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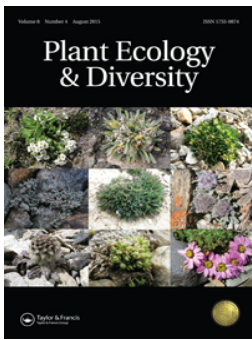
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Hybrid swarms: catalysts for multiple evolutionary events in *Senecio* in the British Isles

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Background: Introgressive hybridisation is an evolutionary catalyst producing novel variants able to explore new ecological niches and evolve as new hybrid taxa. However, the role of ‘hybrid swarms’ – highly variable populations produced following interspecific hybridisation – in generating this evolutionary novelty has been poorly studied.

Aims: We examine the alternative origins of tetraploid hybrid derivatives of *Senecio vulgaris* and *S. squalidus*, via local polytopic formation or long-distance dispersal from a single perennial hybrid swarm around Cork, Ireland.

Methods: Morphometric, isozyme and chloroplast DNA analysis.

Results: The Cork hybrid swarm and UK hybrid swarms exhibited a broad range of morphological variation and contained individuals similar to the stable tetraploid hybrid derivatives; *S. eboracensis* and *S. vulgaris* var. *hibernicus*. Chloroplast DNA analysis shows that *S. eboracensis* did not evolve from the Cork hybrid swarm. However, UK *S. vulgaris* var. *hibernicus* populations exhibit a broad range of variation for both chloroplast and isozyme markers, but were not distinguishable from Cork material.

Conclusions: Our study confirms that *S. eboracensis* did not evolve from the Cork hybrid swarm, and while our analyses could not demonstrate this conclusively for *S. vulgaris* var. *hibernicus* the ease with which hybrid swarms have been generated in the past makes a polytopic origin for *S. vulgaris* var. *hibernicus* the most likely scenario.

Keywords: evolutionary genetics; hybridisation; hybrid taxa; introgression; polytopic origin; *Senecio*

Introduction

Hybrid zones have been labelled natural laboratories for the study of evolution (Hewitt 1988). They may contain ephemeral or long-lived hybrid populations, cause temporary local or permanent widespread introgression, and occasionally generate new hybrid species at the homoploid and polyploid levels. Much of the literature on hybrid zones has concentrated on their genetic structure, dynamics and maintenance (e.g. Barton 1983; Barton and Hewitt 1985; Harrison 1993; Brennan et al. 2009), selection favouring reproductive character divergence of species in secondary contact (Barton and Hewitt 1985; Hewitt 1988; Servedio and Noor 2003) and the role of hybrid zones as bridges for transfer of dependent symbionts between hybridising hosts (Floate and Whitham 1993). However, since the studies of Anderson and coworkers (Anderson 1949; Anderson and Stebbins 1954), attention has also focused on the role of hybrid zones in generating evolutionary novelty (Lewontin and Birch 1966; Arnold 1992; Seehausen 2004; Arnold et al. 2012; Abbott et al. 2013).

Where fertile or partially fertile F₁ hybrids are generated between two species, a wide range of genetic, morphological and ecological variation can be released in backcross (crosses between F₁s and one or both parental species), F₂ (crosses between F₁s) and later hybrid generation progeny. Populations containing a variety of hybrid variants have been labelled ‘hybrid swarms’ (Anderson 1949), the term effectively describing the ‘melting pot’

and diversity of genetic variation that is often liberated by hybridisation.

Depending on fertility constraints, different genomic combinations occurring within hybrid swarms can break down character coherence and give rise to new recombinants and introgressants (Anderson and Stebbins 1954; Rieseberg and Wendel 1993; Rieseberg et al. 2003; Yakimowski and Rieseberg 2014). Indeed, trait expression within many hybrid derivatives can be transgressive (i.e. trait means are higher or lower than those of either parent species) and may lead to new morphological variation, reproductive isolation and adaptation to new habitats (Anderson 1949; Rieseberg et al. 2003; Whitney et al. 2010; Arnold et al. 2012; Yakimowski and Rieseberg 2014).

The frequency of hybrid swarm formation appears to be idiosyncratic, and is now particularly influenced by human activities, occurring often in weedy species within disturbed habitats. Anderson and coworkers (Anderson 1948; Anderson and Stebbins 1954) suggested that habitat disturbance generates the novel and/or graded ecological niches between hybridising species that allows diverse forms such as stabilised introgressants and/or homoploid hybrid species to persist. More recently, the role of newly introduced species as stimulants of hybridisation has been recognised (Seehausen 2004; Vellend et al. 2007) because hybridisation is common when populations invade new environments and potentially elevates rates of response

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to selection, and predisposes colonising populations to rapid adaptive diversification under disruptive or divergent selection. The generation of new recombinant types within hybrid swarms is suspected to have facilitated the evolution of new homoploid hybrid species, for example, in *Helianthus* (Rieseberg et al. 2003), *Iris* (Arnold et al. 2012), *Pinus* (Wang et al. 2011) and *Senecio* (Abbott et al. 2003; Brennan et al. 2012). In the case of new allopolyploid taxa, molecular markers have demonstrated several independent origins at different locations (i.e. polytopic, e.g. in *Tragapogon mirus* and *Tragapogon miscellus*, Novak et al. 1991; Soltis and Soltis 1999; *Senecio cambrensis*, Ashton and Abbott 1992a; Harris and Ingram 1992; Lowe and Abbott 1996; Abbott and Lowe 2004).

Most studies to date, however, have done little to highlight the route of origin of hybrid taxa, or to demonstrate unequivocally the role of hybrid swarms in their origin. In this regard, for very recently evolved taxa – neospecies (i.e. those originating within the last few hundred years) – it is possible to examine herbarium records to search for evidence of hybrid swarms containing individuals that bear morphological similarity to extant neospecies. If long-lived hybrid swarms persist within the range of a hybrid neospecies and are thought to be its source of origin, then different morphometric and molecular approaches may be used to test this. While it may not be possible to catch evolution *in flagrante delicto*, such approaches can be used to consider which hybrid swarms might potentially have been the source of origin of recently established stable introgressants and hybrid neospecies, and which others may be safely discounted from having a role in this.

Within the UK and Ireland, hybridisation between the diploid Oxford ragwort, *Senecio squalidus* L. ($2n = 20$), which is derived from plants introduced from Sicily, Italy, approximately 300 years ago (Harris 2002; James and Abbott 2005; Abbott et al. 2010), and the tetraploid native groundsel, *Senecio vulgaris* var. *vulgaris* L. ($2n = 40$) has resulted in the recent derivation of two tetraploid hybrid taxa (Abbott 1992; Abbott and Lowe 2004) and the allohexaploid, *S. cambrensis*. One of the tetraploid taxa is the inland radiate groundsel, *S. vulgaris* var. *hibernicus* Syme, which official records indicate was first found around Oxford in 1832 (Crisp 1972) but is now commonly found associated with var. *vulgaris* in many parts of Britain and Ireland, particularly in Wales and central England (Abbott et al. 2003). This taxon differs from *S. vulgaris* var. *vulgaris* by the presence of ray florets controlled by genes introgressed from *S. squalidus* (Kim et al. 2008). The second tetraploid hybrid derivative, York groundsel, *Senecio eboracensis* Abbott and Lowe, was first found in York in 1979 (Irwin and Abbott 1992; Lowe and Abbott 2003), where it survived in the wild until early 2000. *S. eboracensis* differs from *S. vulgaris* var. *hibernicus* (and var. *vulgaris*) in a number of morphological characters including achene length, leaf shape and pollen pore number (Irwin and Abbott 1992; Lowe and

Abbott 2003). Morphometric and molecular marker analysis evidence suggests that *S. eboracensis* contains a much higher proportion of genetic material derived from *S. squalidus* than does *S. vulgaris* var. *hibernicus* (Irwin and Abbott 1992; Abbott et al. 2003). While still a product of introgression, the origin of *S. eboracensis* appears to have involved less backcrossing to *S. vulgaris* than var. *hibernicus* (Lowe and Abbott 2000).

Fertile plants with morphologies similar to these two hybrid taxa have been artificially synthesised relatively easily from triploid and tetraploid F_1 hybrids between *S. vulgaris* and *S. squalidus* (Lowe and Abbott 2000). It is feasible that *S. vulgaris* var. *hibernicus* may have originated multiple times at different locations (polytopically), based on its variation in morphology and growth characteristics (Richards 1975; Hull 1976; Oxford et al. 1996), isozyme (Abbott et al. 1992) and cpDNA profiles (Abbott and Lowe 1996). However, such variation could have been generated by a single fertile hybrid derivative through segregation and/or backcrossing to local *S. vulgaris* plants. The situation in *S. eboracensis* is more clear-cut, in that morphological, isozyme and molecular analyses all suggest a single origin (Irwin and Abbott 1992; Abbott et al. 2003; Lowe and Abbott 2003).

Since the mid-nineteenth century, natural hybrid swarms between *S. vulgaris* var. *vulgaris* and *S. squalidus* have been recorded in at least 20 English and Welsh vice-counties and three Irish vice-counties (Benoit et al. 1975: note: vice-counties are geographical divisions of the UK and Ireland used for the purpose of biological recording and other scientific data-gathering; there are 152 vice-counties in total). It is possible that interspecific hybrids arose earlier than this period (since *S. squalidus* has been resident in the wild in the UK for over 200 years, but the lack of written or specimen evidence documenting such hybrids makes this difficult to verify). Crisp and coworkers (Crisp 1972; Benoit et al. 1975) noted that these hybrid swarms contained what appeared to be F_1 , F_2 and backcross products, ranging from sterile triploid and partially fertile tetraploid intermediate hybrids to plants that were only distinguishable from *S. vulgaris* var. *vulgaris* by single characters, for example, possession of ray florets. Crisp (1972) labelled material exhibiting this pattern of variation ‘an introgression sequence’. Based on herbarium specimens collected from several hybrid swarms, it is apparent that some members of an introgression sequence bear a close morphological resemblance to *S. vulgaris* var. *hibernicus* and *S. eboracensis*, suggesting that these taxa may have originated from such swarms (Lowe and Abbott 2003).

Hybrid swarms between *S. vulgaris* and *S. squalidus* are highly dependent on environmental disturbance and tend to persist at most sites for only brief periods. For example, from an examination of herbarium material, Crisp (1972) recorded the presence of hybrid swarms and introgression sequences at the following locations and dates: Cardiff (1904–1906), Bristol (1945–1948), Kings Lynn (1971–1974) and Wrexham (1948). Hybrid

swarms were particularly frequent at different sites during and after the Second World War, when bomb sites and derelict industrial estates provided ideal habitats for colonisation by large mixed populations of *S. vulgaris* and *S. squalidus* (Lousley 1943–1944; Kent 1956; Crackles 1990). If radiate groundsel, *S. vulgaris* var. *hibernicus*, originated polytopically, then its origin and establishment must have been very rapid given that most hybrid swarms exist only briefly.

An alternative hypothesis concerning the origins of *S. vulgaris* var. *hibernicus* and *S. eboracensis* is that all extant and historical populations of these taxa originated from a single hybrid swarm of long duration, while other recorded hybrid swarms played no part in their origin. In fact in contrast to the situation at most locations, a hybrid swarm has persisted around Cork in Ireland, extending to Passage West 8 km away, for more than a century (Praeger 1934; Crisp 1972). The first reliably dated specimen of radiate groundsel from Cork was collected in 1853 (Colgan and Scully 1898), and Syme's description of var. *hibernicus* (1875) is based on material taken from Cork in 1866. However, a poorly labelled specimen was recovered from the Dublin herbarium and purported to be from Cork and dated 1819, that is, 13 years before the first official radiate groundsel specimen was found in Oxford (Crisp 1972). Since that time, hybrid material has been recorded regularly in Cork and its environs and includes specimens similar in morphology to *S. vulgaris* var. *hibernicus* and *S. eboracensis* (Crisp 1972; Lowe and Abbott 2003). It is therefore possible that the hybrid swarm in the Cork area could have been the source of *S. eboracensis* and all populations of *S. vulgaris* var. *hibernicus* in the UK and Ireland. This scenario relies on the possibility that material from a single source in Ireland has effectively dispersed around Britain and Ireland. On this point it is worth noting that *S. squalidus* itself colonised much of Britain in a matter of decades, and that the dispersal of plumed *Senecio* achenes is aided by vortexes of air generated by express trains and cars on train and arterial road networks (Harris 2002; Abbott et al. 2009).

In this paper, we examine further the possible origins of tetraploid hybrid derivatives of *S. vulgaris* and *S. squalidus*, that is, by local polytopic formation or long distance dispersal from a single perennial hybrid swarm around Cork, Ireland, by carrying out the following studies. (1) A comparative morphometric analysis between plants raised from seed collected from a contemporary hybrid swarm near Cork and those raised from seed of *S. vulgaris* var. *vulgaris* and var. *hibernicus*, *S. squalidus* and *S. eboracensis*. (2) A morphometric analysis conducted on historical herbarium specimens collected from a range of hybrid swarms between *S. vulgaris* var. *vulgaris* and *S. squalidus* and also live plants of parental and hybrid taxa as well as synthetic hybrid material of known pedigree (including F₁, F₂ and backcross material) produced from crosses between *S. vulgaris* var. *vulgaris* and *S. squalidus*

(Lowe and Abbott 2000). (3) A comparative survey of isozyme and chloroplast (cp) DNA variation within and between samples from English, Irish, Welsh and Scottish populations of *S. vulgaris* var. *vulgaris*, *S. vulgaris* var. *hibernicus* and *S. squalidus*, and of *S. cambrensis*, *S. eboracensis* and the Cork hybrid swarm. These older molecular techniques were utilised to allow comparison with previous systematic surveys of British *Senecio* populations undertaken by Abbott et al. (1992) Irwin and Abbott (1992), Ashton and Abbott (1992a, 1992b), Harris and Ingram (1992), Abbott and Lowe (1996) and Lowe and Abbott (1996).

Materials and methods

Morphometric comparison between plants from a hybrid swarm near Cork, Ireland, and representatives of S. vulgaris var. vulgaris, var. hibernicus, S. squalidus and S. eboracensis

Plants of *S. vulgaris* var. *vulgaris* from near Cork (Passage West, 10 individuals), York (10) and Edinburgh (6) – together with plants of each of *S. squalidus* from Cork (9), York (10) and Edinburgh (9), *S. eboracensis* from York (10), *S. vulgaris* var. *hibernicus* from Edinburgh (12) and hybrid swarm material from near Cork (Passage West, 19) – were raised from seed in a glasshouse in a fully randomised design. Details of locations from where seed was collected are given in Table A1. Germination and growth conditions were similar to those described in Lowe and Abbott (2000). On the day of full anthesis of the apical capitulum of a plant, a record was taken of 25 morphological characters for that plant. Fifteen of these characters were descriptors of the capitulum, nine described vegetative traits and one was a record of time to flowering (Table 1). Each plant was left to produce seed, before a record was taken of seed fertility, based on the proportion of florets to set seed in the first capitulum. Before analysis, data were tested for normality and heteroscedasticity and those not conforming were transformed. Data were subjected to principal component analysis (PCA) (Wishart, CLUSTAN) to examine clustering of groups. Each of the 26 characters was subjected to one-way analysis of variance with differences between means of groups tested by Tukey–Kramer multiple comparison.

Morphometric comparison of herbarium specimens, live specimens of parental and hybrid taxa, and synthetic hybrid derivatives

Herbarium specimens. A total of 180 herbarium specimens of *Senecio* were examined from eight herbaria: British Museum (BM), Bristol Museum (BRIST), Leicester University (LTR), Liverpool University (LIV), Reading University (READ), Royal Botanic Garden Kew (K), Trinity College Dublin (TCD) and York Museum (YORK). Specimens from Britain and Ireland were placed

Table 1. Means (emboldened text) and standard deviations (95%, normal text) for 26 morphological traits measured on Cork and York *S. squalidus* and *S. vulgaris* var. *vulgaris*, Cork hybrid swarm plants, Edinburgh *S. squalidus* and *S. vulgaris* var. *vulgaris* and var. *hibernicus*, and York *S. eboracensis*.

Taxa/character	<i>S. vulgaris</i> var. <i>vulgaris</i> Edinburgh	<i>S. vulgaris</i> var. <i>vulgaris</i> York	<i>S. vulgaris</i> var. <i>vulgaris</i> Cork	<i>S. vulgaris</i> var. <i>hibernicus</i> Edinburgh	<i>S. eboracensis</i> York	Hybrid swarm Cork	<i>S. squalidus</i> Edinburgh	<i>S. squalidus</i> York	<i>S. squalidus</i> Cork
No. individuals	6	10	10	12	10	19	9	10	9
Plant height (mm)	211.4 21.9	265.2 28.3	264.7 58.8	233.3 32.2	205.6 37.7	259.8 48.6	322.2 64.9	494.7 106.1	356.6 96.0
Inflorescence length (mm)	19.0 2.8	17.9 3.2	18.5 3.7	17.3 2.2	22.1 5.2	17.1 3.3	19.8 2.2	25.1 4.4	26.5 6.5
Capitulum width (mm)	3.6 0.3	3.5 0.1	3.6 0.3	3.8 0.4	4.0 0.2	4.0 0.5	5.2 0.3	4.9 0.5	7.0 5.0
Capitulum length (mm)	8.8 2.7	8.2 2.5	9.0 2.8	7.7 1.9	11.8 4.8	6.9 3.1	9.5 3.7	14.6 4.8	16.4 6.7
No. phyllaries	19.2 1.0	20.3 0.7	20.1 1.5	19.3 2.1	18.2 1.8	20.6 0.8	21.4 1.5	22.6 2.3	21.0 2.2
Prop black tipped phyllaries (arcsin)	85.7 10.6	86.1 6.3	82.2 12.7	76.8 11.2	29.2 17.2	82.0 13.2	79.2 17.9	90.0 0.0	65.9 20.7
No. caliculus bracts	10.5 1.2	10.9 1.6	11.6 4.0	11.7 3.9	6.8 1.5	13.8 2.1	6.1 1.1	7.3 1.6	8.1 2.3
Length caliculus bracts (mm)	3.0 0.5	3.0 0.4	2.5 0.5	3.3 0.6	4.0 0.2	3.6 0.5	3.0 0.2	2.8 0.4	2.9 0.5
No. ray florets	0.0 0.0	0.0 0.0	0.0 0.0	11.7 1.4	8.7 0.9	11.2 1.6	12.6 0.7	13.0 0.0	11.7 2.1
Length ray floret (mm)	0.0 0.0	0.0 0.0	0.0 0.0	5.6 0.4	5.0 0.3	6.8 0.8	12.3 1.1	12.0 1.4	14.0 2.3
Width ray floret (mm)	0.0 0.0	0.0 0.0	0.0 0.0	1.4 0.1	1.4 0.1	1.8 0.2	3.7 0.5	3.1 0.4	3.8 0.5
Length longest leaf (mm)	119.3 29.8	157.8 15.7	133.9 16.0	161.7 18.2	181.7 19.9	142.0 23.9	131.9 14.4	144.6 29.2	112.2 32.4
Length mid-leaf (mm)	98.1 30.7	111.4 6.1	93.3 13.4	103.2 20.3	137.0 24.2	75.1 13.8	74.9 17.9	81.7 15.9	76.4 20.8
No. leaf lobes	11.3 1.0	12.3 0.7	12.8 1.5	11.9 0.9	16.8 1.2	12.9 1.0	10.9 1.5	11.4 1.9	11.0 1.7
Apical angle of mid-leaf (deg.)	132.0 8.8	139.4 17.3	146.0 12.4	137.8 18.6	100.6 14.1	114.6 24.6	85.6 14.6	88.2 14.3	85.9 15.6
Secondary angle of mid-leaf (deg.)	67.8 6.7	59.5 9.6	62.2 7.9	66.2 7.3	57.9 8.5	58.7 9.2	49.7 7.1	45.6 11.7	34.8 12.4
Leaf dissection (mid-leaf)	5.8 1.8	5.7 0.8	5.5 0.6	7.7 1.8	9.4 0.4	8.0 2.1	9.5 2.3	9.3 2.1	6.6 1.6
No. pollen pores	3.0 0.0	3.0 0.0	3.1 0.2	3.0 0.0	4.0 0.0	3.3 0.7	3.0 0.0	3.0 0.0	3.0 0.0
Pore size (µm)	8.3 1.5	8.1 1.3	8.7 1.9	8.7 1.4	7.2 1.2	9.6 1.9	8.0 1.6	8.9 1.4	9.0 0.9

Seed set (%)	53.9	57.2	63.5	60.2	19.6	50.8	3.7	0.6	1.9
	10.9	13.1	9.9	13.6	11.1	18.3	7.7	2.0	3.8
Seed length (mm)	2.4	2.2	2.1	2.5	2.9	2.4	2.3	2.4	2.3
	0.3	0.1	0.1	0.2	0.2	0.2	0.1	0.1	0.3
No. seeds	56.5	68.2	55.5	50.8	63.8	50.8	83.2	90.9	66.1
	10.7	4.2	6.9	10.6	5.7	11.0	11.9	7.3	12.9
Growth time to first flowering (days)	76.0	73.1	75.9	70.8	71.3	86.2	96.4	102.4	96.7
	8.6	6.9	12.5	5.6	3.2	8.6	10.2	10.6	9.3
Square of mid-leaf area	0.4	0.4	0.4	0.4	0.4	0.3	0.3	0.3	0.4
	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.1
Mid-leaf perimeter	2.3	2.3	2.3	3.0	3.5	2.7	3.1	3.2	2.6
	0.7	0.2	0.4	0.8	0.3	0.8	0.9	1.0	0.8

in the following categories based on visual inspection (numbers assigned to each category are in parenthesis): *S. vulgaris* var. *vulgaris* (15), *S. vulgaris* var. *hibernicus* (42), *S. squalidus* (8), *S. × baxteri* (51) – sterile triploid hybrid of *S. vulgaris* and *S. squalidus*, fertile tetraploid hybrid of *S. vulgaris* and *S. squalidus* (49) and *S. cambrensis* (15). Identification of *S. × baxteri* was based on seed sterility and intermediate phenotype, while identification of the fertile tetraploid hybrid was based on morphological similarity to such hybrids artificially synthesised and raised in a glasshouse. Other *Senecio* specimens in the collections were excluded from further analysis. Specimens were collected from numerous sites in England, Wales and Ireland. Where several hybrid specimens (triploid and/or tetraploid) had been collected from the same site, the local population was designated to be a hybrid swarm. In this way, hybrid swarms were identified from the following locations (with dates in parenthesis): Oxford (1886–1889), Cork (1895–1907), Cardiff (1905–1906), Llandoff (1910–1912), London (1943–1944), Norwich (1944–1946), Bristol (1945–1948), Oxford (1946), Eastbourne (1946), Wrexham (1948), Sheffield (1951), Exmouth (1956), Kings Lynn (1971–1974), Manchester (1971–1974), Strathclyde (1974), Liverpool (1976–1977). In total, 82 specimens from these hybrid swarms were examined.

Seven morphometric characters shown previously (1) to be relatively unaffected by variation in growth conditions and (2) to distinguish parental taxa and hybrid derivatives (Lowe, personal observation) were recorded on each of the 180 specimens selected. These included number of ray florets, mean ray floret length (mm), capitulum length (mm), angle of mid-leaf apex (defined as the angle between the apex of the primary vein and the apices of the adjacent marginal tooth sinuses), achene length (mm), leaf length to width ratio (mid-leaf length/mid-leaf width) and leaf width to auricle width ratio (mid-leaf width/width of basal auricle).

Live parental and hybrid taxa. The same seven characters were also recorded on plants raised from seed in a randomised block under glass, which included individuals of *S. vulgaris* var. *vulgaris* from Edinburgh (9) and York (24), of *S. vulgaris* var. *hibernicus* from Edinburgh (5), of *S. eboracensis* (18) and of *S. squalidus* (19) from York.

Synthetic hybrid derivatives of S. vulgaris and S. squalidus. In total, 134 hybrid derivatives of *S. vulgaris* and *S. squalidus* were generated (synthesised) in three different ways (by crossing *S. vulgaris* var. *vulgaris* with *S. squalidus* to produce a triploid F₁ hybrid – route 1, crossing *S. vulgaris* var. *vulgaris* with *S. squalidus* to produce a tetraploid F₁ hybrid – route 2, and crossing *S. vulgaris* var. *vulgaris* with a synthetic tetraploid form of *S. squalidus* to produce a tetraploid F₁ – route 3; see Lowe and Abbott 2000). These progeny were raised under glass and measured at maturity for a range of traits including the seven measured on herbarium specimens and live plants described

above, thus allowing comparisons to be made across all of these individuals. The hybrid progeny (with number in parenthesis) included the following: F₁ tetraploid (4), B₁ (15) and F₃ (5) produced by route 1; B₁ (11) and F₂ (13) progeny produced via route 2; and B₁ (65) and F₂ (21) progeny produced by route 3.

A data set comprising common measurements made on all herbarium specimens and glasshouse grown plants (389 in total) was subjected to PCA. For each trait, untransformed data were standardised to a mean of zero and unit standard deviation before analysis.

Isozyme and cp DNA variation within and between a contemporary Cork hybrid swarm and other Senecio populations

Isozyme variation. A survey of isozyme variation was conducted on plants raised from the hybrid swarm near Cork (Passage West), two populations of *S. eboracensis* (Lendal Bridge and Dalton Terrace, York, the former sampled on two different dates), five populations of *S. vulgaris* var. *vulgaris* (including populations from England – York; Scotland – Edinburgh; Wales – around Wrexham; and Ireland – Passage West, Cork), four populations of *S. vulgaris* var. *hibernicus* (including populations from Scotland – Edinburgh, Grangemouth; Wales – around Wrexham) and two populations of *S. squalidus* (York and Edinburgh) (Table 3). Horizontal starch gel electrophoresis was conducted on crude protein extracts of leaf or flower bud tissue to survey variation for the following enzyme systems: aconitase (ACO), aspartate aminotransferase (AAT), esterase (EST), isocitrate dehydrogenase (IDH), acid phosphatase (ACP) and glutamate dehydrogenase (GDH) using the methods described in Lowe and Abbott (1996). Allozyme variation was scored at each locus where the most anodally migrating allele was defined as *a*. Raw data are presented in Appendix.

A data set of population allele frequencies was constructed, to which were added equivalent values for two populations of *S. cambrensis* obtained from a previous study (Lowe and Abbott 1996). Population allele frequencies were used to calculate the F_{ST} analogue rho as a distance measure between populations by means of the software GenDive 2.0b2.2 (Meirmans and Van Tienderen 2004). The matrix of population pairwise values of rho was subjected to PCA.

Chloroplast DNA variation. Restriction fragment analysis of cp DNA variation was conducted on two individuals of *S. squalidus* and six individuals of *S. eboracensis* collected from two sites in York, Dalton Terrace and Lendal Bridge (Table 2). Details of Southern blotting and autoradiography procedures used are given in Lowe and Abbott (1996). Haplotypes obtained are described according to previous nomenclature (Abbott and Lowe 1996; Lowe and Abbott 1996) and combined for comparison with other previously published data (mainly from Lowe and Abbott 1996).

Results

Morphometric comparison between Cork hybrid swarm plants and S. vulgaris var. *vulgaris*, var. *hibernicus*, *S. squalidus* and *S. eboracensis*

PCA revealed that offspring of *S. vulgaris* var. *vulgaris*, *S. squalidus* and *S. eboracensis* formed distinct phenotypic groups with the first two principal components contributing ~50% of the total variance (Figure 1). As expected, offspring of *S. vulgaris* var. *hibernicus* were positioned close to, though mainly separated from *S. vulgaris* var. *vulgaris*, whereas offspring raised from the hybrid swarm near Cork were more variable and broadly distributed across the plot. Included among the Cork hybrid swarm material were plants bearing a close phenotypic resemblance to *S. vulgaris* var. *hibernicus* at one extreme, and an individual resembling *S. eboracensis* at the other. Additional offspring with intermediate phenotypes were positioned between these extremes.

A comparison of individual traits (Table 1) showed that *S. eboracensis* was intermediate in mean phenotype between *S. vulgaris* var. *vulgaris* and *S. squalidus* for eight of the characters measured, was more similar to *S. squalidus* than *S. vulgaris* for one character and more similar to *S. vulgaris* for six characters. In addition, for seven characters, *S. eboracensis* exhibited a mean outside the range of variation that spanned *S. vulgaris* and *S. squalidus*. In contrast, *S. vulgaris* var. *hibernicus* was intermediate to *S. vulgaris* var. *vulgaris* and *S. squalidus* in mean phenotype for four characters, and for the remaining 22 characters was not significantly different from var. *vulgaris*.

Morphometric comparison of herbarium specimens, live specimens of parental and hybrid taxa, and synthetic hybrid derivatives

A PCA performed on the seven characters measured on all herbarium specimens and glasshouse-raised material showed that the first two principal components (axes) described 32.7 and 18.2% of variation in the data set, respectively. Characters with highest loadings on PC1 were ray floret number (0.557) and length (0.507), capitulum length (0.395) and mid-leaf width/auricle width ratio (0.340), while those with highest loadings on PC2 were mid-leaf apical angle (−0.597), mid-leaf length/width (0.464) and mid-leaf width/auricle width ratio (−0.499). Means and standard deviations for each character are presented in Table 2. For ease of display, plots of individual values against the first two principal components are shown in a series of three figures (Figure 2a–c). In Figure 2a, only plots for herbarium specimens and glasshouse-grown individuals of *S. vulgaris* var. *vulgaris*, *S. squalidus*, *S. vulgaris* var. *hibernicus* and *S. eboracensis* are shown. Added to these in Figure 2b are plots of herbarium specimens of *S. cambrensis*, *S. × baxteri* and hybrid swarm plants. Finally, in Figure 2c plots for the synthetic hybrid progeny raised under glass are displayed in combination with the plots for individuals represented in Figure 2a.

Table 2. Means (emboldened text) and standard deviations (95%, normal text) for seven morphological traits measured on (a) reference plants of *S. vulgaris* var. *vulgaris*, *S. vulgaris* var. *hibernicus*, *S. eboracensis* and *S. squalidus* raised under glasshouse conditions (batch = morphological); (b) herbarium specimens of *S. vulgaris* var. *vulgaris*, *S. squalidus* and *S. cambrensis*, together with fertile (introgression sequence) and sterile hybrid plants (*S. × baxteri*) either occurring singularly or as part of hybrid swarms (batch = herbarium); and (c) material from resynthesised *S. vulgaris* × *S. squalidus* hybrid lineages (from Lowe and Abbott 2000), including F₁, F₂, F₃ and B₁ generations (batch = resynth).

Taxa/ character	<i>S. vulgaris</i> var. <i>vulgaris</i>		<i>S. vulgaris</i> var. <i>hibernicus</i>		<i>S. squalidus</i>		<i>S. eboracensis</i>		<i>S. cambrensis</i>		<i>S. × baxteri</i>		F ₁ hybrid tetraploid		F ₂ hybrid route 2		F ₃ hybrid route 1		B ₁ hybrid route 1		B ₁ hybrid route 2		B ₁ hybrid route 3	
	Morphological	Herbarium	Morphological	Herbarium	Morphological	Herbarium	Morphological	Herbarium	Morphological	Herbarium	Herbarium	Herbarium	Herbarium	Resynth	Resynth	Resynth	Resynth	Resynth	Resynth	Resynth	Resynth	Resynth	Resynth	Resynth
Batch No.	33	15	19	8	5	42	18	15	49	51	4	13	21	5	15	11	65							
No. rays	0.0	0.0	12.5	13.0	8.0	8.0	8.3	11.2	8.1	8.1	12.8	10.2	12.3	11.2	10.7	9.8	9.9							
Ray length (mm)	0.0	0.0	0.5	0.0	2.8	0.0	0.6	1.5	0.7	0.7	0.5	1.9	1.4	1.6	2.1	1.9	3.4							
Capitulum length (mm)	0.0	0.0	10.5	11.0	4.0	5.0	4.0	7.0	5.1	5.0	10.1	8.1	7.4	10.9	4.3	2.6	2.5							
	0.0	0.0	1.2	0.0	0.2	0.0	0.3	0.0	0.9	0.0	0.6	2.5	2.5	0.7	2.2	1.0	1.2							
	7.2	9.6	9.1	10.5	7.6	10.0	8.0	11.9	10.1	9.5	9.4	10.2	9.9	10.9	9.5	10.1	9.8							
Apical angle (deg.)	0.9	1.1	0.6	1.4	0.3	0.9	0.6	1.0	1.4	1.2	0.8	0.9	0.7	0.9	1.0	0.5	0.8							
	117.1	116.4	96.7	90.3	123.6	116.2	98.4	98.1	102.3	93.5	100.3	116.8	106.0	109.4	117.8	111.9	119.8							
Seed length (mm)	31.7	27.5	21.7	22.1	15.8	18.4	14.9	23.7	21.6	25.1	15.7	18.9	18.1	22.5	9.3	20.9	11.8							
	2.3	2.4	2.4	2.3	2.3	2.2	2.9	3.1	2.4	2.5	3.0	2.8	2.7	2.9	2.7	3.0	2.8							
Leaf length/leaf width	0.1	0.0	0.2	0.0	0.1	0.2	0.1	0.1	0.3	0.1	0.1	0.3	0.4	0.3	0.3	0.3	0.3							
	2.4	2.5	2.0	1.9	2.8	2.6	2.6	1.8	2.5	2.6	1.9	2.0	2.3	2.2	2.3	2.0	2.2							
Leaf width/auricle width	0.4	0.7	0.4	0.3	0.2	0.6	0.4	0.4	1.0	1.0	0.6	0.4	0.4	0.6	0.4	0.5	0.4							
	3.5	2.6	7.2	4.1	3.4	2.5	2.8	3.5	2.5	2.2	9.1	4.1	4.6	5.7	4.9	3.1	4.9							
	1.7	1.3	3.8	2.4	1.2	1.1	0.6	1.6	1.2	1.0	4.0	1.6	1.8	2.5	1.4	0.9	1.8							

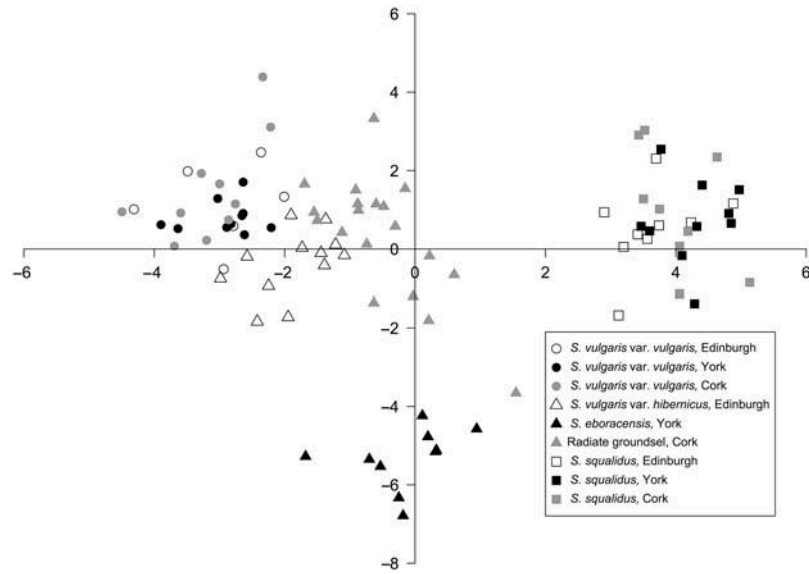


Figure 1. Plot of first and second principal components (x and y axes) based on 26 morphometric characters measured on individuals of *Svalbard* var. *vulgaris* and *S. squalidus* from York, Edinburgh and Cork, and *S. eboracensis*, *S. vulgaris* var. *hibernicus* from Edinburgh and hybrid swarm material from Cork.

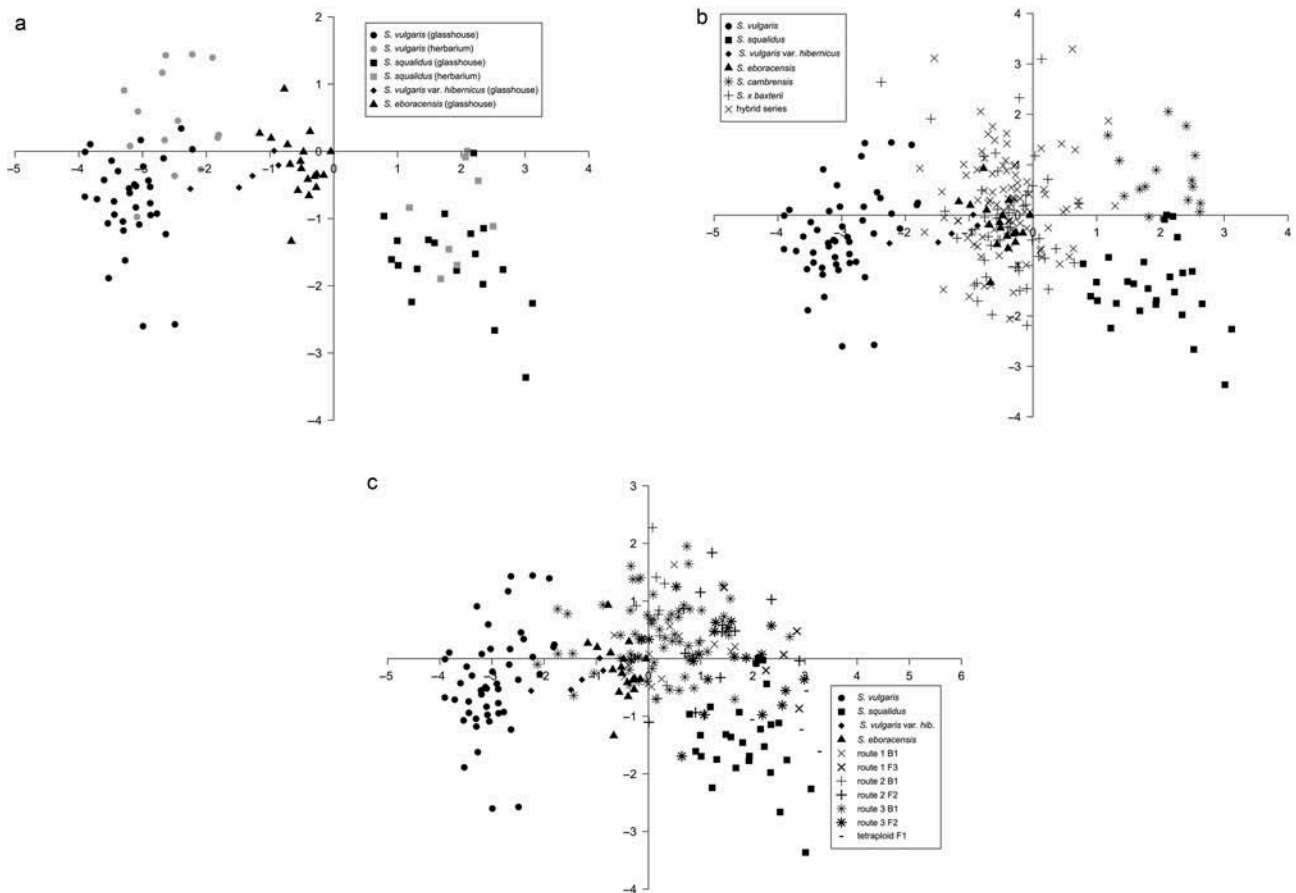


Figure 2. Plot of first and second principal components (x and y axes) based on seven morphometric characters measured on individuals of parental and stabilised hybrid taxa, material of known pedigree generated from a resynthesis study (Lowe and Abbott 2000) and herbarium specimens of potential hybrid derivatives. (a) Plot of first and second principal components (x and y axes) of parental and stabilised hybrid taxa from glasshouse and herbarium sources, that is, *S. vulgaris* var. *vulgaris*, *S. vulgaris* var. *hibernicus*, *S. eboracensis* and *S. squalidus*. (b) Plot of first and second principal components (x and y axes) of parental and stabilised hybrid taxa together with herbarium specimens of fertile material from hybrid swarms (labelled as ‘introgression sequence’) and sterile individuals of the triploid hybrid *S. × baxteri*. (c) Plot of first and second principal components (x and y axes) of parental and stabilised hybrid taxa together with resynthesised tetraploid F_1 hybrids and hybrid segregants (F_2/F_3) and backcrosses (B_1) with *S. vulgaris* via three different resynthesis routes (from Lowe and Abbott 2000).

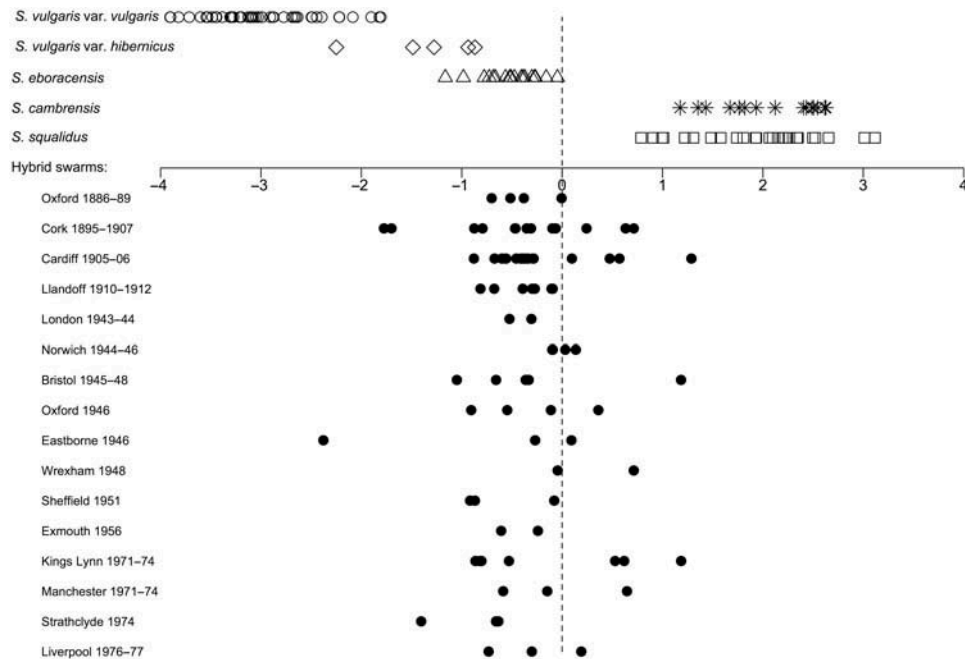


Figure 3. Plot of first principal component (x axis) for herbarium specimens collected from notable hybrid swarms occurring over the last 150 years across the British Isles. Hybrid swarm plants (below axis) are plotted alongside reference samples of *S. vulgaris* var. *vulgaris* and var. *hibernicus*, *S. eboracensis*, *S. cambrensis* and *S. squalidus* (above axis).

It is evident from Figure 2a that although only seven characters were analysed, *S. vulgaris* var. *vulgaris*, *S. squalidus* and *S. eboracensis* are clearly distinguished from each other with *S. eboracensis* exhibiting an intermediate phenotype. In addition, representatives of *S. vulgaris* var. *hibernicus* vary in morphology with some being similar to *S. vulgaris* var. *vulgaris*, while others cluster with *S. eboracensis*.

Examination of Figure 2b shows that herbarium specimens of *S. cambrensis* can be distinguished from *S. squalidus* along PC2, but not along PC1. In contrast, herbarium specimens of historical hybrid swarm material occupy the full range of morphometric space between *S. vulgaris* var. *vulgaris* and *S. squalidus* with many overlapping representatives of *S. eboracensis* and *S. vulgaris* var. *hibernicus* in distribution. Those herbarium specimens classified as the triploid hybrid, *S. × baxteri*, based on seed sterility and intermediate phenotype, were mainly placed as expected in an intermediate position with respect to their parental taxa.

From Figure 2c, it is also evident that synthetic hybrids raised under glass are also broadly distributed in morphometric space between *S. vulgaris* var. *vulgaris* and *S. squalidus* with many individuals overlapping *S. vulgaris* var. *hibernicus* and *S. eboracensis* in distribution. The four synthetic tetraploid F_1 hybrids exhibited a phenotype similar to some representatives of *S. squalidus*, while F_2 and F_3 plants exhibited greatest variation in phenotype, and B_1 plants were more similar to *S. vulgaris* var. *vulgaris* as expected given they were products of backcrossing to this taxon.

To further show the range of phenotypic variation among hybrid herbarium specimens collected from each

designated historical hybrid swarm, relative to reference samples of *S. vulgaris* var. *vulgaris* and var. *hibernicus*, *S. eboracensis*, *S. cambrensis* and *S. squalidus*, a plot was constructed of PC1 values (Figure 3). It was clear that many hybrid swarm individuals have phenotypes overlapping those of the recognised hybrid taxa, *S. vulgaris* var. *hibernicus* and *S. eboracensis*, and occasionally *S. cambrensis*.

Isozyme analysis

Frequencies of the electrophoretic phenotypes in British populations of *S. vulgaris* var. *vulgaris*, var. *hibernicus*, *S. squalidus*, *S. eboracensis* and Cork hybrid swarm material are presented in Table A1. For the eight enzyme systems that could distinguish the parental taxa, all *S. eboracensis* individuals normally expressed the $\alpha Est-1aa$, $\beta Est-3cc$, *Acp-2aa*, *Gdh-1bb*, *Idh-1ab*, *Aco-1aa* and *Aat-3ab* phenotypes commonly found in most British populations of *S. vulgaris*, plus the $\beta Est-1aa$ phenotype diagnostic of *S. squalidus*. Patterns of isozyme variation recorded in *S. vulgaris*, *S. squalidus* and *S. eboracensis* populations for *Acp-1*, *Gdh-1*, *Aat-3*, $\alpha Est-1$, $\beta Est-3$ and $\beta Est-1$ agreed broadly with previous reports for these taxa by Ashton and Abbott (1992a,b) and Irwin and Abbott (1992). Cork hybrid swarm material was fixed for the *Gda-1aa* phenotype, which was also fixed in British populations of *S. squalidus* and found in York populations of *S. vulgaris* var. *vulgaris*.

A PCA analysis based on genetic distances (ρ , an F_{ST} analogue) between populations calculated from allele frequencies (Figure 4) showed that the first two principal

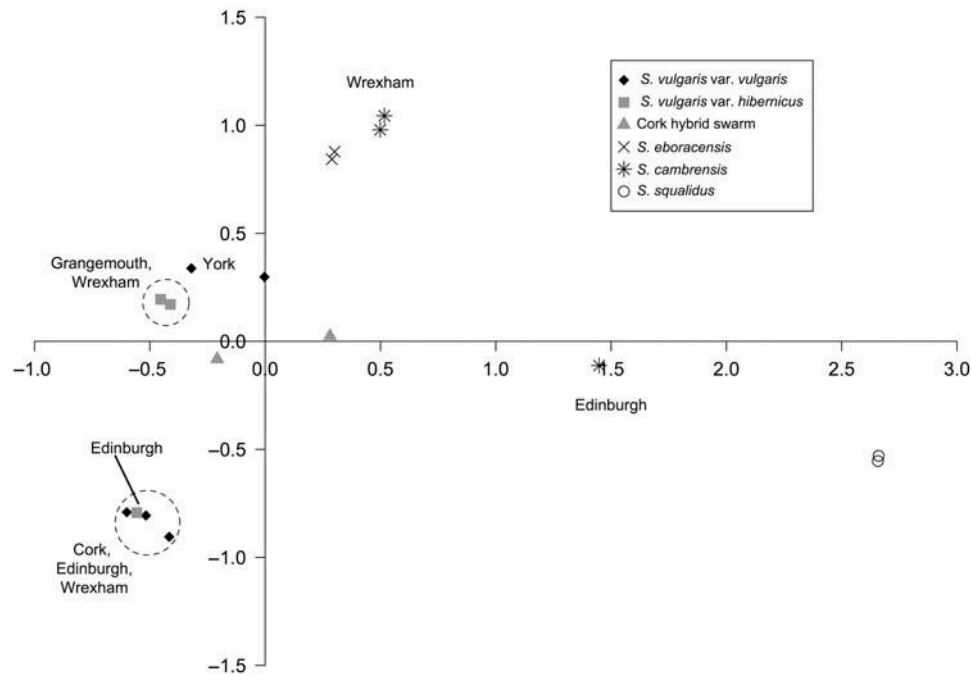


Figure 4. Plot of first and second principal components (x and y axes) based on genetic distances (ρ , an F_{ST} analogue) between populations calculated from allele frequencies for Britain and Irish populations of *S. vulgaris* var. *vulgaris*, *S. vulgaris* var. *hibernicus*, hybrid swarm material from Cork, *S. eboracensis*, *S. cambrensis* and *S. squalidus*.

components had Eigen values of 0.757 and 0.331, ρ values of 0.389 and 0.170, and described 45.37 and 19.82% of the variance in the data set, respectively. Individuals of *S. vulgaris* var. *vulgaris* were clearly separated from *S. squalidus* by PC1, while populations of *S. eboracensis* and *S. cambrensis* were placed in intermediate positions with *S. cambrensis* located closer to *S. squalidus* plants (particularly Edinburgh material) and *S. eboracensis* nearer to *S. vulgaris*. Interestingly, *S. vulgaris* plants clustered into two main groups, with some outliers. One group comprised *S. vulgaris* var. *vulgaris* plants from Cork, Edinburgh and Wrexham, and var. *hibernicus* plants from Edinburgh, while the other group comprised var. *hibernicus* plants from Grangemouth, Wrexham and Bangor, and was close to var. *vulgaris* plants from York. Material from the Cork hybrid swarm was differentiated from the main cluster of British *S. vulgaris* material due to its possession of the *Gda-1a* allele.

Chloroplast DNA analysis

Restriction analysis of cpDNA revealed that six plants of *S. eboracensis* possessed type 3 cpDNA (Table 3). Previous surveys have found type 3 cpDNA in two individuals of *S. vulgaris* var. *hibernicus* from Glasgow and eight individuals of *S. cambrensis* from Wales (Abbott and Lowe 1996; Lowe and Abbott 1996). This survey found that two samples of *S. squalidus* from York possessed type 2 cpDNA, as did 22 samples from a previous sample of *S. squalidus* populations from the UK and Ireland (Abbott et al. 1995). A previous analysis of material from the Cork

Table 3. Summary of the distribution of chloroplast DNA types 1, 2 and 3 among populations of *S. squalidus*, *S. vulgaris* var. *vulgaris* and var. *hibernicus* and the York radiate groundsel.

Species	cpDNA type		
	1	2	3
<i>S. vulgaris</i> var. <i>vulgaris</i> UK	22	12	–
<i>S. vulgaris</i> var. <i>hibernicus</i> UK	4	11	2
Cork hybrid swarm	–	5	–
<i>S. eboracensis</i>	–	1	6
<i>S. squalidus</i> UK	–	24	–

Note: Results include data from Abbott et al. (1995), Lowe and Abbott (1996) and Curnow (unpublished).

hybrid swarm indicated that five plants possessed type 2 cpDNA, whereas two *S. vulgaris* var. *vulgaris* plants from the same location possessed type 1 cpDNA (Abbott and Lowe 1996; Lowe and Abbott 1996). Previous surveys (Abbott and Lowe 1996; Lowe and Abbott 1996) also found type 2 cpDNA in 12 individuals of *S. vulgaris* var. *vulgaris* and 6 individuals of var. *hibernicus* from around the UK, while type 1 occurred in 20 individuals of *S. vulgaris* var. *vulgaris* and 4 individuals of var. *hibernicus* as well as in 2 individuals of *S. cambrensis* from Scotland (Table 3).

Discussion

Introgressive hybridisation can act as an evolutionary catalyst for interspecific genomic reassortment and produce novel recombinant variants that may exhibit beneficial

characters, be able to explore new ecological niches or, more rarely, evolve as new hybrid taxa (Anderson 1949; Arnold 1992; Seehausen 2004; Vellend et al. 2007; Yakimowski and Rieseberg 2014). In many cases, a broad range of genetic variants is produced following cases of natural interspecific hybridisation and subsequent backcrossing. The role of such hybrid swarms thus appears to be central to the generation of successful hybrid derivatives with novel morphological and/or ecological adaptations; however, there are still few cases showing these phenomena in natural populations.

Variation within the hybrid swarm near Cork

Material from the hybrid swarm near Cork exhibited considerable morphological variation broadly intermediate to *S. eboracensis* and Edinburgh *S. vulgaris* var. *hibernicus* plants, but with some overlap with representatives of these two taxa. Thus this hybrid swarm can be considered as an example of an 'introgression sequence' according to Crisp (1972).

While a broad range of variation was observed in the hybrid swarm, it was not as great as that observed within progeny of tetraploid or triploid artificial F₁ crosses generated between *S. vulgaris* and *S. squalidus* (Lowe and Abbott 2000). In addition, no sterile F₁ hybrids were observed in the Cork material; indeed, all individuals raised in the glasshouse and those observed in the field exhibited very high fertility. This pattern of morphology and fertility suggests that the Cork hybrid swarm is a stabilised population comprising backcrossed offspring produced following an earlier hybridisation event between *S. vulgaris* and *S. squalidus*. The fact that a hybrid swarm has been recorded in this area for more than 100 years, and at one time exhibited greater morphological variation (see plot of material collected between 1895 and 1907, Figure 3), suggests that conditions at this location promoted the recurrent formation of F₁ hybrids and/or allowed the survival of intermediate forms, either because of a lack of competition or the existence of a 'hybridised habitat' (Anderson 1948).

The role of the Cork hybrid swarm in the origin of S. eboracensis

While some individuals within the Cork hybrid swarm shared characters that are diagnostic of *S. eboracensis* (e.g. long calyculus bracts and highly dissected leaves), none were identical, and several characters distinguished *S. eboracensis* from the hybrid swarm material (i.e. achene length and leaf lobe number). Isozyme analysis further showed that the vast majority of *S. eboracensis* expressed the β Est-1aa (0.98) and *Gdh-1bb* (0.95) phenotypes, whereas all Cork hybrid swarm plants lacked the β Est-1a allele and expressed the *Gdh-1aa* phenotype. Moreover, whereas *S. eboracensis* possessed type 3 cpDNA all individuals from the Cork hybrid swarm possessed type 2 cpDNA. Indeed, type 3 cpDNA was not present in any

other *Senecio* material surveyed from the Cork area (Table 3). Taken overall, these findings suggest that *S. eboracensis* could not have been derived from material presently comprising the hybrid swarm near Cork, and that *S. eboracensis* most probably is the product of a separate hybridisation event to that which gave rise to the Cork hybrid swarm.

Is the Cork hybrid swarm the source of any British radiate groundsel populations?

Some individuals in the hybrid swarm at Cork were morphologically very similar to those of radiate groundsel, *S. vulgaris* var. *hibernicus*, from Edinburgh and, due to the potential of *Senecio* achenes to disperse great distances either naturally by wind (McEvoy and Cox 1987) or aided by man (Druce 1927; Kent 1956), it is possible that Cork material could have been a source of British radiate groundsel populations. The isozyme survey showed that 14 plants raised from seed collected from the Cork hybrid swarm possessed the *Gdh-1bb* phenotype, which appears to be fixed in UK populations of *S. vulgaris*, and it is therefore possible that *S. vulgaris* var. *hibernicus* is derived from Cork hybrid material. Moreover, five individuals from the Cork hybrid swarm material possessed type 2 cpDNA, which was also found in six *S. vulgaris* var. *hibernicus* individuals from different parts of Britain and Ireland. Another four var. *hibernicus* individuals possessed type 1 cpDNA that was also present in *S. vulgaris* var. *vulgaris* material from the Cork area (two individuals). Based on these findings, it is not possible to rule out the involvement of the Cork hybrid swarm in the origin of *S. vulgaris* var. *hibernicus* populations in the UK and Ireland, and thus a polytopic origin is possible.

It should be noted that the morphological, isozyme and cpDNA restriction fragment length polymorphism markers used in this study (and in previous investigations) are not sufficiently polymorphic to differentiate effectively disjunct populations of *S. vulgaris* var. *hibernicus* in Britain and Ireland. Thus, neither the hypothesis that all populations of this taxon are derived from the Cork hybrid swarm, nor that they arose independently *in situ*, can be supported unequivocally by these studies. Further examination of UK and Irish radiate groundsel populations, Cork hybrid swarm material and the parental taxa using single nuclear polymorphisms distributed throughout the cp and nuclear genomes should shed light on this possibility.

Multiple independent origins of radiate hybrids

Perhaps the only separate origin of *S. vulgaris* var. *hibernicus* that is currently supported by cpDNA comes from an analysis of plants of this taxon in Glasgow. Here, two individuals of the taxon were found to possess the rare type 3 cpDNA haplotype (Abbott and Lowe 1996) and were morphologically distinct from *S. eboracensis* (Lowe and Abbott 2003), which is fixed for type 3 cpDNA.

An important consideration when examining the possibility of independent origins is the ease with which hybrids are generated in the wild. Attempts to resynthesise fertile, tetraploid, hybrid progeny from crosses between *S. vulgaris* and *S. squalidus* have been successful on a number of separate occasions (Ingram et al. 1980; Lowe and Abbott 2000), and it is highly likely that such hybridisation events do occur in the wild, although at low frequency. This speculation is also partially supported by the fact that the F₁ triploid hybrid between *S. vulgaris* and *S. squalidus*, *S. × baxteri*, has been recorded regularly in the UK and Ireland (Crisp 1972; Table 2, Figure 2c) and occurs at low frequency in large mixed populations. In addition, unreduced gametes produced by *S. squalidus* may also play a role in the generation of such tetraploid hybrid derivatives (Lowe and Abbott 2000), and, once generated, tetraploid F₁ hybrids are capable of producing progeny of near full fertility in one generation. In light of these resynthesis studies, it would appear that disjunct populations of *S. vulgaris* var. *hibernicus* are at least equally likely to have arisen by independent origin as compared to dispersal. In addition, the Cork hybrid swarm population is quite distant to the British populations examined here (approximately 500–1000 km). It is possible that intermediary populations may have acted as a bridge; however, separate hybrid swarms between *S. vulgaris* and *S. squalidus* that could have given rise to *in situ* hybrid derivatives have been recorded on at least 16 separate occasions over the last 150 years in locations where populations of *S. vulgaris* var. *hibernicus* were sampled (Oxford 1886–1889, Cork 1895–1907, Cardiff 1905–1906, Llandoff 1910–1912, London 1943–1944, Norwich 1944–1946, Bristol 1945–1948, Oxford 1946, Eastborne 1946, Wrexham 1948, Sheffield 1951, Exmouth 1956, Kings Lynn 1971–1974, Manchester 1971–1974, Strathclyde 1974 and Liverpool 1976–1977; Figure 3; Benoit et al. 1975). These lines of reasoning suggest that independent origins of *S. vulgaris* var. *hibernicus* at different locations in Britain and Ireland are highly likely.

In summary, although the Cork hybrid swarm may have been the source of origin of *S. vulgaris* var. *hibernicus* in this particular part of Ireland, it is likely that other hybrid swarms between *S. vulgaris* and *S. squalidus* gave rise to the taxon in Britain and possibly at other locations in Ireland. Certainly, the findings of our studies have provided no evidence that *S. eboracensis* originated from the Cork hybrid swarm. Instead, this taxon, which has only ever been recorded from York, England, most likely originated following a local hybridisation event between its two parental species.

The detailed understanding of the relative likelihood of a polytopic vs. a single origin followed by dispersal in *Senecio* has important implications for other hybrid systems (Seehausen 2004; Vellend et al. 2007; Yakimowski and Rieseberg 2014). Rather than being considered

evolutionary anomalies, a polytopic scenario demonstrates the adaptive nature of hybridisation allowing the sharing of genes between species and even into new reproductively isolated recombinants when suitable conditions prevail. A single-origin scenario would highlight the special nature of hybridisation, but would place more emphasis on the study of propagule pressure and dispersal and the far-reaching consequences of long distance dispersal in the generation and maintenance of biodiversity.

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Appendix

Table A1. Allozyme phenotype frequencies in samples of *S. vulgaris* var. *vulgaris*, *S. vulgaris* var. *hibernicus*, *S. squalidus*, *S. cambrensis* and *S. eboracensis* collected from the British Isles.

	N	aEst-1			BEst-3			BEst-1			Acp-2			Aat-3			Gdh-1			Aco-1			Idh-1		
		aa	ab	bb	nn	bb	bc	cc	aa	cc	bb	ab	aa	bb	cc	abc	aa	ab	bb	aa	bb	cc	ab	bb	
<i>S. vulgaris</i> var. <i>vulgaris</i>																									
England																									
York, Dalton Terrace	71	1.00	-	-	-	-	1.00	0.01	0.99	1.00	-	-	-	-	-	1.00	0.06	0.14	0.99	0.01	-	1.00	-	-	
York, Lendal Bridge	38	0.92	0.03	0.05	-	0.23	0.03	0.74	-	1.00	1.00	-	-	-	-	1.00	0.08	0.79	0.37	0.60	0.03	1.00	-	-	
Scotland																									
Edinburgh, Leith	20	0.85	0.05	0.10	-	-	0.25	0.75	-	1.00	1.00	-	-	0.05	-	1.00	-	1.00	-	1.00	-	1.00	-	-	
Wales																									
Wrexham	4	-	1.00	-	-	-	-	1.00	-	1.00	1.00	-	-	-	-	1.00	-	1.00	-	1.00	-	1.00	-	-	
Eire																									
Cork, Passage West	9	1.00	-	-	-	-	-	1.00	-	1.00	1.00	-	-	-	-	1.00	-	1.00	-	1.00	-	1.00	-	-	
<i>S. vulgaris</i> var. <i>hibernicus</i>																									
Scotland																									
Edinburgh, Leith	19	1.00	-	-	-	-	-	1.00	-	1.00	1.00	-	-	0.42	0.16	-	1.00	-	1.00	-	1.00	-	1.00	-	
Grangemouth	8	1.00	-	-	-	-	-	1.00	-	1.00	-	-	-	0.15	0.85	-	-	1.00	1.00	-	-	-	-	-	
Wales																									
Mochdre	10	1.00	-	-	-	-	-	1.00	-	1.00	-	-	-	0.10	0.90	-	-	1.00	-	-	-	-	-	-	
Wrexham	24	1.00	-	-	-	-	0.12	0.88	-	1.00	-	-	0.05	0.25	0.41	-	-	1.00	-	-	-	-	-	-	
Cork hybrid swarm																									
Cork	14	1.00	-	-	-	-	-	1.00	-	1.00	1.00	-	-	0.36	-	-	1.00	0.36	-	0.64	1.00	-	-	-	
Passage West, Cork	17	0.23	0.53	0.24	-	-	0.06	0.94	-	1.00	1.00	-	-	0.12	-	-	1.00	-	0.88	0.12	-	1.00	-	-	
<i>S. eboracensis</i>																									
Dalton Terrace	117	1.00	-	-	-	-	-	1.00	0.97	1.00	-	-	-	-	-	1.00	0.02	0.92	0.98	0.02	-	1.00	-	-	
Lendal Bridge	79	1.00	-	-	-	-	-	1.00	1.00	-	-	-	-	0.06	0.94	-	-	1.00	0.94	0.06	-	1.00	-	-	
<i>S. cambrensis</i>																									
Scotland																									
Edinburgh	17	-	-	1.00	-	-	1.00	-	1.00	-	0.43	0.57	-	-	-	1.00	-	0.35	0.65	-	-	1.00	1.00	-	
Wales																									
Mochdre	28	1.00	-	-	-	0.33	0.62	0.05	1.00	-	1.00	-	-	-	-	1.00	-	0.22	0.78	1.00	-	1.00	-	-	
Wrexham	21	1.00	-	-	-	0.43	0.57	-	1.00	-	1.00	-	-	-	1.00	-	-	0.19	0.81	1.00	-	1.00	-	-	
<i>S. squalidus</i>																									
England York	14	-	-	1.00	-	-	1.00	-	1.00	-	-	1.00	0.14	0.43	0.43	-	-	1.00	-	-	-	1.00	-	1.00	
Scotland, Edinburgh	12	-	-	1.00	-	-	1.00	-	1.00	-	-	1.00	0.33	0.50	0.17	-	-	1.00	-	-	-	1.00	-	1.00	