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Can vulnerability among British bumblebee (*Bombus*) species be explained by niche position and breadth?

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ABSTRACT

Comparison of the two flagship species of British bumblebee conservation (*Bombus distinguendus* and *B. sylvarum*) with a widespread, common, and more stable species (*B. pascuorum*) shows (1) that the two rarer and range-declining species in Britain had narrower (more specialized) climatic niches in western Europe even before their most severe declines, and (2) that the areas where they persist in Britain from 2000 onwards are closer climatically to the centres of their pre-decline west-European climatic niches than the areas from which they have been lost. Although data are available for few bumblebee species at present and further tests are needed, the first result supports earlier suggestions that it is bumblebee species with narrower climatic niches that are most vulnerable to decline. The second result supports the suggestion that it is in areas nearer the edges of their climatic niches where these species are most vulnerable to decline, although this can be ameliorated locally by higher food-resource levels. This is not to say that all patterns of bumblebee decline have been influenced by climatic niche, particularly in North America. Nonetheless, in Britain we find that even without climatic change, an interaction between climatic niche and food-plant reductions from land-use change retains the potential to explain at least some of the broader patterns of *which* species have declined, *where* they have declined, and *how* they have declined.

1. Introduction

The question of what is responsible for the decline of some bumblebee species is important because bumblebees are highly valued as pollinators (Osborne and Williams, 1996). Most authors agree that the major driver of bumblebee decline in Britain is agricultural policy affecting changes in land use that in turn affect floral resources (e.g. Williams, 1985, 1986; Prys-Jones and Corbet, 1987; Rasmont, 1988; Rasmont and Mersch, 1988; Carvell, 2002; Edwards, 2003; Goulson, 2003; Macdonald, 2003; Edwards and Williams, 2004; Benton, 2006; Kosior et al., 2007). In contrast, there is much less agreement on the biological mechanism by which floral changes affect the bumblebees, in the sense of how floral changes make some bumblebee species and populations more vulnerable than others (sensu IUCN, 2001). In the 1980s, we investigated (Williams, 1985; Rasmont, 1988; Williams, 1989a) whether bumblebee rarity and decline might depend in a simple way on the degree of food-plant specialization and a declining availability of the corresponding preferred plants. This claim has been repeated more recently (Goulson and Darvill, 2004; Goulson et al., 2005; Rasmont et al., 2005). However, although more data are needed, the degree of specialization in food-plant species alone failed to explain patterns of British bumblebee

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rarity and decline once the effects of the different sample sizes for the different bumblebee species had been taken into account (Williams, 1989b, 2005). In contrast, an earlier idea that rarity and vulnerability to decline might ultimately depend upon interactions between climatic preferences and food-plant preferences was still supported (Williams, 1985, 2005). Here we present an improved test of the climatic component of this idea, beginning with the two bumblebee species on which UK Biodiversity Action Plan studies focused initially as flagships for conservation (Edwards, 1998): *Bombus distinguendus* and *B. sylvarum*. The results show that the climate–food compensation idea has the potential to explain which British bumblebee species are most vulnerable to decline, in which regions of the country they are most vulnerable to decline, and how environmental changes might drive this decline.

A species' pattern of occurrence is often interpreted in terms of Hutchinson's (1957) concept of ecological niche. This idea depends in part on the species' use of food resources and in part on its climatic tolerances. Each species is believed to have its own (1) climatic optimum and (2) breadth of climatic tolerances around this optimum, which together define the climatic space that the species should have the potential to occupy. Presumably these parameters are governed in turn by how physiology responds differently to climate in different species (e.g. Davis et al., 1998). Differences might arise, for example, from species-specific profiles of enzyme activity with temperature, which might affect the regional efficiency with which resources could be converted into more individuals, and hence would limit the species' maximum potential local population sizes. In addition, while these factors may limit the species' potential or 'fundamental niche', barriers to dispersal or competitive and other interactions among species may further constrain the species to a smaller 'realised niche' (e.g. Araújo and Guisan, 2006).

For bumblebees, niches have usually been studied in terms of the relative tongue lengths of the bumblebees and the relative depths of the flowers that they visit (e.g. Heinrich, 1976; Inouye, 1977, 1978; Heinrich, 1979; Prys-Jones, 1982; Barrow, 1983; Ranta, 1984; Williams, 1985; Rasmont, 1988; Neumayer and Paulus, 1999; Goulson and Darvill, 2004; Inoue and Yokoyama, 2006). It has been shown experimentally that bumblebees maximise their foraging profit rates by matching their tongue lengths with the depths of the flowers that they visit (Harder, 1983). This relationship has been found to translate into foraging preferences in the field (e.g. Brian, 1957; Heinrich, 1979). However, bumblebees are social insects and their colonies have a foraging season that is usually long relative to the flowering season of most individual plant species. Therefore, most bumblebee species cannot afford to specialise on just one plant species and need to use a series of food-plant species (the plant species used may vary from place to place) through the season depending on what is most profitable at any one time (with apparent exceptions, see Section 4).

At the other end of the spatial scale, the sub-discipline of macroecology has made a particular study of the relationship between the processes related to niches and abundance, on the one hand, and their expression as macro-scale geographical distribution patterns on the other. Two patterns are of particular interest here. First, a general positive association has been described between species' range sizes and their abundances, and this has been explained in terms of the similar effects of niche breadth on both attributes (Brown, 1984, 1995; Gaston and Blackburn, 2000). Second, a general pattern has been claimed for species to show higher abundances nearer the centres of their geographical ranges (e.g. Andrewartha and Birch, 1954; Hengeveld and Haeck, 1982; Brown, 1984). Recent reviews (Sagarin and Gaines, 2002; Sagarin et al., 2006) have questioned the generality of this second pattern. Nevertheless, some evidence in support of this relationship does exist for British bumble bees (Williams, 1988). However, here we are interested initially in whether bumblebee species show higher abundances in suitable habitats nearer the centres of their distributions within their climatic niche space, and only secondarily in the possible expression of this relationship in geographical space (which may be complicated by many biotic and abiotic factors, see the comments on niche above, including altitude e.g. Gorodkov, 1986a,b; Guralnick, 2006). Much more work is needed to determine the shapes of the maximum abundance responses across the climatic space and which processes might affect abundances in different parts of the range.

A combination of niche ideas and macroecological patterns is expressed graphically in Fig. 1 (Williams, 1985, 1988, 1989b). This illustrates for bumblebees how higher levels of resources (from higher abundances or profitabilities of preferred food plants) in some habitat patches might compensate locally for a lower regional efficiency of conversion of resources into bees (away from the species' climatic optimum), thereby enabling a species to persist in climatically suboptimal but food-rich patches. The precise shape of the abundance curves is not critical: smooth, unimodal curves are unnecessary, because the local maxima (carrying capacities) need only be lower nearer the range edges than closer to the optimum. So even in a uniform patchwork or mosaic of more than one kind of habitat, compensation between regional climate-constrained conversion efficiencies and some richer local resource levels might result in a more patchy distribution for a species within regions where it is closer to the limits of its climatic tolerances. This model fits three patterns observed for bumblebees (Williams, 1988). First, a concentric pattern of nearly ubiquitous distribution near the centre of a species' climatic distribution, surrounded by a more patchy distribution nearer the edges of its climatic range. This appears to be expressed geographically for some species even within Britain, and particularly for declining species like *B. ruderarius* (see map in Alford, 1980). Second, the average abundances of species where they are present within a region are correlated with how widespread they are within that region. Third, those sites that have the rarer bumblebee species present also have the widespread species present in higher abundances on average, as expected if resource levels were higher in these particular habitats. Similar abundance patterns have been found in the Pyrenees (Rasmont et al., 2000a). The apparent absence of the rarer species from areas with generally lower bumblebee abundance is unlikely to be a consequence simply of smaller sample sizes, because occasional records of the rarer species from these areas are almost unknown despite intensive sampling in some cases over

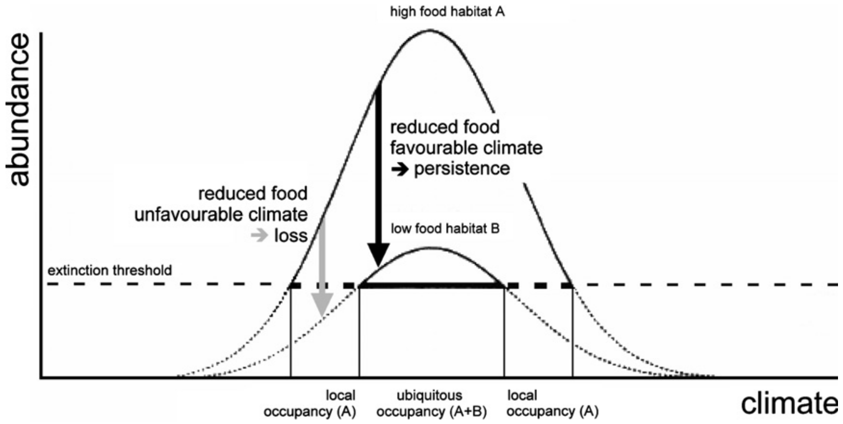

Fig. 1 – Diagram illustrating how an interaction between climate and food-resource levels might govern regional patterns of occurrence across the global climatic range of a single species (redrawn from Williams, 1985, 1988). In this simplified representation, the local abundance of the species on the y-axis depends in part on the species' local food-conversion efficiency, which depends in turn on climate, expressed here as varying (e.g. in temperature) along the x-axis. In addition, the environment is viewed as consisting of a mosaic of just two kinds of habitats, with higher (habitat A) and lower (habitat B) levels of food availability. The differing food-resource levels in the two kinds of habitat result through the food–climate interaction in two abundance curves, with their highest values both centred on the species' climatic optimum. If there were a lower limit to the local abundance that the species could sustain without being extirpated locally (shown by the horizontal dotted line), then the species would have different limits along the climatic axis in the two different kinds of habitat. Consequently, in regions nearer the edges of its climatic range, a species would be more locally restricted to just those habitats with the most food. Similarly, if land-use change were to reduce food resources in one or both habitat types homogeneously across the range, then it would be in the regions nearer the edges of its climatic distribution that a species should be more likely to suffer local extirpation.

many years (Williams, 1988). Recently, an interaction of climate and suitable habitat has also been suggested to govern the distributions of some butterflies near the edges of their ranges in Britain (Hill et al., 1999; Thomas et al., 1999; Bourn and Thomas, 2002).

The idea that higher resources might compensate in part for unfavourable climate near the edge of a species' range (the 'climate–food compensation' idea) has been extended to consider variation in habitat quality through time. If changing land-use practices in some habitat patches were to reduce the abundance of the most profitable food plants (Williams, 1986), then bumblebee abundances are likely to be reduced. With sufficient reduction in abundances, species might become lost from some habitat patches that previously were favourable. From Fig. 1, this is predicted to have two consequences (Williams, 1985). First, the species that should be most generally vulnerable would be those that are everywhere throughout their ranges less efficient in converting resources into more bees, giving them curves of similar breadth to Fig. 1 but with lower maximum abundance. In contrast, species that are efficient only within a particularly narrow range of climates would have narrower curves of otherwise similar shape and similar high maximum abundance (this would not change the pattern of vulnerability relative to their range). However, it is anticipated that many rarer species will combine both of these forms of rarity (Gaston and Blackburn, 2000), making them both more narrowly distributed and more generally vulnerable to reductions in food resources. Second, within the species' range, and among the localities affected by reduced resources, losses should appear first where the species is nearest to the edges of its climatic distribution.

Improved data for the macro-scale distributions of a few British bumblebee species now enable us to begin to test ideas of a possible relationship between differing climatic specialization and range declines. We begin by comparing *B. distinguendus* and *B. sylvarum*, because these became the two initial flagship species for conservation studies of British bumblebees (Edwards, 1998; Edwards and Williams, 2004). These and another species are intriguing because they illustrate three strongly contrasting patterns of change within Britain (Williams, 1982): *B. distinguendus* has declined severely, persisting only in parts of the north; *B. pascuorum* remains widespread; and *B. sylvarum*, which has also declined severely, but which persists only in parts of the south. Macro-scale data compiled for all species world-wide (Williams, 1998) show that (Fig. 2): *B. distinguendus* has a north-Palaearctic distribution; *B. pascuorum* has one of the broadest Palaearctic distributions among all bumblebees; and *B. sylvarum* has a relatively narrow, west-Palaearctic distribution. However, the coarse spatial resolution of these data (compiled to study biogeographic regions) is problematic for gauging with precision the species' climatic niches (Williams, 2005). Fortunately, higher resolution west-European data for these three species are now available (Rasmont et al., 2000b) and data at this resolution do permit a study of climatic niches (e.g. Thuiller et al., 2005). Our questions in this paper assess two predictions of the macro-scale niche-based model: (1) do the rarer and declining species in Britain have narrower (more

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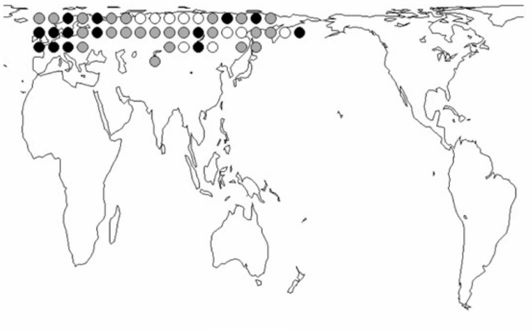
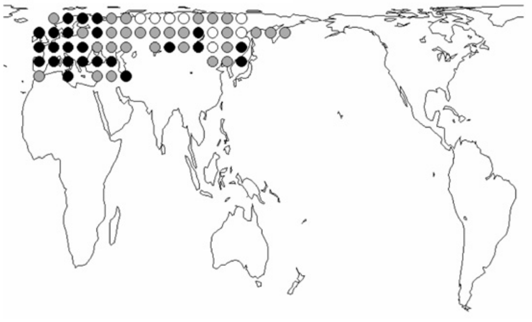


(b) *B. pascuorum*



(c) *B. sylvarum*

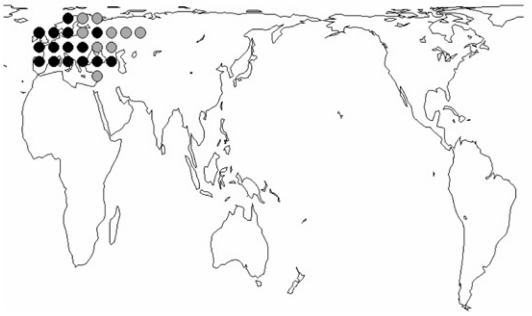


Fig. 2 – Distributions in geographical space of the three bumblebee species world-wide. Data are mapped on an equal-area (611,000 km^2) grid (Williams, 1998). Black: specimens identified by PHW. Grey: literature records. Open circles: expected distribution from adjacent cells with similar climate and habitat.

specialized) climatic niches in western Europe? and (2) are the areas of persistence for declining species in Britain closer to the centres of their west-European climatic niches?

2. Methods

2.1. Distribution data

Within the macro-scale distribution data compiled recently for some west-Palaearctic bumblebees (Rasmont et al., 2000b), the data for western Europe are believed to be the most nearly representative and comparable. Fig. 3 shows the distributions of the three example species recorded for western Europe across all recording periods projected onto the *Atlas Florae Europaeae* (AFE) 50 km × 50 km grid cells

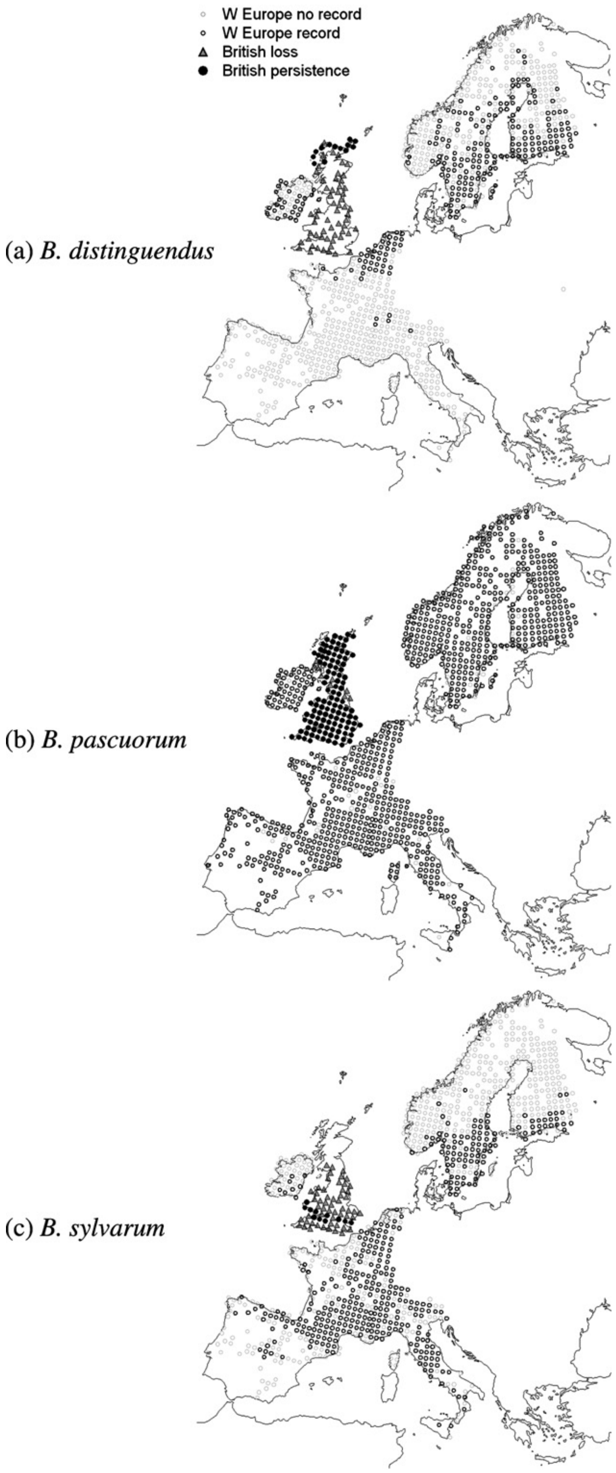


Fig. 3 – Distributions in geographical space of the three bumblebee species in western Europe (Norway, Finland, Sweden, United Kingdom, Ireland, Netherlands, Belgium, Luxembourg, France, Switzerland, Italy, Andorra, Spain, Portugal). Data are mapped on the 50 km × 50 km AFE grid. Black spots: persistent (2000 onwards) distributions from British BWARS/HBRG data. Grey triangles: range losses (pre-2000 only distributions) from British BWARS data. Black circles: all other west-European records (Rasmont et al., 2000b). Grey circles: west-European records for the other two species (Rasmont et al., 2000b).

(e.g. Jalas et al., 1972; Williams et al., 2000). Together these species occupy 1030 grid cells (none of these species is recorded from Iceland, Svalbard, or northern Africa).

For Britain, improved re-compilations of data for the three bumblebee species have been made by the Bees, Wasps, and Ants Recording Society (BWARS: e.g. maps in Benton, 2006) and the Highland Biological Recording Group (HBRG: e.g. maps in Macdonald and Nisbet, 2006). The BWARS/HBRG data are more reliable than earlier British compilations in that all records are referenced to specimens. However, it is apparent by comparison with independent earlier field work in relatively few but widely scattered areas (mapped in Fig. 1.2 in Williams, 1985) that many BWARS map cells probably have yet to be recorded sufficiently thoroughly for even the common species. Since we analysed the BWARS/HBRG data at the scale of a 50 km × 50 km grid, this should be less of a problem (Williams, 2005). On the other hand, highly directed sampling by the UK Biodiversity Action Plan's Bumblebee Working Group (Edwards, 2003), which focussed on the rarest species, has probably yielded a nearly complete picture for *B. distinguendus* and *B. sylvarum*.

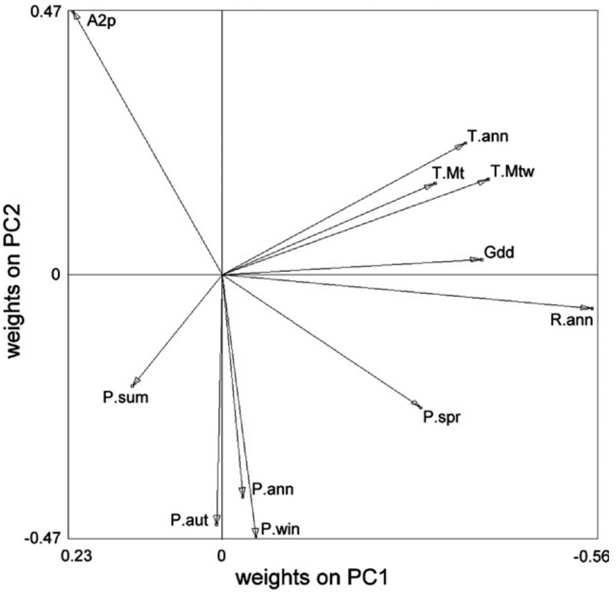
For assessing British declines, all 1900–1999 BWARS/HBRG records together are taken to represent former distributions, whereas records from 2000 to 2006 are used to represent current distributions. The threshold of 2000 was adopted because when the BWARS data were mapped by 20-year time slices, the largest proportional decline appears to have occurred for *B. sylvarum* between the 1960–1979 and 1980–1999 data slices (with little subsequent change), and for *B. distinguendus* between the 1980–1999 and 2000–2006 data slices, despite particularly intensive sampling for both species in 2000–2006 (no gains in range are recorded for these species between these time periods). For the following analyses, cells with 2000-onwards records are classed as 'persistence' data, whereas cells with pre-2000 but no 2000-onwards records are classed as 'loss' data (alternatively, adopting the threshold of 1980 for *B. sylvarum* would have a negligible effect on the map for this species).

2.2. *Comparing climatic niche breadths*

Principal components analysis (PCA) was used to create a 'climatic space' that summarises variation within climatic variables among the 1030 AFE grid cells for western Europe occupied by the three bumblebee species. Climatic data were taken from the UEA database (New et al., 2002). The climatic variables chosen (listed in Fig. 4) were selected because they are often interpreted as governing factors for the distribution of many species, particularly among plants (e.g. Woodward and Williams, 1987; Prentice et al., 1992). All climatic variables for each grid cell were averaged for 1961–1990 (Araújo et al., 2004) and therefore represent the climatic situation prior to the most recent British bumblebee decline mapped here.

To answer our first question, of whether declining species have more specialized climatic niches, we use the multivariate tolerance index (T_m) of Dolédec et al. (2000) to characterise the climatic niche breadths of the three bumblebee species in western Europe. PCA and tolerance-index analyses were performed with ADE4 software (http://pbil.univ-lyon1.fr/ADE-4/).

(a) climatic variables



(b) species

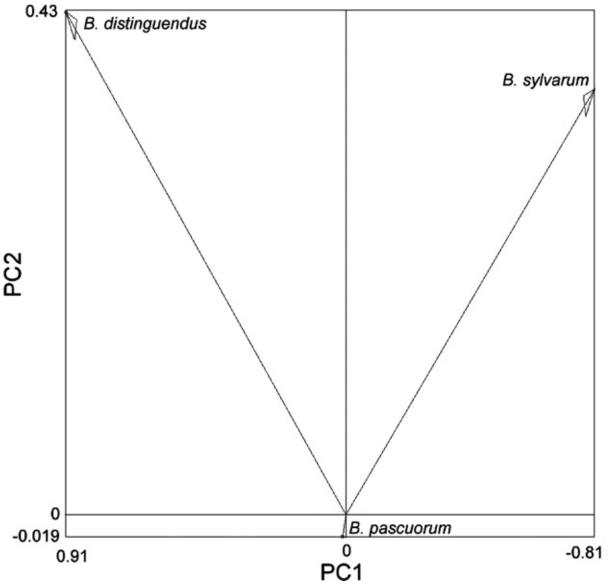


Fig. 4 – Climatic niche space summarised by principal components analysis (PCA) for the sampled region of western Europe. (a) Weights of each environmental variable on the first two PCA axes: mean annual temperature (T.ann); mean temperature of the coldest month per year (T.Mtc); mean temperature of the warmest month per year (T.Mtw); annual solar long-wave radiation (R.ann); mean annual precipitation (P.ann); mean winter precipitation (P.win); mean summer precipitation (P.sum); mean spring precipitation (P.spr); mean autumn precipitation (P.aut); mean annual growing degree days (>5 °C) (Gdd); and the moisture index (A2p) calculated as the ratio of mean annual actual evapotranspiration (AET) over mean annual potential evapotranspiration (PET). (b) Mean position of the three bumblebee species on the first two PCA axes.

2.3. *Comparing distances of areas from the centre of the climatic niche*

To answer our second question, of whether the areas of range persistence for declining species in Britain are closer than expected by chance to the centres of their west-European climatic niches, we use a simulation test (Manly, 1991). We do this by measuring the cell's distance from the climatic niche centre, without attempting to define the climatic niche edge, which is more difficult statistically (edges may have complex geometry, and this geometry may be uncertain because individual extreme observations are unreliable estimates of edge). Asking whether areas of persistence are closer to the niche centre is equivalent to asking whether losses are further from the niche centre, but it is only an approximation to asking whether areas of persistence are further from niche edges or whether losses are closer to the niche edges. To use our approach we have to accept a simplifying assumption that the climatic niche centre is close to the climatic optimum for the species (i.e. the average occupied position on these niche axes is assumed to be the most favourable). This form of bell-shaped response has been the standard model in multivariate studies for species distributions along a gradient for the last century (e.g. Austin, 1985).

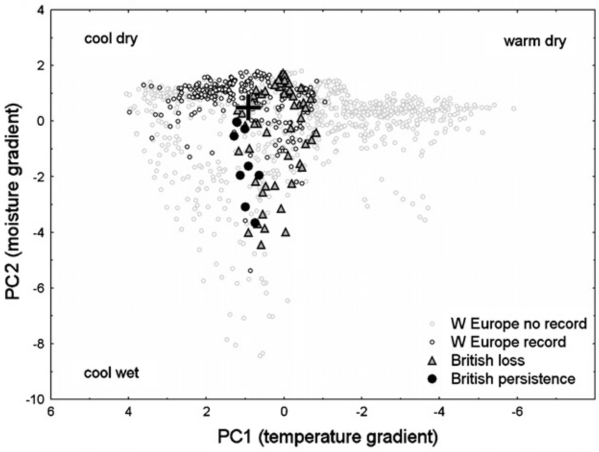
The centre of each species' climatic niche within western Europe is calculated as the mean (centroid) among the combined west-European and British presence records on PCA axes 1 and 2. We then use a simulation of 10,000 random draws from within the species' former British range of the same number of cells as have observed British persistences. This allows us to estimate the distribution of distances from the west-European climatic niche centre of areas of persistence among British cells that would be expected if these areas of persistence were unrelated to climatic niche. Observed areas of persistence for a species are considered significantly closer to the climatic niche centre if the observed mean distance among persistence cells is in the lower 5% tail of the expected random persistence distances distribution. Computational software for the mapping and randomisation tests was written in C.

3. Results

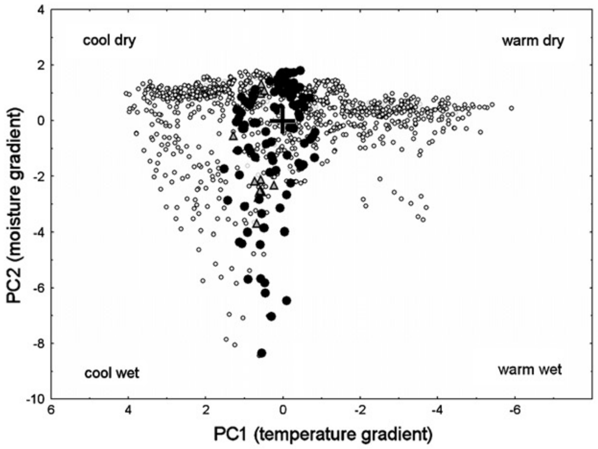
3.1. *Characterising climatic niches*

Fig. 4a shows the contribution of the climatic variables to the 1960–1990 climatic space for western Europe as summarised by the PCA. Principal component 1 (Fig. 4a *x*-axis, henceforth PC1) represents a temperature gradient and is most strongly related (negatively) to annual solar long-wave radiation, so warmer cells occur towards the more negatively scoring end of the axis. Principal component 2 (Fig. 4a *y*-axis, henceforth PC2) represents a moisture gradient and is most strongly related (positively) to the moisture index AET/PET and (negatively) to mean winter precipitation, so drier areas occur towards the higher end of the axis. The first two axes are successful in accounting together for almost all (94.7% with PC1; another 3.8% with PC2) of the total variance in the climatic data for those west-European grid cells that have records for the three species of bumblebees.

(a) *B. distinguendus*



(b) *B. pascuorum*



(c) *B. sylvarum*

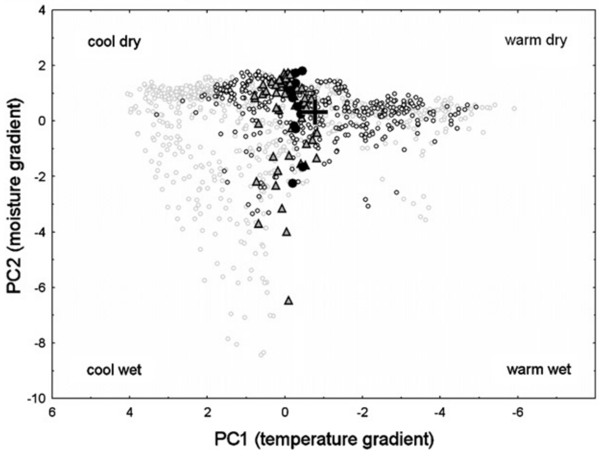


Fig. 5 – Distributions in climatic niche space of the three bumblebee species in western Europe. Scores are mapped from the 50 km × 50 km AFE grid onto the first two PCA axes (*x*-axis reversed). Black spots: persistent (2000 onwards) distributions from British BWARS/HBRG data.
Grey triangles: range losses (pre-2000 only distributions) from British BWARS data. Black circles: all other west-European records (Rasmont et al., 2000b). Grey circles: west-European records for the other two species (Rasmont et al., 2000b). Crosses: west-European climatic range centroids from all records for each species.

Table 1 – Climatic niche centre positions of British former ranges from 1960 to 1990 climatic data

	Distance of the mean among British former (pre-2000 + 2000 onwards) records from the west-European centroid for each species on the PCA axes:	
	PC1 temperature gradient	PC2 moisture gradient
B. distinguendus	−0.606	−0.906
B. pascuorum	0.254	−0.655
B. sylvarum	0.701	−0.135

Table 2 – Results of the simulation tests

	Observed mean distance from the European climatic range centre of the British records for each species on the PCA axes:			
	PC1 temperature gradient		PC2 moisture gradient	
	Persistence (2000 onwards) records	Range-loss (pre-2000) records	Persistence (2000 onwards) records	Range-loss (pre-2000) records
B. distinguendus	0.198 ($p < 0.01$)	0.743	1.954 (ns)	1.375
B. pascuorum	0.481 (ns)	0.621	1.692 (ns)	2.000
B. sylvarum	0.480 ($p < 0.02$)	0.749	1.013 (ns)	1.269

Parentheses show probability comparison with the simulation; ns = no significant difference.

The British grid cells (approximated by the combined grey triangles and black spots in Fig. 5b) share nearly the same centre in the climatic space with the overall centre occupied by all three species within western Europe (approximated by the open black circles in Fig. 5b). On the temperature gradient (Fig. 5b *x*-axis), the British cells occupy less than one third of the range of all west-European scores. On the moisture gradient (Fig. 5b *y*-axis), British cells span the entire range of west-European scores.

3.2. *Do rarer and declining species have more specialized climatic niches?*

The west-European climatic niches of the three bumblebee species as measured here for records of all date classes show substantial overlap (Fig. 5). Nonetheless, there are differences among the three bumblebee species in the positions and breadths of their climatic niches. The niche-breadth (tolerance) statistic T_m (Dolédec et al., 2000) shows that climatic niche breadth is greater in western Europe for the widespread and relatively stable *B. pascuorum* ($T_m = 6.383$). In comparison, the two rarer and strongly declining species, *B. distinguendus* ($T_m = 4.173$) and *B. sylvarum* ($T_m = 3.894$), did have narrower and thus more specialized climatic niches within western Europe, even before their recent declines.

B. distinguendus is associated with the cooler and drier ends of the combined west-European gradients (Fig. 4b and Fig. 5a centroid cross). The former British distribution of *B. distinguendus* (Fig. 5a triangles and black spots, mainly to the right of the cross) was predominantly at the warmer end of this species' west-European climatic niche (Table 1, with a more negative mean value in Britain on PC1), which is reached at sea level just south of Britain in Normandy.

B. pascuorum is essentially unassociated with any of the climatic variables within the 1030 studied grid cells of western Europe (Fig. 4b and Fig. 5b centroid cross), because its distribution covers most of the climatic range occupied by these three species within the region. Here the species is found from the Mediterranean coast in the south throughout mainland Britain to the Barents Sea in the north, and at altitudes from sea level to more than 3000 m in the Alps.

B. sylvarum is associated with the warmer and drier ends of the combined west-European gradients (Fig. 4b and Fig. 5c centroid cross). The former British distribution of *B. sylvarum* (Fig. 5c triangles and black spots, almost all to the left of the cross) was towards the cooler end of this species' west-European climatic niche (Table 1, with a more positive mean value in Britain on PC1), which is reached in southern Scandinavia.

3.3. *Are areas of persistence closer to a species' range centre in climatic niche space?*

Fig. 5 shows systematic patterns of change between the distributions of British areas of persistence (black spots) and British range losses (grey triangles) by 2000 for the three species within their west-European climatic niche space. Table 2 shows that for all three species, the areas of persistence are not significantly closer to their west-European climatic niche centres (black crosses in Fig. 5) on PC2 (moisture gradient axis), the axis that explains little climatic variance. However, the results differ among species for PC1 (temperature gradient axis), the axis that explains almost all of the climatic variance.

For *B. distinguendus*, the British persistence records are significantly closer to the west-European temperature-niche centre on PC1 than expected by chance (Table 2), with most of the British losses scattered further towards the warmer end of the axis (grey triangles mainly to the right of the cross in Fig. 5a).

For *B. pascuorum*, the British persistence records are not significantly closer to the west-European climatic niche centre on PC1 than expected by chance (Table 2). The apparent losses overlap broadly with the other British records within the climatic space (grey triangles in Fig. 5b).

For *B. sylvarum*, the British persistence records are significantly closer to the west-European temperature-niche centre on PC1 than expected by chance (Table 2), with most of the British losses scattered more towards the cooler end of the axis (grey triangles almost all to the left of the cross in Fig. 5c).

4. Discussion

This analysis shows that, at least for the two flagship species of British bumblebee conservation (*B. distinguendus* and *B. sylvarum*) in comparison with the more stable species (*B. pascuorum*), (1) the more vulnerable and declining species in Britain had narrower (more specialized) climatic niches in western Europe even before their most severe declines, and (2) that their areas of persistence in Britain are closer to the centres of their pre-decline west-European climatic niches than their apparently more vulnerable areas of loss.

4.1. *Caveats*

The results are potentially sensitive to all of the usual problems arising from species misidentification, biased sampling, and errors in recording, both of the species' distribution data and of the climatic data. Apparent range declines could in some cases be artefacts of insufficient sampling, particularly when samples from a long period (pre-2000) are compared with samples from a short period (2000–2006). This is likely to explain the apparent British 'losses' for *B. pascuorum* in Fig. 3. Many of the areas of apparent loss for this species are in southern Scotland and northern England, which are areas with few of the rarer bumblebees (Alford, 1980; Benton, 2006) and few bumblebee recorders (BWARS data). Consequently, there is little incentive to invest much effort in travelling far to record a very common species such as this. In practice, *B. pascuorum* appears to be found in almost all mainland areas of Britain (except at the highest altitudes) when they are searched thoroughly (PHW, pers. obs.). In contrast, sampling problems are unlikely to be the reason for apparent declines of *B. distinguendus* and *B. sylvarum*, which have been specially targeted intensively throughout their known ranges since 2000 by the UK Biodiversity Action Plan's Bumblebee Working Group (Edwards, 2003).

We cannot be certain that we have identified the climatic variables that most closely affect the processes governing the distributions of these bumblebees. There is inevitably a spatial mismatch between the point locations where the bees were collected and where the climatic data were collected, leading to imprecision in the climatic niche models. Measurements of climatic niche breadth are unlikely to be independent of the extent of geographical range, although pre-decline niche breadth could in principle be independent of declines. An approximately bell-shaped response curve for bumblebee abundance along the climatic niche axes follows the common assumption of ecological methods for the last century (e.g. Austin, 1985), but has not been demonstrated for these bumblebees. However, our approach based on empirical measurement of the niche is very similar in all of these problems to the climatic suitability models and abundance models that are now routinely applied in ecological (e.g. Austin et al., 1990), evolutionary (e.g. Graham et al., 2004), and conservation studies (e.g. Araújo and Williams, 2000).

An issue that is more particular to this study is that the climatic centroid is assumed to approximate the climatic optimum for western Europe (discussed in Section 2), which needs further study. Furthermore, not all of the global distribution of the three bumblebee species is included in the climatic niche model, so the west-European centroid will not be the same as the global centroid. It is possible that climatic preferences might vary across a species' distribution, especially over vast longitudinal distances. However, we are interested in the characteristics of the west-European populations of the three species, and the climatic niche models should be indicative for these because their entire west-European latitudinal ranges are included. It is unlikely that any of these sources of error would be sufficient to change the conclusions by shifting the estimated climatic optima to the opposite sides of the species' British distributions on PC1.

Most of the variation in climatic niche detected here in western Europe is related primarily to temperature (PC1). Bumblebee distributions might also be expected to depend on moisture gradients (e.g. Banaszak, 1996). Bumblebees depend on plants for nectar, and nectar secretion must be affected to some extent by moisture availability. However, Table 2 shows that changes in the distributions of the three bumblebee species appear surprisingly to be unrelated to the weak moisture gradient (PC2). Perhaps if bumblebees are not narrow specialists on particular plants, so that different food plants could be substituted across their ranges, then bumblebees would be buffered from the effects of the moisture gradient by the differing moisture-extracting abilities of the various food-plant species.

4.2. *Climate and explanations for declines in British bumblebees*

Several explanations for declines in British bumblebees have been proposed (e.g. Williams, 1986, 1989b; Goulson, 2003; Edwards and Williams, 2004; Williams, 2005; Benton, 2006). Our results are discussed in relation to some of these ideas below.

4.2.1. *Introduced pathogens*

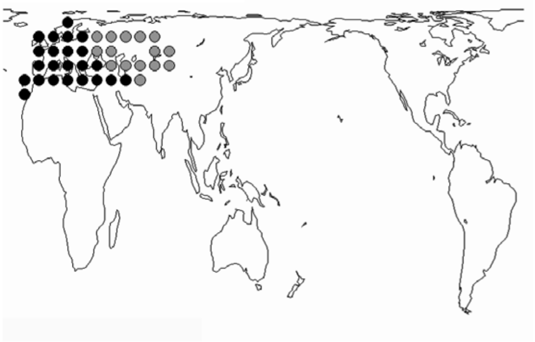
Some patterns of bumblebee decline seem particularly unlikely to have been influenced by climatic niche. In North America, several closely related species of the subgenus *Bombus* (*B. affinis*, *B. terricola*, and *B. franklini*) have shown rapid and severe declines in the late 1990s across their entire geographical ranges (Thorp and Shepherd, 2005; Winter et al., 2006). These declines have been interpreted as possibly a result of introduced pathogens (Thorp and Shepherd, 2005; Winter et al., 2006), although this is unproven. *B. franklini* always had one of the smallest ranges among all bumblebee species (Thorp et al., 1983), but unusually had not been found since

Table 3 – Apparent changes in climatic niche within Britain for each species from the 1960–1990 climatic data

	Mean position of the British records on the PC1 temperature gradient:		Difference before and after 2000:
	Former (pre-2000 + 2000 onwards) records	Persistence (2000 onwards) records	
B. distinguendus	0.316	1.019	0.703
B. pascuorum	0.262	0.224	−0.038
B. sylvarum	−0.078	−0.299	−0.221

2003 until a single worker was sighted in 2006 (R. Thorp, in litt. 2006). *B. terricola* (including the western form *B. occidentalis*) was formerly one of the most widespread and common North American bumblebees. For example, one of us (PHW) found it commonly in southern Ontario in 1983, but failed to find it in transects of California (1999–2001) and of southern British Columbia (2001), or in southern Ontario (2003–2004) and the eastern US (Ohio, Kentucky, Tennessee, South Carolina, North Carolina, Virginia, Pennsylvania, New York, 2006), with only two individuals found in southern Ontario (2005–2006). *B. affinis* was formerly widespread and common in the east (e.g. PHW southern Ontario 1983), but has not been seen for several years (e.g. PHW southern Ontario 2003–2006), with only one recent record in 2005 and one in 2006 (S. Colla, in litt. 2006). In contrast to the North American situation, the British species have declined more slowly over a period of several decades (BWARS data). Many of the declining British species also remain common elsewhere in Europe or Asia. But perhaps more challenging for the pathogen hypothesis in Britain, many of the declining British species are not closely related to one another, but are scattered among several subgenera. Other British species in some of the same subgenera seem unaffected. Much more work is needed to identify and track the effects of pathogens in bumblebees before pathogens can be associated definitely with any bumblebee declines. However, it is quite possible that the most severe bumblebee declines in North America have causes that are quite different from the causes of many bumblebee declines in Europe.

(a) *B. terrestris*



(b) *B. lapidarius*

(c) *B. soroeensis*

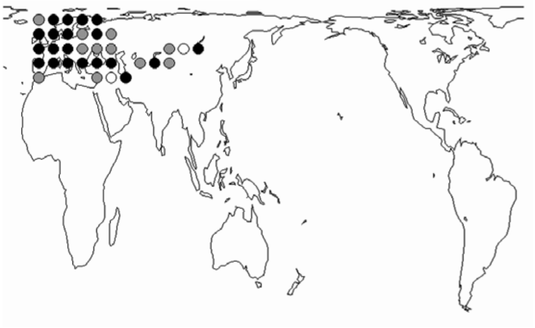


Fig. 6 – Distributions in geographical space of three bumblebee species world-wide. See the caption to Fig. 2.

4.2.2. Climatic change

A popular explanation for changes in distribution ranges in the recent literature is climatic change, especially with a warming of the climate in western Europe (e.g. Thomas et al., 2006). Climatic change would not alter the equilibrium position of a species' climatic optimum in climatic space (Fig. 1) but is likely to alter the position of its climatic optimum in geographical space (depending on geography and the scale of study). Recent range expansions of *B. terrestris* and *B. lapidarius* in Scotland may be related to this phenomenon (Macdonald, 2001). However, climatic warming has been rejected as a general explanation for declines in British bumblebees (Williams, 1986, 1989b), because while some species have retreated northwards (e.g. *B. distinguendus*), others (e.g. *B. sylvarum*) have simultaneously retreated southwards. If there had been a uniform warming (or cooling) of Britain before the second sampling period (from pre-2000 to 2000 onwards), then we would expect all non-ubiquitous species to show a range shift in the same latitudinal (geographical) direction. This is can be seen more clearly from the climatic data here. Species are expected to retain the same underlying climatic tolerances, so if their distributions were projected into climatic spaces measured with contemporary climatic data (for pre-2000 and 2000 onwards respectively), then they ought to remain in broadly the same climatic spaces. Unfortunately, climatic data are available only for the pre-2000 period. The consequence of this is that because the pre-2000 climatic data are used to plot the 2000-onwards geographically shifted species' data, there should appear to be range shifts in the climatic space (which would not be real). However, Table 3 shows that the apparent mean positions on the temperature gradient (PC1) for these two species seem to have moved in opposite directions in the pre-2000 climatic space. Therefore a simple unidirectional climatic change in Britain could not explain these opposing geographical range shifts.

Nonetheless, it remains possible that an increase in the climatic variance could have affected adversely both the warm- and cool-adapted bumblebee species simultaneously, by alternately imposing increasingly extreme cool and extreme warm climates. Consequently, more detailed studies are needed, and future impacts of expected climatic change should be anticipated.

4.2.3. *Climate–food compensation and land-use change*

The essence of this idea (described in Section 1) is that any land uses reducing the levels of food resources are particularly likely to cause local extirpation near the edges of a bumblebee species' climatic range, where it is more vulnerable further from its climatic optimum. Our results add support to two lines of evidence that are consistent with this view.

First, measures of rarity and decline among all social British bumblebee species have been found previously to be negatively correlated with their European geographical range sizes (Williams, 2005). The strength of the correlation was increased as expected when geographical ranges were adjusted to reduce the effect of altitude on estimates of climatic range. But as an improved test, the present study shows that declining species have narrower climatic niches when measured more directly in western Europe, although data for more species will be needed to test the generality of the pattern. This tells us which bumblebee species are most likely to decline by this mechanism.

Second, this study shows that after range declines, areas of persistence tend to be closer to a species' climatic niche centre (Table 2). This tells us from where a declining bumblebee species is most likely to be lost. Within a small country like Britain, it also helps to discern which species are more likely to be lost. Assessing proximities to climatic niche centres in this paper is a more direct test of the proposed underlying niche-based mechanism than the previous study by Williams (2005), which found no association. That study used geographical range as a proxy for climatic range and used only very coarse-scale data (e.g. Figs. 2 and 6), for which the resolution was considered problematic, so that the results were expected to require confirmation (Williams, 2005).

In contrast, four observations appear to challenge the climate–food compensation idea. First, the pattern of concentration of local extirpations further from species' climatic range centres that is observed here might be expected only when the level of threats is relatively mild and also relatively uniform or random across the range. The pattern of peripheral loss could always be overwhelmed by a wave of extirpation anywhere within the climatic range if the levels of threats were sufficiently high (Channell and Lomolino, 2000). Confounding of the pattern of loss is quite likely at the within-Britain scale because the country is small relative to the global ranges of most bumblebee species and because strong regional differences in patterns of resource decline are likely. Resource decline appears to have followed agricultural policy and land-use changes, and the relative nature and intensity of agricultural land-use change is known to be related to existing regional patterns of land-use (Williams, 1986). So a strongly regionally biased pattern of resource decline would be expected to create a corresponding regional pattern of bumblebee decline (Williams, 1986), which would then be concentrated not necessarily nearest to species' climatic range edges at the within-Britain scale. Therefore, the regional pattern of agricultural intensification could explain why bumblebee declines are concentrated in the central region of Britain (Williams, 1986) and in the eastern region of Ireland (Fitzpatrick et al., 2007). But even in this case, the climate–food compensation idea could still explain why the declines are expected to affect primarily those species for which central Britain and eastern Ireland fall within the margins of their global climatic ranges.

Second, Goulson et al. (2005) noted that contrary to what might be expected from Fig. 1, the widespread and abundant *B. lapidarius* and *B. terrestris* are near the northern edges of their latitudinal ranges in northern Britain. As a contrast, they described *B. soroeensis* as declining and yet near the centre of its range in Britain. However, our data (Fig. 6) show that *B. lapidarius* and *B. terrestris* have some of the broadest latitudinal ranges among European bumblebees, extending into North Africa. They occur at relatively low altitudes in both northern and southern Europe (e.g. Rasmont, 1988; PHW, pers. obs.), so it is likely that their climatic niches will also prove to be particularly broad (estimated by Williams, 2005: Table 1 as 'Adjusted total European range'), fitting the broad-niche pattern shared by the less vulnerable species here. In contrast, *B. soroeensis* has a slightly narrower European latitudinal range (Fig. 6). But crucially, in southern Europe *B. soroeensis* is restricted to higher altitudes (e.g. Rasmont, 1988; PHW, pers. obs.), so its climatic niche is likely to be correspondingly narrower (Williams, 2005: Table 1), which is shared here by the more vulnerable species. Although this inverse relationship between 'Adjusted total European range' (as a proxy for climatic niche breadth) and decline was demonstrated at a coarse scale for all social British species by Williams (2005), fine-scale analyses like those presented here are needed for many more of the British species in order to confirm the generality of this relationship with climatic niche-breadth.

Third, Carvell (2002) noted that contrary to what might be expected from Fig. 1, densities of the rare and declining *B. humilis* and *B. sylvarum* on Salisbury Plain in Britain were sometimes higher than densities of some widespread species. Similarly, numbers of *B. humilis* on Dungeness could sometimes be relatively high (Williams, 1989a). Despite this high variation in abundance among sites, numbers of the rare and declining species in Kent were on average lower among the sites where they occur than numbers of the widespread species (Williams, 1988), as described in Fig. 1.

Fourth, Goulson et al. (2006) describe how many of the rare and declining British species that currently have narrow habitat preferences were formerly much less specialised in Britain. Furthermore, they describe how some species are now associated with apparently very different habitats in the north and in the south of Britain. However, both observations are consistent with the climate–food compensation idea, which describes how, with widespread reductions in food availability, species would be expected to become more restricted to those habitats that retain the highest food availability (Williams, 1985, 1988), even if most British bumblebee species do seem otherwise to have only weakly differentiated habitat specializations (Williams, 1986). If higher resource levels have become associated consistently with certain kinds of habitat (Williams, 1988), then species might appear to become greater habitat specialists, just as they describe. Indeed, Goulson et al. (2006) agree with the earlier suggestions (Williams, 1985, 1988, 1989b) that the habitats where the rare and declining species persist probably do have higher floral density and diversity than the intensively farmed countryside. Furthermore, the same shared need for high resource levels near range edges could drive the increasingly narrow habitat specializations of the different species to diverge in apparently very different directions once their different climatic specializations are superimposed. The two strongly declining bumblebee species considered here both now tend to be restricted to a narrow range of tall, flower-rich grasslands: *B. distinguendus* with Scottish machair; and *B. sylvarum* with some southern chalk and coastal grasslands (e.g. Edwards and Williams, 2004). These grasslands appear to share particularly high densities of deep-flowered food-plants. However, climatic niches could explain why both bumblebee species are not found in both habitats. For example, with a mild reduction in food resources across Britain, persistence of a northern, relatively cool-adapted species like *B. distinguendus* even in slightly damaged machair habitat might still be likely in the climatically more favourable north. Nonetheless, with some reduction in resources over large areas, loss of *B. distinguendus* might be likely from even a relatively flower-rich habitat like Salisbury Plain in the south because it is climatically less favourable to this species. The reverse argument could also be applied to *B. sylvarum*, with cool climates in Scotland keeping it from the machair.

4.3. *Further work*

First, when data become available the tests described here should be extended to all of the British species to test the generality of the pattern. Second, it would be important to assess the profile of bumblebee abundances in a replicated range of habitats and resource levels at sites across Europe. There are many difficulties with assessing available floral resources (e.g. Zimmerman and Pleasants, 1982), but progress should be possible. Third, it would be ideal to assess colony sizes and reproductive rates in relation to climatic niche and resource levels. It is tempting to start with the effects of latitude (cf. Yalden, 1982), but it might be easier when developing the methods to look at the effects of altitude within a narrower, mountainous region.

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