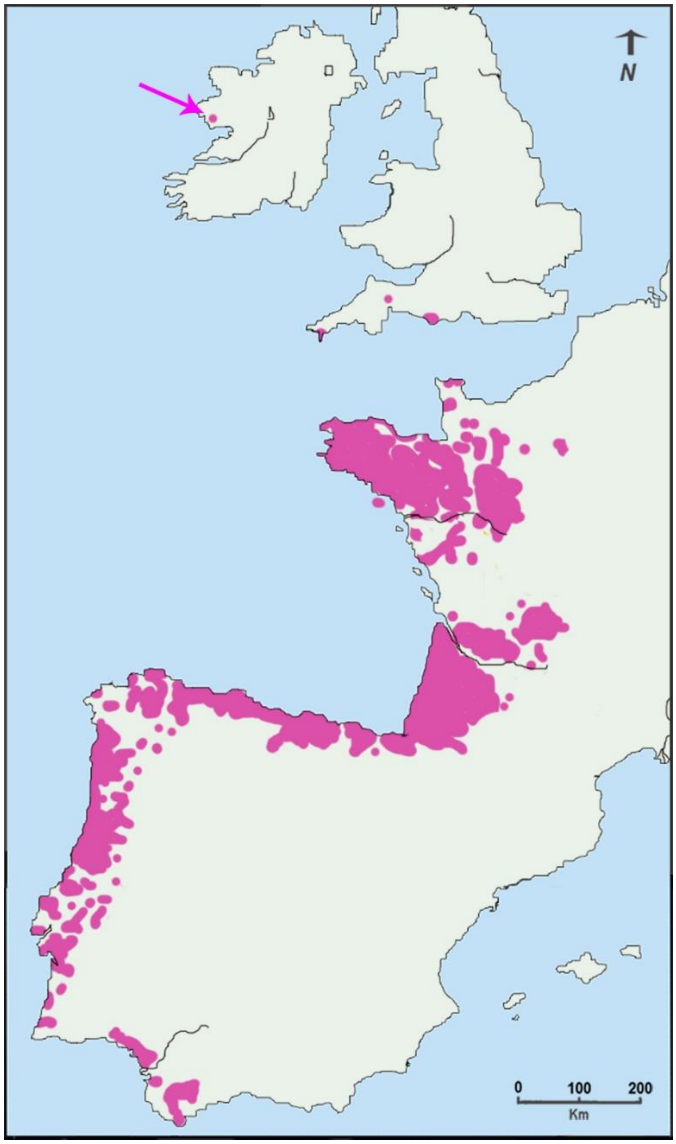

Figure 8. Distribution of *Erica ciliaris*

***Daboecia cantabrica* (St Dabeoc's Heath)**

Daboecia cantabrica was first described from northern Spain in 1694 and was discovered only 6 years later in Ireland where it grew *"in most of the mountains of Galloway and Mayo"* (Lhwyd, 1712 in Nelson, 2011). It does indeed grow throughout much of this area, but in Ireland it *only* occurs there and not in other extensive areas of similar habitat. Elsewhere (Fig. 9) *D. cantabrica* is confined to northern Spain, northern Portugal and the western French Pyrenees (the outlying population in central France is thought likely to be an introduction, as are probably the isolated populations in Spain and Portugal, since this species is a common garden plant).

In Ireland *D. cantabrica* occurs on thin peaty soils over rock; it is not present on the extensive bogs of Connemara/west Mayo, but on the rock outcrops amidst the peatlands (Woodell, 1958). It is confined to weakly acidic poor soils and does not occur on limestone. In France and Spain, it also occurs on dry poor soils including mountainsides (Woodell, 1958).

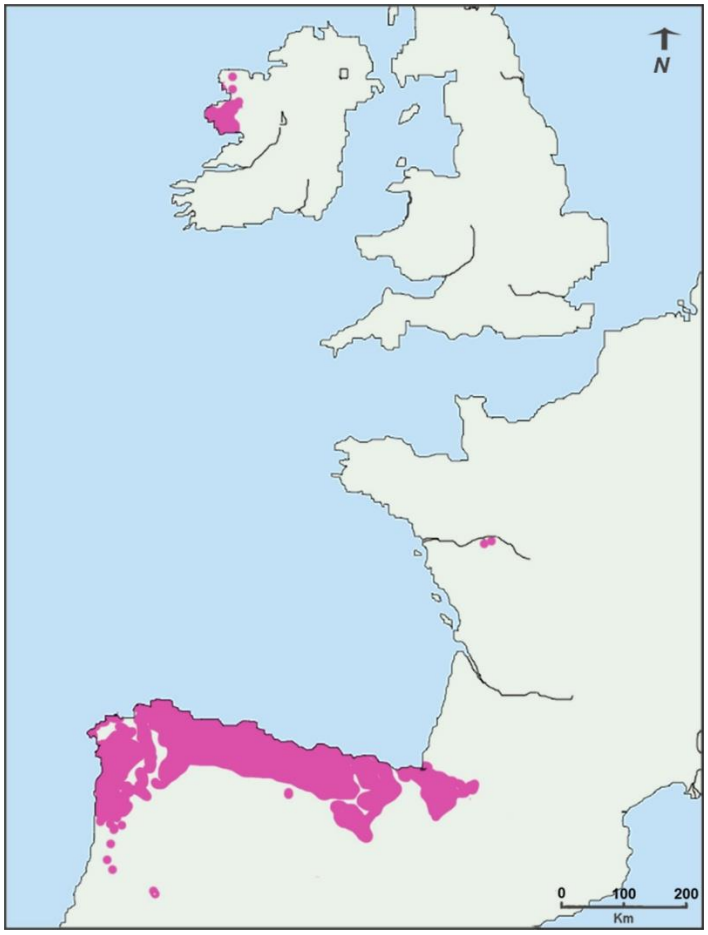

Figure 9. Distribution of *Daboecia cantabrica*

First records for Ireland for each 10 km square in the BSBI online database using three date classes appear to indicate that *D. cantabrica* is still spreading into Co. Mayo (Fig. 10). It was not possible to include an earlier date class as, at least for Ireland, the database is missing many of the records used to produce the first printed BSBI atlas (Perring & Walters, 1962) which included all records up to 1960. That atlas used the British grid squares throughout, but subsequently Irish grid squares have been used for Ireland, which only partially overlap with the British ones, so that comparison of the data requires caution. The 10 km square dots from the 1962 atlas (pre- and post-1930 categories combined) are lain over the database results in Fig. 10. This appears to show that the expansion of *D. cantabrica* since 1960 has only been northwards into Co. Mayo, and that it had by then already been found in all the available hectads south of Clew Bay. It also shows that the first records for Gorumna and adjacent islands in south Connemara were also in fact before 1960, which is consistent with the causeways to these islands being present by then.

Kingston and Waldren (2006) undertook a genetic analysis of *D. cantabrica* sampled from Spain, France and Ireland and found that the Irish population had restricted diversity which they attribute to a founder effect, i.e. the population had arisen from a small number of individuals, and also that there was clear differentiation from the Spanish and French populations. They concluded that the species had arrived by natural dispersal along the European coast a long time ago

and that the intervening populations had since been lost. A later genetic analysis of *D. cantabrica* sampled from Spain and Ireland (Beatty & Provan, 2013) also found that Spanish populations exhibited substantially higher genetic diversity than Irish populations at all the loci studied, with few private haplotypes found in the Irish populations. The results of both studies support the hypothesis that *D. cantabrica* was introduced by humans to Ireland from Spain, long enough ago to produce the genetic differentiation, but neither study considers this. Kingston and Waldren (2006) instead propose two refugia during the last ice age, one in Galicia and the other in the Bay of Biscay, with the Irish population derived from the latter, without attempting to explain why *D. cantabrica* is not now present in southwest Ireland, on the Cork/Kerry peninsulas, which would logically be on any post-glacial migration route to Connemara from further south. The location of their suggested refugia is derived by palaeodistribution modelling based on the present distribution and climatic envelope of the species, without considering that if the Irish populations were introduced by humans from Spain, then this would generate a false need for an additional refugium.

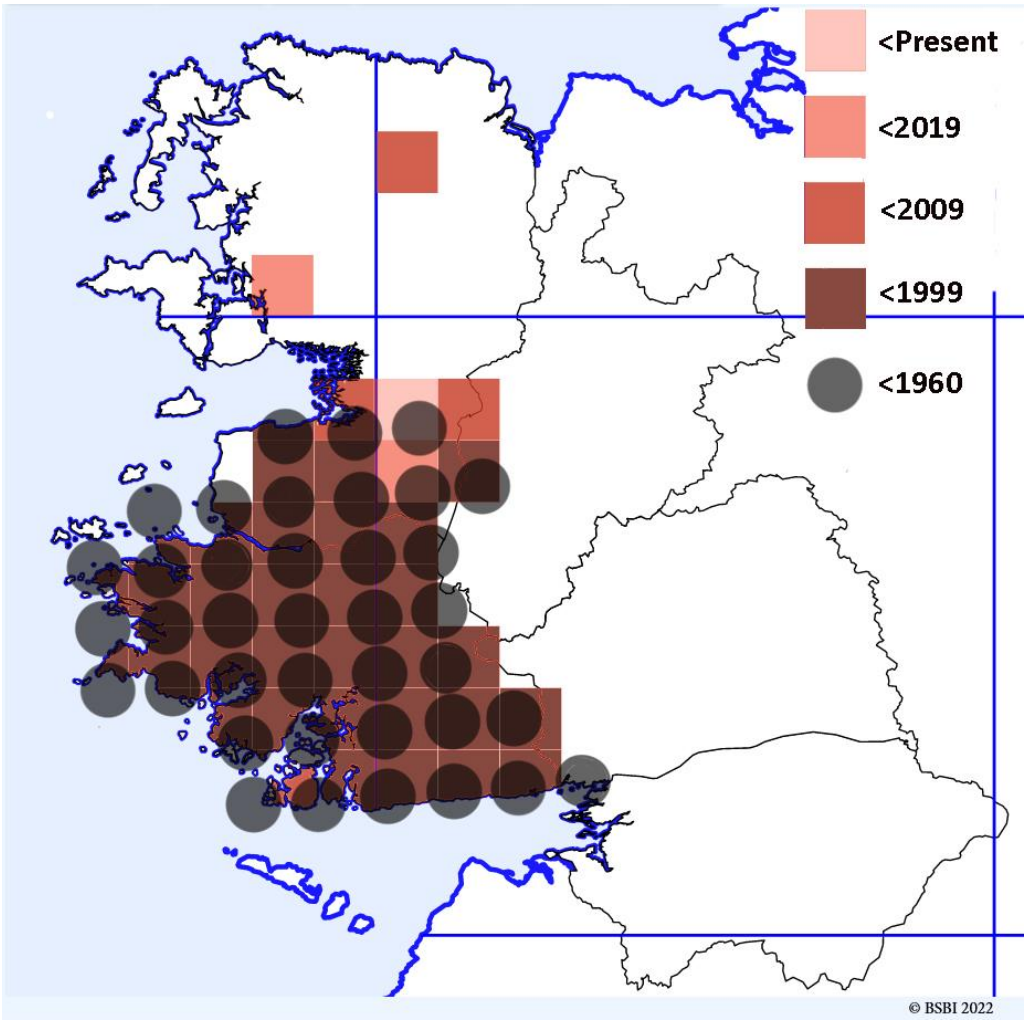

Figure 10. First records of *Daboecia cantabrica* in 10 km Irish grid squares by date class from the BSBI data base (except for islands which are shown individually) and <1960 records based on 10 km UK grid square records, shown as dots, from the first printed atlas (Perring & Walters, 1962)

Pene Eftonga (unpublished PhD 2013) obtained more confused results for *D. cantabrica*. Irish populations were again distinct genetically from those from Spain and France, and all but one exhibited comparatively low genetic diversity, while remaining within the overall diversity range. The author concluded that the Irish populations were originally derived from those of southern France either by land migration, with the intervening populations since becoming extinct, or by a direct natural dispersal event possibly from two sources.

Discussion

Origin

The Iberian Peninsula appears to hold the primary centre of species richness for heathers, which, it has been suggested, probably evolved there, or near to there, in adaptation to the Atlantic fringe, with the much greater number of heather species on the Cape of South Africa suggested to have come through a secondary evolutionally diversification (Mugrabi de Kuppler *et al*., 2015). Extensive heathland is not fully continuous along Europe's Atlantic coast, occurring mainly on the rocky promontories, particularly western and northern Iberia, Brittany, western Britain, western Ireland and western Norway. The gaps between these create potential barriers to migration northwards for any species unable to grow further inland, due either to frost sensitivity or to other dependence on an ecological niche specific to the Atlantic fringe. This means that with the common oceanic climate it would be possible for a heather species which originally grew no further north than the Iberian Peninsula, to establish and thrive in Ireland and Britain, if introduced there.

Heathland was once the principal habitat of northern Spain: stretching from the tops of the Cantabrian mountains northwards down through the foothills, to the coast (Fagúndez & Izco, 2016). Except for mountain tops and wind-swept cliff tops, this heathland was originally open acidic woodland, with heathland species occurring within it, which was then cleared by humans. Today most of this ex-woodland heathland has been improved to create grassland or planted as commercial forest, but patches remain, as does much of the original open heathland on mountain and cliff tops (Fagúndez & Izco, 2016).

In northern Spain farm animals are housed overnight because of the prevalence of wolves. The traditional bedding for the animals is harvested heathland vegetation (heathers, gorse, bracken), which after use, is then spread on the fields. In 2015, we met an old couple in northwest Galicia loading a trailer with cuttings in which we spotted *D. cantabrica* as well as *Erica arborea*. Seed on the coats of ponies and mules bedded overnight on this vegetation could have been transferred in turn to any cargo they carried.

Heathland still occurs near the ports on Spain's north coast, particularly on cliff tops (Fig. 11). Foss and Doyle (1990) suggest that harvested heathland could have also been used as packing in boats. While in northern Spain for that study, Peter Foss actually saw this use in a boat moored in a Spanish port (pers. comm.). Such packing, called dunnage, was very important in sailing ships, as any movement of the cargo at sea could capsize the boat. Heather used as dunnage has been identified in a wreck of a Mediterranean sailing ship (Wicha, 2005).

Figure 11. Heathland on Cabo Peñas, Asturias. This headland juts out northward between the ports of Avilés and Gijón. August 2015. Image: Nick Scott

The prevalence of heathland and its harvesting for bedding and other uses could well be why six of the sixteen Lusitanian plant species found on the west coast of Ireland are heathland species: the five heathers plus *Simethis mattiazzii* (Lupton & Sheehy Skeffington, 2020).

Carriage

To establish how these heathers may have been brought to western Ireland, we need to consider evidence for direct traffic between North Spain and the west of Ireland over time. The earliest evidence is provided by another Lusitanian species, *Arbutus unedo* L (Strawberry-tree), which was found as charcoal in archaeological horizons dating from 4,200 BP at the Ross Island copper mine in Co. Kerry. We have proposed that *A. unedo* was probably introduced with the first copper miners around 4,400 BP as part of this new influx of people who came from north Spain (Sheehy Skeffington & Scott, 2021). This was at the start of the Early Bronze Age, during which Ireland and Britain became major producers of copper, tin and gold which were traded along the Atlantic coast. Ancient Greek sources reported that the Phoenicians acquired copper from 'Celtic lands' via Tartessos (Freeman, 2010). This is the culture suggested to be proto-Celtic by Cunliffe and Koch (2010), which was based on the southwest Spanish coast, near to the Phoenician trading port at Cádiz (Aubet, 2001).

Later, the Romans must have used the direct crossing from the Iberian Peninsula to Ireland and Britain as they knew the Galician port of A Coruña, on the north-west corner, as 'Portus Brittanniae', with Britanniae used to mean both

Islands. Its famous 'Torre de Hércules' is a restored first-century Roman lighthouse which is referred to by Paulus Orosius in his fifth century history *as "erected … for looking towards Britanniae"* (González Garcés, 1972).

Links between western Ireland and Iberia feature prominently in the *Lebor Gabála Érenn*, the 'Book of Invasions', a collection of origin narratives for the peoples of Ireland, preserved in a variety of manuscripts (Macalister, 1938-56). These stories recount the coming of a series of ruling elites, who land in several places in Ireland, depending on the account. Prominent among the landing places is the Dingle Peninsula in the far southwest and they appear to have always set sail from A Coruña, as the tales mention the Torre de Hércules lighthouse, referring to it as the tower of Breoghan. The earliest known version of this story is a 9th century Irish poem (Ritari, 2017). If this myth is based on original migrations, they happened long before the tower was built.

The many cultural affinities between western Ireland and North Africa have been suggested as evidence for a continuing ancient trade route along the Atlantic coast. For instance, the traditional unaccompanied *sean-nós* singing of western Ireland is very unlike any other folk singing in northern Europe, but similar to North African singing; the bodhrán hand-held drum is also found in both places (Quinn, 2005). It is still unclear where the early Celtic monastic Christianity of western Britain and Ireland came from. It flourished in Ireland and then spread further into Britain and to Northern Europe. It seems to have arrived at the end of the 4th century and was already well established when the national saint, Patrick, came on his mission to Ireland in 432 AD. The first monasteries were on coastal islands, particularly along the west coasts (Kehnel, 2019). It has many elements in common with the Christian hermitic movement that arose in the eastern Mediterranean in the 2nd century which led to the Christian monasteries of Egypt (the desert fathers) (Dunn, 2003; Telepneff, 2002). St Anthony, an important monastic saint in the Coptic church, is depicted on carved Irish crosses and the Coptic church's list of martyrs includes seven who died in Ireland (Quinn, 2005). The word desert occurs in Irish placenames (as *díseart*), meaning hermitage in Irish (Logainm, 2023). Early Celtic art, particularly associated with the monastic tradition, is very similar to Coptic art (Henry, 1963). These cultural connections suggest the same route through the Mediterranean and north along the Atlantic coast as that proposed for the earlier origins of the Celtic languages (Cunliffe & Koch, 2010).

Prior to the Norman invasion of Ireland in the 12th century, the ruling families on Ireland's west coast had extensive inland territories and their own merchant ships, trading directly with France and Spain (O'Halloran, 1916; Robinson, 2006). Much of their lands were lost to the Normans, but they continued to trade.
From the 13th century, two ports developed on Ireland's west coast through their trade with Spain. Dingle, in southwest Ireland is due north of A Coruña. It was paying customs on exports in 1257 and once had such a strong connection with Spain that the first Spanish diplomatic envoy to Ireland landed there in 1529 to sign a treaty. Galway, in the centre of Ireland's west coast, came to prominence based on its trade with Spain, particularly in wine (O'Sullivan, 1942). To this day, Galway has a harbour entrance to the old town walls called 'Spanish Arch' and has town houses built in the Spanish style. Galway's merchant families swapped sons with trading partners in north Spanish ports as a way of cementing trust (O'Sullivan, 1942).

When the English tried to suppress Irish direct trade at the end of the 16th century, the old ruling families were able to continue. Initially, this trade was open in nature as the British Government had little control along Ireland's western fringe, but with increasing sea patrols and eventually the establishment of a system of 'water bailiffs' (Platt, 2011) on land (later renamed the Coast Guards) this trade became hidden. Smuggling became so prevalent through the 18th century that it underpinned a rapid growth in population. It was this increased population, with little income after the smuggling was finally completely stopped in the 1830s, that suffered terribly when the potato crop failed in 1845 (Gibbons, 2004). With increasing suppression by the English, illicit trade would have evolved from the open landing of goods at quays in the early 18th century, to landing the goods via small boats in hidden bays and then more furtively at night, carrying the goods inland to hide them.

For these heathers to become established, their seeds need to be delivered to the right habitat. Early trade, before there were proper ports and roads, would have used natural harbours, which on many parts of Ireland's west coast would have been adjacent to heathland. This would still have been the case in the 15th century when *Erica erigena* is likely to have been introduced to Mayo (Foss & Doyle, 1988). Later illicit trade, which avoided the by now established ports and proper roads, would also have used this habitat. There is extensive heathland along the wild stretches of coast that was so ideal for smuggling.

The Irish populations of *Simethis mattiazzii*, are all associated with a discrete cove or other landing place near to Derrynane at the end of the Iveragh Peninsula, Co. Kerry (Lupton & Sheehy Skeffington, 2020). This is the principal family home of the O'Connells, who are known to have openly traded with France and Spain until the trade was suppressed by the British (MacDonagh, 1988). A family member has told us that his uncle used to tell them that the Kerry Lily came with the wine barrels. The only small Irish population of *Erica mackayana* adjacent to the coast is also next to a discrete cove, at Carna in Connemara. The rest are all approximately fifteen kilometres inland beside small roads or tracks. The more westerly of the two populations in Mayo (Fig. 12) is beside a long-abandoned track, now difficult to discern. 19th century maps show that this led to the shore of Blacksod Bay, part of the west coast screened from the open ocean by several islands and headlands. This is classic terrain for smugglers, who feared detection both from the land and the open sea. When smugglers had landed their goods, then *"to be avoided at all costs was to be caught in possession of the incriminating tubs, so hides and dumps for contraband near the coast were of great value"* (Platt, 2011). They would usually carry the goods inland, often at night, and hide them somewhere unlikely to be found, but somewhere, if found, that would not implicate them. The men were *"capable of moving their 90lb burden at a pace described as a very brisk walk for ten miles or more."* (Platt, 2011).

There is even a description of a smuggling ship entering Blacksod Bay in an account by an Englishman staying in a shooting lodge just inland from the coast and adjacent to the same track as *E. mackayana* occurs (Maxwell, 1832). The one population of *Erica mackayana* in Co. Kerry (Fig. 12) is beside a minor road which leads to a small coastal community with another house owned by the O'Connell family. The short track from there to the sea is still known as the "smugglers path" (Sheehy Skeffington & Van Doorslaer, 2015).

Establishment and Spread

That these species of heather establish easily is illustrated by recent non-native records for them in Britain and Ireland as garden escapes (Stroh *et al*., 2023). *Erica mackayana, E. erigena* and *E. vagans* are all reported as establishing easily from cuttings and can spread by branches taking root after being trampled into the ground by cattle or through being cut into for turf (Sheehy Skeffington & Van Doorslaer, 2015; Foss & Doyle, 1988; Nelson & Coker, 1974). This form of vegetative reproduction needs wet conditions, which are common in the west of Ireland. It would also explain their association with disturbance, which is not the case in Spain.

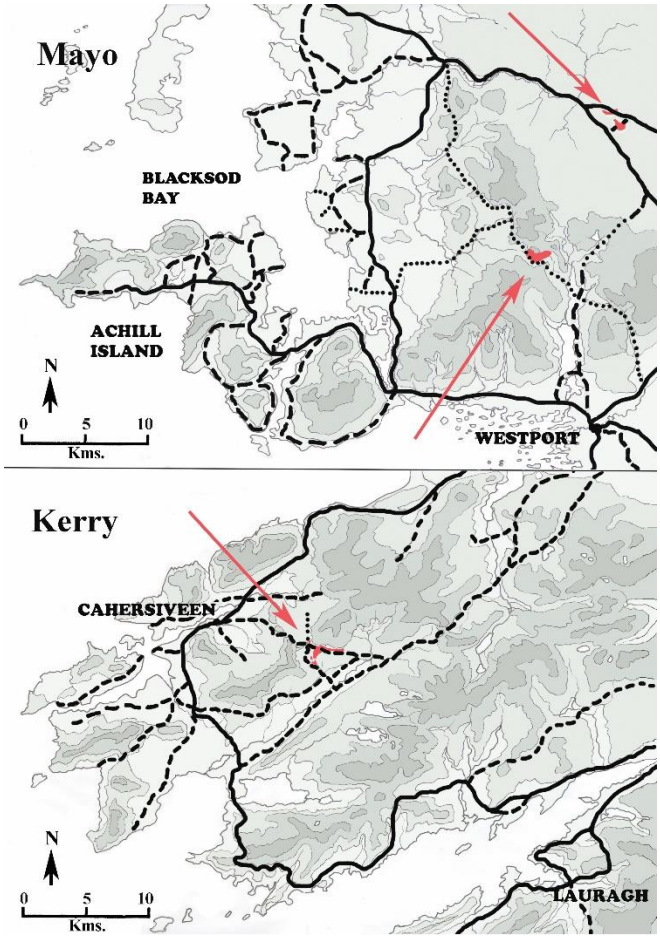

Figure 12. *Erica mackayana* in Co. Mayo and Co. Kerry in relation to terrain and roads. Major roads (——), minor roads (- - -) and tracks (•••). Contours represent 100 m, 200 m and 400 m altitude (from Sheehy Skeffington & Van Doorslaer, 2015).

The apparent failure of *Erica mackayana, E. vagans* and *E. ciliaris* to set seed in Ireland is likely to be because their populations have been derived from a single introduced individual which was self-incompatible. The lack of variation in the populations of the latter two species is evidence of this. If each of the *E. mackayana* populations on the west coast of Ireland is the result of a separate introduction

(Fagúndez & Díaz-Tapia, 2023), then individuals collected from each population should be able to cross-fertilize.

Each of the four *Erica* species, but not *D. cantabrica,* is associated with disturbed habitats in Ireland which are conducive to their spread: roads, tracks, stream sides, lake shores, coastal sites and cut-away bog. *Erica mackayana, E. erigena* and *D. cantabrica* are still actively spreading into new areas. While *Erica ciliaris* and *E. vagans* are confined to small colonies in Ireland, they are actively spreading in southwest England, where they set seed.

It is difficult to estimate the rate of spread for any of the heathers in Ireland. However, we can presume that for any one species the extent of spread in one population, as compared to another, is related to how long they have been present, while needing to acknowledge any disturbance or potential carriage that may have aided their spread. We can also presume that the rate is much slower when a species is not setting seed and so can only spread vegetatively through cuttings or trampled branches. This would account for the small size of the *E. mackayana, E. vagans* and *E. ciliaris* colonies in Ireland. It was the small size of the colonies of *E. mackayana* which made it possible to identify their likely original point of introduction, and lead to the realisation of the importance of smuggling.

When?

Where these five heathers occur in Ireland gives a clue as to when they might have originated. All but one of the populations of *E. mackayana,* the population of *E. erigena* at Roundstone in Connemara and the one population each of *E. ciliaris* and *E. vagans* are inland at places suitable for hiding smuggled goods at a distance which they could have been carried to overnight. None of these populations was discovered before the 18th century and all, except for *E. mackayana* on Roundstone Bog, are small enough in size to have originated from a single established plant during the late 18th century when this type of smuggling occurred.

Eighteenth century smuggling cannot be responsible for the populations of *D. cantabrica* and the principal population of *E. erigena*, as these populations are too large. First records also show they must have arrived much earlier. Pollen of *Erica erigena* dating back to the early 15th century was found where it is most extensive today, (Foss & Doyle, 1988). It may have occurred for much longer on the nearby coast, only spreading inland with the opening of the habitat that was also recorded then. *D. cantabrica* was first discovered in Ireland in 1700; reported by Richard Lhuyd as occurring in most of the mountains of Galway and Mayo (Nelson, 2011). Lhuyd was travelling down the west coast of Ireland and there is no evidence for how far he penetrated inland, but even if it grew only in the heathland near the coast, this would still mean that this species must have been present for some considerable time by then. *E. mackayana* on Roundstone Bog must also long pre-date smuggling as it is far more widespread in comparison to its other sites in Ireland and the hybrid is far more common.

A pre-historical introduction of *D. cantabrica,* and of the population of *E. mackayana* on Roundstone Bog is also indicated by genetic studies which all report reduced genetic diversity in line with a founder effect but genetic compositions which, while within that of plants sampled from north Spain, are distinct (Kingston and Waldren 2006, Beatty & Provan 2013, Pene Eftonga 2013, Fagúndez & Díaz-Tapia, 2023).

The conglomeration of records in southwest Connemara, where *E. mackayana*, *E. ciliaris*, *E. erigena* and *D. cantabrica* all grow (Fig. 2) may partially be related to the direct trade between Galway and Spain from the 14th century onwards (O'Sullivan, 1942). To avoid the British prohibition on international trade, imposed in the 1690s, the merchants of Galway, in collusion with the local garrison, loaded and unloaded goods on the south shore of Connemara from sailing ships calling into Galway. A 1737 report to the government detailing this activity mentions Roundstone Bay (Gibbons, 2004; Robinson, 2006). The large ornate house at Ballynahinch, to the north of Roundstone Bay, now an upmarket hotel, is known to have been built by the Martin family on the proceeds of smuggling (Robinson, 2006). Larkin's 1819 map of Co. Galway shows the estate and a track from the house, leading to the west shore of Roundstone Bay (Fig. 2). This is the location today of the small port of Roundstone, which developed around a harbour built in the 1820s, after this map was produced. Larkin's map shows only a few cottages scattered along the shore. Robinson (2006), who lived in Roundstone, found an old stone shed beside remnants of a simple quay, where this track would have ended. It had an insignia and the date 1731 carved into one of the stones. Larkin has 'store' marked at this point on his map.

The nearby location of *E. erigena,* behind Errisbeg Hill, would have been an ideal temporary hiding place for smuggled goods arriving at Roundstone Bay. Ballynahinch house was built where the track met the road to Galway. The population of *E. mackayana,* hidden amongst boulders, on the small bay at Carna could represent an alternative landing place for smuggled goods. Larkin's map shows no roads or tracks in this area.

It is likely this use of Roundstone Bay, and possibly others in southwest Connemara, would have preceded the suppression since the 1690s of international trade from Irish ports, simply as a way of avoiding paying taxes. It also seems likely that the bay's excellent natural harbour was used for collecting goods such as animal hides and wool, which were exported to Spain from west Connemara. The O'Flaherty's, once Lords of Connemara, had a castle on an island in Ballynahinch lake plus three castles on Connemara's west coast, one just to the west of Roundstone Bog, and owned ships for trading wool for wine and port back to the 12th century (Robinson, 2006).

It would also seem plausible that the bays on the southwest corner of Connemara, including Roundstone, could have been used much earlier, even the Bronze Age, for maritime trade to the south, and that the bog road follows a traditional route from the west coast to the head of Roundstone Bay and thus onward along the south coast of Connemara.

Such a possibility could account for the introduction of both *D. cantabrica*, and of the population of *E. mackayana* on Roundstone Bog. It could also account for the small population of *E. ciliaris* growing beside the track crossing the bog and near the centre of this *E. mackayana* population It is even possible they were all introduced together with *E. ciliaris* then unable to spread, while *E. mackayana* spread slowly, vegetatively and *D. cantabrica,* able to set seed, spread much more rapidly to cover much of Connemara today. The present distribution of *D. cantabrica*, confined by limestone to the east and by coast to the west and south, yet apparently only recently spreading into northern Connemara (Fig. 10), does appear to indicate an original introduction in south Connemara.

The suggestion that *E. erigena* may have been introduced through the pilgrimage to Santiago de Compostela (Foss & Doyle, 1988) appears compelling. The pilgrimage first became popular in the 12th century but initially only involved the recently arrived Anglo-Norman ruling class who went overland visiting other pilgrimage sites *en route*. Direct crossings by sea from Ireland are recorded from the 14th century and by the start of the 15th century the Gaelic Irish were frequently travelling there on pilgrimage (Cunningham, 2018). They embarked from a variety of places on the coast, not just recognised ports, and landed at A Coruña. The journey inland from there took them past sites for *E. erigena.* Notably, the one site for *E. erigena* in France is on a traditional pilgrimage route overland to Santiago de Compostela.

Should these species still be regarded as native?

The botanists who first found these heathers assumed they were native, as they were still discovering many new plant species in Britain and Ireland in the eighteenth and early nineteenth century. Even Praeger (1938), reporting *E. vagans* for the first time in Ireland, over 100 years later, concluded that this was a native species which would prove to have a much more extensive population in the then little-recorded hills and mountains of southwest Fermanagh.

Despite coming to realise how incongruous their distribution is, there has been an unwillingness to admit that these heather species might not be native. They have become an accepted, and treasured, part of the relatively limited Irish island flora. These heathers are elegant, some grown commonly as garden plants, and very local. None other than eminent Irish botanist Prof. D.A. Webb, setting out criteria for recognizing whether a plant species is native, warns of the '*curious emotional bias which I have found very widespread (and from which I may not be entirely free of myself) which favours native status for an attractive plant or for a botanist's home country*' (Webb, 1985). But when proposing as one of the criteria a failure to set seed, he then gives *E. mackayana* in Ireland as an exception, thus contradicting his warning.

When the first author's PhD student, Lieveke Van Doorslaer first attempted in the 1990s to publish the work on *E. mackayana* in BSBI's *Watsonia*, it was turned down because it suggested the species might not be native. *E. erigena* and *E. mackayana* continued to be treated as native to Ireland in some floras (Stace, 2019) and plant atlas (Preston *et al*., 2002) despite the published work of Foss & Doyle (1988, 1990) and Sheehy Skeffington & Van Doorslaer (2015). This reluctance might also explain why previous genetic work on *D. cantabrica* and *E. mackayana* failed to consider the possibility that they might have been introduced through human activity as an explanation for the results obtained (Kingston & Waldren, 2006; Beatty & Provan, 2013)

Zoologists, dealing with organisms that can more clearly migrate, have not had the same reluctance in more recent years. The Kerry Slug, *Geomalacus maculosus,* another Lusitanian species, is thus named for being long known only in Co. Kerry; and occurs elsewhere only in northern Spain. Irish populations genetically most resemble populations near Santander, on Spain's north coast, so that it was suggested that the Irish population may have derived from one or two founder individuals, introduced inadvertently through trade with Spain (Reich *et al*., 2019). The Banded Snail, *Cepaea nemoralis,* is widespread in Ireland, yet a genetic study

suggests that it was introduced to Ireland from north Spain with Mesolithic peoples, possibly brought as a food (Grindon & Davison 2013). Amongst the vertebrates, the genetic structure of the Irish population of the Eurasian Pygmy Shrew, *Sorex minutus* led to the suggestion that it also probably originated from a single founder event and that it has close affinity to Spanish animals, but not to those of Britain or the rest of Europe (Mascheretti *et al*., 2003).

Implications of human introduction

If the possibility that these five heathers were introduced through human activity is accepted, then a comparison of their distribution, along with that of *Simethis mattiazzii*, in Ireland gives some indication of how this may have happened. Fig. 13 shows the three mountainous regions with acidic soils that protrude into the Atlantic from Ireland's west coast. These are separated from each other by low-lying areas with limestone-influenced soils. All but *E. vagans* are species of acidic heathland habitats and in Ireland they all only occur on these three mountainous headlands. All but *E. mackayana* occur on only one of the headlands. It thus seems likely that each of these species, except *E. mackayana*, is derived from one introduction, as otherwise they are likely to occur in more than one part of the west coast. The small population of *E. erigena* at Roundstone may be the one exception.

Mountainous acidic habitat also occurs at places along the rest of Ireland's coastline, if less frequently, but none of these heather species is found there. The prevalence of smuggling along the wilder west coast and the pilgrimage to Santiago de Compostela from the west coast appear to explain recent introductions, but not those which must be earlier.

There are at least four other Lusitanian plant species which are that widespread in Ireland today that an introduction through human activity within historical times does not seem possible. The present distribution of *Euphorbia hyberna* (Irish Spurge), *Pinguicula grandiflora* (Large-flowered Butterwort), *Saxifraga hirsuta* (Kidney Saxifrage), and the slightly more widespread *S. spathularis* (St Patrick's Cabbage), might also suggest an original introduction on the west coast of Ireland in prehistoric times. There is thus evidence for a trade route between the Iberian Peninsula and specifically Ireland's west coast that has continued into historical times from some time in the distant past, perhaps even from the start of the Bronze Age and the introduction of *Arbutus unedo* to Kerry around 4,400 years ago (Sheehy Skeffington & Scott, 2021).

A human-aided introduction of any of the Lusitanian plant species from the Iberian Peninsula before the search for metals which brought in the Bronze Age, seems highly unlikely. Thus Jessen's (1949) discovery of fossil leaves of *Erica mackayana* on Roundstone Bog from the Boreal time appears unlikely and requires further investigation, particularly as the identification was subsequently questioned (Jessen, 1959).

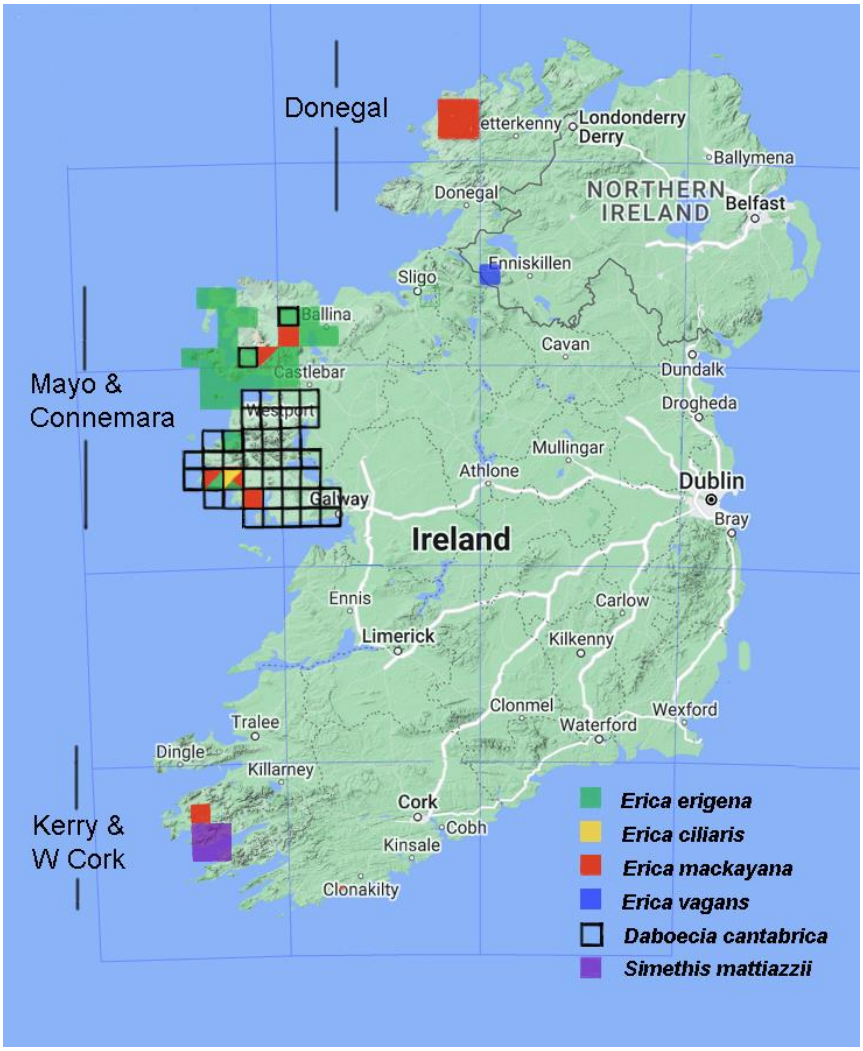

Figure 13. Irish distribution of heathland Lusitanian species using 10 km grid squares. From BSBI database (DDb) accessed December 2022. The three regions with acid rocks jutting into the Atlantic are indicated

It would seem possible that a direct crossing of the Bay of Biscay was enabled by the fact that the southwest tip of Ireland is directly north of the northwest corner of the Iberian Peninsula so that a boat sailing for several days out of sight of land could be guided by the north star. This is also the shortest direct crossing to Ireland from the Iberian Peninsula. This in turn would account both for A Coruña, on that corner of the Iberian Peninsula, being called 'Portus Brittanniae' and the reference to its lighthouse in the Irish 'Book of Invasions' as indicating the port of embarkation.

The concentration of Lusitanian heather records in the southwest of Connemara seems to indicate that southwest Connemara is particularly significant on this trade route. At present it is not possible to see why this might be so.

Prehistoric maritime connections within Europe are currently of great interest to archaeologists (e.g., https://www.gu.se/en/research/maritime-encounters). Our work on *Arbutus unedo*, which attempts to explain how this Lusitanian species may have arrived in Ireland in prehistoric times, proved to be very helpful for archaeologists trying to understand how peoples and past cultures first came to Ireland. More precise evidence for the prehistoric arrival of some of these heathland

species has the potential to be equally helpful, as well as confirming our suspicion that none is native. To this end we suggest a genetic investigation of *E. ciliaris*, *E. vagans*, *E. erigena*, *D. cantabrica* and *Simethis mattiazzii* similar in detail to that undertaken for *E. mackayana* (Fagúndez & Díaz-Tapia, 2023). This could potentially show where each came from and whether they came as more than one introduction. Populations of *E. vagans* and *E. ciliaris* in southwest England and *E. ciliaris* in northern France should be included. Such a genetic investigation needs to be supplemented by evidence for when their introduction might have occurred. Of particular interest is the arrival of *E. mackayana* to Roundstone Bog and *D. cantabrica* to Connemara. Estimating their rate of invasion in recent years might help, but several detailed cores examining both pollen and macrofossils would have greatest potential.

Conclusion

We now understand enough about the ecology and genetics of plant invasions to question the status of these five heather species as native to Ireland. We have discussed how they all have many characteristics indicative of an introduced species. They also all occur in places where they could easily have been introduced, and we have provided possible explanations for their carriage and introduction from the Iberian Peninsula.

These five species grow in heathland habitat both in the Iberian Peninsula and in Ireland. Thus, the evidence for the introduction of each of the individual species is cumulative and as such seems overwhelming. Although there may be less evidence that *D. cantabrica* has been introduced through human activity, if it is accepted that the other species have probably been introduced, then the most feasible explanation for the incongruous distribution of *D. cantabrica* in Ireland is that it was also originally introduced through human activity, but long enough ago to account for the subsequent genetic differentiation from the parent population. This is also the case for the population of *E. mackayana* on Roundstone Bog.

Further evidence that these species have been introduced would provide valuable information to archaeologists studying ancient trade routes and human migrations. Genetic studies of their Irish, and English, populations along with those in the Iberian Peninsula could demonstrate where they probably originated from, as for the Kerry Slug, *Geomalacus maculosus,* (Reich *et al*., 2019), Strawberry Tree, *Arbutus unedo* (Sheehy Skeffington & Scott, 2021) and now also Mackay's Heath, *Erica mackayana,* (Fagúndez & Díaz-Tapia, 2023). Palaeoecological studies might demonstrate when they first arrived in Ireland and even, as with *Arbutus unedo* in Kerry, where they arrived and how they spread. However, the evidence already gathered here, is such that all five species should now be regarded as probably naturalised. Until further studies provide evidence for when each species first arrived, we suggest they be all regarded as archaeophytes, defined as species that have arrived prior to 1500 AD (Preston *et al*., 2004). We also suggest that the listing of *E. vagans* in the Wildlife (Northern Ireland) Order 1985, as amended by the Wildlife and Natural Environment Act (Northern Ireland) 2011, might be revised.

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