Jarvis, Susan; Fielder, Hannah; Hopkins, John; Maxted, Nigel; Smart, Simon. 2015. **Distribution of crop wild relatives of conservation priority in the UK landscape**.

Distribution of crop wild relatives of conservation priority in the UK landscape

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Abstract

Many crop species suffer from a lack of genetic diversity which reduces the ability of cultivars to withstand new pests or environmental stresses. The wild relatives of crop plants are an important source of genetic variation and can be used to introduce new traits into existing crops. Identification and conservation of crop wild relatives (CWR) is, therefore, an important step to safeguard future food security. Recent efforts have identified geographical hotspots of CWR diversity in several countries but, as yet, there have been no surveys to identify the habitats and landscape features within these areas that might be most suitable for conservation efforts. Here, we use a UK-wide vegetation survey covering a range of both habitats and landscape features (e.g. fields, hedgerows, waterways and roadsides) to identify the habitats and features with the highest proportion of CWR identified as priority taxa for conservation. Priority CWR were most abundant in grassland habitats, although this was most striking in CWR related to forage and fodder crops. CWR related to food crops were most common in cropped and weedy areas, fertile grassland and lowland woodland. Within habitats, CWR occurrence was significantly associated with linear features including hedgerows, roadsides, field boundaries and field margins. Our findings indicate that CWR of conservation interest are often associated with disturbed habitats and landscape features that are not considered as priorities under site-based conservation measures. We suggest that efforts to maintain linear features in hotspots of CWR diversity would be most effective at conserving the UK's CWR resource.

Keywords

Agriculture; conservation; crop wild relatives; field margins; landscape; road verges

1. Introduction

Crop wild relatives (CWR) are wild plant species that are close relations of domesticated plants (Harlan and de Wet, 1971; Maxted et al., 2006). Concerns about the lack of genetic diversity in many crop species have led to an increased interest in utilising the wider pool of genetic variation present in closely related plants to improve food security in the face of threats such as pests and disease. Food security is likely to be increasingly at risk in the longer term as climate change is predicted to reduce crop yields by an estimated 2% per decade, with the forecast set to worsen beyond 2050 (Porter et al., 2014).

CWR host genetic diversity that could be used to tackle these issues through the introduction of traits such as pest and disease resistance, stress tolerance and increased yield to improve crops. The introduction of traits from wild relatives to cultivated plants has already led to a vast literature describing new varieties with improved characteristics (Maxted and Kell, 2009). For example, sugar beet (*Beta vulgaris* subsp. *vulgaris*) varieties with resistance to *Cercospora* leaf spot and Rhizomania have been developed with traits introduced from the wild relative, sea beet (*Beta vulgaris* subsp. *maritima*) (Biancardi et al., 2002; Grimmer et al., 2007; Lewellen et al., 1987; Munerati, 1932). More recently sea beet accessions with abiotic stress tolerant traits have been identified and are being considered for use in breeding programs (Stevanato et al., 2013). Other examples of wild relative use in crop improvement include the transfer of mustard aphid resistance from wild *Brassica fruticulosa* Cirillo into cultivated *B. rapa* L. (Chandra et al., 2004), the transfer of powdery mildew resistance from wild *B. carinata* A. Braun into cultivated *B. oleracea* L. (Tonguc and Griffiths, 2004) and the transfer of potato leafroll virus resistance from the wild Mexican species *Solanum verrucosum* Schtdl. to cultivated potato (Carrasco et al., 2000).

Until recently little was known about the global distribution and abundance of CWR. The creation of the Harlan and de Wet Inventory of CWR in 2013 (Vincent et al., 2013) marked a significant advance in our understanding of the number of global priority CWR taxa (1667 CWR taxa with potential or proven use for crop improvement related to 173 crops of global importance) and their distributions. The inventory identified several global hotspots including a high concentration of CWR taxa around the Fertile Crescent, an area noted as both a historical centre of crop domestication and parts of which are subject to ongoing conflict. Thus efforts to establish active and systematic in situ and ex situ CWR conservation have been driven by the realisation that a lack of genetic diversity in crop plants is becoming a significant problem and that many CWR occur in areas where conservation is difficult to achieve.

Although the United Kingdom does not have the CWR diversity of the Fertile Crescent it does host a wide range of CWR taxa, many of which are related to crops of economic value such as the food crops brassicas, barley and sugar beet as well as forage and fodder crops including grasses, clovers and vetches. Current in situ CWR conservation in the UK is focused on a few very rare and threatened species. For example, *Pyrus cordata* is listed as Endangered in the English Red Data Book and has its own species recovery programme (Jackson, 1995; Stroh et al., 2014) while *Asparagus prostratus*, which is Endangered according to the Vascular Plant Red Data List for Great Britain, has undergone hand pollination and re-introduction to increase population sizes in the most vulnerable of sites (Cheffings and Farrell, 2005; King et al., 2007; King and Edwards, 2007). There are currently no habitat based conservation measures targeted towards active CWR conservation, though approximately 35% of priority English CWR do gain some level of passive protection through presence within protected areas (Fielder et al., 2015). Active conservation measures are, however, being developed on the Lizard Peninsula in Cornwall, based on genetic analyses of multiple CWR taxa, with a view to establishing this location as the first UK CWR genetic reserve (Fielder, 2015). Though ideally conservation strategies targeting CWR populations would consider genetic diversity (Frankel et al., 1995; Magos Brehm et al., 2012), such analyses are not always possible due to high costs. A more pragmatic approach is to support habitat based conservation measures as a tool for establishing targeted and active management of CWR populations in key locations.

Designation of sites or habitats of conservation interest for CWR has been hampered by the absence of an inventory of priority CWR and by a lack of knowledge regarding the habitats with the highest concentrations of CWR (Maxted, 2003). There is evidence to suggest that some CWR, such as wild oat (*Avena fatua*) and wall barley (*Hordeum murinum*), are more often associated with disturbed early-successional communities rather than perennial-dominated mid to late-successional communities (Grime, 1977; Hopkins and Maxted, 2011; Maxted and Kell, 2009). These disturbed habitats tend to have high levels of anthropogenic influence and as such, are not normally considered for conservation designation (JNCC, 2013). The abundance of CWR may also vary within habitats. Linear features such as road verges, field boundaries and streamsides are often relatively highly disturbed but act as important refuges for species not favoured in the modern intensively managed countryside (Smart et al., 2006a, 2002) and could be important for CWR diversity. Whilst the margins of arable fields have attracted interest and agri-environment support as a refuge for rare arable weeds, food plants for lowland farmland birds and nectar plants for pollinating insects (Marshall and Moonen, 2002), their role in supporting CWR has never been examined and, as yet, there has been no formal analysis of the preferences of UK CWR for different habitats and landscape locations.

Recent research effort has produced inventories listing CWR of priority conservation interest for the UK as a whole and also in separate inventories for England, Scotland and Wales (Fielder, 2015; Fielder et al., 2015). This has led to more complete geographic analyses of hotspots of CWR abundance within each country. Here, we seek to extend this work by utilising the UK CWR inventory to assess the habitats and landscape features with the highest richness of UK CWR. Identification of habitats and features with the highest number of CWR will inform conservation efforts for this valuable resource in the UK.
In the current study, the following hypotheses were addressed:

1. CWR are more likely to be located in disturbed habitats and areas with high anthropogenic influences than more stable communities, due to their often weedy growth habits (Jain, 1975; Maxted et al., 1997).
2. Combining the fact that CWR would be expected to be adapted to agricultural disturbance but not preferred by intensive cultivation we would expect CWR to be more likely to be found in linear features, particularly arable field margins.
3. If forage and fodder species are primarily grasses then it would be expected that either high or low productivity grasslands would be their preferred habitats. Since high productivity grasslands are more species poor we would expect lower productivity grasslands to be richer in CWR.
4. CWR that are more closely related to their associated crop are predicted to show more similar habitat preferences and so be more likely to be associated with agricultural habitat and landscape features.

2. Methods

2.1 Data collection

Data on the distribution of CWR in the UK landscape (excluding Northern Ireland) were taken from vegetation surveys conducted as part of the Countryside Survey of 2007 (Bunce et al., 2014; Carey et al., 2008). The detailed survey methodology of the Countryside Survey makes it an ideal resource for identifying habitat and landscape distribution patterns. The dataset consists of 11 685 quadrats from a stratified random sample of 589 1 km squares across the UK. Priority CWR in each quadrat were identified according to the UK and regional priority inventories (Fielder, 2015; Fielder et al., 2015). The priority inventories contain CWR taxa that are considered to be most in need of conservation and differ between the regions due to differences in regional conservation priorities and species pools; for example, only the Welsh inventory considers CWR related to forestry crops (Appendix A Table A1). The UK priority list is not simply a product of the corresponding regional inventories as different conservation priorities were defined at each scale and criteria used to assign priority to CWR in each region were selected by the relevant stakeholders in each case. The UK priority CWR were then based on a new selection of criteria and were agreed between all regional stakeholders. Criteria used in the UK were: the use of the related crop, the native status of the CWR, the degree of relatedness of the CWR to the crop, the economic value of the related crop, the threat assessment of the CWR and the presence of any additional designations (Fielder, 2015). Only native or archaeophyte priority CWR were included in this analysis because non-native taxa may show different habitat preferences or, having recently arrived, may not yet have fully occupied preferred niche space. Nomenclature for CWR follows (Stace, 2010).

2.2 Landscape drivers

Habitat types were defined using the aggregate classes from the Countryside Vegetation System (Bunce et al., 1999). Eight classes (crops and weeds, tall grass and herbs, fertile grassland, infertile grassland, lowland woodland, upland woodland, moorland grass mosaic, heath and bog) were identified. The habitat classes are defined by separation along two axes representing fertility and disturbance e.g. crops and weeds are both highly fertile and highly disturbed whereas lowland woodland can be relatively fertile but has low disturbance. Within habitats, some Countryside Survey quadrats were targeted on linear landscape features such as hedgerows, field margins, the banks of watercourses and road verges (Table 1). Fields, unenclosed land and other areas of habitat were sampled by other randomly located quadrat types (U and X). Quadrats designed to sample unusual or interesting habitats (Y quadrats) were excluded from the analysis as these were not sampled randomly. Plots sampling only woody taxa (D quadrats) were also excluded. Other variables that might influence the proportion of CWR were also considered (Table 2) including the proportion of arable and urban areas in the surrounding 1 km square which reflect potential associations of CWR with agricultural activities or human activity. Road area in the surrounding 1 km was similarly included to reflect the potential influence of transport routes and road verges on CWR occurrence. Note that the 1 km square refers to the Countryside Survey sample square and therefore the quadrat may be at the edge of the square. The proportional cover of woody and annual plants and bare ground were chosen to reflect the successional stage and disturbance regime associated with the vegetation in each quadrat; CWR are often ruderal plants and might be expected to occur where the cover of annuals and bare ground is higher (Maxted and Kell, 2009). Finally, the Easting and Northing of the sites were included to account for any geographic variation in CWR abundance not explained by the other variables.

2.3 Statistical analysis

To assess the relationships between habitat and landscape drivers and the occurrence of CWR it was necessary to account for the variation in size of the quadrats used (Table 1). Because quadrat type was of interest to the study, using the area of quadrat as an offset in a model of CWR counts risked confounding quadrat size and location effects on CWR richness. Instead, the proportion of taxa defined as priority CWR was calculated for each quadrat, thus accounting for variation in total species richness between quadrats as a result of varying quadrat size. The relationships between the landscape drivers and CWR occurrence were assessed with binomial mixed models with a logit link. The proportion of priority CWR taxa per quadrat was the response variable in all models and all terms in Table 2 were included as fixed terms. Continuous variables were standardised and centred prior to analysis. Collinearity between continuous predictors was tested for using variance inflation factors (Zuur et al., 2009) and found to be low (all variance inflation factors below 2) so all predictors were retained. Interaction terms between fixed effects were not included due to the high number of factor levels assessed. Due to the design of the survey the quadrats are nested within 1 km squares and therefore the 1 km square was included as a random intercept term to account for any unexplained between-square variation in the proportion of CWR.

A total of twelve models were constructed with the same fixed and random effect structures but varying response variables. Firstly, to assess the variables related to the overall distribution of CWR, a model was constructed with the proportion of all CWR from the UK inventory as the response variable. Four additional models were constructed to assess whether different types of CWR from the UK inventory were affected by different drivers. In this study, CWR were divided into those related to food crops and those related to forage and fodder crops. Forage/fodder CWR were defined as those related to crops used for fodder or forage for animal feed. Food CWR included plants related to crops used as vegetables, oil/fat producers, nuts, pseudocereals, pulses, fruits, flavourings, cereals, seeds or sugar (USDA, 2015). Due to the different species present in each group (e.g. forage/fodder CWR comprise mostly grasses and forbs while food CWR are more variable including tree and shrub taxa) different patterns of occurrence in the landscape might be expected. The proportions of food or forage/fodder CWR from the UK inventory in each quadrat were calculated as response variables. Several CWR taxa are related to both food and forage/fodder crops and were included in both models.

CWR can also be grouped based on the degree of relatedness to their domesticated relatives. Relatedness can be defined by the ability to successfully cross taxa (the Gene Pool Concept, Harlan and de Wet, 1971) or, if crossing information is not available, by phylogenetic distance (the Taxon Group Concept, Maxted *et al*., 2006). CWR with the ability to cross easily with their related crop, or that are in the same species, are classed as Taxon Group (TG) or Gene Pool (GP) 1b (where TG or GP 1a are the cultivated varieties of a species). Taxa that are in the same genus as the crop, or that have limited ability to cross are placed in TG 2 to 4 or GP 2 and 3. Some CWR are related to multiple crop taxa and in such cases the most closely related species was used to define the GP or TG. The proportions of CWR taxa from the UK inventory in GP and TG 1 or 2 to 4 in each quadrat were used as response variables in the next two models.

There was some evidence that forage/fodder CWR in the dataset were more likely to be in TG or GP 1b, so four more models were constructed to assess whether differences in drivers associated with relatedness were maintained within each usage group. In each case the response variable was the proportion of taxa each usage/relatedness combination from the UK priority inventory.

Finally, to investigate regional differences in the drivers of CWR occurrence, three models were specified using the proportion of CWR derived from the English, Scottish and Welsh priority inventories respectively. For regional analyses, only quadrats from that region were included in the model.

Parameters for all twelve models were estimated using Markov chain Monte Carlo sampling implemented in the R package MCMCglmm (Hadfield, 2010). Uninformative inverse Wishart prior distributions were used for the fixed effects. An uninformative parameter expanded (Cauchy) prior was used for the random effect to help convergence and estimation of the random effect variance. The prior on residual variation was fixed at 1. Models were run for 30,000 iterations with a 5,000 iteration burn in period and a thinning interval of 10 iterations. Three separate models were run to assess chain convergence visually and using the Gelman-Rubin statistic (Gelman *et al*., 2004). All analysis was conducted in R v.3.0.3 (R Core Team 2014).

3. Results

Of the 211 native and archaeophyte taxa present across the four (UK and national) priority inventories of CWR, 129 were recorded in the 2007 Countryside Survey (Appendix A Table A1). The most commonly recorded species were *Holcus lanatus*, a fodder CWR, and *Rubus fruticosus* agg. (bramble), closely related to cultivated blackberry and more distantly related to raspberry. The number of priority CWR per quadrat was generally less than 10 and was a small proportion of the total number of taxa (Figure 1). Numbers of CWR were variable between habitats and landscape features, but variation in quadrat size associated with different landscape features (Table 1) complicates interpretation of these results. Therefore, numbers of CWR were assessed as a proportion of total richness in the modelling work.

Gelman-Rubin statistics for all chains in all models were between 1 and 1.01 after 30,000 iterations and were considered to be sufficiently converged. In each model, parameter estimates for the habitat and landscape feature levels are differences (contrasts) from the proportion of CWR expected in crops and weeds (the reference habitat type) and randomly located quadrats (the reference feature type).

Model coefficients for the model with all CWR from the UK Inventory as the response are shown in Figure 2 a. Coefficients are available in Appendix A Table 2. CWR were more likely to occur in grasslands than highly disturbed habitats (the baseline level of crops and weeds) but less likely to occur in heath and bog. Woodland areas and moorland grass mosaics had similar numbers of CWR taxa to cropped and weedy habitats. Priority CWR were more common in several landscape features compared to randomly selected quadrats. Arable field margins, hedgerows, field boundaries (including fences and walls) and road verges were all preferred localities for CWR taxa. By contrast, quadrats situated next to waterways had lower proportions of priority CWR than randomly located quadrats. Of the covariates included, negative associations were seen with the cover of woody and annual plants and bare ground in the quadrat. Overall, priority CWR were more frequent in the south and east of the UK.

CWR related to food and forage/fodder plants had different patterns of occurrence in the landscape (Figure 2, Appendix A Table 2). Forage/fodder CWR were most common in grasslands whilst food CWR occurred most often in disturbed areas, fertile grassland and lowland woodland. Forage/fodder CWR dominated the preference for particular landscape features observed for all CWR, with food CWR occurring at similar frequencies in most landscape features, being slightly more frequent in roadsides and less frequent next to waterways. Food CWR were more likely to occur in quadrats with high cover of woody plants and quadrats in the south and east of the UK whilst forage/fodder CWR had a strongly negative association with cover of woody plants.

Overall, CWR in taxon or gene pool groups 2–4 (TG/GP 2-4) were found most often in the baseline crops and weeds habitat type while more closely related CWR were more likely to be found in grassland or woodland habitats (Figure 2, Appendix A Table A2). CWR differing in relatedness did not differ greatly in associations with landscape features, although there was a larger association with roads and verges for TG/GP 2-4 taxa and unenclosed land had proportionally more TG/GP 2-4 and fewer TG/GP 1b taxa. Because the usage of the related crop and relatedness were found to be confounded (forage/fodder CWR were more likely to be closely related to their cultivated relative; mean gene pool/taxon group for forage/fodder CWR = 2.11, food CWR = 2.67, $t_{1,97} = 2.13$, $P = 0.04$; see species lists in Appendix A Table A3), distribution patterns of CWR in different relatedness groups were also assessed within each usage group (Figure 3, Appendix A Table A4).

Differentiating CWR based on both characteristics showed that closely related (TG/GP 1b) forage/fodder CWR dominated the overall CWR response, being much more common in all types of grasslands than the other groups. Less closely related forage/fodder CWR (TG/GP 2-4), dominated by *Festuca rubra* agg., had similar habitat preferences to food CWR, being most frequent in disturbed and infertile grassland habitats, but shared landscape preferences with the closely related forage/fodder CWR, showing high frequencies in linear landscape features. Variation in habitat preferences were seen within food CWR with taxon/gene pool group 1b CWR being most common in lowland woodland and least common in heaths and bogs. Less closely related food CWR were most common in disturbed habitats and fertile grassland. Both groups of food CWR showed a preference for roads and verges.

Although there were some differences in patterns between the different regions of the UK (Appendix A Figure A1), the uncertainty surrounding parameter estimates was much higher for the Welsh and Scottish CWR due to the smaller sample sizes and therefore although there was some variation in posterior means there was significant overlap in posterior distributions for most parameters.

4. Discussion

Despite the growing importance of conserving the diversity of CWR as a means of securing future agricultural production the analysis presented here is the first systematic analysis of the ecological preferences of priority CWR for a country, made possible through national interest in CWR conservation and the extensive dataset developed through the Countryside Survey in Great Britain. Understanding the habitats and landscape features with the greatest diversity of CWR is important for informing in situ conservation strategies for crop genetic diversity to facilitate targeted management and monitoring in the most appropriate locations.

The first hypothesis that CWR would be most diverse in disturbed habitats with high anthropogenic influences was only partly supported by our data. Overall CWR were most common in fertile and infertile grasslands, the former of which is likely to be subject to human influence and disturbance through fertilisation and grazing. However, the habitat with the highest disturbance (the baseline crops and weeds habitat) had similar frequencies of CWR to woodlands and moorlands suggesting no overall preference for disturbed habitat types. The high proportion of CWR in grasslands was driven by the high proportion of forage and fodder CWR in the dataset, supporting the third hypothesis that forage and fodder CWR would be most likely to be found in grasslands. In particular, this pattern was driven by the more closely related forage and fodder CWR (those in taxon/gene pool group 1b). This group is dominated by several of the most common grass species in the UK including *Holcus lanatus* and *Lolium perenne* which are commonly found in both fertile and infertile grasslands; fertile grasslands are likely to be managed to promote their occurrence. These taxa, and the dominant forage and fodder CWR in taxon/gene pool groups 2–4, also drive the overall association of CWR with linear landscape features, being more likely to be found in field boundaries, field margins, hedgerows and alongside roads than in randomly located quadrats. In particular, those forage and fodder CWR which are less tolerant of grazing e.g. *Arrhenatherum elatius* (Dostálek and Frantík, 2012), were commonly found in linear features (Appendix A Table A5). The second hypothesis that CWR would be more frequent in linear features than the surrounding habitat is therefore supported, and it appears that arable field margins have particularly high proportions of CWR related to forage and fodder crops.

The importance of linear features as refuge features for plant species in Britain has been previously linked to the relatively lower impact of heightened macronutrient availability and extremes of disturbance, which is frequently either intense or absent, that typify intensively farmed landscapes in the temperate zone (Smart et al., 2006a, 2002). These twin pressures non-randomly filter species based on their traits. Thus ‘winners’ tend to be tall woody species or fast growing forbs and grasses while ‘losers’ are more likely to be shorter, slower-growing forbs (Smart et al., 2006b; Tamis et al., 2005; Walker et al., 2009). Where linear features are subject to intermittent or frequent removal of biomass and lack of direct fertilizer application, conditions mimic lower intensity agriculture. Thus the many CWR species that are favoured by modern management regimes can coexist alongside CWR species less adapted to intensive farming regimes, resulting in higher proportions of CWR on linear features. Low occurrence of CWR on watersides compared to randomly located plots was a feature of both food and forage and fodder CWR. This suggests that few CWR are adapted to either high soil moisture or to the late to mid-successional conditions increasingly prevalent on lowland stream and riversides in Britain (Carey et al., 2008).

Food CWR were positively associated with road verges and negatively associated with waterways, although the effects were relatively small. Food CWR may show fewer strong patterns of occurrence with landscape features due to both the lower proportions recorded and the wider range of functional types within the group, which includes grasses, herbaceous plants and trees. The cultivated relatives of food CWR are generally grown in either arable fields or orchards. These habitats are likely to be classed as crops and weeds, although some orchards more closely resemble lowland woodland. Food CWR did have high abundance in both the baseline crops and weeds habitat type and in lowland woodland, suggesting that the distribution of CWR mirrored the habitats in which their cultivated relatives were grown, however fertile grasslands also had high numbers of food CWR. When food CWR were separated by relatedness it was apparent that the association with lowland woodland was driven by more closely related food CWR, while less closely related CWR were more common in fertile grassland and crops and weeds. Common closely related food CWR included the fruit and nut relatives *Rubus fruitcosus* agg. and *Corylus avellana*, both of which are late successional woody taxa common in lowland wooded areas. The most common of the more distantly related food CWR (in taxon/gene pool groups 2–4) was *Trifolium repens*. Although *Trifolium* spp. are grown primarily as forage/fodder crops in the UK and are therefore strongly associated with fertile grasslands, they can also be used as food crops and therefore their relatives are classed as both food and forage and fodder CWR. Therefore, for food CWR, there was limited support for the fourth hypothesis that more closely related CWR would be more likely to share habitat preferences with their related crops. There was more support for this hypothesis in forage and fodder crops as closely related forage and fodder CWR were much more likely to be associated with fertile grasslands than less closely related forage and fodder CWR.

Overall, the proportion of CWR found was slightly higher in the south and in the east of the UK, a pattern also evident in the analysis of the UK geographic distribution of CWR taxa (Fielder, 2015). Many archaeophyte CWR, non-native taxa introduced before AD 1500, are likely to have their biogeographic origins in Mediterranean, eastern European or Asian biomes (Vincent et al., 2013). This is may have led to the patterns observed in the UK with CWR being slightly less prevalent in the climatically harsher north of the country, though further analysis would be required to fully investigate this. There were few regional differences in patterns of CWR occurrence despite the variation in both available species pools and conservation priorities between regions. There was an indication that woody cover had a more negative effect in England and westerly areas were more impoverished in Scotland but for most parameters credible intervals overlapped, partly a reflection of the smaller amount of data used in each model.

Most crops were originally domesticated from wild and weedy plant species (Maxted and Kell, 2009). Many of the patterns of occurrence in CWR found in the current study can be explained in this context. Weedy or ruderal plants are usually stress intolerant and found in early successional habitats with high levels of persistent disturbance and potentially high productivity (Grime, 1977). As a consequence, CWR are unlikely to occur in stressful or late successional environments and more likely to be typical of disturbed and productive habitats. Tree species, generally used to cultivate fruits and nuts, are an exception to this rule. The wild relatives of these taxa are more commonly associated with stress tolerance and are found in mid- to late successional environments (Grime, 1977), although the pressures to obtain maximum yield means that species with highly stress-resistant traits were less likely to be domesticated.

The main caveat to our analysis is that it was not possible to assess the habitat and landscape of the rarest CWR as many of these taxa were not recorded in the Countryside Survey. Of those priority CWR taxa listed in the Great Britain Threatened Plants list (Cheffings and

Farrell, 2005) only seven were recorded in the 2007 Countryside Survey with a total of only 19 records. Our results, therefore, cannot necessarily be generalised to these rarer taxa and should instead be considered to reflect the habitat preferences of the more common CWR species. Several of the common taxa, while listed in the priority inventory on the basis of their relatedness to and economic importance of cultivated relatives, are unlikely to ever be considered for conservation as they are highly prevalent in the UK countryside. To assess the conservation needs of the rarer taxa, targeted surveys are required in combination with the broad scale analysis conducted here. In addition, the Countryside Survey does not effectively sample coastal areas, partly because the total area of coastal habitat in the UK is small. Many CWR of conservation importance have a coastal distribution (Preston et al., 2002) and therefore the ability of the Countryside Survey to record these species was limited by the small number of coastal locations surveyed.

Geographical analyses have already been carried out within the UK (Fielder, 2015; Fielder et al., 2015) to identify both hotspots of CWR diversity and minimum areas which are sufficient to contain all priority CWR. Within these outlined areas we can identify protected areas and establish conservation measures within them. The analysis conducted here means that we can also prioritise specific habitats and features within hotspots (whether within or outside of protected areas) allowing much more specific targeting of in situ CWR conservation. In particular, the results of this analysis suggest maintaining linear features such as field margins and road verges would be particularly useful. The continuation of prescriptions to maintain arable field margins in agri-environment schemes is therefore predicted to be important for CWR conservation. It will also be important to identify the distribution of genetic variation within CWR taxa, something that is not addressed here but which has been studied in detail on the Lizard Peninsula in Cornwall (Fielder, 2015). Genetic diversity of key CWR found on the Lizard and across the rest of the southwest of the UK was found to be geographically structured which suggests that UK conservation efforts for CWR will need to be widespread.

5. Conclusion

This study presents the first analysis of the habitat and landscape feature preferences of multiple CWR taxa. This is possible within the UK due to the abundance of vascular plant survey data and the recent identification of CWR of highest priority for conservation. The results emphasise the importance of diverse approaches to conservation of CWR. Traditional conservation within protected areas alone may not be sufficient to conserve the full range of genetic diversity in CWR and should be complemented by conservation outside of protected areas, particularly in sites associated with linear features. Conservation outside of protected areas however, will present novel challenges for establishing long-term monitoring and active management and will require involvement and commitments from landowners. Nevertheless, if CWR (and the genetic diversity within) are to be comprehensively conserved across the country in order to meet the UK's commitments to the Convention on Biological Diversity (CBD, 2010a, 2010b, 1992) and the International Treaty for Plant Genetic Resources for Food and Agriculture (FAO, 2001), these challenges must be addressed. Since agri-environment schemes are likely to be a significant pan-European mechanism for delivering CBD commitments, it would be both desirable and relatively straightforward to evaluate whether existing UK scheme options will indirectly foster favourable conditions for CWR in their preferred habitats and locations.

Acknowledgements

This work was funded by the EU Seventh Framework Programme funded project, PGR Secure ‘Characterization of biodiversity resources for wild crop relatives to improve crops by breeding’ (Grant agreement 266394) and Natural England (Grant agreement ECM 6269 ITT 748). SJ also acknowledges support for this research from CEH/NERC National Capability funding. The Countryside Survey of 2007 was funded by a partnership of nine government funded bodies led by the Natural Environment Research Council (NERC) and the Department for Environment, Food and Rural Affairs (Defra). Data and reports are available from the Countryside Survey website (http://www.countrysidesurvey.org.uk/). The sponsors had no role in designing the study; in the collection, analysis and interpretation of data; in the writing of the report; or in the decision to submit the article for publication. We also thank Pete Henrys for statistical advice and two anonymous reviewers for useful comments.

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Figure legends

Figure 1. Boxplots of the number of crop wild relatives (CWR) from the UK priority CWR inventory and total species richness by a) habitat and b) quadrat type. Lines represent the median values, boxes are 25 and 75% percentiles and whiskers represent the most extreme data point within 1.5 times the interquartile range. Unshaded bars show number of CWRs, shaded bars show the total number of taxa. Note that quadrats vary in size (see Table 1 for details).

Figure 2. Parameter estimates for modelled effects of variables on the proportion of crop wild relatives (CWR) in a quadrat. Panel a) shows parameter estimates for all CWR types from the UK Inventory, panel b) shows the difference between CWR classified as either fodder/forage or food and panel c) groups CWR by taxon/gene pool group (TG/GP 1b vs TG/GP 2-4). Points are the mean of the posterior distribution and lines indicate the 95% credible interval. Coefficients are presented in Appendix A Table A2.

Figure 3. Parameter estimates for modelled effects of variables on the proportion of crop wild relatives (CWR) in a quadrat. Panel a) shows fodder/forage CWR patterns when additionally grouped by taxon/gene pool group (TG/GP 1b vs TG/GP 2-4), panel b) shows the same groupings for food CWR. Points are the mean of the posterior distribution and lines indicate the 95% credible interval. Coefficients are presented in Appendix A Table A4.

Table 1. Location of Countryside Survey quadrats in the landscape and quadrat characteristics (adapted from Carey *et al*., 2008).

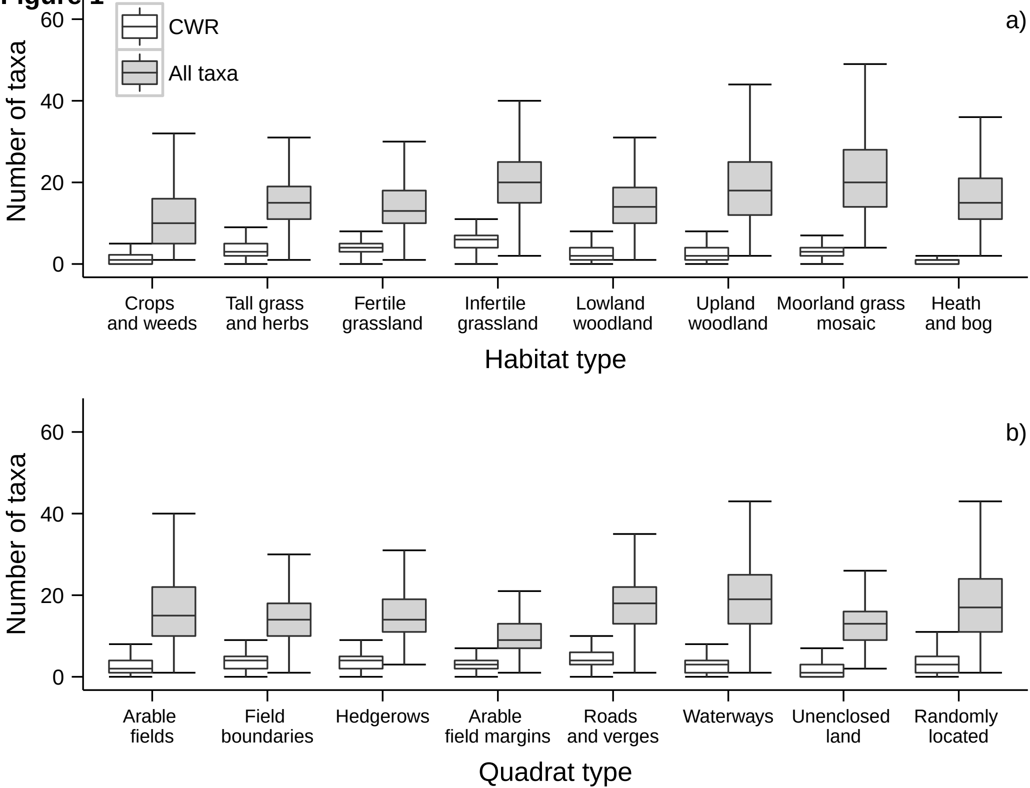
Quadrat type	**Associated landscape feature**	**Quadrat size**	**Number of quadrats per 1 km survey square**
A	Arable fields	100 m^2	5
B	Adjacent to field boundaries (hedges, walls or fences)	10 m^2	5
H	Hedgerows	10 m^2	2
M	Arable field margins	4 m^2	Up to 15
R/V	Next to roads	10 m^2	5
S/W	Next to watercourses	10 m^2	5
U	Unenclosed land	4 m^2	Up to 10
X	Randomly located	200 m^2	5

Table 2. Explanatory variables included in models of landscape drivers of crop wild relative (CWR) occurrence

Variable	Description	Range
Habitat type	Aggregate vegetation class (Bunce *et al.*, 1999)	N/A – see section 2.2
Quadrat type	Landscape feature in which quadrat occurred	N/A – see Table 1
Proportion arable area	Proportion of 1 km square covered by arable land parcels	0 - 0.95
Proportion urban area	Proportion of 1 km square covered by urban land parcels	0 - 0.91
Road area	Total area covered by roads in 1km square (hectares)	0 - 20
Proportion woody cover	Proportion of total cover due to woody plants in quadrat	0 - 1
Proportion annual cover	Proportion of total cover due to annual plants in quadrat	0 - 1
Proportion bare ground	Proportion of bare ground in quadrat	0 - 1
Easting[1]	Longitudinal position of 1 km square	072243 - 650966
Northing[1]	Latitudinal position of 1 km square	037121 - 1217913

[1]British National Grid coordinate system

Figure 1



CWR
All taxa
a)
Number of taxa
60
40
20
0
Crops and weeds
Tall grass and herbs
Fertile grassland
Infertile grassland
Lowland woodland
Upland woodland
Moorland grass mosaic
Heath and bog
Habitat type
b)
Number of taxa
60
40
20
0
Arable fields
Field boundaries
Hedgerows
Arable field margins
Roads and verges
Waterways
Unenclosed land
Randomly located
Quadrat type

Figure 2 colour

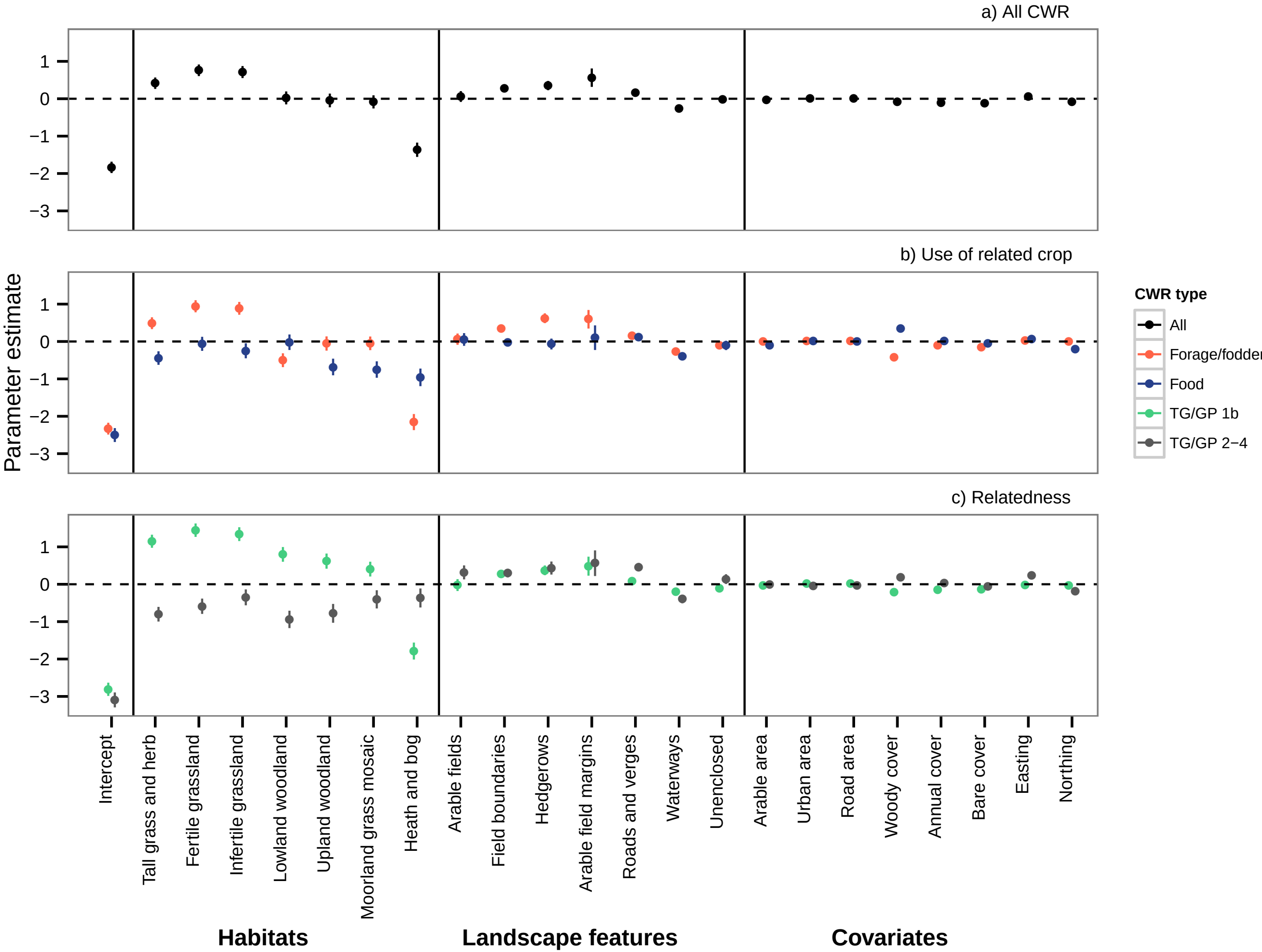
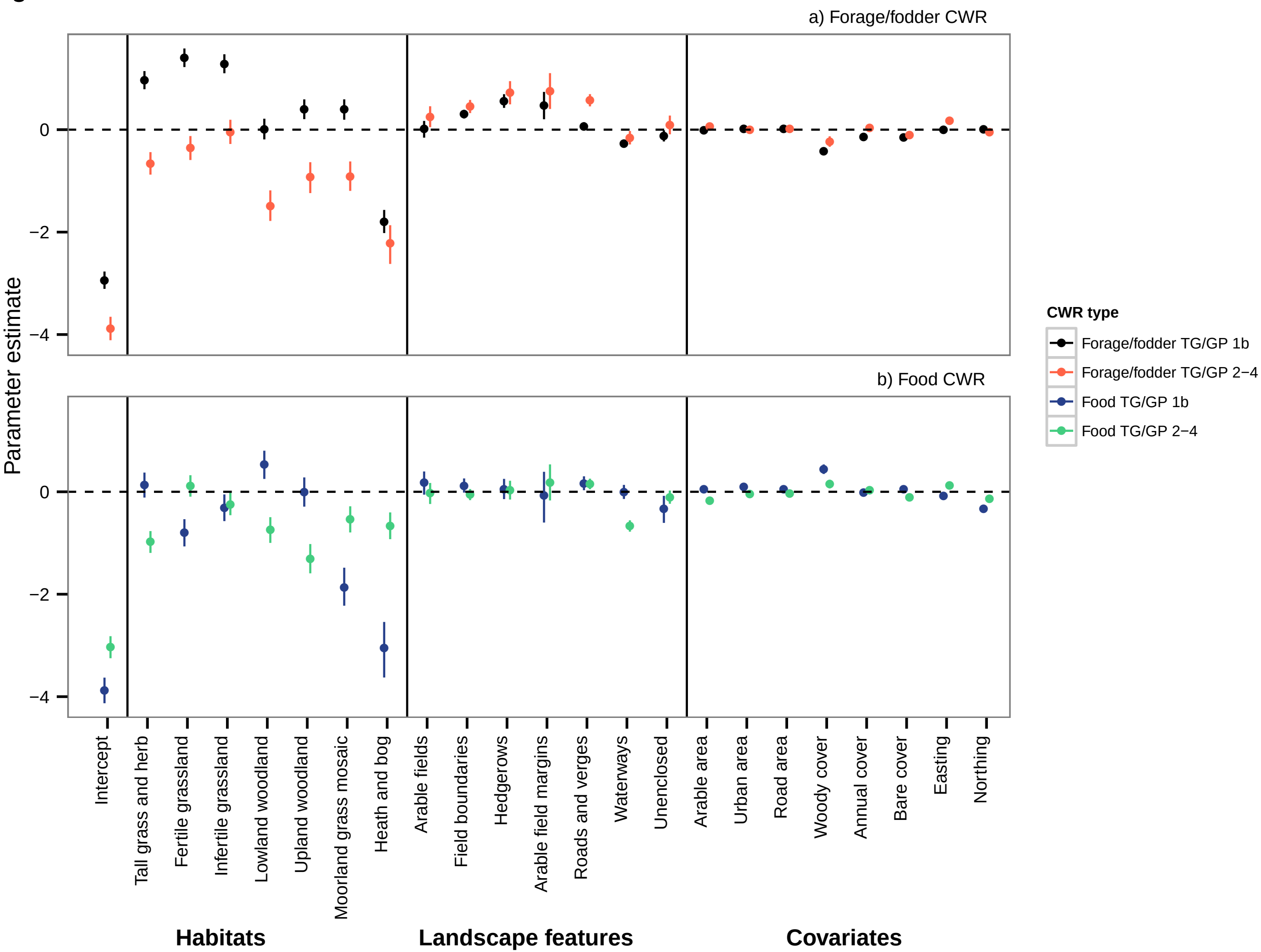


Figure 3 colour



Appendix A

Table A1. Priority crop wild relatives (CWR) recorded in the Countryside Survey of 2007 with closest domesticated relatives, use of crops, relatedness and presence in regional inventories.

Table A2. Coefficients for models of all CWR, fodder/forage CWR, food CWR, taxon group/gene pool 1b CWR and taxon group/gene pool 2-4 CWR as shown in Figure 2.

Table A3. Crop wild relative (CWR) taxa recorded in the Countryside Survey grouped by both usage (food or fodder/forage) and relatedness (taxon or gene pool group).

Table A4. Coefficients for models of fodder/forage CWR and food CWR grouped by taxon group/gene pool as shown in Figure 3.

Table A5. Frequency of crop wild relatives (CWR) in the UK priority inventory recorded in each CS quadrat type.

Figure A1. Parameter estimates for modelled effects of variables on proportion of priority crop wild relatives (CWR) in England, Scotland and Wales.

Table A1. Crop wild relative taxa in study (i.e found in Countryside Survey (CS) 2007) with closest relative, taxon/gene pool group, use of related crop, occurrence in regional inventories (E = England, S = Scotland, W = Wales, UK = United Kingdom). Species with an asterisk (*) are described as Vulnerable, Near Threatened, Endangered or Critically Endangered in the UK Red List for Vascular Plants (Cheffings and Farrell, 2005).

Crop wild relative	Closest domesticated relative(s)	Common name of domesticated relative(s)	Use of related crop(s)	Highest taxon or gene pool group	Regional inventories	Number of records in CS[1]
Acer campestre	*Acer campestre*	Field maple	Wood	1	W	651
Agrostis canina	*Agrostis capillaris; A. gigantea*	Common bent; black bent	Fodder; Forage	4	E	11
Agrostis capillaris	*Agrostis capillaris*	Common bent	Fodder; Forage	1	E, S, W, UK	3377
Agrostis curtisii	*Agrostis capillaris; A. gigantea*	Common bent; black bent	Fodder; Forage	4	E	47
Agrostis gigantea	*Agrostis gigantea*	Black bent	Fodder; Forage	1	E, S, W, UK	66
Allium ursinum	*Allium cepa; A. chinense; A. fistulosum; A. ampeloprasum; A. sativum; A. schoenoprasum; A. tuberosum*	Onion; Chinese onion; spring onion; leek; garlic; chives; Chinese chives	Vegetable; Flavouring	4	E, S, W, UK	36
Allium vineale	*Allium ampeloprasum; A. sativum*	Leek; garlic	Vegetable; Flavouring	2	E, S, W, UK	6
Alopecurus geniculatus	*Alopecurus pratensis*	Meadow foxtail	Fodder; Forage	4	E	144
Alopecurus myosuroides	*Alopecurus pratensis*	Meadow foxtail	Fodder; Forage	4	S, UK	224
Alopecurus pratensis	*Alopecurus pratensis*	Meadow foxtail	Fodder; Forage	1	E, S, W, UK	305
Anthoxanthum odoratum	*Anthoxanthum odoratum*	Sweet vernal grass	Forage	1	E, S, W, UK	2367
Apium graveolens	*Apium graveolens* var. *dulce; A. graveolens* var. *rapaceum*	Celery; celeriac	Vegetable	1	E, S, W, UK	2
Arrhenatherum elatius	*Arrhenatherum elatius*	False oat-grass	Forage	1	E, S, W, UK	2856

*Asparagus officinalis**	*Asparagus officinalis*	Asparagus	Vegetable	1	E	1
Atriplex glabriuscula	*Atriplex nummularia*	Old man saltbush	Forage	4	E	2
Atriplex portulacoides	*Atriplex nummularia*	Old man saltbush	Forage	4	E	12
Avena fatua	*Avena sativa*	Oat	Cereal; Starch; Fodder; Forage	1	UK	179
Beta vulgaris subsp. *maritima*	*Beta vulgaris* subsp. *vulgaris*	Beetroot	Sugar; Vegetable; Fodder	1	E, S, W, UK	7
Betula pendula	*Betula pendula*	Silver birch	Wood	1	W	157
Betula pubescens	*Betula pubescens*	Downy birch	Wood	1		95
Brassica nigra	*Brassica nigra*	Black mustard	Vegetable; Flavouring; Oil/fat; Fodder; Forage	1	E, S, W, UK	2
Brassica oleracea	*Brassica oleracea*	Cabbage; broccoli; cauliflower; kale; Brussels sprouts; kohlrabi	Vegetable; Flavouring; Oil/fat; Seeds; Fodder; Forage	1	E, W, UK	20
Brassica rapa	*Brassica rapa*	Turnip	Vegetable; Flavouring; Oil/fat; Fodder; Forage	1	E, S, W, UK	16
Bromus hordeaceus	*Bromus inermis*	Smooth brome	Fodder	4	S, UK	426
Calamagrostis epigejos	*Calamagrostis canadensis*	Bluejoint	Fodder; Forage	4	E, S, UK	7
Capsella bursa-pastoris	*Brassica rapa; B. napus; B. oleracea*	Turnip; oil seed rape; cabbage; broccoli; cauliflower; kale; Brussels sprouts; kohlrabi	Vegetable; Oil/fat; Fodder; Forage	3	E, S, W, UK	268
Chenopodium album	*Chenopodium quinoa*	Quinoa	Pseudocereal	4	E, S, W, UK	292
*Chenopodium bonus-henricus**	*Chenopodium quinoa*	Quinoa	Pseudocereal	4	E, S, W, UK	9
Chenopodium ficifolium	*Chenopodium quinoa*	Quinoa	Pseudocereal	3	E, S, W, UK	4
*Chenopodium murale**	*Chenopodium quinoa*	Quinoa	Pseudocereal	4	E, W, UK	1
Chenopodium polyspermum	*Chenopodium quinoa*	Quinoa	Pseudocereal	4	E, S, W, UK	5
Chenopodium rubrum	*Chenopodium quinoa*	Quinoa	Pseudocereal	4	E, S, W, UK	5

Comarum palustre	*Fragaria* × *ananassa*	Strawberry	Fruit	1	E, S, W, UK	30
Corylus avellana	*Corylus avellana*	Hazelnut	Nut; Oil/fat	1	E, S, W, UK	1517
Cynosurus cristatus	*Cynosurus cristatus*	Crested dog's-tail	Fodder; Forage	1	E, S, W, UK	1161
Dactylis glomerata	*Dactylis glomerata*	Cock's-foot	Fodder; Forage	1	E, S, W, UK	3790
Daucus carota	*Daucus carota* subsp. *sativus*	Carrot	Vegetable	1	E, S, W, UK	71
Diplotaxis tenuifolia	*Diplotaxis tenuifolia*	Rocket	Oil/fat; Seeds; Vegetable; Flavouring; Forage; Fodder	1	E, S, W, UK	1
Erodium cicutarium	*Erodium cicutarium*	Common stork's-bill	Fodder	1	E, S, W, UK	12
Erodium maritimum	*Erodium cicutarium*	Common stork's-bill	Fodder	4	S, UK	1
Fagus sylvatica	*Fagus sylvatica*	Beech	Wood	1	W	328
Festuca ovina agg.	*Schedonorus arundinaceus; S. pratensis*	Tall fescue; meadow fescue	Forage	4	E	1197
Festuca rubra agg.	*Schedonorus arundinaceus; S. pratensis*	Tall fescue; meadow fescue	Forage	4	UK	2946
Fragaria vesca	*Fragaria* × *ananassa*	Strawberry	Fruit	3	E, S, W, UK	34
Fraxinus excelsior	*Fraxinus excelsior*	Ash	Wood	1	W	1770
Holcus lanatus	*Holcus lanatus*	Yorkshire fog	Fodder	1	E, S, W, UK	5083
*Hordeum marinum**	*Hordeum vulgare*	Barley	Cereal; Fodder	3	E, W, UK	4
Hordeum murinum	*Hordeum vulgare*	Barley	Cereal; Fodder	3	E, S, W, UK	97
Hordeum secalinum	*Hordeum vulgare*	Barley	Cereal; Fodder	3	E, W, UK	45
Koeleria macrantha	*Koeleria macrantha*	Crested hair-grass	Fodder; Forage	1	E, S, W, UK	10
Lactuca serriola	*Lactuca sativa*	Lettuce	Vegetable; Oil/fat; Fodder	1	E, S, W, UK	47

Lactuca sp.†	*Lactuca sativa*	Lettuce	Vegetable; Oil/fat; Fodder	3	E	1
Lathyrus linifolius	*Lathyrus cicera; L. ochrus; L. sativus*	Chickling vetch; Cyprus vetch; Indian pea	Vegetable; Fodder; Forage	4	E	33
*Lathyrus palustris**	*Lathyrus cicera; L. ochrus; L. sativus*	Chickling vetch; Cyprus vetch; Indian pea	Vegetable; Fodder; Forage	4	S, W, UK	1
Lathyrus pratensis	*Lathyrus cicera; L. ochrus; L. sativus*	Chickling vetch; Cyprus vetch; Indian pea	Vegetable; Fodder; Forage	4	E	496
Lathyrus sylvestris	*Lathyrus cicera*	Chickling vetch	Vegetable; Fodder; Forage	2	E, S, W, UK	2
Lepidium campestre	*Lepidium sativum*	Cress	Vegetable	4	S, UK	1
Lepidium coronopus	*Lepidium sativum*	Cress	Vegetable	4	UK	68
Lepidium heterophyllum	*Lepidium sativum*	Cress	Vegetable	4	E	1
Lepidium latifolium	*Lepidium sativum*	Cress	Vegetable	4	UK	3
Linum bienne	*Linum usitatissimum*	Flax	Oil/fat; Seeds; Fodder	2	E, W, UK	8
Linum catharticum	*Linum usitatissimum*	Flax	Oil/fat; Seeds; Fodder	4	E, S, W, UK	67
Lolium perenne	*Lolium perenne*	Perennial ryegrass	Fodder; Forage	1	E, S, W, UK	3513
Lotus corniculatus	*Lotus corniculatus*	Bird's foot trefoil	Fodder; Forage	1	E, S, W, UK	520
Lotus glaber	*Lotus corniculatus; L. pedunculatus*	Bird's foot trefoil; greater bird's foot trefoil	Fodder; Forage	4	UK	1
Lotus pedunculatus	*Lotus pedunculatus*	Greater bird's foot trefoil	Fodder; Forage	1	E, UK	293
Malus sylvestris	*Malus domestica*	Apple	Fruit	1	E, S, W, UK	66
Medicago arabica	*Medicago truncatula*	Strong-spined medick	Vegetable; Fodder; Forage	2	E, W, UK	20
Medicago lupulina	*Medicago sativa; M. truncatula*	Alfalfa; strong-spined medick	Vegetable; Fodder; Forage	4	E, S, W, UK	131
Medicago polymorpha	*Medicago truncatula*	Strong-spined medick	Vegetable; Fodder; Forage	2	E, UK	1
Nasturtium officinale	*Nasturtium officinale*	Watercress	Vegetable	1	E, S, W	44
Ornithopus perpusillus	*Ornithopus sativus*	Common bird's foot	Forage	4	E	8

Pastinaca sativa	*Pastinaca sativa* subsp. *sativa*	Parsnip	Vegetable	1	E, W, UK	32
Phalaris arundinacea	*Phalaris arundinacea*	Reed canary-grass	Fodder; Forage	1	E, S, W, UK	221
Phleum bertolonii	*Phleum pratense*	Timothy	Fodder; Forage	2	E, S, W, UK	89
Phleum pratense	*Phleum pratense*	Timothy	Fodder; Forage	1	E, S, W	637
Plantago lanceolata	*Plantago lanceolata*	Ribwort plantain	Fodder	1	S, W	1668
Plantago media	*Plantago lanceolata*	Ribwort plantain	Fodder	4	S	27
Poa annua	*Poa pratensis*	Smooth meadow grass	Fodder; Forage	4	E	2267
Poa nemoralis	*Poa pratensis*	Smooth meadow grass	Fodder; Forage	4	E	59
Poa pratensis	*Poa pratensis*	Smooth meadow grass	Fodder; Forage	1	E, S, W	907
Poa trivialis	*Poa pratensis*	Smooth meadow grass	Fodder; Forage	4	E	2512
Populus tremula	*Populus tremula*	Aspen	Wood	1	W	22
Prunus avium	*Prunus avium*	Cherry	Fruit; Nut; Seeds	1	E, S, W, UK	73
Prunus domestica	*Prunus domestica*	Plum	Fruit; Nut; Seeds	1	E, S, W	71
Prunus padus	*Prunus armeniaca; P. avium; P. cerasifera; P. cerasus; P. domestica; P. dulcis; P. persica*	Apricot; cherry; cherry plum; dwarf cherry; plum; almond; peach	Fruit; Nut; Seeds	4	E, S, W, UK	16
Prunus spinosa	*Prunus domestica*	Plum	Fruit; Nut; Seeds	2	E, S, W, UK	2207
Quercus petraea	*Quercus petraea*	Sessile oak	Wood	1	W	145
Quercus robur	*Quercus robur*	Pedunculate oak	Wood	1	W	921
Raphanus raphanistrum subsp. *maritimus*	*Raphanus sativus*	Radish	Oil/fat; Vegetable; Forage	1	E, S, W, UK	4
Raphanus raphanistrum subsp. *raphanistrum*	*Raphanus sativus*	Radish	Oil/fat; Vegetable; Forage	1	E, S, W, UK	34
Ribes rubrum	*Ribes rubrum*	Redcurrant	Fruit	1	E, S, W, UK	12
Rorippa sylvestris	*Rorippa indica; Nasturtium officinale*	Variableleaf yellowcress; watercress	Vegetable	4	E	2

Rubus caesius	*Rubus fruticosus*	Blackberry	Fruit	3	E, S, W, UK	57
Rubus chamaemorus	*Rubus fruticosus; R. idaeus*	Blackberry; raspberry	Fruit	4	E, S, W, UK	47
Rubus fruticosus agg.	*Rubus fruticosus*	Blackberry	Fruit	1	UK	4627
Rubus idaeus	*Rubus idaeus*	Raspberry	Fruit	1	E, S, W	98
Rubus saxatilis	*Rubus fruticosus; R. idaeus*	Blackberry; raspberry	Fruit	4	E, S, W	1
Schedonorus arundinaceus	*Schedonorus arundinaceus*	Tall fescue	Forage	1	E, S, W, UK	145
Schedonorus giganteus	*Schedonorus arundinaceus; S. pratensis*	Tall fescue; meadow fescue	Forage	3	E, S, W, UK	28
Schedonorus pratensis	*Schedonorus pratensis*	Meadow fescue	Forage	1	E, S, W, UK	129
Sinapis alba	*Sinapis alba*	White mustard	Flavouring; Oil/fat; Vegetable; Seeds; Fodder; Forage	1	E, S, W	4
Sinapis arvensis	*Brassica nigra*	Black mustard	Flavouring; Oil/fat; Vegetable; Seeds; Fodder; Forage	2	E, S, W	137
Sinapis arvensis/alba‡	*Brassica nigra*	Black mustard	Flavouring; Oil/fat; Vegetable; Seeds; Fodder; Forage	2	E, S, W	5
Trifolium arvense	*Trifolium pratense; T.incarnatum subsp. incarnatum*	Red clover; crimson clover	Flavouring; Fodder; Forage	2	E, S, W	5
Trifolium campestre	*Trifolium pratense; T. repens; T. incarnatum subsp. incarnatum; T. subterraneum*	Red clover; white clover, crimson clover, subterranean clover	Flavouring; Fodder; Forage	4	E	14
Trifolium fragiferum	*Trifolium pratense; T. repens; T. incarnatum subsp. incarnatum; T. subterraneum*	Red clover; white clover, crimson clover, subterranean clover	Flavouring; Fodder; Forage	3	E, S, W	1
Trifolium medium	*Trifolium pratense; T.*	Red clover; crimson	Flavouring; Fodder;	2	E, S, W	13

	incarnatum subsp. incarnatum	clover	Forage			
Trifolium micranthum	*Trifolium pratense; T.repens; T.incarnatum subsp. incarnatum; T. subterraneum*	Red clover; white clover, crimson clover, subterranean clover	Flavouring; Fodder; Forage	4	UK	12
Trifolium ornithopodioides	*Trifolium pratense; T. repens; T.incarnatum subsp. incarnatum; T. subterraneum*	Red clover; white clover, crimson clover, subterranean clover	Flavouring; Fodder; Forage	3	E, UK	2
Trifolium pratense	*Trifolium pratense*	Red clover	Flavouring; Fodder; Forage	1	E, S, W, UK	520
Trifolium repens	*Trifolium repens*	White clover	Flavouring; Fodder; Forage	1	E, S, W, UK	3001
Trifolium striatum	*Trifolium pratense; T.incarnatum subsp. incarnatum*	Red clover; crimson clover	Flavouring; Fodder; Forage	2	E, S, W, UK	1
Trisetum flavescens	*Trisetum flavescens*	Yellow oat-grass	Fodder	1	E, S, W, UK	93
Ulmus glabra	*Ulmus glabra*	Wych elm	Wood	1	W	79
Ulmus procera	*Ulmus procera*	English elm	Wood	1	W	195
Vaccinium myrtillus	*Vaccinium oxycoccos*	Cranberry	Fruit	4	E, S, W, UK	1163
Vaccinium oxycoccos	*Vaccinium oxycoccos*	Cranberry	Fruit	1	E, S, W, UK	22
Vaccinium uliginosum	*Vaccinium oxycoccos*	Cranberry	Fruit	4	E, S, UK	3
Vaccinium vitis-idaea	*Vaccinium oxycoccos*	Cranberry	Fruit	4	E, S, W, UK	165
*Vicia bithynica**	*Vicia faba*	Broad bean	Pulse; Fodder; Forage	3	E, S, W, UK	2
Vicia cracca	*Vicia articulata; V.ervilia*	One flower vetch; bitter vetch	Pulse; Fodder; Forage	3	E, S, W, UK	209
Vicia hirsuta	*Vicia articulata; V.ervilia*	One flower vetch; bitter vetch	Pulse; Fodder; Forage	3	E, S, W, UK	27

Vicia lathyroides	*Vicia faba*		Pulse; Fodder; Forage	3	E, S, W, UK	1
*Vicia orobus**	*Vicia articulata; V.ervilia*	One flower vetch; bitter vetch	Pulse; Fodder; Forage	3	S, W, UK	1
Vicia sativa	*Vicia sativa*	Common vetch	Pulse; Fodder; Forage	1	E, S, W, UK	171
Vicia sepium	*Vicia faba; V.narbonensis; V.pannonica; V.sativa*	Broad bean; narbon bean; Hungarian vetch; common vetch	Pulse; Fodder; Forage	3	E, S, W, UK	252
Vicia sylvatica	*Vicia articulata; V.ervilia*	One flower vetch; bitter vetch	Pulse; Fodder; Forage	3	E, S, W, UK	1
Vicia tetrasperma	*Vicia articulata; V.ervilia*	One flower vetch; bitter vetch	Pulse; Fodder; Forage	3	E, S, W, UK	51

[1] Excluding D and Y plots which were not analysed in this study

† Not recorded to species in survey, most likely to be *Lactuca serriola*, *L. sativa* or *L. virosa* as the plot is in an inland location so *L. saligna* and *L. tatarica* are very unlikely to occur

‡ These species could not always be distinguished so were sometimes recorded as an aggregate

Table A2. Parameter estimates and 95% credible intervals (in brackets) for each parameter in models of crop wild relative (CWR) occurrence either ungrouped (All CWR) or grouped by usage or relatedness (taxon/gene pool groups 1b or 2-4). Parameters where 95% intervals do not overlap zero are highlighted in bold. Factors show contrasts from the reference (baseline) levels: crops and weeds (Habitats) and randomly located quadrats (Landscape features).

Parameter	All CWR	Food CWR	Fodder CWR	TG/GP 1b CWR	TG/GP 2-4 CWR
Intercept	**-1.84** (-1.99, -1.68)	**-2.5** (-2.69, -2.32)	**-2.33** (-2.49, -2.17)	**-2.81** (-2.99, -2.63)	**-3.09** (-3.29, -2.89)
Habitats					
Tall grass and herb	**0.42** (0.26, 0.57)	**-0.44** (-0.62, -0.26)	**0.49** (0.33, 0.65)	**1.15** (0.98, 1.33)	**-0.8** (-1, -0.61)
Fertile grassland	**0.76** (0.61, 0.92)	-0.06 (-0.25, 0.13)	**0.94** (0.78, 1.1)	**1.45** (1.27, 1.63)	**-0.59** (-0.79, -0.38)
Infertile grassland	**0.71** (0.55, 0.87)	**-0.25** (-0.45, -0.05)	**0.89** (0.72, 1.06)	**1.34** (1.16, 1.53)	**-0.35** (-0.56, -0.14)
Lowland woodland	0.02 (-0.15, 0.20)	-0.02 (-0.23, 0.19)	**-0.5** (-0.69, -0.32)	**0.8** (0.6, 1)	**-0.94** (-1.17, -0.71)
Upland woodland	-0.04 (-0.23, 0.14)	**-0.69** (-0.9, -0.46)	-0.05 (-0.24, 0.14)	**0.62** (0.42, 0.82)	**-0.78** (-1.03, -0.53)
Moorland grass mosaic	-0.08 (-0.26, 0.09)	**-0.75** (-0.97, -0.53)	-0.05 (-0.23, 0.13)	**0.4** (0.21, 0.6)	**-0.4** (-0.65, -0.16)
Heath and bog	**-1.36** (-1.56, -1.17)	**-0.96** (-1.19, -0.72)	**-2.15** (-2.37, -1.94)	**-1.79** (-2.01, -1.56)	**-0.36** (-0.62, -0.11)
Landscape features					
Arable fields	0.06 (-0.09, 0.20)	0.05 (-0.12, 0.22)	0.06 (-0.09, 0.21)	-0.02 (-0.18, 0.14)	**0.32** (0.13, 0.5)
Field boundaries	**0.28** (0.2, 0.36)	-0.03 (-0.13, 0.07)	**0.35** (0.27, 0.44)	**0.27** (0.19, 0.36)	**0.3** (0.18, 0.41)
Hedgerows	**0.35** (0.23, 0.48)	-0.07 (-0.21, 0.08)	**0.62** (0.49, 0.75)	**0.37** (0.24, 0.5)	**0.44** (0.26, 0.61)
Arable field margins	**0.56** (0.32, 0.81)	0.11 (-0.23, 0.43)	**0.6** (0.35, 0.84)	**0.48** (0.23, 0.74)	**0.57** (0.22, 0.91)
Roads and verges	**0.16** (0.09, 0.23)	**0.12** (0.03, 0.22)	**0.16** (0.09, 0.24)	**0.09** (0.01, 0.16)	**0.46** (0.35, 0.57)
Waterways	**-0.26** (-0.34, -0.19)	**-0.4** (-0.49, -0.3)	**-0.27** (-0.35, -0.19)	**-0.2** (-0.27, -0.12)	**-0.4** (-0.51, -0.29)
Unenclosed	-0.02 (-0.11, 0.08)	-0.11 (-0.23, 0.02)	-0.1 (-0.21, 0)	**-0.11** (-0.22, -0.01)	**0.14** (0.01, 0.27)
Covariates					
Arable area	-0.03 (-0.06, 0.01)	**-0.1** (-0.15, -0.05)	0 (-0.04, 0.04)	-0.02 (-0.06, 0.01)	0 (-0.07, 0.06)
Urban area	0.01 (-0.02, 0.04)	0.02 (-0.02, 0.06)	0.01 (-0.01, 0.04)	0.03 (0, 0.05)	-0.04 (-0.09, 0.01)
Road area	0.01 (-0.02, 0.03)	0 (-0.04, 0.04)	0.01 (-0.02, 0.04)	0.02 (-0.01, 0.05)	-0.03 (-0.08, 0.02)
Woody cover	**-0.08** (-0.13, -0.02)	**0.35** (0.28, 0.41)	**-0.42** (-0.48, -0.36)	**-0.21** (-0.27, -0.15)	**0.19** (0.11, 0.26)
Annual cover	**-0.10** (-0.13, -0.07)	0.02 (-0.02, 0.05)	**-0.1** (-0.13, -0.07)	**-0.15** (-0.18, -0.11)	0.03 (-0.01, 0.07)
Bare cover	**-0.12** (-0.15, -0.09)	**-0.04** (-0.08, -0.01)	**-0.16** (-0.19, -0.12)	**-0.13** (-0.16, -0.1)	**-0.05** (-0.1, -0.01)
Easting	**0.07** (0.03, 0.10)	**0.07** (0.02, 0.11)	0.03 (0, 0.06)	-0.02 (-0.05, 0.01)	**0.24** (0.18, 0.3)
Northing	**-0.08** (-0.11, -0.05)	**-0.2** (-0.24, -0.16)	0 (-0.03, 0.03)	-0.03 (-0.06, 0)	**-0.18** (-0.24, -0.13)

Table A3. CWR taxa from the UK priority inventory recorded in the Countryside Survey grouped by both usage (food or fodder/forage) and relatedness (taxon or gene pool group). The taxon or gene pool group reflects the closest relation to a crop of that usage e.g. *Raphanus raphanistrum* subsp. *maritimus* is closely related to the food crop *Raphanus sativus* (gene pool group 1) but less closely related to the fodder crop *Brassica napus* (gene pool group 3).

Food CWR		***Fodder/forage CWR***	
Taxon/gene pool group 1	**Taxon/gene pool groups 2-4**	**Taxon/gene pool group 1**	**Taxon/gene pool groups 2-4**
Apium graveolens	*Allium ursinum*	*Agrostis capillaris*	*Alopecurus myosuroides*
Avena fatua	*Allium vineale*	*Agrostis gigantea*	*Brassica nigra*
Beta vulgaris subsp.maritima	*Capsella bursa-pastoris*	*Alopecurus pratensis*	*Brassica rapa*
Brassica nigra	*Chenopodium album agg.*	*Anthoxanthum odoratum*	*Bromus hordeaceus*
Brassica oleracea	*Chenopodium bonus-henricus*	*Arrhenatherum elatius*	*Calamagrostis epigejos*
Brassica rapa	*Chenopodium ficifolium*	*Avena fatua*	*Capsella bursa-pastoris*
Comarum palustre	*Chenopodium murale*	*Beta vulgaris subsp.maritima*	*Crambe maritima*
Corylus avellana	*Chenopodium polyspermum*	*Brassica oleracea*	*Diplotaxis tenuifolia*
Daucus carota	*Chenopodium rubrum*	*Cynosurus cristatus*	*Erodium maritimum*
Diplotaxis tenuifolia	*Fragaria vesca*	*Dactylis glomerata*	*Festuca rubra agg.*
Lactuca serriola	*Hordeum marinum*	*Erodium cicutarium agg.*	*Hordeum marinum*
Malus sylvestris	*Hordeum murinum*	*Holcus lanatus*	*Hordeum murinum*
Pastinaca sativa	*Hordeum secalinum*	*Koeleria macrantha*	*Hordeum secalinum*
Prunus avium	*Lathyrus palustris*	*Lactuca serriola*	*Lathyrus palustris*
Raphanus raphanistrum subsp. *maritimus*	*Lathyrus sylvestris*	*Lolium perenne*	*Lathyrus sylvestris*
Raphanus raphanistrum subsp. *raphanistrum*	*Lepidium campestre*	*Lotus corniculatus*	*Linum bienne*
Ribes rubrum	*Lepidium coronopus*	*Lotus pedunculatus*	*Linum catharticum*
Rubus fruticosus agg.	*Lepidium latifolium*	*Phalaris arundinacea*	*Lotus glaber*
Rubus idaeus	*Linum bienne*	*Schedonorus arundinaceus*	*Medicago arabica*
Sinapis alba	*Linum catharticum*	*Schedonorus pratensis*	*Medicago lupulina*
Sinapis arvensis	*Medicago arabica*	*Sinapis alba*	*Medicago polymorpha*
Sinapis arvensis/alba	*Medicago lupulina*	*Sinapis arvensis*	*Phleum bertolonii*
Trifolium pratense	*Medicago polymorpha*	*Sinapis arvensis/alba*	*Raphanus raphanistrum* subsp. *maritimus*
Vaccinium oxycoccos	*Prunus padus*	*Trifolium pratense*	*Raphanus raphanistrum* subsp. *raphanistrum*
	Prunus spinosa	*Trifolium repens*	*Schedonorus giganteus*
	Rubus caesius	*Trisetum flavescens*	*Trifolium arvense*
	Rubus chamaemorus	*Vicia sativa*	*Trifolium fragiferum*
	Rubus saxatilis		*Trifolium medium*
	Trifolium arvense		*Trifolium micranthum*

	Trifolium fragiferum	*Trifolium ornithopodioides*
	Trifolium medium	*Trifolium striatum*
	Trifolium micranthum	*Vicia bithynica*
	Trifolium ornithopodioides	*Vicia cracca*
	Trifolium repens	*Vicia hirsuta*
	Trifolium striatum	*Vicia lathyroides*
	Vaccinium myrtillus	*Vicia orobus*
	Vaccinium uliginosum	*Vicia sepium*
	Vaccinium vitis-idaea	*Vicia sylvatica*
	Vicia bithynica	*Vicia tetrasperma*
	Vicia cracca	
	Vicia hirsuta	
	Vicia lathyroides	
	Vicia orobus	
	Vicia sativa	
	Vicia sepium	
	Vicia sylvatica	
	Vicia tetrasperma	

Table A4. Parameter estimates and 95% credible intervals for each parameter in each model of crop wild relative (CWR) occurrence grouped by relatedness (taxon/gene pool groups 1b or 2-4) within each usage group as shown in Figure 3 a, b. Parameters where 95% intervals do not overlap zero are highlighted in bold. Factors show contrasts from the reference (baseline) levels: crops and weeds (Habitats) and randomly located quadrats (Landscape features).

	Forage/fodder CWR		**Food CWR**	
Parameter	**TG/GP 1b**	**TG/GP 2-4**	**TG/GP 1b**	**TG/GP 2-4**
Intercept	**-2.94** (-3.12,-2.77)	**-3.88** (-4.1,-3.66)	**-3.86** (-4.12,-3.62)	**-3.04** (-3.25,-2.82)
Habitats				
Tall grass and herb	**0.97** (0.79,1.14)	**-0.66** (-0.88,-0.45)	0.12 (-0.11,0.36)	**-0.98** (-1.19,-0.76)
Fertile grassland	**1.4** (1.22,1.58)	**-0.35** (-0.58,-0.13)	**-0.81** (-1.07,-0.55)	0.12 (-0.08,0.34)
Infertile grassland	**1.28** (1.1,1.47)	-0.05 (-0.28,0.18)	**-0.34** (-0.6,-0.08)	**-0.24** (-0.46,-0.01)
Lowland woodland	0.01 (-0.2,0.21)	**-1.49** (-1.77,-1.21)	**0.51** (0.26,0.78)	**-0.74** (-0.98,-0.48)
Upland woodland	**0.4** (0.19,0.61)	**-0.93** (-1.22,-0.64)	-0.02 (-0.3,0.26)	**-1.3** (-1.58,-1.02)
Moorland grass mosaic	**0.4** (0.2,0.6)	**-0.92** (-1.19,-0.65)	**-1.89** (-2.23,-1.56)	**-0.53** (-0.78,-0.27)
Heath and bog	**-1.8** (-2.03,-1.56)	**-2.19** (-2.54,-1.84)	**-3** (-3.51,-2.5)	**-0.67** (-0.93,-0.39)
Landscape features				
Arable fields	0.01 (-0.15,0.17)	**0.25** (0.04,0.45)	0.17 (-0.05,0.4)	-0.03 (-0.24,0.18)
Field boundaries	**0.3** (0.22,0.39)	**0.45** (0.32,0.59)	0.12 (-0.02,0.26)	-0.06 (-0.17,0.06)
Hedgerows	**0.56** (0.42,0.7)	**0.71** (0.49,0.94)	0.05 (-0.13,0.23)	0.03 (-0.16,0.22)
Arable field margins	**0.47** (0.22,0.73)	**0.74** (0.39,1.1)	-0.07 (-0.61,0.42)	0.17 (-0.2,0.54)
Roads and verges	0.07 (-0.01,0.14)	**0.57** (0.46,0.69)	**0.17** (0.03,0.3)	**0.15** (0.05,0.25)
Waterways	**-0.28** (-0.35,-0.19)	**-0.16** (-0.29,-0.02)	0 (-0.14,0.14)	**-0.67** (-0.78,-0.55)
Unenclosed	**-0.12** (-0.23,-0.02)	0.1 (-0.09,0.28)	**-0.35** (-0.62,-0.09)	-0.1 (-0.24,0.03)
Covariates				
Arable area	-0.01 (-0.05,0.03)	0.06 (0,0.13)	0.05 (-0.01,0.12)	**-0.18** (-0.24,-0.11)
Urban area	0.02 (-0.01,0.05)	0 (-0.06,0.05)	**0.1** (0.05,0.14)	-0.04 (-0.09,0.01)
Road area	0.01 (-0.01,0.04)	0.02 (-0.03,0.07)	0.05 (0,0.1)	-0.04 (-0.09,0.01)
Woody cover	**-0.42** (-0.48,-0.35)	**-0.24** (-0.34,-0.13)	**0.44** (0.35,0.52)	**0.15** (0.07,0.23)
Annual cover	**-0.14** (-0.17,-0.11)	0.04 (-0.01,0.08)	-0.02 (-0.06,0.03)	0.04 (0,0.08)
Bare cover	**-0.15** (-0.18,-0.12)	**-0.11** (-0.16,-0.06)	0.05 (0,0.1)	**-0.11** (-0.16,-0.06)
Easting	0 (-0.04,0.03)	**0.18** (0.11,0.24)	**-0.08** (-0.15,-0.02)	**0.13** (0.07,0.18)
Northing	0.01 (-0.02,0.04)	-0.05 (-0.1,0.01)	**-0.33** (-0.39,-0.27)	**-0.13** (-0.18,-0.08)

Table A5. Frequency of crop wild relatives (CWR) in the UK priority inventory (97 taxa) recorded in each CS quadrat type. Note R and V plots and S and W plots were combined for analysis.

	A	B	H	M	R	S	U	V	W	X
Agrostis capillaris	18	593	121	7	261	257	458	364	378	946
Agrostis gigantea	13	16	1	5	4	1	1	2	4	19
Allium ursinum	0	2	0	0	1	12	0	0	20	2
Allium vineale	0	1	0	0	1	0	0	3	0	1
Alopecurus myosuroides	105	21	1	3	5	1	0	2	1	85
Alopecurus pratensis	3	57	13	3	31	16	3	38	32	110
Anthoxanthum odoratum	3	252	29	2	117	255	453	174	416	700
Apium graveolens	0	0	0	0	0	2	0	0	0	0
Arrhenatherum elatius	87	749	306	27	387	232	18	546	326	179
Avena fatua	75	29	7	7	6	1	1	4	1	48
Beta vulgaris subsp.maritima	0	4	0	0	0	0	0	0	0	3
Brassica nigra	0	0	0	0	0	1	0	0	0	1
Brassica oleracea	5	1	0	0	0	1	0	0	1	12
Brassica rapa	4	2	0	1	1	0	0	0	1	7
Bromus hordeaceus	72	216	46	28	104	30	4	148	20	192
Calamagrostis epigejos	0	2	1	0	1	0	0	0	0	3
Capsella bursa-pastoris	76	23	3	12	17	0	0	37	0	100
Chenopodium album	81	20	4	9	25	3	1	45	4	98
Chenopodium bonus-henricus	1	1	1	0	3	0	0	1	0	2
Chenopodium ficifolium	1	0	0	0	1	0	0	1	0	1
Chenopodium murale	0	1	0	0	0	0	0	0	0	0
Chenopodium polyspermum	1	0	0	0	0	0	0	0	0	4
Chenopodium rubrum	3	1	0	0	0	0	0	0	0	1
Comarum palustre	0	2	0	0	1	5	8	0	6	8
Corylus avellana	4	194	143	0	58	85	1	67	124	55
Crambe maritima	0	0	0	0	0	0	0	0	0	0

Cynosurus cristatus	7	197	19	24	89	99	56	113	144	425
Dactylis glomerata	145	847	297	41	578	186	40	858	292	505
Daucus carota	6	13	1	3	5	0	5	14	1	26
Diplotaxis tenuifolia	0	1	0	0	0	0	0	0	0	0
Erodium cicutarium	4	1	0	0	0	0	2	0	0	6
Erodium maritimum	0	0	0	0	0	0	0	0	0	1
Festuca rubra agg.	50	552	145	35	377	187	221	564	310	520
Fragaria vesca	0	3	2	0	10	1	1	9	2	6
Holcus lanatus	120	997	235	46	456	448	320	656	667	1149
Hordeum marinum	1	1	0	0	1	1	0	0	0	0
Hordeum murinum	7	24	2	0	20	0	0	28	1	15
Hordeum secalinum	0	12	1	0	2	0	0	4	4	24
Koeleria macrantha	0	2	0	0	0	0	4	0	0	4
Lactuca serriola	9	9	1	0	9	2	0	6	2	9
Lathyrus palustris	0	0	0	0	0	1	0	0	0	0
Lathyrus sylvestris	0	0	0	0	0	0	0	1	1	0
Lepidium campestre	0	0	0	0	0	0	0	0	0	1
Lepidium coronopus	31	6	0	0	6	0	0	6	1	18
Lepidium latifolium	0	2	0	0	0	0	0	1	0	0
Linum bienne	1	3	0	0	0	0	0	1	0	3
Linum catharticum	0	7	0	0	7	2	22	12	5	17
Lolium perenne	114	667	140	39	547	102	37	750	168	950
Lotus corniculatus	3	45	7	2	45	31	68	77	64	188
Lotus glaber	0	0	0	0	0	0	0	0	0	1
Lotus pedunculatus	0	26	1	0	12	53	30	23	79	71
Malus sylvestris	2	11	5	0	1	4	0	2	4	1
Medicago arabica	0	1	0	0	7	1	0	9	0	2
Medicago lupulina	4	22	1	1	12	2	8	47	0	38
Medicago polymorpha	0	0	0	0	0	0	0	1	0	0

Pastinaca sativa	10	16	0	2	8	0	6	4	0	18
Phalaris arundinacea	0	17	1	2	1	70	6	3	112	11
Phleum bertolonii	1	15	1	2	11	2	5	15	0	42
Prunus avium	1	11	4	0	2	3	0	2	1	17
Prunus padus	0	3	2	0	0	4	0	0	2	1
Prunus spinosa	30	311	248	1	95	40	3	136	65	40
Raphanus raphanistrum subsp. *maritimus*	0	1	0	0	1	0	1	0	1	0
Raphanus raphanistrum subsp. *raphanistrum*	12	2	0	0	0	3	0	1	2	14
Ribes rubrum	0	2	2	0	0	1	0	1	0	3
Rubus caesius	0	9	5	0	2	4	0	11	10	3
Rubus chamaemorus	0	0	0	0	0	2	21	0	2	29
Rubus fruticosus agg.	69	722	402	6	270	280	46	421	387	261
Rubus idaeus	0	6	4	0	7	16	1	16	11	21
Rubus saxatilis	0	0	0	0	0	0	0	0	1	0
Schedonorus arundinaceus	4	10	4	7	26	11	4	41	15	23
Schedonorus giganteus	0	3	1	0	1	8	0	3	8	4
Schedonorus pratensis	12	18	3	8	17	5	1	26	9	30
Sinapis alba	1	1	0	0	1	0	0	1	0	0
Sinapis arvensis	59	21	2	1	3	4	0	8	2	37
Sinapis arvensis/alba	2	1	0	0	0	0	0	0	0	2
Trifolium arvense	0	0	0	0	0	0	1	3	0	1
Trifolium fragiferum	0	1	0	0	0	0	0	0	0	0
Trifolium medium	0	1	0	0	4	1	1	3	1	2
Trifolium micranthum	0	2	0	0	1	0	0	4	2	4
Trifolium ornithopodioides	0	0	0	0	2	0	0	0	0	0
Trifolium pratense	11	46	5	5	54	18	18	103	41	225
Trifolium repens	58	460	39	35	373	161	143	519	242	983
Trifolium striatum	0	0	0	0	0	0	0	0	0	1
Trisetum flavescens	0	22	3	0	7	4	10	11	2	39

Vaccinium myrtillus	0	55	0	0	14	72	441	28	118	478
Vaccinium oxycoccos	0	0	0	0	0	1	10	0	2	8
Vaccinium uliginosum	0	0	0	0	0	0	2	0	0	1
Vaccinium vitis-idaea	0	5	0	0	3	8	56	3	7	90
Vicia bithynica	1	0	0	0	0	0	0	1	0	0
Vicia cracca	5	32	19	2	35	12	2	43	31	27
Vicia hirsuta	2	5	1	0	3	2	0	8	2	4
Vicia lathyroides	0	0	0	0	0	0	0	1	0	0
Vicia orobus	0	0	0	0	0	0	0	0	0	1
Vicia sativa	4	62	18	4	52	16	0	102	18	66
Vicia sepium	3	32	18	1	55	15	0	84	31	12
Vicia sylvatica	0	0	0	0	0	0	0	0	0	1
Vicia tetrasperma	3	12	2	2	2	5	1	4	6	14

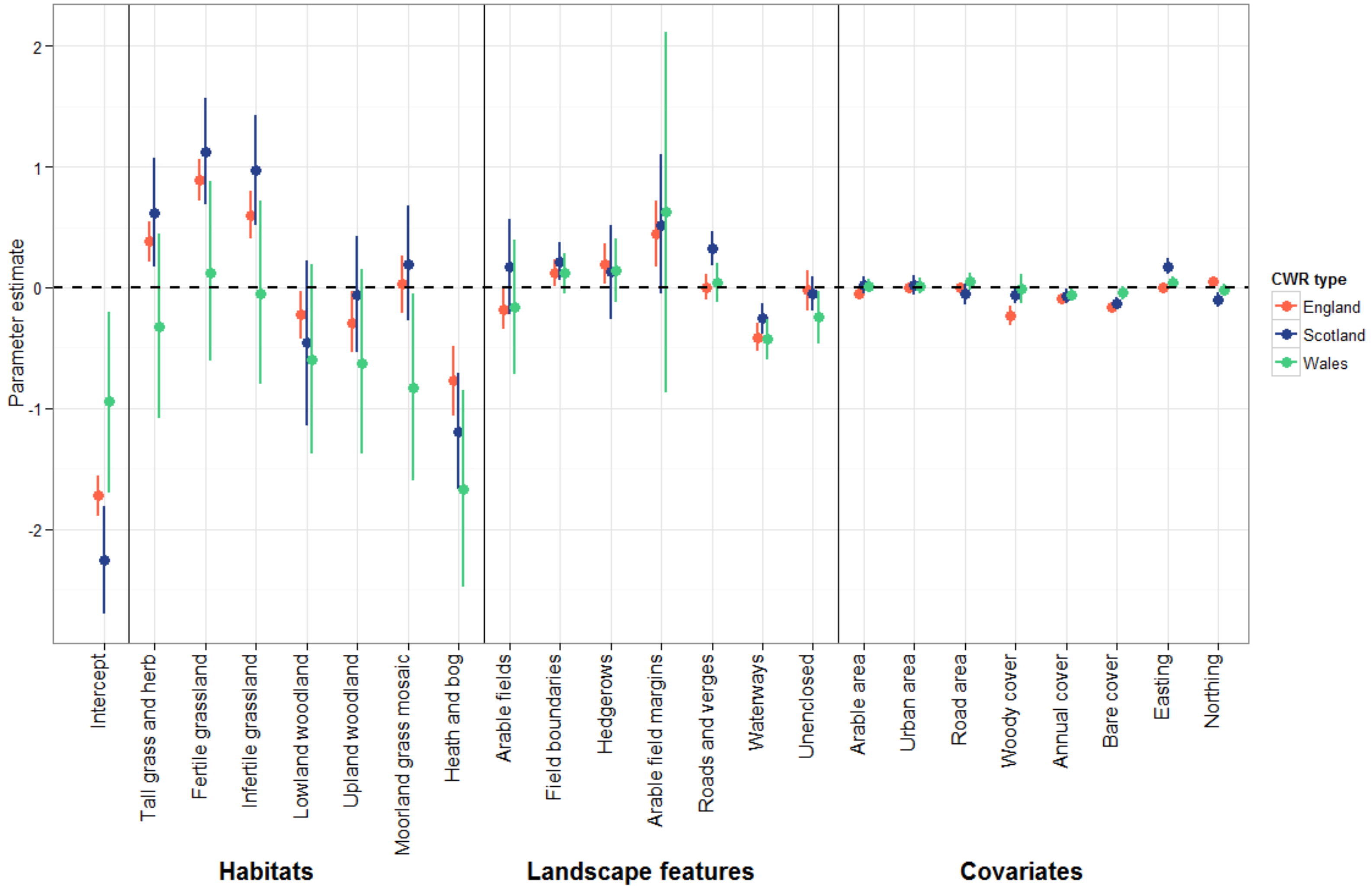


Figure A1. Parameter estimates for modelled effects of variables on proportion of priority crop wild relatives (CWR) in England, Scotland and Wales using the corresponding regional priority CWR inventory. Lines indicate 95% credible intervals.