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Snake's-head Fritillary *Fritillaria meleagris* (Liliaceae) in Britain: its distribution, habitats and status

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Abstract
Snake's-head Fritillary *Fritillaria meleagris* L. (Liliaceae) is a scarce plant of unimproved meadows where it was formerly considered to be a native British species. A review of 593 British sites showed that 80% of British populations were located in other habitats where it had been planted or had established from introductions nearby. Of the 118 populations located in unimproved meadows, 53 occurred in floodplain grassland in central and southeast England where it has long been considered to be native. However, recent evidence suggests that it is more likely to be a modern introduction (neophyte). It seems inconceivable that such an attractive plant would have been overlooked in the wild by herbalists in the fifteenth and sixteenth centuries. Furthermore, the rapid growth of introduced populations in meadows in Sweden and England has shown that populations of *F. meleagris* in Britain could have reached their present size in the 300 years since they were first recorded in the wild. Historical accounts prove that it was being grown for ornament in large gardens in the sixteenth century, from where it presumably escaped along rivers to colonise meadows downstream. Regardless of its status, however, it remains a much-loved and valued component of the British flora and a flagship species for the conservation of floodplain grasslands.

Keywords: floodplain meadows; genetics; population growth; neophyte.

Introduction

In Britain *Fritillaria meleagris* L. (Liliaceae), Snake's-head Fritillary, is a Nationally Scarce plant that was formerly considered to be native in wet, species-rich eutrophic meadows on alluvial soils and gravels in lowland England (King & Wells, 1993; Wells, 1994). Most of these populations are, or were, on the floodplains of the River Thames and its tributaries between Cirencester, Oxford and Reading with outlying populations in Suffolk, Herefordshire, Staffordshire and Buckinghamshire, although populations occur in floodplain meadows in other regions (Jefferson & Walker, 2019). In these areas presumed native populations are located in unimproved meadows that have been traditionally managed for hay and support species-rich grasslands related to *Alopecurus pratensis-Sanguisorba officinalis* (MG4) grassland of the British National Vegetation classification (Rodwell, 1992; Jefferson & Pinches, 2011). Away from meadows *F. meleagris* has also been widely planted as an ornamental and naturalises readily in private gardens and semi-wild and wild

locations such as on roadsides or in nature reserves. Some of these planted populations persist in drier and more shaded habitats than in floodplain meadows although in Europe it is often found as a native in woodlands and in relatively dry alpine pastures (Jefferson & Walker, 2019).

More has probably been written about the status of *F. meleagris* in Britain than any other plant species. Oswald (1992) argued that meadow populations adjacent to major rivers in central and southeast England are likely to be the remnants of a 'Greater Rhineland' population that extended across the North Sea (Doggerland) after the end of the last glaciation. These populations were gradually cut-off from Continental Europe by rising sea-levels, isostastic adjustments and possibly finally by tsunamis caused by the Storegga submarine landslide around 8,200 years ago (Coles, 2000).

However, the very late year of discovery in the wild in Britain (1737) has led many botanists to question its native status. Harvey (1996) argued that it would have been inconceivable that earlier botanists of the calibre of Ray and Turner would have missed such an attractive species if it was growing in the wild during their lifetimes. Others cite the lack of references to it in literature, art, architecture, local folklore and placenames and its absence from the fossil record (Godwin, 1976; Pennington, 1977). Weighing up arguments on both sides Pearman (2007, 2013) concluded that it was most likely an ornamental introduction to monastic gardens that escaped to colonise semi-natural habitats in the eighteenth century, especially in the vicinity of Swindon and Oxford.

Due to the lack of definitive evidence either way, the authors of the *New Atlas of the British and Irish flora* treated *F. meleagris* as 'native or alien' mapping hectads with populations in unimproved meadows in south, east and central England as native and hectads with occurrences in other habitats such as parks, churchyards, and road verges as alien (Preston *et al.*, 2002). Meadow populations were generally accepted as native if they were located in floodplain meadows and had a long history. Recent floras have followed suit describing it as 'doubtfully' or 'possibly' native (Stace, 2010, 2019) despite its official status having been changed to neophyte in 2010 (Leach, 2010, 2019).

In this paper I review some of the evidence used to assess the status of *F. meleagris* in Britain and Ireland namely (1) its distribution and occurrence in different habitats, (2) its discovery in the wild, and (3) population growth at sites where it is known or suspected to have been introduced.

Methods

In order to assess its distribution and occurrence in different habitats I used *c.*1300 distribution records of *F. meleagris* held in the BSBI's Distribution Database (BSBI DDb accessed March 2019; https://database.bsbi.org/) to differentiate populations that occurred in unimproved meadows from other habitats where it was known or suspected to have been planted or had become established from introduced populations nearby. I assigned each record to a unique site and habitat using digital maps and satellite imagery (https://www.bnhs.co.uk/2019/technology/grabagridref/gagr.php) combined with information submitted with the records or provided in county floras, rare plant registers and published papers. All populations were assumed to have been introduced with the exception of those located in unimproved meadows. These were

categorised as either native or introduced, the latter where their origin was uncertain or where they were known or suspected of having been originally introduced or had established from introduced populations nearby.

The year of discovery in the wild for each population was taken from a variety of sources including dates in the BSBI DDb, county Floras and published papers (e.g. Kent, 2001) and compared to the year of discovery in the wild for all other British native species. Dates of discovery for natives were taken from Pearman (2017).

Information on the growth of an introduced population on Kunsängen Meadow in southern Sweden was taken from Zhang (1983) and Zhang & Hyttteborn (1985). Information on the establishment of a population on Portholme Meadow SSSI, Huntingdonshire, were taken from published counts and more latterly annual monitoring carried out by Lynne Farrell, myself and co-workers (L. Farrell, pers. comm.). Information on the establishment of Fritillary at Aubert Ings SSSI, North Yorkshire, was based on annual counts undertaken by the author since 2003. Monitoring at both sites usually took place in the first half of April and was based on counts of flowerheads as well as vegetative shoots and flowers that had been bitten off. The numbers of purple and white flowers were also counted at both English sites.

Results

Distribution and number of populations

593 unique site-populations were identified from BSBI records held in the DDb. These sites were widely scattered across Great Britain with a single site in southeast Ireland (Fig. 1). The majority of populations were located in south central and south eastern England especially in Surrey (n=37), Oxfordshire (n=34), Berkshire (n=30), Buckinghamshire (n=26), North Wiltshire (n=24) and Middlesex (n=22). Large concentrations of populations were also found in the Midland counties of Leicestershire (n=20), Worcestershire (n=19) and Staffordshire (n=19) and in East Suffolk (n=17) where it has long been known from ancient, unimproved meadows (Trist, 1960, 1978, 1981). Elsewhere in England it was more thinly scattered, as in Wales and Scotland where most recent records, especially in north and northwest, were from private gardens. The only Irish site was on a roadside near to Adamstown, County Wexford, in the Republic of Ireland.

Although widespread *F. meleagris* remains a very localised plant in Britain with 281 hectads (72%) supporting single populations. Only 10 hectads supported five or more populations and two hectads, both near Oxford (SP50, SP70), supported 18 and 12 populations respectively although virtually all the meadows in SP70 have now been destroyed.

Habitats

Non-meadow habitats

Of the 593 populations included in this study 475 (80%) originate from deliberate plantings or as escapes into non-meadow habitats (Table 1). Most of these populations were located in urban areas such as parks, amenity grassland and educational establishments (21%) or in the grounds or parkland of large country houses (15%). *F. meleagris* has a strong association with religious sites and has often been planted in churchyards, cemeteries and in the grounds of convents (14%) where in some cases it has been established for many decades. Increasingly

F. meleagris has also being planted on roadside verges or alongside other boundary habitats (14%), in some cases in large numbers as part of road development schemes, although some of these populations may have originated as escapes from private gardens. It has also been planted in a range of grasslands (6%) including on riverbanks or in riverside grasslands where plants may have originated from seed dispersed from populations upstream. It is also now a popular garden plant due to its attractive flowers, hardiness, and ease of growth. As a consequence there were records from residential gardens (6%) although this is likely to be a significant underestimate given that botanists generally do not submit records from private gardens (Walker, Pearman & Stroh, 2016). In recent years it has also been planted in many country parks or in nature reserves (6%) managed by national and local conservation organisations presumably to increase the wildlife interest of the site as well as to raise awareness of the loss of species and habitats. Finally, a number of private landowners have planted *F. meleagris* in woodlands, plantations or orchards (6%) where in some cases it has persisted for several decades.

Meadow habitats

F. meleagris has been recorded in 118 unimproved meadows supporting species-rich vegetation (Table 1). In 53 of these meadows there was no evidence that it had been deliberately introduced or had colonised from introduced populations nearby and consequently, these hectads were mapped as native in Preston *et al*. (2002). Most of these meadows were located on the floodplains of the River Thames and its tributaries between Cirencester and Oxford and around Reading and Thame (Fig. 2). These include the famous Wiltshire Fritillary meadows at North Meadow, Clattinger Farm and Oaksey (Grose, 1957; King & Wells, 1993) and those close to Oxford such as Iffley Meadow, Magdalen Meadow and Ducklington Mead (Erskine *et al*., 2019).

In the past, there was also a large concentration of Fritillary meadows along tributaries of the River Thames to the east of Oxford between Haddenham and Ford in Buckinghamshire but the majority of these have now been improved and *F. meleagris* probably now only survives at one site (Fritillary Field, Haddenham). In East Suffolk Fritillary occurred in a handful of meadows where it was formerly thought to be native including the famous Fox Fritillary Meadow, near Framsden where the public are encouraged to visit the Fritillary's each spring (Trist, 1981).

In Staffordshire it was considered native on Mottey and Broad Meadow near Tamworth (Hawksford *et al*., 2011). Elsewhere there are single putative native populations on Portholme Meadow in Huntingdonshire, Lugg Meadow in Herefordshire, Stanford End on the Berkshire and North Hampshire border and Stanfield in Norfolk.

Of the 53 populations in unimproved meadows that were formerly thought to be native only 23 are thought to survive (Table 2). The reasons for this decline, which has largely taken place since the 1970s, is due to the drainage and conversion of hay meadows to arable and improvement for more intensive production of silage (Horton & Jefferson, 2006). Most of the surviving sites have now been designated as Sites of Special Scientific Interest (SSSI) and are managed as hay meadows to ensure the survival of *F. meleagris* and its associated hay meadow flora. However, in a few cases populations numbers of *F. meleagris* have declined on SSSIs due to improvement and as a result sites have been denotifed such as Coleshill Meadow, Upper Waterhay, Long Meadow, Inglesham Meadows (Horton & Jefferson, 2006).

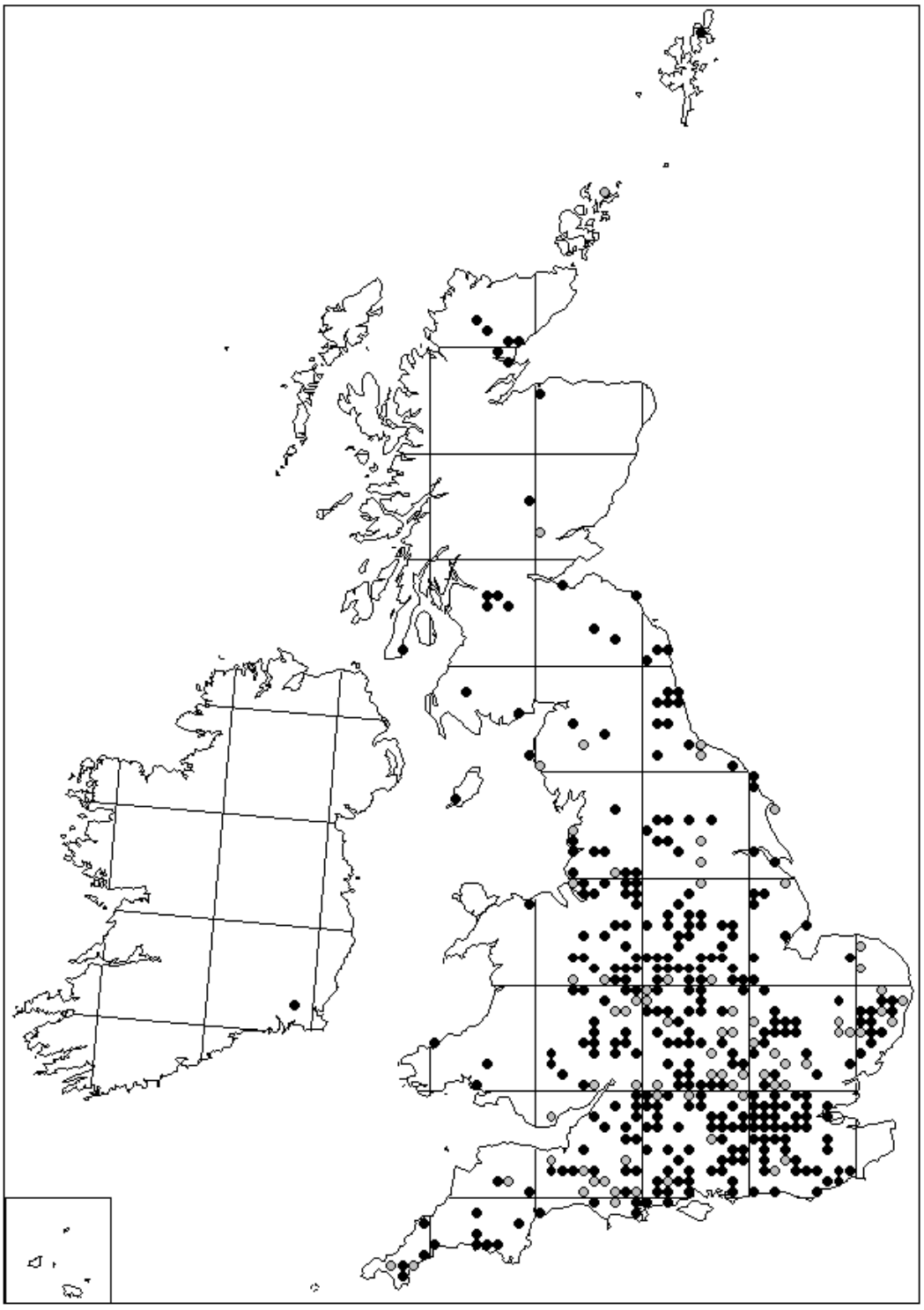

Figure 1. Distribution of *Fritillaria meleagris* in Britain and Ireland. Grey circles indicate where *F. meleagris* was recorded before 2000 and black circles where it was recorded between 2000-2019.

Table 1. The number of populations of *Fritillaria meleagris* in different habitats in Britain and Ireland. The numbers are derived from records held within the BSBI's Distribution Database. The habitats (see notes below table) are divided into meadow and non-meadow habitats and are listed in rank order and within BSBI recording date-classes.

Habitat	Before 1930	1930-1969	1970-1986	1987-1999	2000-2019	Total	%
(a) Non-meadow							
Urban (non-residential)	1	2	6	16	101	122	21
Formal gardens and parkland	5	5	23	22	46	87	15
Religious buildings and grounds	1	1	11	20	53	82	14
Road verge and boundary	0	0	1	6	38	42	7
Grassland (non-meadow)	0	0	2	9	30	37	6
Residential garden	1	1	3	2	30	37	6
Country parks & nature reserves	0	0	2	10	31	36	6
Woods, plantations, orchards	0	2	4	6	22	32	5
Total	8	11	52	91	351	475	80
(b) Unimproved meadow							
Native	7	19	43	33	23	53	9
Origin uncertain	2	0	2	10	27	36	6
Planted	4	0	1	4	23	29	5
Total	13	19	46	47	73	118	20
Total	21	30	98	138	424	593	100

Notes on habitats: 'Urban (non-residential)' – occurrences in urban areas outside of private gardens, mainly urban parks/amenity grassland but also including plantings in school and university grounds; 'Formal gardens and parkland' – mainly plantings in formal gardens of large country houses and estates, including meadows and rough grassland; 'Religious building and grounds' – mainly plantings in churchyards or cemeteries but also includes the gardens of religious buildings such as convents; 'Road verge and boundary' – in grassland next to roads, cycleways, tracks and footpaths; 'Grassland (non-meadow)' – occurrences in wide variety of other grasslands types including rough, marshy, calcareous, coastal, riverside, etc.; 'Residential garden' – private gardens including abandoned gardens that are now semi-wild; 'Country parks and nature reserves' – mainly plantings in rural (country) parks and nature reserves; 'Native' – unimproved meadows supporting species-rich eutrophic grasslands (e.g. MG4) where *F. meleagris* has long been thought to be

native (see Table 2 for further details); 'Origin uncertain' – likely to have been planted or colonised from introduced populations nearby; 'Planted' – unimproved meadows where Fritillary is known to have been planted.

Today the largest populations occur on the floodplains of tributaries of the River Thames near to Swindon and Oxford. At North Meadow near Cricklade numbers have been estimated to exceed half a million in some years (Rothero *et al.*, 2016) and nearby at Upper Waterhay and Clattinger Farm there are an estimated 30,000 and 35,000 respectively. Near Oxford an estimated 30-70,000 plants grow in a meadow by the Thames at Iffley (Wolstenholme, 2011) and at Ducklington Mead near to Witney an estimated 100,000 plants grow in a meadow by the River Windrush (Erskine *et al.*, 2018). All other extant populations hold fewer than 2,000 plants, and many have less than a few hundred blooms.

Although considered to be native at other sites it is possible that *F. meleagris* was deliberately planted at some of these, such as Portholme Meadow, Huntingdon, where it was first recorded in 1925. The famous botanist E.W. Hunnybun lived close to the meadow for much of his life (1848-1912) and so it seems unlikely that he would have missed it during his lifetime. At Lugg Meadow in Herefordshire the dominance of white flowers has led some to suggest that the entire population may have arisen from an original planting (Brian & Thomson, 2002). Likewise at one meadow in Suffolk *F. meleagris* grows with a range of garden plants which may indicate that part of the meadow once formed part of a garden or orchard (Trist, 1981).

As well as the native sites *F. meleagris* also occurs in 65 species-rich meadows where it is known or strongly suspected to have been deliberately planted or had become naturalised (Table 1). These meadows are widely distributed throughout lowland England, mainly in the southeast and midlands with outliers in northern England, such as Owston Meadows SSSI near to Doncaster (Secombe, 1983, 2011), Aubert Ings SSSI near to Knaresborough in North Yorkshire and Billingham Beck Valley near to Middlesborough (Fig. 2). Some of these populations occur in species-rich meadows close to putative native sites, such as Chimney Meadows SSSI in Oxfordshire, where *F. meleagris* has been introduced as part of a large hay meadow restoration scheme.

Discovery in the wild

F. meleagris was first discovered in the wild at Mauld Fields, Middlesex in 1737, where it had been present for at least 40 years (Kent, 2001; Pearman, 2017). Over the subsequent 60 years it was found in 11 vice-counties including two sites where it still occurs today: at Magdalen Meadow, Oxford, in 1785 and Mottey Meadow, Staffordshire in 1787 (Kent, 2001). In the first half of the nineteenth century it was recorded from a further 15 vice-counties with sites where it still occurs today including Stanford End, Berkshire in 1802, Lugg Meadow, Herefordshire in 1805, Mickfield Meadow, Suffolk in 1829, Broad Meadow, Staffordshire in 1835, Fox Fritillary Meadow, Suffolk, 1836 and Spring Farm Meadow, Suffolk, 1837. However, many of its most famous sites in Wiltshire and Oxfordshire were not discovered till the second half of the nineteenth century, most notably North Meadow, Cricklade in 1860, Iffley Meadows in 1869 and Ducklington Mead in 1886. Populations continued to be found throughout the twentieth particularly in the latter half when many

planted and naturalised populations were recorded in regions away from areas where it had traditionally been considered to be native (Fig. 3). However, eight apparently native populations were discovered after 1900 including Clatter Farm in 1969, which holds one of the largest British populations (Gibbons, 2001) and most recently New Marston Meadows and Hinksey Meadow near to Oxford, the latter discovered as recently as 2006 and possibly a colonist from meadows further upstream.

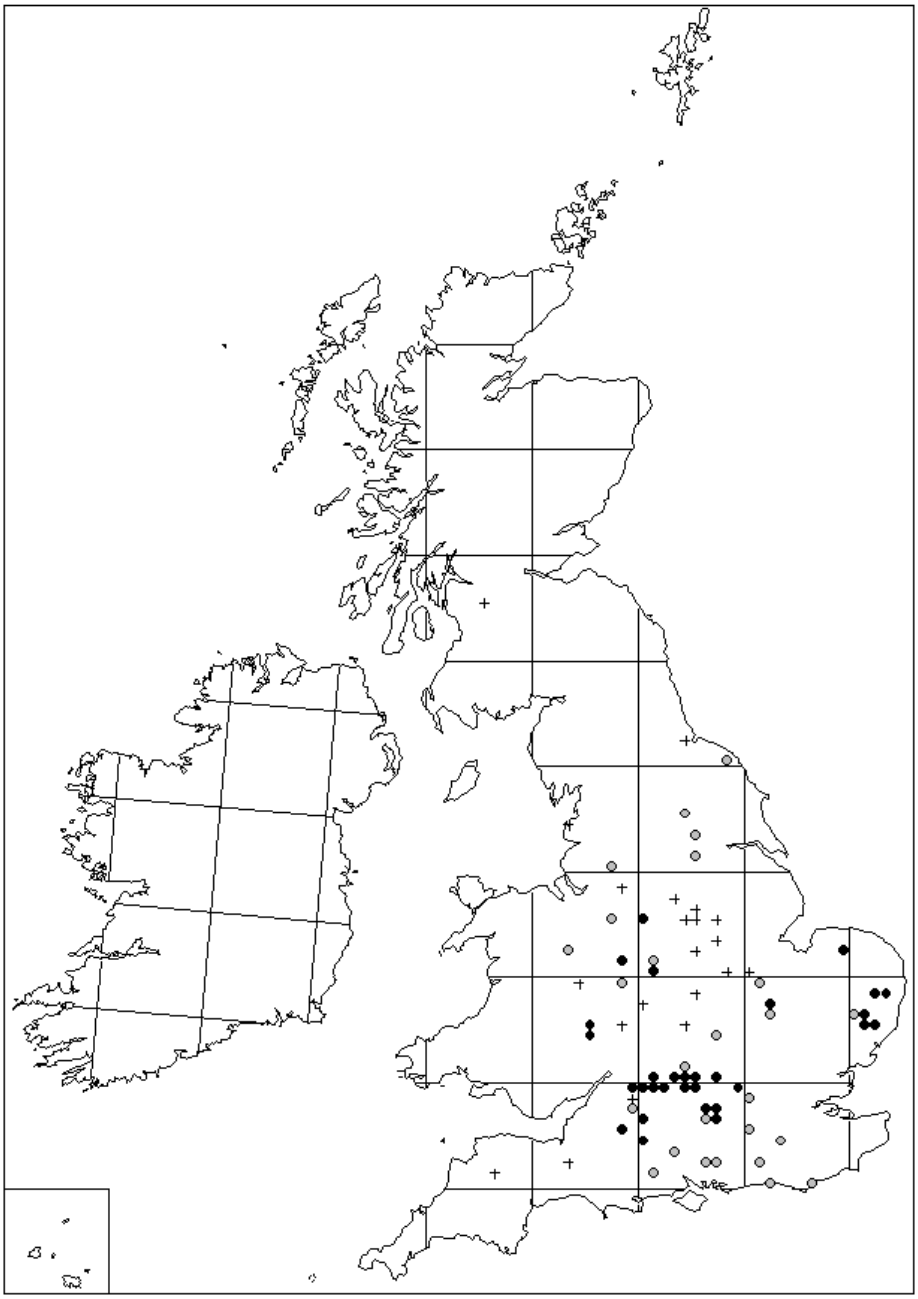

Figure 2. Distribution of *Fritillaria meleagris* populations in species-rich hay-meadows and pastures. Black circles indicate species-rich meadows where *F. meleagris* was formerly considered to be native; grey circles are hectads where *F. meleagris* is suspected of having been introduced and the crosses indicate known introductions.

Table 2. Extant populations of *Fritillaria meleagris* in unimproved meadows where formerly considered native.

Site name	First year	No. of plants	Details
Oaksey Meadows, Wiltshire	1862	?	Formerly in a number of meadows near to Oaksey; now confined to one area.
North Meadow SSSI/NNR, Cricklade, Wiltshire	1860	>500,000	Lammas meadow with c.80% of the entire GB population (Wolstenholme, 2011).
Upper Waterhay SSSI, Wiltshire	1949	10-30,000	Species-rich meadow dominated by white form (Pilkington, 2007).
Clattinger Farm SSSI, Wiltshire	1969	35,000	A series of species-rich meadows with an exceptionally rich flora (Gibbons, 2001).
Coleshill Meadow, Wiltshire	1897	<200	Decline since 1970s due to improvement (Horton & Jefferson, 2006).
Upper Inglesham, Lynt Farm, Wiltshire/Berkshire	1888	2,000	Semi-improved but *F. meleagris* still present (Pilkington, 2007).
Stanford End Meadow, Hampshire/Berkshire	1802	100s	A large population mostly in Berkshire (Crawley, 2005; Rand & Mundell, 2011).
Iffley Meadows SSSI, Berkshire	1869	30-70,000	Famous meadow population close to Oxford (Wolstenholme, 2011)
Grafton Lock Meadow SSSI, Berkshire/Oxfordshire	1970	50-200	Species-rich meadow adjacent to the River Thames.
Ducklington Mead SSSI, Oxfordshire	1886	100,000	Species-rich meadow by the River Windrush, near Witney (Erskine *et al.*, 2018).
Hinksey Meadow (Osney Mead), Oxfordshire	2006	300	Species-rich flood meadow near to Oxford (King, 2018).
Magdalen Meadow, Oxfordshire	1785	1,000s	Species-rich meadow within the Magdalen College grounds.
New Marston Meadows SSSI, Oxfordshire	1978	<20	Small populations scattered across three species-rich meadows (Webb, 2011).
Fritillary Field, Haddenham, Buckinghamshire	1971	?	Formerly in a number of meadows now possibly confined to a single field.

Fox Fritillary Meadow SSSI, Framsden, Suffolk	1836	100s	Species-rich meadow with both purple and white forms (Sanford & Fisk, 2010).
Mickfield Meadow SSSI, Suffolk	1829	500-1,000	Species-rich meadow, possibly introduced (Trist, 1978; Sanford & Fisk, 2010).
Martins Meadow NR, Monewden, Suffolk	1956	300-400	Species-rich meadow, possibly introduced (Sanford & Fisk, 2010).
Spring Farm Meadow, Suffolk	1837	1,000	Damp, species-rich meadow (Sanford & Fisk, 2010).
Fritillary meadow, Stanfield, Norfolk	1990	?	
Portholme Meadow SSSI, Huntingdonshire	1925	500-1,000	Meadow by River Great Ouse where it was possibly introduced (Doody, 2007).
Lugg Meadows SSSI, Herefordshire	1805	1-2,000	Lammas meadow where white form dominates (Brian & Thomson, 2002)
Mottey Meadows SSSI/NNR, Staffordshire	1787	250	Species-rich alluvial flood meadow (Hawksford *et al.*, 2011).
Broad Meadow, Tamworth, Staffordshire	1835	600	Species-rich alluvial flood meadow (Hawksford *et al.*, 2011).

When compared against other species we see that almost three-quarters of British and Irish plants had been recorded by the time *F. meleagris* was found growing in the wild (Fig. 3). If it was a native species then it seems inconceivable that it would have been found so late, especially given that the core of its distribution was so close to such a well botanised area as Oxfordshire. As Druce mused in his *Flora of Oxfordshire*: "It is not a little singular that the Fritillary, so conspicuous a plant of the Oxford meadows, should have so long remained unnoticed by the various botanists who had resided in or visited Oxford" (Druce, 1886, p.387). Grigson (1955) goes further adding: "It seems not only singular, but impossible. The only explanation is that the Fritillaries were not there, that they are not native, that they spread from foreign plants set in the Tudor or Jacobean garden". Harvey (1996) came to similar conclusions adding that *F. meleagris* would have been impossible to overlook and it was unthinkable that such eminent botanists such as Turner, Gerard, Parkinson, Johnson, and Ray would have missed it during their lifetimes. He concludes, "firmly though regretfully" that they were not there, a sentiment echoed by Pearman (2007) in his review of the status of Fritillary.

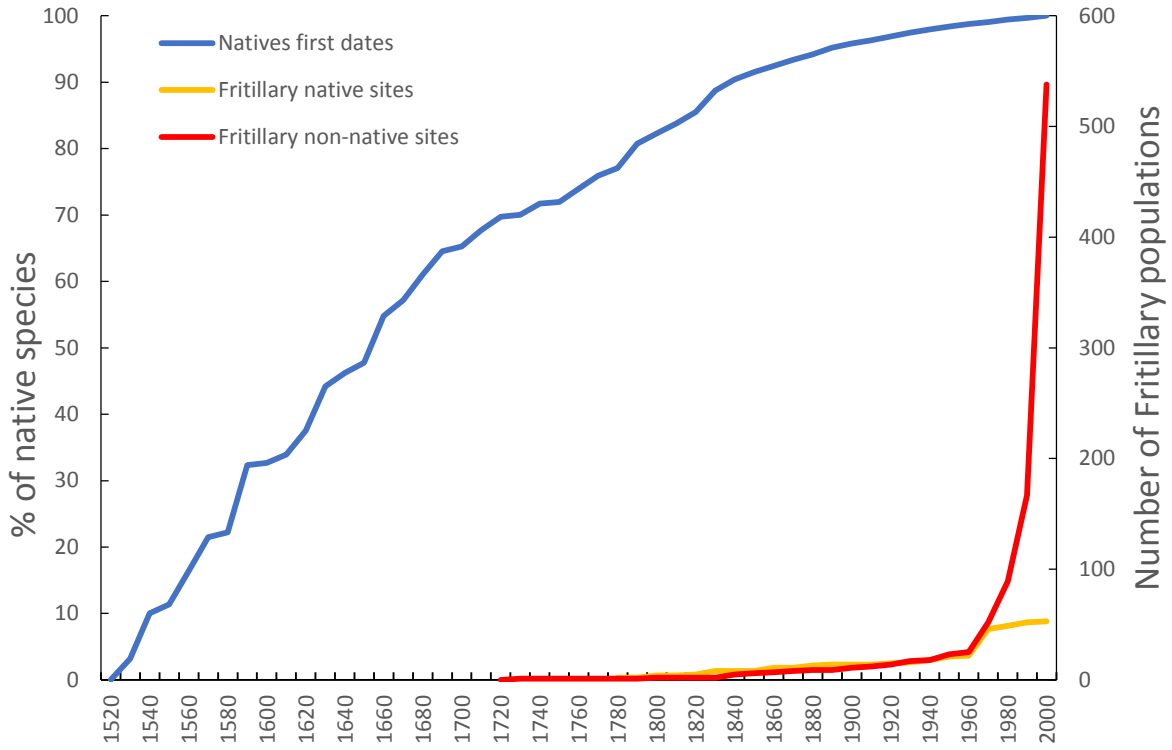

Figure 3. Graph showing the cumulative percentage of native plant species discovered in the wild in Britain and Ireland within each decade (blue line) against the cumulative number of non-native (red line) and native (orange line) populations of *F. meleagris*. The year of discovery for native species was taken from Pearman (2017) and the first records for Fritillary populations were compiled as part of this study.

Growth of introduced populations

One of the main arguments for *F. meleagris* being native is its abundance in ancient grasslands, most famously at North Meadow, Cricklade, where its numbers exceed half a million plants in some years (Wolstenholme, 2011; Rothero *et al.*, 2016). The sheer size of these populations has led to an assumption that they must be native. However, it is now clear that introduced populations can grow rapidly under a traditional hay management regime. The main evidence for this comes from Kungsängen [King's] Meadow near to Uppsala in Sweden. Documentary evidence has shown that *F. meleagris* escaped from a nearby botanic garden and colonised the meadow shortly before 1742 (Zhang, 1983). Over the following two centuries *F. meleagris* spread throughout all but the lowest lying areas of the meadow and the population increased and now comprises hundreds of thousands of blooms each spring (Fig. 4). This meadow lies on the floodplain of the River Fyris and like those in Oxfordshire and Wiltshire it supports MG4 grassland that is shut-up for hay in the spring and summer and aftermath grazed by sheep during the winter months (Zhang & Hytteborn, 1985).

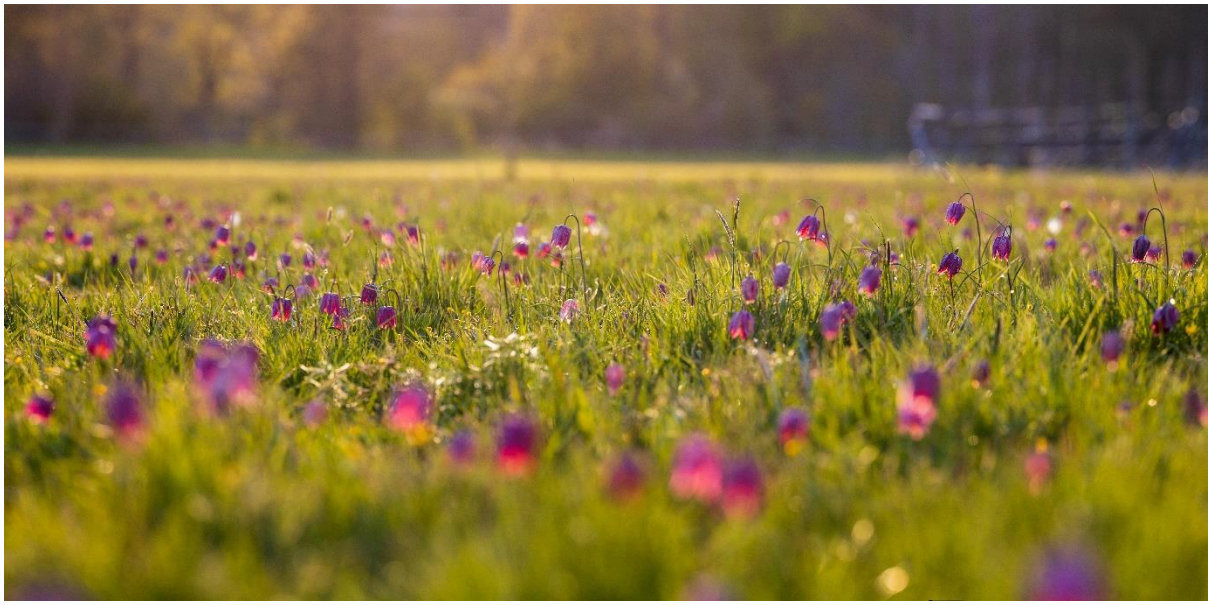

Figure 4. *Fritillaria meleagris* on Kungsängen Meadow near to Uppsala in Sweden. *F. meleagris* first colonised this meadow in 1742 after escaping from the Uppsala Botanic Garden. Image: Ulf Bodin, shared under license CC BY-NC-SA 2.0 (https://www.flickr.com/photos/ulfbodin/49895507936).

A similar pattern is emerging on Portholme Meadow SSSI in Huntingdonshire where *F. meleagris* is likely to have been introduced shortly before 1925 (Druce, 1926; Wells, 2003). For many years a single clump was present adjacent to a low-lying depression but monitoring by local botanists revealed a dramatic increase in numbers after about 70 years (Fig. 5). Since then the original colony has continued to increase and now has more than 1000 flowers in some years. *F. meleagris* has also spread to other parts of the meadow in some cases up to 600 m away from the main colony presumably as a result of the dispersal of seed during hay-cutting or winter floods. At current (exponential) growth rates the population will increase to tens of thousands of plants over the coming century.

Since 2003 I have also been monitoring a small colony on river floodplain near to Knaresborough in North Yorkshire. Like Portholme, it is located in MG4 grassland in an ancient meadow, Aubert Ings SSSI, that is cut for hay and aftermath grazed by sheep. Its origin is unknown but is likely to have originated from seed brought in by floodwaters from the adjacent River Nidd. Since I noticed a single plant in 2003, the population has spread over about a hectare of meadow with numbers increasing to more than 119 plants by 2019.

All three sites show that *F. meleagris* has the capacity to regenerate rapidly under a traditional hay meadow regime where plants are able to shed seed during the hay-making period and aftermath grazing and flooding reduces the competitive dominance of the surrounding sward.

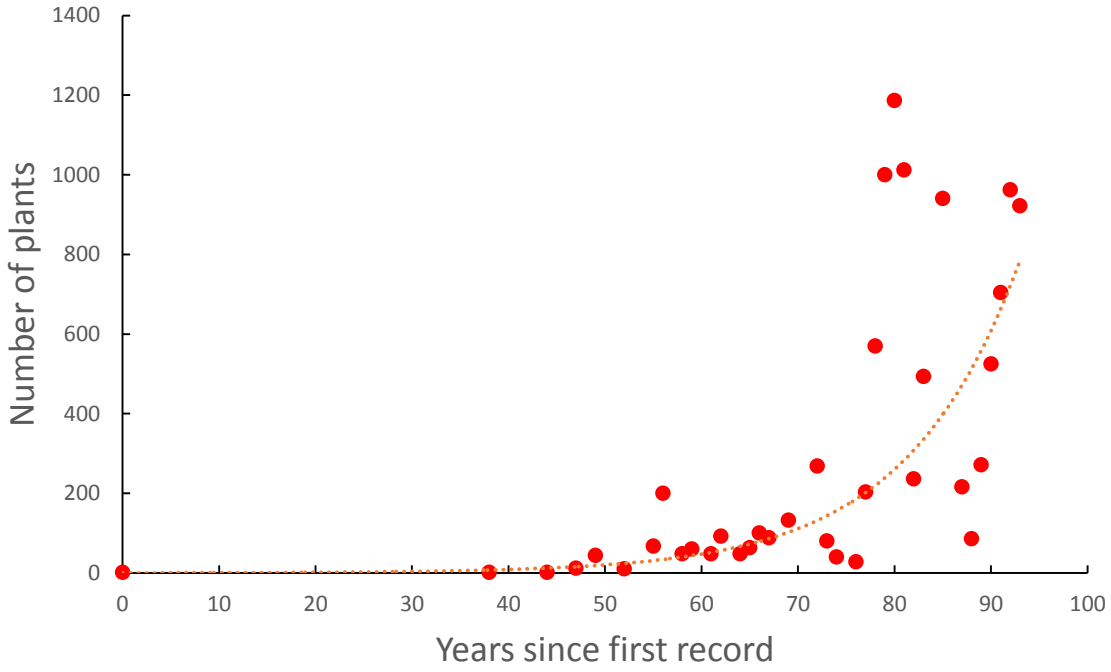

Figure 5. The number of *Fritillaria meleagris* recorded on Portholme Meadow, Huntingdonshire relative to the year it was first recorded (1925).

Conclusions

We will possibly never know the true status of *F. meleagris* in Britain but on balance the evidence points to it being a modern introduction. A genetic study by Day (2017) showed that British *F. meleagris* forms part of a much broader Northern European population and is not distinct from it. Whilst that alone does provide strong evidence either way, it's very late year of discovery in the wild suggests that it was most likely brought to Britain by plant collectors from one of these Northern European regions after 1568 when the species was first described in Europe (Day, 2017). *F. meleagris* became popular as an ornamental species and was widely planted in large houses and gardens along the Thames Valley from where it presumably escaped to colonise floodplain meadows downstream. The failure of botanists to find such an attractive plant in the wild before 1737 strongly supports this garden origin. Once established it presumably increased rapidly under a hay meadow management regime. Its behaviour at Kunsängen and Portholme Meadow provides evidence for this and

shows that large colonies, such as at North Meadow, could have developed naturally within the last 300 years.

Although *F. meleagris* remains an iconic species of floodplain meadows the results of this study have shown that it is now far more common in non-meadow habitats where it has either been deliberately planted or has naturalised from introduced populations nearby. Although the dramatic increase in populations in recent decades may be due to better recording of alien species and alternative habitats, there is no doubt that it is being more widely planted than in the past, especially in semi-wild and wild locations such as amenity areas, nature reserves, country parks and urban roadsides. This is not surprising given its beauty, the ease with which it can be grown from bulbs, its widespread availability in garden centres and association with wild habitats. This widespread introduction is possibly also resulting in an increase in established populations in semi-natural habitats, as at Aubert Ings SSSI, where it appears to have colonised 'under its own steam'. The origin of such populations is likely to be gardens backing onto large rivers that frequently flood. This further supports its non-native status as it shows that Fritillary has the capacity to spread from gardens to the wild.

The change in the status of *F. meleagris* from native to neophyte (Pearman, 2007) has led to its removal from the British Red Data List (Leach, 2010) where it was formerly considered Vulnerable due to marked losses of meadow populations since the 1970s (Cheffings & Farrell, 2005). Regardless of its status, however, Fritillary remains a much loved and valued component of our nation's flora. Nearly all the meadows in which it occurs are Sites of Special Scientific Interest (SSSI) and it remains a flagship species for the conservation of floodplain meadows, as witnessed by its prominence in efforts to raise the profile of this threatened habitat over recent years (Rothero *et al.*, 2016). It also remains the county flower of Oxfordshire and recently adorned the cover of *Oxfordshire's Threatened Plants* (Erskine *et al.*, 2018). For many a visit to a Fritillary meadow in April will continue to bring great joy even with the knowledge that it might not be native there.

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