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Rarity and decline in bumblebees – A test of causes and correlates in the Irish fauna

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ABSTRACT

Bees are believed to be in decline across many of the world's ecosystems. Recent studies on British bumblebees proposed alternative theories to explain declines. One study suggested that greater dietary specialization among the rarer bumblebee species makes them more susceptible to decline. A second study disputed this theory and found that declines in British bumblebees were correlated with the size of species' European ranges, leading to the suggestion that climate and habitat specialization may be better indicators of the risk of decline. Here we use a new and independent dataset based on Irish bumblebees to test the generality of these theories. We found that most of the same bumblebee species are declining across the British Isles, but that, within Ireland, a simple food-plant specialization model is inadequate to explain these declines. Furthermore, we found no evidence of a relationship between declines in Irish bumblebees and the size of species' European ranges. However, we demonstrate that the late emerging species have declined in Ireland (and in Britain), and that these species show a statistically significant westward shift to the extremity of their range, probably as a result of changing land use. Irish data support the finding that rare and declining bumblebees are later nesting species, associated with open grassy habitats. We suggest that the widespread replacement of hay with silage in the agricultural landscape, which results in earlier and more frequent mowing and a reduction in late summer wildflowers, has played a major role in bumblebee declines.

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1. Introduction

Bees, which provide the essential ecosystem service of pollination (Klein et al., 2006), are believed to be declining across many of the world's ecosystems (Buchmann and Nabhan, 1996; Kearns et al., 1998). A series of recent initiatives, including the International Pollinator Initiative (IPI, see Williams, 2003), have been aimed at the conservation of this important

group. While there is some debate about whether pollination *per se* is in crisis (Ghazoul, 2005a; but see Biesmeijer et al., 2006), there is no doubt that pollinators themselves, and specifically bees, are an increasingly threatened component of the world's fauna (Steffan-Dewenter et al., 2005; Ghazoul, 2005b; Biesmeijer et al., 2006). In general, this decline appears to be driven by habitat loss and fragmentation, mainly due to intensification of agriculture and urbanization (Williams,

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1986; Benton, 2006). In addition, it is clear that, whilst some species of bee are in decline, others remain abundant, suggesting that species or taxon-specific factors may also play a role in explaining decline. For example, a recent study by Biesmeijer et al. (2006) found that narrow habitat range, flower specificity, and univoltinism were all associated with decline in solitary bees in Britain and the Netherlands. Nevertheless, Biesmeijer et al. (2006) noted that their conclusions were based on a relatively small number of 10×10 km grid squares and cautioned the extrapolation of their conclusions to the broader spatial scale. Few quantitative and geographically broad datasets exist to enable us to test the role of these and other potential factors in the decline of bees.

One such dataset is the distribution of bumblebees in Great Britain. A series of studies have interrogated this dataset in an attempt to understand the factors involved in causing the general decline of this group (Williams, 1982; 1986) and finer patterns of species-specific decline (Goulson and Darvill, 2004; Goulson et al., 2005; Goulson et al., 2006; Williams, 2005). Two recent papers assessed the potential roles of foraging niche width (Goulson et al., 2005) and species-range patterns (Williams, 2005) in bumblebee decline in Great Britain.

The food-plant specialization hypothesis (Goulson and Darvill, 2004; Goulson et al., 2005) proposes that species that now have restricted geographic distribution (i.e., are rarer) in Britain are more specialized foragers and have a narrower dietary breadth for pollen. Consequently, it argues that these species have declined because of changes in plant communities, largely attributable to the loss of unimproved flower-rich grasslands, a habitat rich in Fabaceae.

Williams (1985, 1989b) rejects a food-plant specialization model and proposes the marginal mosaic model (Williams, 1985, 1988, 1989b), suggesting that species near the edge of their geographic range or near their niche limit (those with particularly narrow ranges) might have marginal growth rates, be present at lower local densities and be most patchy in their local distributions. Reductions in foraging profits and consequent further reductions in density mean that these species would be most susceptible to local extinctions and so show range declines. Thus, it is not necessarily specialization in particular food plants that is limiting but maybe specialization in other aspects of the niche. Williams (2005) found no evidence for a relationship between rarity and declines in British bumblebees and their dietary breadth, the strength of their dietary preference or their proboscis length. That study (Williams, 2005) instead found support for a relationship between rarity and decline within Britain and the sizes of species' European ranges, particularly when these measures are adjusted to represent their ranges near sea level. Williams (2005) argues that adjusted range sizes may reflect overall niche breadth and that climatic and habitat specialization may be a better indicator of risk of decline than food plant specialization.

While these studies did not come to a clear consensus, it does seem that both species-range and niche differences have played a part in the decline of the British bumblebee fauna. However, in the absence of other equivalent datasets, it is impossible to ascertain the generality of these conclusions. Here we use a new dataset based on the bumblebee fauna

of Ireland to provide a comparative analysis of bumblebee decline and to test the British conclusions, and whether they allow generalizations to be drawn that are relevant across a wider geographic range.

2. Methods

2.1. Measuring rarity and decline in Irish distribution ranges

This study uses distribution maps generated from a database of Irish Bees developed by the authors and contains ca. 8000 records from Ireland. Records were sourced from the Bees, Wasps and Ants Recording Society (BWARS), which collates data for British and Irish bees; from museum collections held in the Ulster Museum; collated from published sources (predominantly records published in the *Irish Naturalists' Journal* and the *Bulletin of the Irish Biogeographical Society*); taken from the personal databases of John Breen and Don Cotton; and collected in recent country-wide studies (Veronica Santorum, Úna Fitzpatrick, Tomás Murray, Rob Paxton and Mark Brown). Rarity and decline in British bumblebees have traditionally been assessed by comparing records pre- and post-1960 (Alford, 1980; Williams, 2005), mainly due to a massive recording effort undertaken in the 1970s and the ensuing production of *The Atlas of the Bumblebees of the British Isles* (1980). However, declines in both solitary and social bee species in Britain have recently been assessed by comparing records pre- and post-1980 (Biesmeijer et al., 2006). Unlike Britain, Ireland does not have a strong historical tradition of natural history recording and thus has considerably fewer records per unit area. The Irish dataset was interrogated and 1980 chosen as the equivalent point from which to assess decline as the data has a roughly equal spread of records pre and post this date. In addition, and more importantly, this reflects the slightly later transition towards intensive agricultural land-use in Ireland (Feehan, 2003), which has been suggested to be a major causal factor in bumblebee decline (Santorum and Breen, 2005).

We performed the analyses of range decline for each bumblebee species on distribution data at the regional scale by using a rectangular grid of 50×50 km cells, to enable direct comparison with British data that used the same grid area (Williams, 2005). Coastal cells do not have equal areas to the inland cells but, as in Williams (2005), have been left in the analysis because of the importance of coastal distributions. Again, as in Williams (2005), the data quality means that measuring range declines is dependent on the assumption that a 1980 onwards record on the map implies its pre-1980 presence while a pre-1980 record implies its post-1980 absence. To minimize the impact of false decline, in our recent recording we specifically targetted under-recorded 50×50 km cells to maximize the number of species recorded. Nevertheless, it should be noted that this methodology and assumptions may result in decline being exaggerated and thus borderline declines should be treated with caution.

The former range sizes of each Irish species are the number of cells on a 50 km grid for all known records. Present range sizes are the number of cells on a 50 km grid for records from 1980 onwards. Range decline is measured as the propor-

tional change in the number of cells on a 50 km grid (there are a total of 54 squares in Ireland): $1 - [(1980 \text{ onwards records}) / (\text{pre-1980} + 1980 \text{ onwards records})]$.

2.2. Measuring relative dietary breadth

There are few sites where a wide range of bumblebee species occurs together, which has resulted in few datasets that permit quantitative comparisons of forager choice. One exception is the dataset from Dungeness in Britain, used by Williams (2005). Unfortunately no such dataset is available for Ireland so we measured relative dietary breadth and dietary preference from new data gathered across a range of habitat types (see below), thus taking a landscape scale view of foraging specialization.

As part of a broader study on the habitat requirements of Irish bees, we carried out surveys on 44 protected sites (Special Areas of Conservation or National Parks) distributed across the island of Ireland (Fig. 1). In 2004, eight dry calcareous grassland sites, eight bog sites, eight sand dune sites and four machair grassland sites were surveyed, and in 2005 we surveyed eight dry heath and eight woodland sites. Within each habitat type (with the exception of machair which is restricted to the north and west of Ireland) two sites were chosen from each of the four provinces (which roughly divide Ireland into quarters) to ensure a geographic spread across the country (see Fig. 1). Each of the 44 sites was visited three times across the season (spring, early summer and late summer) and on each visit a 2-hour standardized ‘Pollard’ walk

was carried out, where all bees observed and what they were foraging on, was recorded (no distinction was made between nectar or pollen collection). For each species, information on their forage sources was amalgamated across all visits on all sites and used to calculate a value for rarefied dietary breadth and maximum dietary preference, using the methodology of Williams (2005). The final dataset contained a total of 2086 records.

A major problem in measuring dietary breadth is the statistical artifact that can arise as a result of the differing sample sizes among bumblebee species depending on their rarity (Williams, 1989b). This problem was overcome using a rarefaction procedure (Gotelli and Colwell, 2001) which compares the number of plant species the different bumblebee species would be expected to visit for a standardized number of visits by each bee species. Following Williams (2005) we made a sub-sample of 20 visits from the observed frequency distribution of visits by each bee species, but chosen at random without replacement 1000 times. This provides an estimate of the mean number of plant species that each bumblebee species would be expected to visit in 20 flower visits. For the Irish data, there were insufficient records of *Bombus distinguendus*, *B. ruderarius* and *B. sylvarum* to calculate a relative dietary breadth. *Bombus lucorum* and *terrestris* workers could not be distinguished as bees were identified on the wing during Pollard walks, and were regarded as *B. lucorum* agg in the dietary analyses.

2.3. Measuring relative dietary preference

The Irish dataset was used to calculate relative dietary preference, again following the methodology of Williams (2005). Relative dietary preferences of bumblebee species were measured by comparing the deviations of their observed frequencies of flower visits from those expected using a contingency table (Williams, 1989a). The frequencies of visits that would be expected if foragers were unselective and encountered the same flowers was calculated from the product of the marginal totals of recorded visits (total numbers of visits by one bee species \times total number of visits to one plant species) divided by the total of all visits to all flowers. An index of preference of a bee for a plant is provided by the deviation of observed from expected frequencies of visits, divided by the expected frequency. The strongest preference is the largest positive index value (Table 1).

2.4. Emergence time of Irish species

The emergence time of each species in Ireland is the earliest known record of the species (by month), based on the information held in the Irish database developed by the authors.

2.5. Range decline correlations

For each of the Irish species, we correlated range decline with relative dietary breadth, relative dietary preference, time of emergence, and with European range sizes and proximity to range edges (data taken directly from Williams (2005)). We also correlated Irish range decline with relative dietary breadth and dietary preference values calculated using the

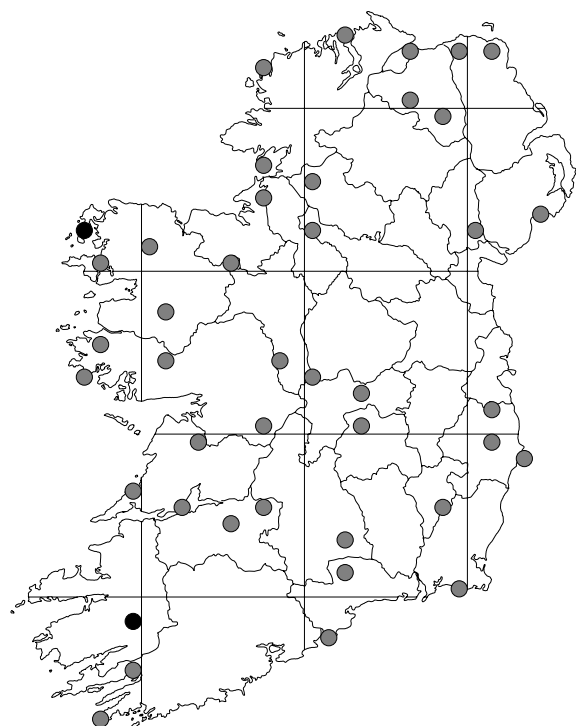


Fig. 1 – Map showing the location of the 44 sites from which foraging data were collected and used to calculate relative dietary breadth and dietary preference in Ireland (black dots indicate areas within which two separate sites were surveyed).

Table 1 – Irish bumblebee distributional data and biological traits compiled for the analyses

Species	Former regional range (no. 50 km cells)	Former local range (no. 10 km cells)	Range decline (proportion of 50 km cells)	% Total populations in the west pre 1980	% Total populations in the west 1980 onwards	Emergence month of overwintered queens	Rarefied dietary breadth (no. plant species in 20 visits)	Maximum dietary preference (obs-exp)/exp	Pollen maker or pollen storer
<i>distinguendus</i>	31	68	0.710	47	93	4		27.19	Maker
<i>hortorum</i>	51	261	0.157	57	51	1	10.83	38.36	Maker
<i>jonellus</i>	45	174	0.089	58	54	1	6.62	9.18	Storer
<i>lapidarius</i>	49	181	0.204	62	56	1	9.31	22.71	Storer
<i>lucorum</i>	51	284	0.098	49	45	1	8.45 ^a	0.86 ^a	Storer
<i>monticola</i>	7	13	0.000	–	–	3	1.99	33.38	Storer
<i>muscorum</i>	46	174	0.239	60	60	3	12.63	21.67	Maker
<i>pascuorum</i>	53	379	0.038	57	49	1	13.16	4.11	Maker
<i>pratorum</i>	43	176	0.093	34	43	2	8.55	16.98	Storer
<i>rudericus</i>	34	99	0.588	62	80	4		17.30	Maker
<i>sylviarum</i>	15	33	0.533	57	85	5		10.07	Maker
<i>terrestris</i>	42	150	0.190	31	39	1			Storer

^a Represents the value for *Bombus lucorum* agg.

British Dungeness data (data taken directly from Williams (2005)). In addition, British range decline (Williams, 2005) was correlated with Irish emergence data. To evaluate whether the Irish data provide a substantively different dataset from the British data, the British data were also re-analyzed using only those species common to both regions. Correlations are Spearman rank, performed in SPSS version 12.0.1. *Bombus monticola* was not included in any of the correlations as it was first recorded in 1974 and is suspected to be a recent arrival to Ireland (Speight, 1974).

2.6. Assessing changes in species distributional ranges from 1980 onwards

Changes in the broad distributional range of each species were assessed by comparing the percentage of populations of each species in the western and eastern halves of the island of Ireland pre-1980 and post-1980. *B. monticola* was not assessed as it was first recorded in Ireland in 1974 and to date is only distributed in upland areas of eastern Ireland. A rectangular grid of 50 × 50 km cells was superimposed onto Ireland using the Irish grid, and we defined the eastern and western halves as lying on either side of the midpoint of this grid (Figs. 3–5). We first compared the number of 10 km cells for which bumblebee records were available in the two halves of the country pre-1980 and post-1980. Then, for each species, we controlled for sampling effort in each half of the country by dividing the number of positive cells (cells with a species record) by the number of cells from which any *Bombus* records existed. We then compared the distribution of these cells to the null hypothesis that a species was equally likely to be found in either half of Ireland for both pre- and post-1980 data. Species comparisons were done at both the 10 and 50 km scales, using chi-square tests.

3. Results

3.1. Rarity and decline in Irish regional ranges

Former distribution ranges at the scale of 10 and 50 km grids are positively correlated ($r_s = 0.98$, $p < 0.01$). Species with the greatest former distribution range at the 50 km square level also have the greatest range when assessed at the 10 km square level. Species with intermediate regional range sizes within Ireland are disproportionately rarer within regions (Fig. 2).

There was a significant negative relationship between former range and decline ($r_s = -0.69$, $p < 0.05$). The historically rarer species, with smaller former ranges, have declined most in Ireland (see data in Table 1 and Fig. 2).

3.2. Correlating rarity and decline in Ireland and in Britain

Similar species are declining in Ireland and Britain, with declines in Ireland positively correlated with declines in Britain ($r_s = 0.84$, $p < 0.01$; Fig. 3 for species comparisons). Traditionally rarer species in Ireland are also traditionally rarer in Britain, with former range in Ireland positively correlated with former range in Britain ($r_s = 0.86$, $p < 0.01$).

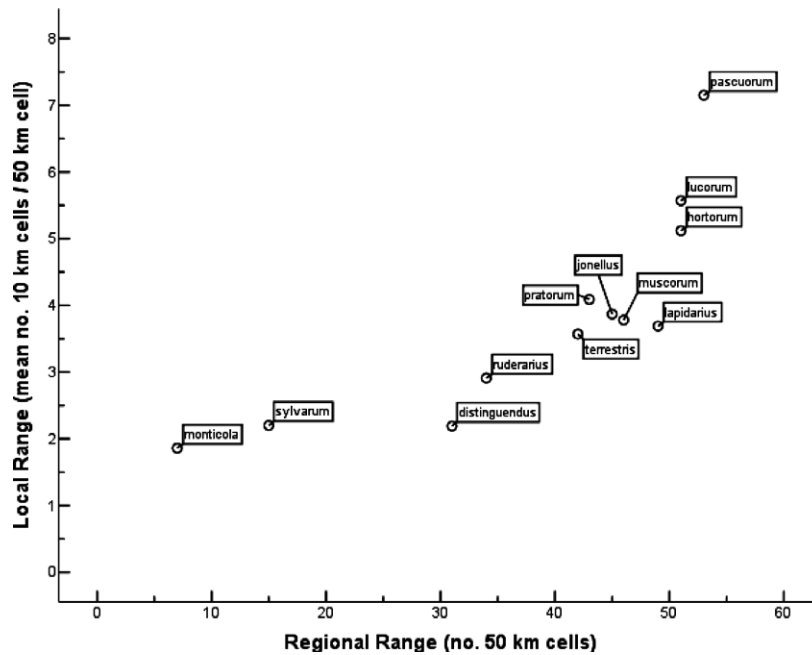


Fig. 2 – Scatterplot showing the relationship between former ranges of Irish bumblebee species (pre-1980 and 1980 onwards), measured (x-axis) as numbers of 50 × 50 km grid cells and (y-axis) as mean numbers of 10 × 10 grid cells per occupied 50 × 50 km grid cell. The exponential relationship is driven by species with intermediate regional range sizes being disproportionately rarer at the local scale.

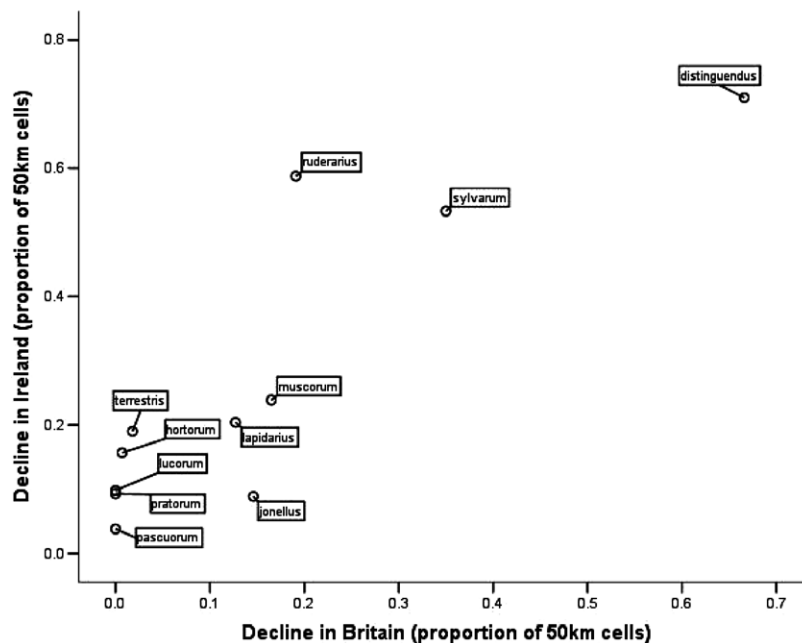


Fig. 3 – Scatterplot showing the relationship between range decline (proportion of 50 km cells) in Ireland and Britain (data from Williams (2005)) for 11 species that are common to both regions.

3.3. Correlating rarity and decline with dietary breadth and dietary preference

Rarefied dietary breadth (calculated from the total Irish forage data) is uncorrelated with Irish former regional range size among species ($r_s = 0.52$, n.s.) and is uncorrelated with regional decline among species ($r_s = 0.18$, n.s.). Relative maximum

dietary preference is uncorrelated with Irish former regional range size among species ($r_s = -0.20$, n.s.) and is uncorrelated with regional decline among species ($r_s = 0.58$, n.s.). These relationships were qualitatively the same when subsets of foraging data from the six specific habitats were used in the analysis (data not shown). Similarly, no significant correlations were found between Irish former regional range size

or regional decline and rarefied dietary breadth ($r_s = 0.20$, n.s. and $r_s = 0.10$, n.s., respectively) or relative maximum dietary preference ($r_s = 0.02$, n.s. and $r_s = 0.16$, n.s., respectively) using the British Dungeness data (taken from Williams (2005)). These data provide no evidence of a relationship between declines in Irish bumblebees and their dietary breadth or strengths of their dietary preferences.

3.4. Correlating rarity and decline with European range sizes and edges

Adjusted European range size is positively correlated with Irish former regional range size among species ($r_s = 0.67$, $p < 0.05$) but is uncorrelated with regional decline among species ($r_s = -0.35$, n.s.; Fig. 4). Those species with the greatest former ranges in Ireland also have the greatest European range sizes, but there is no evidence for a significant relationship between declines in Irish bumblebees and their European range size in these data. The lack of correlation is not simply due to a loss of power caused by the smaller Irish species list. Williams (2005) found that the adjusted European range size was positively correlated with British former regional range size among species ($r_s = 0.68$, $p < 0.05$) and was negatively correlated with regional decline among species ($r_s = -0.65$, $p < 0.05$). We repeated these analyses with the British data after reducing the species list to contain only those species present in Ireland and the relationships remained significant ($r_s = 0.70$, $p < 0.05$ and $r_s = -0.61$, $p < 0.05$, respectively; Fig. 4).

European range-edge proximity is uncorrelated with Irish former regional range size among species ($r_s = 0.38$, n.s.) and is uncorrelated with regional decline among species ($r_s = 0.09$, n.s.). These data provide no evidence of a relationship between declines in Irish bumblebees and their European range-edge proximity.

3.5. Correlating rarity and decline with emergence time

Species that emerge later in the year have declined most in Ireland, with emergence time positively correlated with regional decline among species ($r_s = 0.75$, $p < 0.01$). Declines in Brit-

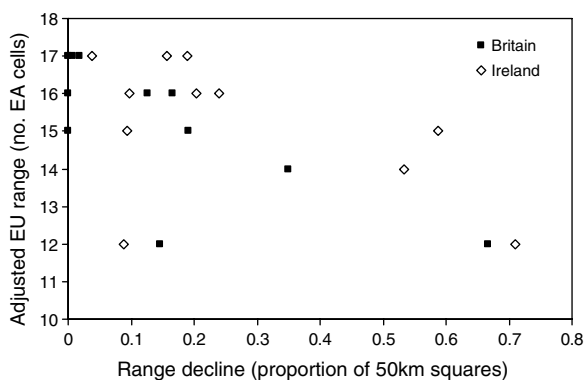


Fig. 4 – Scatterplot showing the relationship between adjusted EU range (data from Williams (2005)) and range decline (proportion of 50 km cells) in Ireland and in Britain (data from Williams (2005)).

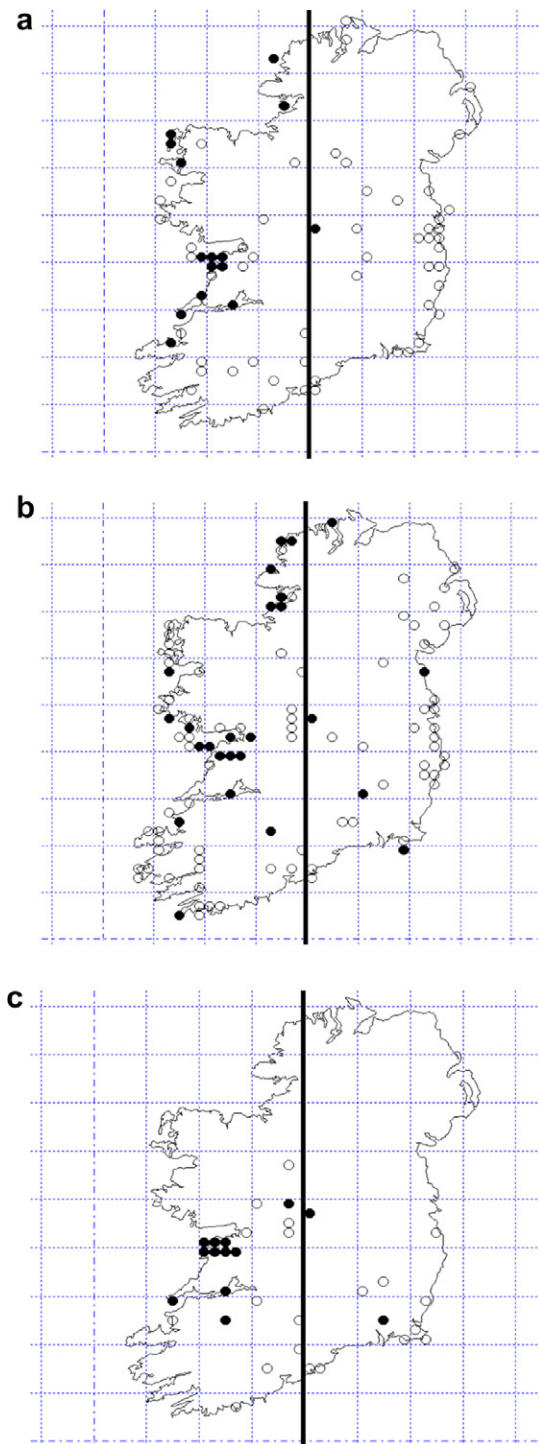


Fig. 5 – (a) Map showing the distribution of *Bombus distinguendus* at the 10 km² level pre 1980 (hollow circles) and from 1980 onwards (filled circles). The solid vertical line denotes the midpoint used to divide Ireland into east and west. (b) Map showing the distribution of *Bombus rudrararius* at the 10 km² level pre 1980 (hollow circles) and from 1980 onwards (filled circles). The solid vertical line denotes the midpoint used to divide Ireland into east and west. (c) Map showing the distribution of *Bombus sylvarum* at the 10 km² level pre 1980 (hollow circles) and from 1980 onwards (filled circles). The solid vertical line denotes the midpoint used to divide Ireland into east and west.

Table 2 – χ^2 Test of differences in the % of populations of *Bombus distinguendus*, *B. sylvarum* and *B. ruderarius* in the west compared to the null hypothesis that a species was equally likely to be found in either half of Ireland for post 1980 data

Species	10 km ² level	50 km ² level
<i>Bombus distinguendus</i>	$\chi^2_1 = 8.28, p < 0.005$	$\chi^2_1 = 23.39, p < 0.001$
<i>Bombus sylvarum</i>	$\chi^2_1 = 4.68, p < 0.05$	$\chi^2_1 = 6.05, p < 0.025$
<i>Bombus ruderarius</i>	$\chi^2_1 = 6.87, p < 0.01$	$\chi^2_1 = 5.88, p < 0.025$

ish bumblebees are also positively correlated with time of emergence based on Irish emergence data ($r_s = 0.73, p < 0.05$).

3.6. Assessing changes in species distributional ranges from 1980 onwards

The three species that have undergone the biggest declines in Ireland and Britain – *B. distinguendus*, *B. ruderarius* and *B. sylvarum* – showed a dramatic and statistically significant increase in the percentage of their populations occurring in the west of Ireland from 1980 onwards, with at least 80% of the currently known populations of each now existing in the west (Table 1; Fig. 5(a–c)).

There was no difference in the percentage of 10 km cells from which we had bumblebee records between the western and eastern halves of Ireland pre- and post-1980 ($\chi^2_1 = 0.03$, n.s.). Pre-1980, only *B. terrestris* had a distribution significantly different from that expected by the null hypothesis, with a greater percentage of its populations occurring in the eastern half of Ireland at the 10 km grid scale ($\chi^2_1 = 4.09, p < 0.05$). However, at the 50 km grid scale this difference disappeared ($\chi^2_1 = 0.52$, n.s.). In contrast, post-1980 *B. distinguendus*, *B. ruderarius* and *B. sylvarum* all had significantly greater proportions of their populations in the western half of the country than expected, at both the 10 and 50 km scales (Table 2). There were no significant differences in east–west distribution of any of the remaining species.

4. Discussion

This study clearly shows that the later emerging bumblebees are declining in Ireland and that there is a significant westward shift in the range of these species, probably caused by changing land use. We found no evidence for a relationship between rarity and decline in Irish bumblebees and overall niche breadth (based on adjusted European range size) or between decline and dietary breadth or dietary preference. Bumblebee species are, however, reacting similarly across the British Isles, with range declines in Irish bumblebees positively correlated with declines in Britain. The probable drivers of these trends, namely changes in and intensification of agriculture, may apply across a much larger geographic range.

This study found three bumblebee species to be in serious decline in Ireland – *B. distinguendus*, *B. sylvarum* and *B. ruderarius*. Within Ireland, *B. distinguendus* is at the southern edge of its European distribution (Williams, pers. comm); while in contrast; *B. ruderarius* and *B. sylvarum* are both at the northern

edge of their European range (Goulson et al., 2005). Despite these differences, each of the three species shows a similar westward shift in its range from 1980 onwards. A species' former range may be constrained by climatic tolerances (Williams, 2005), but our data provide no evidence that range contractions are being driven towards climatically favorable regions, given this shift to the west, where the climate is cooler and wetter (Keane et al., 2004) and thus presumably less conducive for supporting bumblebee populations.

Much of the urbanization and agricultural intensification of Ireland has centered on the east and midlands of the island (Feehan, 2003) with distribution data showing an almost complete regional extinction of the three species from these areas. Declining bumblebees are found in the pockets of floral rich habitat that remain in Ireland (isolated grasslands in the midlands, the western limestone pavement of the Burren in Co. Clare and coastal sites along the west coast) and have no clear associations with distinct habitat type. This is mirrored in Britain where the rare species are restricted to a broad range of biotypes that have escaped the ravages of modern agriculture (Williams, 1986; Goulson et al., 2006).

Williams (2005) showed that rare and declining species in Britain tend to have smaller geographic ranges within Europe and suggested that range sizes may reflect overall niche breadth and therefore that climatic and habitat specialization may be a better indicator of risk of decline from changing food plant availability than food plant specialization. Irish data show no evidence of a relationship between declining species and their geographic range size across Europe. Williams (1982) identified a central impoverished region in Britain, analogous to the eastern impoverished region in Ireland. It may be that the differing location of this region within each country is contributing to the relationship, or lack of, between decline and adjusted range size. For example, if species with a smaller former range size only reached to the central region in Britain, a centrally located impoverished region would result in a correlation between decline and range size, irrespective of the actual cause of the impoverishment.

Bombus distinguendus, *B. ruderarius* and *B. sylvarum* are traditionally rare in Ireland (Stelfox, 1927) supporting the theory that regionally rarer species tend to be found at lower local abundances where they are present. So, if abundances were decreased further in general, it is likely to be the least abundant that would be extirpated first (Williams, 1988). As regionally rare species, found at lower local abundances, they may have a greater difficulty in colonizing new areas or exploiting alternative niches in a backdrop of habitat loss and fragmentation, and it is possible that it is this initial rarity combined with subsequent habitat loss that is driving their range decline rather than more specific climatic or habitat specializations.

It has been suggested that many rarer species have more specialized diets (Goulson et al., 2005). Our data support the findings of Williams (2005) who found no relationship between range decline and dietary specialization. While the Irish data do not show a relationship between decline and dietary specialization, whether declines have been driven by overall food plant availability (linked to habitat change) or loss of specific plant species remains unknown. In Britain

it has been suggested that the widespread decline in wildflowers traditionally associated with hay meadows, pasture and hedgerows may have contributed to declines (Williams, 1986, 1988, 1989a, 1989b; Goulson et al., 2006). We propose that declines are more specifically explained by the movement from hay to silage production, which has largely happened within the past 30 years in Ireland (Feehan, 2003) and is a similarly recent phenomenon in Britain (MAFF et al., 1997). The first silage harvest is usually taken in May, a month or more before hay, which is usually cut in late June–August (Vickery et al., 2001). In comparison to silage, hay making allows considerable flowering (Smith and Jones, 1991); because the process is dependent on having a period of settled dry weather it tends to be delayed until mid summer (Vickery et al., 2001). Thus, the transition from hay making to silage production not only results in a general decline in the extent of wildflowers across the agricultural landscape, but more specifically a sudden decline in the presence of these floras later in the season.

The transition from hay making to silage production and the subsequent decline in wildflowers has previously been suggested to have had significant effects on butterflies (Ferber et al., 1996); we propose that it has also had a detrimental effect on bumblebees and most specifically on the late emerging species. Bumblebee species differ in the time of year at which the queen emerges from hibernation. Previous discussion of British data suggested an association between late emerging species and decline (Edwards and Williams, 2004; Goulson et al., 2005). Here we show a significant positive correlation between decline and time of emergence for Irish bumblebees (and demonstrate a similar statistically significant effect for the British data), and draw attention to the possible relationship between the decline of these species and the transition from hay to silage production. Late emerging species may have traditionally been dependent on hay meadows and their associated wildflowers, and thus it may be the loss of this element of the landscape that is contributing most to their decline.

Our data show that in Ireland, the four species that have declined most (*B. distinguendus*, *B. ruderarius*, *B. sylvarum* and *B. muscorum*) are later emerging species, associated with open grassy habitats. The only other species to show major evidence of a decline in Ireland is *B. lapidarius*. This species is not late emerging but has been largely lost from the agricultural landscape in Ireland (Santorum and Breen, 2005). Santorum and Breen (2005) suggest that *B. lapidarius* may have always had a more patchy distribution, and be prone to population fluctuations in Ireland (Stelfox, 1927). It remains abundant in the limestone pavement area of the Burren in western Ireland, where the agricultural landscape is dominated by low intensity farming (Santorum and Breen, 2005); and is also common on flower rich grasslands and sand dunes around Ireland (Fitzpatrick and Murray, 2006; unpublished report). A recent study of bumblebees in Dublin city found that it accounted for less than 2% of the individuals observed and was only observed where floral sources were abundant and diverse (Brown, 2002; unpublished report). *B. lapidarius* is not declining in Britain where it is one of the 'big six' common and ubiquitous species (Goulson et al., 2005). Clearly, it is reacting differently in Britain and Ireland and the reasons for

these differences in its ecology and pattern of decline are worthy of further study.

One of the most intriguing elements of bumblebee ecology is why some species have declined while others remain abundant. Attempting to identify taxon-specific factors involved in decline can be problematic, given the influence of the decline itself on the ecology of the species. In Ireland *B. distinguendus* currently has a very restricted range and could be mistaken for a habitat specialist, while historical data indicate that it previously occupied a much broader range of habitats; a situation that is mirrored in Britain (Williams, 1982; Goulson et al., 2006). A more pertinent question, and unfortunately one that is now difficult to assess in Ireland, is why the declining species were rare in the first place. Taxon-specific factors may have been involved in the rarity of *B. distinguendus*, *B. ruderarius* and *B. sylvarum* but not necessarily directly in their decline.

There is no clear evidence that bumblebees as a group are declining in Ireland, although the assemblage is changing. *Bombus pratorum* (first recorded in 1947) and *B. monticola* (first recorded in 1974) are the most recent arrivals, with the former now widespread and abundant and the latter currently expanding its range. *B. monticola* has declined in Britain and is currently in a species recovery program (SRP) being run by the UK governmental conservation agency, Natural England. Identifying why *B. monticola* is expanding in Ireland yet declining in Britain makes these islands an important place to understand bumblebee ecology and how bumblebees utilize the landscape. While many species are reacting similarly in Britain and Ireland, in addition to *B. lapidarius*, there are other fine scale patterns that are very different. *B. sylvarum* is now known from only seven populations in Britain and shows a markedly coastal distribution where once it was widespread inland (Williams, 1982; Goulson et al., 2006). This is not the case in Ireland where the species has declined from eastern Ireland but is known from 15+ populations, and retains its historical association with inland sites. *B. muscorum sladenii* also now shows a markedly coastal distribution, having significantly declined from inland Britain (Williams, 1982; Goulson et al., 2006). These levels of decline are not mirrored in Ireland where *B. muscorum* remains widespread and is often found in urban environments. Comparative studies in the two systems offer enormous potential for a greater understanding of the factors driving declines.

5. Conclusions

Late emerging bumblebees are declining in Ireland but no evidence has been found for a relationship between these declines and food plant specialization or niche breadth (as indicated by the European range). Similarly, evidence indicates that declines are not resulting in range contractions towards climatically favorable regions. This new dataset finds a significant positive correlation between time of emergence and decline, and we suggest that the widespread replacement of hay with silage in the agricultural landscape since the 1970s in both Britain and Ireland, which results in earlier, more frequent mowing and a reduction in late summer wildflowers, has played a major role in bumblebee declines.

Habitat loss may be the major driving factor but little is known about the subtleties of localized extinctions. Studies are urgently needed on the precise habitat requirements of the rare species across the British Isles, including research into pollen foraging at sites where a rich assemblage of bumblebee species remains, including those that are declining. While declines in food-plant density may play a role in local declines, increases in food plants may be insufficient to ensure recovery (Williams, 2005). As suggested by many authors (Edwards, 2003; Edwards and Williams, 2004; Goulson et al., 2005; Carvell et al., 2006), maintaining Fabaceae-rich grasslands in areas where populations remain, combined with specific management to support the later emerging species, may be the best immediate conservation actions. Banaszak (1992) recommends that a minimum of 25% of land cover should be semi-natural habitat in order to conserve a region's bee diversity. There is a clear need to address this – in Ireland a recent national red list of Irish bees found that one third of the entire fauna (102 species) is already threatened (Fitzpatrick et al., 2006). One solution may be to change agricultural practices and provide economic support for schemes that introduce networks of small semi-natural habitat patches back into the agricultural landscape.

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