The last thirty five years: recent changes in the flora of the British Isles

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ABSTRACT

In 1970 Max Walters predicted a number of changes that have taken place in the British and Irish flora over the last 35 years. Although few species became nationally extinct during this period, losses at the local scale were dramatic, particularly in S.E. England where land use pressures were greatest. Despite these losses the British flora has become increasingly diverse due to the introduction, naturalisation and spread of alien species. Research into their habitats, modes of dispersal, and competitive inter-actions with native species has provided valuable ecological insights. Hybridisation events have produced some of the best studied examples of hybrid speciation. In the future, such naturalisation events may also provide important evidence for major environmental perturbations such as climate change.

KEYWORDS: aliens, diversity, extinction, hybridisation, naturalisation, neophytes, urban habitats.

INTRODUCTION

In 1970 Max Walters concluded *The flora of a changing Britain* conference by predicting a number of changes that were likely to take place in the British flora over the subsequent twenty-five years (Walters 1970). Although brief, his paper dealt with floristic richness, aliens, extinctions, plant conservation and land abandonment. The aim of this paper is to review three of these predictions in view of the major changes which have taken place: (1) floristic richness has increased as a result of man's activities; (2) the number of national and regional extinctions has continued to increase; and (3) much has been learnt from the naturalisation of alien species. In addressing these three predictions I have intentionally drawn heavily (but not exclusively) on research published within this journal, especially the review by Brenan (1982) which deals with many of the same topics. Wherever possible, I have also referred to changes in Max's home county of Cambridgeshire (v.c. 29). I do not deal with changes in plant conservation, land use, or the ten activities he proposed for the society as these now form the basis of much of the society's current work (e.g. monitoring common species, research on rare species, publication of handbooks).

1. FLORISTIC RICHNESS WILL CONTINUE TO INCREASE AS A RESULT OF MAN'S ACTIVITIES

As Max predicted species invasions have exceeded extinctions by an order of magnitude leading to a dramatic net increase in the number of plant species recorded in the British Isles (Fig. 1). Despite localised losses only 21 native species have gone extinct nationally since records began in the sixteenth century (Stace 2002). Nine of these species have been lost in the last 35 years, although some are either dubiously native (e.g. *Galeopsis segetum*) or are likely to have been over-looked (e.g. *Epipogium aphyllum*) (Table 1). During the same period an equal number of species have been discovered or newly described of which only two are of questionable origin (*Cystopteris diaphana*, *Serapias parviflora*) and one (*Epipactis youngiana*) may be a recently evolved ecotype (Hollingsworth *et al*. 2006). In comparison to these rather modest changes to the native flora, there has been a dramatic increase in the number of naturalised aliens and casuals (Fig. 1): by the middle of the 1950s the number of recorded casuals exceeded the number of natives whereas there were around 600 naturalised aliens (30% of the native flora). By 2000 the number of casuals and naturalised aliens had increased to make up 45% and 18% of the entire British flora respectively.

Historically alien plants have arrived unintentionally as escapes from botanic gardens or as contaminants in the ballast of ships, grain, animal fodder and waste products of

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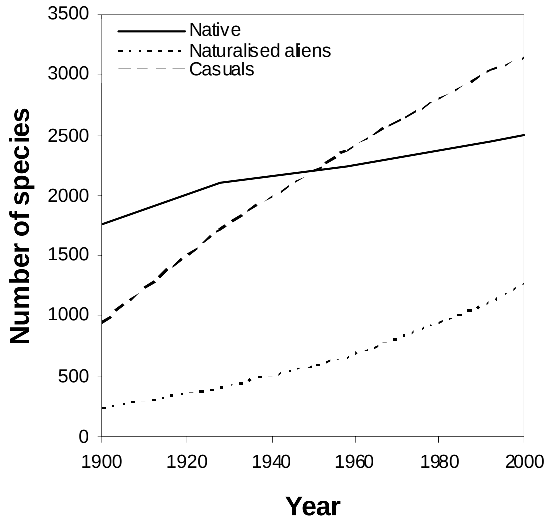

FIGURE 1. The number of native taxa, naturalised aliens and casuals in the flora of Great Britain according to various sources (Druce 1908; Druce 1928; Dandy 1958; Kent 1992; Kent & Stace 2000). 'Native' includes agamospecies such as *Hieracium*, *Rubus* and *Taraxacum*. Adapted from Stace (2002).

TABLE 1. NATIVE SPECIES DISCOVERED OR KNOWN TO HAVE BECOME EXTINCT IN BRITAIN (INCLUDING ISLE OF MAN) SINCE 1970. UPDATED FROM STACE (2002). SPECIES IN THE CRITICAL GENERA *ALCHEMILLA*, *EUPHRASIA*, *HIERACIUM*, *LIMONIUM*, *RUBUS*, *SORBUS* AND *TARAXACUM* ARE OMITTED

Species	First/last record	V.C.	Comment
(a) Discovered			
Epipactis youngiana	1976	67	Probably only an ecotype of *E. helleborine*
Senecio eboracensis	1979	63	Derived from spontaneous hybrid
Crepis praemorsa	1988	69	
Utricularia stygia	1988	97	
Serapias parviflora	1989	2	Native status uncertain
Callitriche palustris	2000	99	
Cystopteris diaphana	2000	2	Native status uncertain
Carex salina	2004	105	
(b) Extinct			
Arnoseris minima	1971	24	Probable archaeophyte. Re-introduced
Bromus interruptus	1972	29	Probable neophyte. Re-introduced
Schoenoplectus pungens	1972	59	Only native on Jersey. Re-introduced
Galeopsis segetum	1975	49	Probable archaeophyte
Saxifraga rosacea subsp. *rosacea*	1978	49	Still occurs in Ireland
Crepis foetida	1980	15	Probable archaeophyte. Re-introduced
Epipogium aphyllum	1986	22	Unconfirmed records since 1990
Neotinea maculata	1986	71	Occurs in Ireland. Formerly Isle of Man
Senecio eboracensis	2000	61	Possibly extinct?

Luzula pallidula is included as extinct by Stace (2002) but there are a number of confirmed records from Holme Fen in Huntingdonshire (v.c. 31).

TABLE 2. CHANGE IN THE NUMBER OF TAXA RECORDED IN BERKSHIRE (V.C. 22). ADAPTED FROM CRAWLEY (2005)

	Druce (1897)	Bowen (1968)	Crawley (2005)	% change	
				1897–1968	1968–2005
Native & archaeophyte	820	883	955	+8	+8
Neophyte	300	629	710	+110	+13
Apomictic	63	84	184	+33	+119
Subspecies & varieties	400	38	41	-91	+8
Hybrids	70	99	181	+41	+83

clothing manufacture (skins, wool, tan-bark) (Lousley 1953). Although introductions via these agencies declined during the second half of the twentieth century (Shimwell 2006), the numbers originating from horticulture, either as escapes or outcasts from gardens, have increased dramatically. For example, the *New Atlas* showed that eight of the 10 most rapidly spreading species since the 1960s are neophytes which were originally introduced as garden plants (*Buddleja davidii*, *Cotoneaster simonsii*, *Laburnum anagyroides*, *Linaria purpurea*, *Lysimachia punctata*, *Prunus cerasus*, *P. laurocerasus*, *Syringa vulgaris*) (Preston *et al*. 2002).

Changes at the vice-county level show a similar pattern. Berkshire (v.c. 22) has one of the best studied floras in the country, particularly with regard to alien species, and this has allowed an assessment of changes in floristic richness over the past 100 years (Table 2; Crawley 2005). Whereas the number of native and archaeophyte additions has been rather modest there has been a dramatic increase in the number of recorded neophytes (Bowen 1968). Similarly, critical and hybrid taxa have been much better studied since 1968 whereas the vast majority of infraspecific taxa formerly recognised by Druce (1897) are not included in the modern floras of Bowen and Crawley.

Based on his experiences in Cambridgeshire Max Walters predicted that urban areas would accrue more alien species than rural areas and therefore, that urbanised 10-km squares would be the richest. However, unlike continental Europe, British urbanised tetrads are not significantly richer overall than their rural

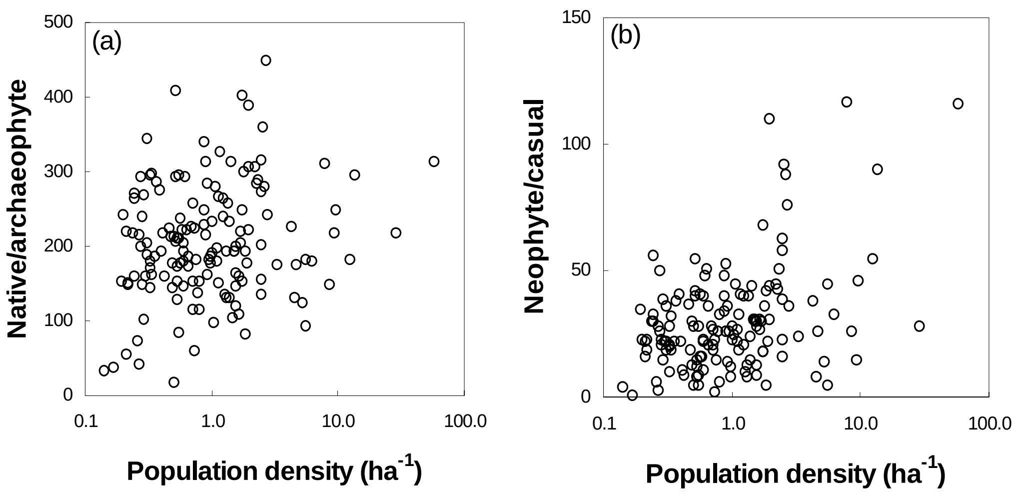

FIGURE 2. The relationship between human population density (displayed on a log scale) and (a) the number of natives and archaeophytes and (b) neophytes and casuals recorded in Cambridgeshire parishes (v.c. 29) between 1987–2000 (*n*=151). Human population densities were calculated from Population Census Returns for 2001.

counterparts, although they do support a greater number (and proportion) of introduced alien species (Roy *et al.* 1999). The results for agriculturally ravaged Cambridgeshire were as predicted by Max with more densely populated (and therefore urbanised) parishes tending to be marginally more species-rich (R^2=4·2%, F=6·5, p <0·05) whereas differences in the number of natives and archaeophytes were not significant due to large variation in numbers of species between parishes (R^2=1·9%, F=2·9, p=0·09; Fig. 2a). In contrast, urbanised parishes have significantly more neophytes and casuals with several of the ten richest parishes being almost entirely urban (R^2=16·9%, F=30·3, p <0·001; Fig. 2b). The slight discrepancy between Cambridgeshire and the national picture (i.e. more species in urban areas) may be due to local factors. Some urban parishes in the county have been extraordinarily well recorded by resident botanists (e.g. Cambridge, Chesterton, Ely, Whittlesey) whereas the majority of rural parishes are relatively species-poor due to the intensity of arable farming in the county.

2. NATIONAL AND REGIONAL EXTINCTIONS WILL CONTINUE AT AN ALARMING RATE

As discussed above relatively few species have gone extinct at the national level and, with the possible exceptions of *Bromus interruptus*, which may be a recently evolved neo-endemic (Rich & Lockton 2002), and *Senecio eboracensis*, none have become globally extinct. Of the nine species that have disappeared since 1970 (Table 1) five were probably originally introduced (*Arnoseris minima*, *Bromus interruptus*, *Crepis foetida*, *Galeopsis segetum*, *Schoenoplectus pungens*; but see Rich & Lockton (2002) and Rich & Pryor (2003) for alternative views), *Saxifraga rosacea* and *Neotinea maculata* still occur in Ireland and there are unconfirmed records for *Epipogium aphyllum* in the last decade. In contrast, *Senecio eboracensis* is probably the shortest-lived addition to the British flora, having possibly gone extinct within 17 years of its discovery in 1979 (Abbott *et al*. 2005).

In contrast to these rather modest changes at the national level, there has been a dramatic loss of species at the regional and county level since the nineteenth century. Twenty-three native species have gone extinct in the most intensively populated region of lowland England which includes all vice-counties to the east of a line running from Poole in Dorset to Goole in S.W. Yorkshire ('the Poole to Goole line'; Table 3). The vast majority are Northern (Boreal) species at the southern edge of their range in lowland England that disappeared following the widespread loss of lowland heaths and bogs (e.g. *Diphasiastrum* spp., *Huperzia selago*, *Gymnocarpium dryopteris*, *Listera cordata*, *Pseudorchis albida*, *Pyrola media*, *Scheuchzeria palustris*, *Selaginella selaginoides*, *Trientalis europaeus*, *Vaccinium vitis-idaea*). Others have been lost due to drainage of fenland (*Tephroseris palustris*), hybridisation (*Schoenoplectus triqueter*), ploughing of calcareous grassland (*Cirsium tuberosum*) and changes to aquatic habitats (*Elatine hydropiper*, *Luronium natans*) or simply because their extreme rarity in S.E. England has made them highly susceptible to other factors (*Asplenium obovatum*, *A. viride*, *Genista pilosa*, *Mertensia maritima*, *Orobanche alba*, *Vicia orobus*). Species which still occur in S.E. England but have suffered dramatic declines are also listed in Table 3. These show a similar pattern to extinctions with the majority of species associated with rivers and wetlands (*Damasonium alisma*, *Leersia oryzoides*, *Potamogeton praelongus*, *Teucrium scordium*), infertile grasslands and heaths (*Antennaria dioica*, *Gentianella campestris*, *Orchis militaris*, *Potentilla neumanniana*) and lowland bogs and mires (*Carex limosa*, *Liparis loeselii*, *Viola persicifolia*, *Utricularia intermedia*).

The loss of species at the county level has been much greater than at the national or regional scale (Walker 2003). Fig. 3 shows the average decadal rate of extinction (actually the number of last records) using the most recent information for eighteen vice-counties in England (data available from the author on request). This shows a gradual increase in the number of extinctions from less than one species per decade at the start of the nineteenth century to 3 species per decade by 1850 and 4 species per decade by 1900. Numbers were more variable during the first half of the twentieth century, but were probably around 5 species per decade up to 1950 increasing to 6 species per decade in the 1960s and 1970s. The apparent decline in the 1980s is undoubtedly an underestimate as more time is usually needed to declare a species as extinct. Although the figures for the nineteenth century are less reliable due to lower recording intensities, they

TABLE 3. EXTINCT AND DECLINING SPECIES IN SOUTH EAST ENGLAND[1]

(a) Extinct in S.E. England	Loss	(b) Marked decline in S.E. England[2]	Extant	Loss
Tephroseris palustris	26	*Gastridium ventricosum*	5	71
Huperzia selago	24	*Potamogeton praelongus*	5	55
Gymnocarpium dryopteris	13	*Damasonium alisma*	3	46
Genista pilosa	7	*Gentianella campestris*	5	46
Pseudorchis albida	7	*Antennaria dioica*	1	34
Schoenoplectus triqueter	6	*Lactuca saligna*	3	33
Elatine hydropiper	5	*Cynoglossum germanicum*	3	30
Listera cordata	4	*Teucrium scordium*	1	20
Epipogium aphyllum	3	*Atriplex pedunculata*	1	17
Selaginella selaginoides	3	*Utricularia intermedia* s.l.	1	17
Asplenium viride	2	*Liparis loeselii*	2	16
Luronium natans	2	*Orchis militaris*	3	16
Orobanche alba	2	*Alchemilla glabra*	4	14
Scheuchzeria palustris	2	*Leersia oryzoides*	3	14
Asplenium obovatum	1	*Viola persicifolia*	3	14
Cirsium tuberosum	1	*Campanula patula*	3	13
Diphasiastrum alpinum	1	*Vicia bithynica*	5	13
Diphasiastrum complanatum	1	*Carex limosa*	3	12
Mertensia maritima	1	*Erodium maritimum*	3	10
Pyrola media	1	*Potentilla neumanniana*	5	10
Trientalis europaeus	1	*Lotus angustissimus*	5	9
Vaccinium vitis-idaea	1	*Salicornia nitens*	3	9
Vicia orobus	1	*Hypochaeris maculata*	5	8

[1] Includes vice-counties 10–32 & 53–56. [2] Species recorded in $\leq$5 10-km squares between 1987 and 2000 (Preston *et al*. 2002). 'Loss' is the number of 10-km squares in which a species was recorded prior to 1987. A further 65 species occur in $\leq$ 5 10-km squares in S.E. England but have been excluded because they are either (a) very rare (*n*=21), (b) rare but showing only localised declines (*n*=23) or (c) northern/western species at the extreme edge of their range in S.E. England (*n*=21):

(a) *Apium repens, Artemisia campestris, Calamagrostis stricta, Cephalanthera rubra, Cyperus fuscus, Eriophorum gracile, Gnaphalium luteoalbum, Goodyera repens, Ludwigia palustris, Orchis simia, Orobanche artemisiae-campestris, Petrorhagia nanteuilii, Phyteuma spicatum, Polygala amarella, Potamogeton nodosus, Salicornia obscura, Scleranthus perennis, Scilla autumnalis, Senecio paludosus, Stachys germanica, Thymus serpyllum, Veronica spicata, Veronica verna*.

(b) *Alisma gramineum, Atriplex longipes, Bupleurum baldense, Carex depauperata, Carex filiformis, Clinopodium menthifolium, Eleocharis parvula, Gentianella ciliata, Lobelia urens, Luzula pallidula, Maianthemum bifolium, Najas marina, Ophioglossum azoricum, Ophrys fuciflora, Orobanche caryophyllea, Pilosella peleteriana, Polygonum maritimum, Pulmonaria obscura, Selinum carvifolia, Seseli libanotis, Thlaspi perfoliatum*.

(c) *Allium scorodoprasum, Asplenium marinum, Blysmus rufus, Carum verticillatum, Dactylorhiza purpurella, Equisetum variegatum, Euphorbia portlandica, Festuca altissima, Fumaria purpurea, Gymnocarpium robertianum, Hymenophyllum tunbrigense, Juncus acutus, Juncus filiformis, Lavatera arborea, Melica nutans, Phegopteris connectilis, Rosa mollis, Rubus saxatilis, Salix myrsinifolia, Sibthorpia europaea, Sparganium angustifolium, Stellaria nemorum.*

suggest an overall increase in the rate of extinction during the twentieth century, especially since the 1960s. As can be seen from Fig. 3, rates in Cambridgeshire were generally higher than average throughout this period, particularly during the first half of the nineteenth century when many infertile grassland and bog species (e.g. *Drosera intermedia*, *D. anglica*, *Herminium monorchis*, *Narthecium ossifragum*, *Ophrys sphegodes*) were lost as a result of parliamentary enclosure (Preston 2000). Rates approached one species a year (10 species per decade) for the majority of the twentieth century, particularly after the 1950s, when species of infertile semi-natural habitats continued to decline at an alarming

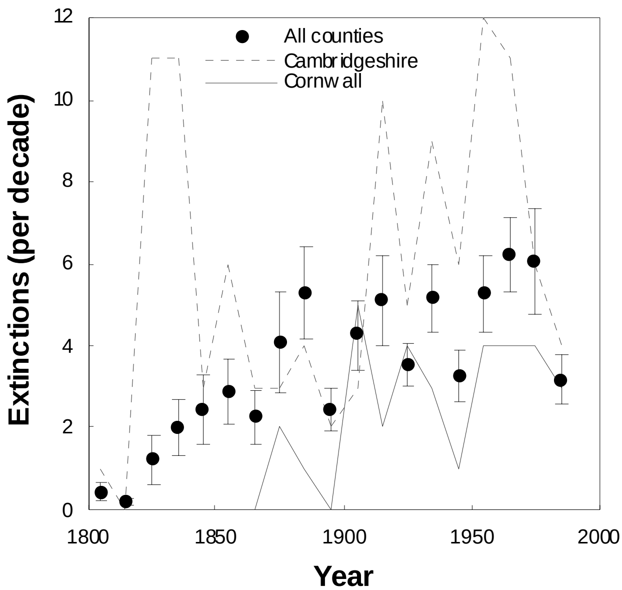

FIGURE 3. The average decadal 'extinction' rate (±1 SE) based on figures for 18 lowland vice-counties in England for which recent (post-2000) data were available (v.c. 1/2, 9–10, 13/14, 21–22, 24, 27/28, 29–32, 39–40, 59–60, 81, Bristol Region). Values for Cambridgeshire (v.c. 29) and Cornwall (v.c. 1 & 2) are displayed for comparison.

rate, presumably due to the conversion of semi-natural grasslands to arable production (e.g. *Cirsium tuberosum*) but also as a result of more gradual changes brought about by eutrophication (e.g. *Alisma gramineum*, *Eleogiton fluitans*) and falling water tables (e.g. *Eriophorum angustifolium*, *Parnassia palustris*, *Pinguicula vulgaris*, *Utricularia minor*). At the other extreme, losses in Cornwall have been much lower than average since 1800, particularly during the nineteenth century when only three species were reported to have gone extinct (*Clinopodium acinos*, *Lathraea squamaria*, *Hypochaeris glabra*). Rates were more variable at just under 4 species per decade during the twentieth century with no obvious increase following the 1939–1945 war.

3. WE CAN LEARN MUCH FROM RECENT NATURALISATION EVENTS

Of the 8,000 or so plant species which have been deliberately or accidentally introduced into the British Isles, less than 100 have become widely naturalised (Preston *et al.* 2002) and of these vanishingly few (<0·1%) are regarded as problem plants (Crawley *et al.* 1996). On the contrary, their introduction, spread and interactions with the native flora (e.g. competition, hybridisation) have provided fascinating ecological and evolutionary insights. To use Max Walters' own words: "Most of them are unplanned experiments, but if we watch we can learn a great deal from them" (Walters 1970, p.136). Table 4 lists some of the most successful invaders discussed in this paper.

SUCCESSFUL INVADERS

Clear ecological differences appear to exist between the British native and alien floras. British aliens tend to be larger, have larger seeds and occur in more fertile conditions than their native counterparts (Crawley *et al.* 1996; Williamson & Fitter 1996). They are also more likely to flower earlier or later in the year, have longer-lived seed banks and be pollinated by insects (Crawley *et al.* 1996). Although some of these differences are due to the predilections of gardeners and horticulturalists (e.g. woody species, attractive flowers) they also appear to reflect real ecological differences. The most

TABLE 4. ALIENS SHOWING THE MOST DRAMATIC INCREASES IN RANGE AND ABUNDANCE IN BRITAIN DURING THE TWENTIETH CENTURY

Species	Origin	First record	Main spread	Change Index
Senecio squalidus[1]	Italy	1794	1870-	+0·77
Impatiens glandulifera	Himalayas	1855	1940-	+1·85
Matricaria discoidea	N & S Asia	1871	1900-	-0·49
Fallopia japonica	E Asia	1886	1920-	+1·83
Epilobium ciliatum	N America	1891[2]	1930-	+3·88
Epilobium brunnescens	New Zealand	1904	1930-	+1·42
Galinsoga quadriradiata	C & S America	1909	1960-	+1·07
Buddleja davidii	C & W China	1922	1945-	+3·73
Veronica filiformis	N Turkey/Caucasus	1927[3]	1930-	+2·69
Crassula helmsii	Australia/New Zealand	1956	1970-	No data
Conyza sumatrensis	S America	1961[4]	1980-	No data
Hyacinthoides ×massartiana	Cultivation	1963	1960-	No data
Elodea nuttallii	N America	1966	1970-	No data
Lemna minuta	N & S America	1977	1989-	No data

[1] Possibly arose spontaneously as a result of hybridisation at Oxford Botanic garden in the 1890s. [2] Known from a single site in Leicestershire up till 1934. [3] There is an earlier record for 1838. [4] The first record was from Guernsey. The first record in England was from S Essex in 1974.

widely naturalised species are either highly competitive woody or thicket-forming species capable of excluding native vegetation (e.g. *Fallopia japonica*) or rapidly maturing species that succumb to competition during secondary succession but spread rapidly via disturbed niches (e.g. *Epilobium ciliatum*, *Senecio squalidus*). Some of these invaders display higher growth rates than their native or introduced congeners. For example, stems of *Elodea nuttallii* elongate faster than those of *E. canadensis*, and this has been shown to cause displacement of the latter, formerly invasive species, in some sites (Simpson 1984, 1990). Similarly, the rapid development of leaves in *Lemna minuta* can exclude other native floating aquatics (Leslie & Walters 1983). In ruderal habitats, the dramatic spread of *Epilobium ciliatum* may be due, in part, to a faster growth rate and longer flower period than native willowherbs (Preston 1988). The lack of natural pests and pathogens within the introduced range may also provide exotic species with a competitive advantage thereby making them more invasive (the ‘enemy release hypothesis’; Keane & Crawley 2002). Perhaps the most notoriously invasive plant in the British flora, *Fallopia japonica* var. *japonica*, provides a good example. Plants in Japan suffer damage from a range of invertebrate pests which attack rhizomes, stems and leaves. No such pests have been found on British plants and no doubt this has aided its dramatic spread following its escape from cultivation in 1886 (Bailey & Connolly 2000).

HABITAT

The habitats occupied by naturalised species can provide fascinating ecological insights as well as providing novel conditions in which to study interactions with native congeners (e.g. competition, hydridisation). The vast majority of alien plants occur in man-made habitats (e.g. waste ground, railway lines, walls, urban sites) close to habitation (‘the 100 m rule’; Crawley *et al.* 1996). These habitats provide disturbed, and often drought-stressed niches (e.g. cinder tips, clinker of railway lines, asphalt, quarries, rubble, wasteland) similar to conditions occupied in the native range. Some of the best examples are primary colonists of volcanic rocks (e.g. *Senecio squalidus*, *Fallopia japonicus* var. *japonicus*) and river shingles and gravels (e.g. *Epilobium brunnescens*). *Buddleja davidii* is a perennial shrub native to central and western China where it typically occurs as dense thickets on shingle beaches adjacent to rivers (Owen & Whiteway 1980). Its spread in southern Britain was one of the most dramatic of the twentieth century and followed the sudden availability of lime-rich rubble created by bombing during the 1939–1945 war. Its ability to thrive on compacted, drought-prone soils combined with prolific seed production (>1 million seeds per plant) has allowed it to colonise a wide variety of ruderal niches (e.g. railway sidings, quarries, stone structures) and as a result it is now one of the most familiar weeds of urban and waste areas (Clay & Drinkall 2001). Similarly, *Epilobium brunnescens* has spread throughout much of northern and western Britain where it is now common on moist, gravely substrates similar to its native riverbed habitat in New Zealand (Kitchener & McKean 1998). Urban niches also provide suitable conditions for more southerly species such as the subtropical plant *Conyza sumatrensis* which is confined to arid, sun-baked niches such as pavement cracks (Wurzell 1988). In contrast, it's more temperate cousin *Conyza canadensis* has spread further and more rapidly along railway-lines since the 1939–1945 war (Salisbury 1961).

INTRODUCTION AND SPREAD

Although some naturalised aliens were introduced unintentionally the vast majority, including many pernicious plant invaders, were brought in as garden ornamentals (Crawley *et al.* 1996). Their subsequent spread has long fascinated botanists and as a result many have been studied in great detail (e.g. *Elodea* spp., *Fallopia* spp., *Senecio* spp.). The time lag between escape into the wild and invasion can be surprisingly long given how widespread some species eventually become. For example, *Epilobium ciliatum* was known for over 40 years from a single site in Leicestershire before it began its dramatic spread throughout southern England in the 1930s (Preston 1988). However, most plant invasions have been shown to follow a rather generalised pattern with a pioneer phase of scattered primary occurrences followed by a rapid expansion from primary foci ('infection' *sensu* Salisbury 1961) and a final era of consolidation. The naturalisation of *Fallopia japonica* var. *japonica* in the British Isles provides the classic example. Its spread began in the early 1900s with initial foci in industrial areas in South Wales but also private gardens, estates, nurseries and botanic gardens from which dispersal by escape, exchange, gift, sale or disposal took place (Bailey & Connolly 2000). Indeed today clusters of hybrids with *F. sachalinensis* (*F.* ×*bohemica*) often indicate proximity to gardens where it was originally planted (Bailey & Conolly 2000). It spread modestly up till the 1939–1945 war but rapidly thereafter, especially around urban areas, before consolidating its range in the 1970s (Conolly 1977). In contrast, wind dispersed aliens have shown a much more continuous pattern of spread, particularly where colonisation took place along transport corridors (e.g. railway sidings). For example, *Epilobium ciliatum* showed a more or less even spread after the 1930s reflecting a more natural expansion of an established population rather than introduction by man at different sites (Preston 1988).

Although most aliens consolidate their distributions, a small number have subsequently declined. One of the best examples is *Elodea canadensis*: between 1850 and 1880 this North American species spread vigorously in the east of England, where it blocked drains, sluices and watercourses much to the chagrin of college rowers and swimmers in Cambridge (Simpson 1984). However, it quite inexplicably declined in abundance and invasiveness, more latterly due to displacement by *E. nuttallii* which was first recorded near Oxford in 1966 (Simpson 1990). *Spartina anglica*, the allopolyploid derivative of *S. maritima* and the North American *S. alterniflora*, has suffered a similar 'die-back' in some areas due to successional changes (Ainouche *et al*. 2004).

DISPERSAL MODE

Research on the dispersal modes of aliens has identified two distinct groups of successful invaders: tall, competitors that spread largely by vegetative fragments in garden waste and small, short-lived species with high reproductive outputs which are dispersed in soil or as airborne propagules (Hodkinson & Thompson 1997). The most extreme example of the former group is *Fallopia japonica* var. *japonica*. British populations are male-sterile and so spread is entirely by vegetative fragments from a single extraordinarily vigorous clone (Conolly 1977; Hollingsworth & Bailey 2000). Plants can establish from tiny root fragments dispersed in topsoil or garden waste, making it almost impossible to eradicate or control. The spread of the diminutive rockery plant *Veronica filiformis* has received less attention but is no less dramatic. Despite setting virtually no seed, it has colonised almost every lowland hectad in less than 70 years, presumably by vegetative fragments transported on mowing machinery. Likewise, the astonishing spread of *Spartina anglica* along the Western seaboard of Europe has occurred as a result of dispersal of rhizome fragments by sea currents.

The spread of *Epilobium ciliatum* and *Senecio squalidus* are relatively easier to understand as both produce copious amounts of plumed seed capable of dispersal over large distances. For example, Druce (1927, p.241) famously observed the dispersal of seeds *S. squalidus* during a railway journey between Oxford and Reading (c. 40 miles): "…the vortex of air following the express train carries the fruits in its wake. I have seen them enter a railway-carriage window near Oxford and remain suspended in the air in the compartment until they found an exit at Tilehurst". No doubt many other 'railway yard' aliens have been spread in a similar fashion (e.g. *Buddleja davidii*, *Conyza canadensis*, *Senecio viscosus*). Invasion of riparian habitats via waterborne dispersal of seeds, fruits and vegetative propagules have been no less dramatic. Since the 1940s *Impatiens glandulifera* (incidentally Britain's tallest annual plant) has spread rapidly along riverbanks throughout the British Isles and now occurs in dense mono-specific stands where it can suppress native perennials such as *Urtica dioica* (Tickner *et al*. 2001). Less invasive examples include the dispersal of seeds of *Lathraea clandestina*, bulbils of *Cardamine bulbifera* and vegetative fragments of *Arenaria balearica* along watercourses (Atkinson 1996; Corner 1996; Wallace 2005). The transport of seeds in soils or waste manures (e.g. wool shoddy) has also led to the spread of many species, although relatively few aliens have become widely naturalised via this agency. Possibly the most successful example is *Matricaria discoidea* which was originally introduced, into Ireland at least, with American corn fed to poultry (Reynolds 1996) but has since spread rapidly in soil attached to animals, shoes and motor vehicles (Hodkinson & Thompson 1997). A more recent invasion has been the spread of *Galinsoga quadriradiata* in urban areas, initially due to the effects of bombing during the 1939–1945 war, but more latterly in soil amongst horticultural produce (Lacey 1957).

HYBRIDISATION AND SPECIATION

Occasionally naturalised species hybridise with native congeners or other introduced species. Of the estimated 800 or so angiosperm hybrids known to occur in the UK 87 combinations involve at least one non-native taxon and 26 are hybrids between two or more alien species (Preston *et al.* 2002). Many originated allopatrically and are therefore unique to the British Isles most notably hybrids between *Fallopia* and *Epilobium* taxa. As British populations of *Fallopia japonica* var. *japonica* are entirely male sterile all seed produced is inevitably of hybrid origin. The most frequent pollen donor appears to be the common garden plant, *F. baldschuanica* although instances of the hybrid *F. ×conollyana* establishing in the wild have been astonishingly rare given the amount of seed produced annually (Bailey 2001; but see Bailey & Spencer 2003). In contrast, the hybrid with *F. sachalinensis* (=*F. ×bohemica*) displays many of the invasive tendencies of *F. japonica* var. *japonica* and is currently colonising roadsides, waste ground, riversides and railway banks throughout the British Isles (Bailey *et al*. 1996).

Harsh, man-made environments often create novel abiotic conditions in which evolutionary changes can take place (e.g. heavy metal tolerance on colliery waste tips). They can also stimulate allopatric speciation events and new hybrid combinations. Good examples are hybrids between the naturalised willowherb *Epilobium brunnescens* and native *E. lanceolatum*, *E. montanum*, *E. obscurum*, *E. palustre* and *E. parviflorum*. All have arisen relatively recently on damp, acid substrates associated with former mining activities (e.g. quarry slopes, granite aggregates, mine wastes, china clay gravels) in Cornwall (Kitchener & McKean 1998; Kitchener 2003a). Native plants are very slow to colonise these habitats and as a consequence primary colonists, such as willowherbs, have ample to time to establish and hybridise (Kitchener 2003b). In addition, the relatively sunny and warm Cornish climate may encourage hybridisation by allowing flowers to remain open longer thereby increasing chances of cross-pollination by insects (Kitchener 2003b).

The evolutionary implications of such novel hybridisation events are well documented and provide some of the clearest examples of speciation by allopolyploidy. Possibly the best studied is the neoallopolyploid *Spartina anglica* which originated from hybridisation between the native species *S. maritima* and East American *S. alterniflora* following its introduction to Southampton Water in the 1820s. The sterile first generation hybrid, *S.* ×*townsendii*, was first observed in 1870 and within twenty years gave rise to the fertile allopolyploid *S. anglica* following genome duplication (Ainouche *et al.* 2004). More recent examples have involved *Senecio squalidus*, a diploid ragwort introduced from Mount Etna, Sicily, at the beginning of the eighteenth century (Harris 2002). This species may have originated in Oxford as a stabilised diploid hybrid between two Sicilian species, *S. aethnensis* and *S. chrysanthemifolius* (Abbott *et al.* 2000, 2002; although Sell & Murrell (2006) treat both as subspecies of *S. squalidus*). Hybridisation between *S. squalidus* and *S. vulgaris* is relatively rare in the wild yielding highly sterile triploid (=*S.* ×*baxteri*) or partially fertile tetraploid hybrids. Segregation from either of these hybrids, or following backcrossing to *S. vulgaris*, has been shown to produce the 'York radiate groundsel' *S. eboracensis* (Lowe & Abbott 2003) in England and the allohexaploid 'Welsh groundsel' *Senecio cambrensis* in Wales and Scotland (Abbott *et al.* 1983; Ashton & Abbott 1992). Although reproductively isolated from their parents due to self-compatibility mechanisms and flowering times (Lowe & Abbott 2004) both are currently threatened: the Edinburgh lineage of *S. cambrensis* was recently destroyed by redevelopment (Abbott & Forbes 2002) and York populations of *S. eboracensis* have declined as a result of over-zealous street cleansing and may be extinct (Abbott *et al.* 2005). Introgression of *S. squalidus* into *S. vulgaris* subsp. *vulgaris* has also been implicated in the origin of radiate forms of groundsel, *S. vulgaris* var. *hibernicus*, which is now a common variety of town and wasteland floras in many parts of the British Isles (Abbott *et al.* 1992). *Senecio squalidus* also hybridises with the introduced *S. viscosus* to form the sterile hybrid *S.* ×*subnebrodensis* and it has been suggested that subsequent introgression may have led to the spread of *S. viscosus* during the twentieth century (Crisp & Jones 1978).

CONCLUSION

The rather depauperate nature of the British flora has meant that, with the possibility of *Bromus interruptus*, *Senecio eboracensis* and a few critical taxa, no species have become globally extinct, and relatively few have been lost in the UK as a whole. However, as Max Walters (1970) predicted this belies real losses at the local scale over the last 35 years, particularly in the intensively managed lowlands of southern England, where land use pressures have been greatest. Here the extinction of species of infertile habitats shows now sign of abating, and it seems likely that many of the species listed in Table 3 could well go extinct within the next 35 years. However, these localised losses have been more than compensated by the discovery of new species, mainly within critical genera, and, even more so by the introduction and spread of casuals and neophytes. Although Max's prediction that urban areas will be the most diverse is not strictly true, they are certainly the centres of alien plant diversity in the UK and, as the results from Cambridgeshire show, they may well become the richest areas if we continue to lose native species from the countryside at the same alarming rate. In recent decades many non-native species have been treated as unwelcome additions which will threaten our native flora. However, British botanists have learnt a great deal from their means of arrival, dispersal, habitats and competitive interactions with the native flora. In addition, the naturalisation of species from all over the globe has provided evolutionary biologists with unique opportunities to study the intricacies of diploid hybrid speciation. Future naturalisation events may also provide evidence of major environmental changes, such as climate change, as conditions become more suitable for Mediterranean and subtropical species.

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