Ground flora of field boundary dry stone walls in the Burren, Ireland

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Abstract
Despite the fact that field boundary (dry) stone walls are globally common in rural landscapes, very little research has been carried out regarding them. Dry stone walls may act as refuges for a range of plants and animals, especially in areas where conditions do not favour a high biodiversity or areas of high exposure. They may also provide connectivity via habitat corridors and may even serve as a habitat in their own right. This paper reports on a case study survey of the forb assemblages of field boundary dry stone walls in terms of species richness, biodiversity, and composition in comparison to the surrounding landscape, and aims to provide some insight into the floral ecology characteristics of dry stone walls. To accomplish this, the forbs growing in and immediately adjacent to 18 segments of dry stone wall in the Burren region of western Ireland, were surveyed. The forb assemblages growing within the walls were compared with those growing in the 0.5 m closest to the walls and those growing the areas 0.5-1.0 m on either side of the walls. The wall assemblages were shown to have lower species richness and each category of assemblage was shown to have significantly different species composition. This research indicates that the dry stone walls of the Burren may be associated with a distinct floral ecology, and therefore may act as habitat corridors in an otherwise exposed landscape.

Key words: field boundaries; floral ecology; corridors; agricultural ecology; forb; limestone pavement.

Introduction
Despite their prevalence in many landscapes globally, the ecological aspects of field boundary dry stone walls are a largely unexplored area (Collier, 2013; Collier & Feehan, 2003). There are some studies with data for a specific animal or plant species on or near a field boundary stone wall; however, no studies exist where dry stone walls are the primary research subject, though some new and promising studies are beginning the process (Manenti, 2014). Awareness of the presence of biota on walls of all types is nothing new; there is a long history of botanical and zoological surveys of the species found on walls (Darlington, 1981; Francis, 2010; Francis & Lorimer, 2011; Segal, 1972) but the main focus has been on mortared walls and walls in urban areas. With respect to flora, some surveys of field boundary stone walls exist (e.g. Brandes, 2002; Brandes & Brandes, 1999; Haslam, 2001; Holland, 1972; Kent, 1961; Nedelcheva & Vasileva, 2009; Payne, 1978; Risbeth,
1948), though these focus almost exclusively on flora on walls and not adjacent to them. In short, the scientific community has paid little attention to how walls relate to their surroundings from an ecological standpoint (Collier, 2013; Francis, 2010). This paper reports on research into forb assemblages adjacent to dry stone walls in western Ireland.

**Stone wall ecology**

A limited number of systematic studies into field boundary dry stone walls exist. However, of these, the stone wall element was not the subject of the main area of the reported research (Collier, 2013). Some authors refer to their potential for micro-habitats (Moreira & Russo, 2007), while others discuss their potential classification as ‘small biotopes’ (Agger & Brandt, 1988) or ‘ecotopes’ (Naveh, 1984). However, without evidence from systematic studies there is no evidence that dry stone walls act as refuges or corridors in the same manner that, for instance, hedgerows (fencerows) do. Some floristic surveys and observations have described differing types of vegetation that appear with regularity on dry stone walls. Lichens and algae, while not true plants, are often included in those botanical wall studies that exist. This is perhaps because they appear to colonize all types of walls, since they are often the first pioneers of a stone or anthropogenic structure. Bryophytes are also common on both dry and mortared walls, and some moss species appear to have little difficulty growing on bare stones and often act as second-stage colonizers. With a paucity of data, these assumptions have not been systematically validated for field boundary stone walls, though research in cliffs and other bare rock indicates that this may be similar to the succession processes on dry stone walls (Larson et al., 2005). Though there were many writers and commentators in the past, Segal (1969) introduced the idea that walls may have a unique ecology worthy of study, and his concepts were later expanded upon by Darlington (1981). While these works form the foundation of our understanding of wall ecology in general, including crucial concepts, such as the division of walls into height-based zones and the process of succession in mural communities, they also remain two of the few major publications on the subject, especially with regards to flora. There is a small collection of localised studies into stone wall flora (Cherrill & McClean, 1997; Duchoslav, 2002; Francis, 2010; Haslam, 2001; Jim, 1998; Jim & Chen, 2010; Johnson & Ouimet, 2016; Manenti, 2014; Müller, 2013; Nedelcheva, 2011; Thorson, 2005; Tokuoka & Hashigoe, 2015) with most focussing on old masonry urban walls (Jim, 2013; Jim & Chen 2010; Li et al., 2016; Lo & Jim 2015). Contrast this with the volume of research into other field boundaries such as hedgerows and field margins, which mirror stone walls in extent and function, but not in form. The importance of hedgerows as refuges and corridors in the landscape is well established (e.g. Barr & Petit, 2001; Baudry et al., 2000; Burel & Baudry, 1990; Corbit et al., 1999; Dover, 2019; Marshall & Moonen, 2002; Petit et al., 2003; Roy & de Blois, 2008; Wehling & Diekmann, 2009). The manifest lack of systematic research into field boundary stone wall ecology is unfortunate, not only from a scholarly standpoint, but also due to the possibility that dry stone walls may be of ecological significance, especially considering their age and longevity in many landscapes.

Not all dry stone walls are necessarily vegetated. It may take a very long time for lichens to colonize a wall and even longer for true plants. Segal (1972) estimates that vascular plants will generally begin growing on mortared walls after about 50-
100 years, while Gilbert (1992) gives an estimate of 40-80 years. The presence of plants, especially vascular plants, on a wall requires some degree of loose substrate in which flora can anchor themselves and withdraw nutrients from. In mortared walls, this is generally achieved through the natural breakdown of mortar or the accumulation of dirt and sediments in crevices. Dry stone walls are different; by definition they are ‘dry’ or ‘un-mortared’. This lack of mortar not only means that there no available substrate, but also that wind and rain can permeate the gaps between stones and remove accumulated sediment (McAfee, 1997). While this may provide opportunities for invertebrates and other fauna (Manenti, 2014) it can mean that forbs, which are perhaps more widely associated with stone walls along with other spontaneously occurring vegetation, such as grasses, shrubs and even trees, are mostly located at the base and adjacent to the wall. To date, anecdotal observations of dry stone walls appear to indicate that they may support a variety of lichens, plants, invertebrates, birds, and mammals. Some contend that stone walls act as corridors and refugia for plants and animals just as hedgerows do (Gilbert, 1992; MacWeeney & Conniff, 1986; Millsopp, 2001; Simkins, 2004; Stewartry of Kirkcudbright Drystane Dyking Committee, 1976; Thomson, 1988; Thorson, 2005; Woodell & Rossiter, 1959) and while observation and commentary are useful as starting points, such assumptions have yet to be corroborated by systematic studies.

**Materials and Methods**

**Case study area: the Burren**

The Burren region of County Clare is dominated by Karst limestone pavement (Cabot & Goodwillie, 2018; D'Arcy, 2006; O'Rourke, 2005) (Fig. 1). It is an exposed landscape where there is not enough soil for any type of field boundary except stone walls, which pervade throughout and consist of large stones extracted from the pavement (Fig. 2). The limestone pavement has shaped the region’s agricultural environment for centuries, exemplified by the use of winter grazing on high land and summer lowland grazing (the opposite of most such systems). This grazing regime has given rise to a unique floral assemblage in the Burren (Cabot & Goodwillie, 2018) so as a socio-ecological system it is very high in biodiversity. Stone walls are still used as active barriers to livestock, and therefore they are very prevalent.

For the purposes of this study, forbs – herbaceous plants that are not grasses, sedges, or rushes – were focused on exclusively, as forbs have been known to be notable members of both wall and field habitats (Holland, 1972; Payne, 1978; Risbeth, 1948). Forbs are the only floral type that dry stone wall communities might typically share with meadows and pastures and are therefore the most valid assemblages with which to compare. The purpose of this research was to document one aspect of dry stone wall ecology that might be a significant element of their modern values in the larger agricultural landscape. If, like mortared walls, dry stone walls act as a platform for unique assemblages of plant species, and if, like hedgerows, those assemblages growing upon and beside them are distinct from those of adjoining pastureland, then these patterns should be apparent in an examination of the floral communities.
In order to establish the nature of the forb assemblages growing in and around the walls, it was first necessary to closely examine the flora at dry stone wall sites throughout the Burren. To this end, 20 segments of wall 10 m in length were
selected to be surveyed over a period of three weeks in June of 2018, though ultimately two of these sites had to be rejected due to adverse weather conditions. The 18 sites used in this study may be seen in Fig. 3.

Figure 3. Geographical map of the Burren (top, © Ordnance Survey Ireland, 2017), and location of survey sites (bottom)
Wall selection
Following Holland's (1972) wall selection criteria, the walls surveyed were between 0.8 and 1.2 m in height and were not mortared or with interior substrate. Although transects and regular series of quadrats are common in botanical studies, they can create a strong locational bias when used in agricultural areas (Kent, 2011). To avoid this, each of the survey sites used segments of different walls, or, if on the same wall, segments which were at least 50 m away from each other. No more than two quadrats were thrown on the same wall. In order to avoid any overlap of wall-affected areas, intersections with other walls on the same side as the survey segment were avoided by at least 5 m. It was presumed that age is a key factor in ensuring that stone walls were established long enough to have been colonized by plants or impacted surrounding plant communities. Aside from the generalized speculations of Segal (1969) and Darlington (1981), there is almost no research on successional (seral) progression in dry stone walls, though studies of mortared walls indicate that colonization and successional stages are extremely lengthy processes (Francis, 2010; Gilbert, 1992). Without knowing the minimum age a wall must be in order to be useful to this study, it was necessary to follow Holland's (1972) “quasi-experimental” method of interviewing local farmers and landowners to identify the oldest walls and to limit the independent variables. Unfortunately, some landowners did not know the age of the walls in question, while others had recently rebuilt walls upon an older foundation. However, information supplied by landowners was supplemented with the 1842 Ordnance Survey map of County Clare in which 12 of the 18 study sites were recorded as field boundaries (Table 1). All walls were constructed using the Burren style and all were limestone (Fig. 2).

| Site | Age                     | Extant in 1842 |
|------|-------------------------|---------------|
| 1    | Unknown                 | Y             |
| 2    | >20 yrs                 | N             |
| 3    | ~120 yrs                | Y             |
| 4    | ~120 yrs                | Y             |
| 5    | >20 yrs                 | N             |
| 6    | 2-3 yrs                 | Y             |
| 7    | 2-3 yrs                 | N             |
| 8    | Unknown                 | N             |
| 9    | 5-10 yrs                | Y             |
| 10   | 5-10 yrs                | Y             |
| 11   | 5-10 yrs                | N             |
| 12   | 5-10 yrs                | N             |
| 13   | 5-10 yrs                | Y             |
| 14   | Upper structure, 5-10 yrs; foundation >50 yrs | Y |
| 15   | Upper structure, 5-10 yrs; foundation >50 yrs | Y |
| 16   | Unknown                 | Y             |
| 17   | Unknown                 | Y             |
| 18   | Unknown                 | Y             |
Data recording

At each location, a 10 m long segment of wall was randomly selected as well as an area extending to 1 m perpendicular to the wall, forming an overall quadrat measuring 10x1 m². This was separated into three sections: the 0.5 m furthest from the wall (A section), the 0.5 m closest to the wall (B section), and the wall itself (W section) (see Figs. 4 and 5). These divisions, as well as the overall size of the quadrat, were adapted from the methodology of studies of hedgerows (Corbit et al., 1999; Wehling & Diekmann, 2009). Once the sites were chosen, the forbs growing in each of the A, B, and W sections were identified by species and counted. If an individual fell on the line between the A and B sections, it was counted as part of the A section. Those species that could not be identified on-site were given a numerical designation, photographed, and described in the survey notes for later off-site identification. A full list of species and their counts recorded at each site may be found in Supplementary Table 1 (downloadable separately). In addition, weather, location, and geographic coordinates were recorded as well as wall height, aspect (e.g., North to South, facing West), gradient and direction of any slope, coverage by moss, shade, and vines in 25% increments, as well as best estimate of age. These data can be viewed and downloaded separately as Supplementary Tables 2 and 3 (site data). Information regarding the overall location was also documented.

Figure 4. The A, B, and W sections into which each site was divided, demonstrated in the first meter of site 6.
Figure 5. Floral composition shows a difference from the surrounding habitat more than 1 m from the wall, as demonstrated by the high numbers of *Rumex crispus* at site 2 both within and without the quadrat. The 1 m distance from the wall is marked in red, and lack of *R. crispus* in the main area of the pasture can be seen in the background.

**Results**

The A, B, and W sections were compared to establish species richness, Shannon diversity index, and Simpson’s diversity index using a series of ANOVAs with Tukey post-hoc tests (for the derivation of these indices see DeJong, 1975). The species found at each site were also examined with regard to type. Species unique to a particular section were identified (for instance, species only appearing in the A section of any given site), and the relative abundances of common species were compared using a chi-squared analysis. The sections were also compared using Jaccard’s coefficient of similarity. 103 species were recorded across the 18 sites, with 19,823 individual forbs counted altogether (Appendix 1, end of paper). Generally, more plants were found in the A and B sections than the W sections, with the A sections typically having the most (Fig. 6). Similarly, the W sections were shown to have significantly fewer species on average than either the A (p<0.001) or B (p<0.001) sections (Fig. 7). However, there is no significant difference in species richness between the A and B sections (p=0.866) (overall: p<0.001, F=33.690).

When Shannon’s index of diversity was calculated for each section at each site (Table 2), the overall biodiversity of the W sections was found to be significantly lower than the A (p<0.001) or B (p<0.001) sections. The Shannon indices of the A and B sections were not seen to be significantly different (p=0.998) (overall: p<0.001, F=17.39). However, when the Simpson’s indices of diversity were similarly
calculated and compared (Table 2), no significant difference was found to exist between any of the sections (p=0.300, F=1.233).

Figure 6. Number of individual forbs recorded within each section of each site

Figure 7. Species richness found within each section of each site

When comparing the patterns of distribution seen within the respective sections, 8 species were found only within A sections, 11 species were only found within B sections, and 2 species were only found within W sections (Table 3). The
species common to the A and B sections did appear in significantly different abundances ($p<0.001$, $\chi^2=3969.285$, $df=79$), as did those common to the A and W sections ($p<0.001$, $\chi^2=10037.420$, $df=46$) and to the B and W sections ($p<0.001$, $\chi^2=7782.937$, $df=47$). When compared using Jaccard’s coefficient of similarity, the A and B sections were found to be 81.0% similar, while the W sections were only around 50% similar to each of the others (Table 4). Although each species was matched with its typical habitat according to the general literature (Appendix 2, see end of paper), many of these species are associated with multiple habitats. This, coupled with the proximity of many study sites to different habitats or the fact that they exist within a mosaic area, meant that no conclusive patterns could be ascertained based on species’ habitat preferences.

**Table 2. Biodiversity of each section at each site, as represented by Shannon’s and Simpson’s indices of diversity**

| Site | Section: | A     | B     | W     | A     | B     | W     |
|------|----------|-------|-------|-------|-------|-------|-------|
| 1    |          | 2.136 | 2.128 | 0.929 | 0.832 | 0.841 | 0.557 |
| 2    |          | 1.343 | 1.784 | 1.413 | 0.616 | 0.781 | 0.699 |
| 3    |          | 1.432 | 1.517 | 1.120 | 0.668 | 0.673 | 0.470 |
| 4    |          | 2.156 | 1.556 | 1.337 | 0.830 | 0.654 | 0.683 |
| 5    |          | 1.522 | 1.949 | 2.114 | 0.698 | 0.805 | 0.871 |
| 6    |          | 2.133 | 2.337 | 1.208 | 0.797 | 0.859 | 0.645 |
| 7    |          | 2.609 | 2.387 | 1.073 | 0.906 | 0.179 | 0.640 |
| 8    |          | 2.283 | 2.332 | 2.250 | 0.850 | 0.841 | 0.926 |
| 9    |          | 2.662 | 2.297 | 1.273 | 0.883 | 0.875 | 0.778 |
| 10   |          | 2.400 | 2.378 | 2.037 | 0.865 | 0.841 | 0.843 |
| 11   |          | 2.668 | 2.595 | 1.079 | 0.918 | 0.902 | 0.762 |
| 12   |          | 2.908 | 2.907 | 1.609 | 0.930 | 0.930 | 1.000 |
| 13   |          | 2.609 | 2.070 | 1.003 | 0.917 | 0.804 | 0.583 |
| 14   |          | 2.414 | 2.502 | 2.112 | 0.880 | 0.890 | 0.827 |
| 15   |          | 2.206 | 2.636 | 2.068 | 0.776 | 0.912 | 0.881 |
| 16   |          | 2.183 | 2.523 | 1.889 | 0.820 | 0.891 | 0.843 |
| 17   |          | 2.303 | 2.045 | 1.359 | 0.858 | 0.822 | 0.756 |
| 18   |          | 2.150 | 2.313 | 1.581 | 0.835 | 0.868 | 0.833 |
Table 3. Species found only within the A, B, or W sections of any given site and the number of recorded individuals of each of these species.

| Species                  | Section | Count |
|--------------------------|---------|-------|
| Calystegia sepium        | B       | 2     |
| Crepis capillaris        | B       | 1     |
| Galium palustre          | B       | 6     |
| Lapsana communis         | B       | 2     |
| Medicago lupulina        | A       | 3     |
| Neottia cordata          | B       | 2     |
| Ophrys insectifera       | B       | 1     |
| Plantago major           | A       | 1     |
| Polypodium cambricum     | W       | 2     |
| Polypodium vulgare       | W       | 2     |
| Potentilla erecta        | B       | 2     |
| Rhinanthus minor         | A       | 17    |
| Scorzoneroideae autumnalis | A  | 2    |
| Sonchus asper            | A       | 2     |
| Sonchus oleraceus        | B       | 3     |
| Veronica serpyllifolia   | B       | 2     |
| Unidentified 1           | A       | 8     |
| Unidentified 2           | A       | 2     |
| Unidentified 4           | B       | 2     |
| Unidentified 5           | B       | 1     |
| Unidentified 6           | A       | 2     |

Table 4. Degree of similarity between each section class, as represented by Jaccard’s coefficient of similarity.

| Sections compared | Jaccard’s coefficient of similarity |
|-------------------|------------------------------------|
| A and B           | 81.0%                              |
| A and W           | 50.0%                              |
| B and W           | 53.3%                              |

Discussion
The differences in species richness, abundances, and Jaccard coefficient between the W sections from both the A and B sections implies that wall assemblages may generally be different from their surrounding habitats. Based on the data, it appears that fewer forb species are likely to occur on a dry stone wall than in a meadow or pasture, and the species that do grow on walls tend to be present in different relative abundances. Although it was ultimately not possible to determine any trends associated with the known habitat preferences of the wall assemblages, a few patterns can nevertheless be discerned regarding the types of species found in W sections. The stone wall habitat appears to ‘favour’ ferns such as Asplenium ruta-
muraria, Asplenium ceterach, and Polypodium cambricum, as well as the crane’s-bills Geranium robertianum and G. rotundifolium, as these were the most common groups to appear across all sites. This finding supports both Segal (1969) and Darlington’s (1981) assertions that ferns and fern allies are generally the most frequent vascular plants to appear on walls, as well as D’Arcy’s (2006) observation that G. robertianum can commonly be found in and around the Burren’s field boundary walls. While at first glance, it appears that Bellis perennis is a similarly common wall species, it should be noted that almost all instances of this species were recorded at sites 3 and 4. Therefore, for the purposes of this study, it should not be considered a common wall species.

Despite such patterns distinguishing the W sections from the A and B sections, it is not clear whether the same holds true with regard to biodiversity. The incongruity between the Shannon’s and Simpson’s indices of diversity makes it unclear whether the W sections are truly less diverse than the A and B sections. While this inconsistency may be reflective of the nature of floral diversity in the wall habitat (as Simpson’s index of diversity is weighted in favour of dominant species), there is a strong likelihood that it is the product of a statistical anomaly. In either case, more surveys will be needed before any definitive statements can be made concerning the biodiversity of wall assemblages, and how it compares to the diversity of the surrounding habitat.

While the W sections exhibit several differences from the other two sections, the B sections are very similar to the A sections. The B sections are comparable with the A sections in terms of species richness and biodiversity (according to both Shannon’s and Simpson’s index of diversity), as well as sharing a relatively high Jaccard coefficient of similarity. However, there is an important way in which these two sections are distinct: the relative abundances of their species. The A and B sections have notably higher numbers of species unique to them compared to the W sections, and the species held in common by both sections occur in different relative abundances. This suggests that forb assemblages do, in fact, change with proximity to stone walls. It also implies that if any difference does exist between wall-adjacent areas and their surrounding habitats, it has more to do with species distribution than any other factor.

As with the W sections, the inability to typify the species observed based on their preferred habitats does not mean that they cannot be characterized altogether. The B sections featured comparatively high counts of Galium aparine, Circaea lutetiana, Glechoma hederacea, Rumex acetosella, Geranium robertianum, and Geranium rotundifolium, all of which rely, at least in part, on animals for seed dispersal (Cox, 2003; Harris, 2019). This is in line with Darlington’s (1981) contention that small animals sheltering in walls distribute the seeds of zoophilous plants around wall bases. However, this is not necessarily a definitive trend, as some zoophilous plants are more populous in the A sections, such as Geum urbanum (Darlington, 1981), and many of the plants frequently occurring in the B sections are propagated by wind dispersal, including Epilobium montanum and Urtica dioica (CABI, 2019; Myerscough & Whitehead, 1966). Dry stone walls in this study appear to impact proximate floral communities in some way, and they do seem to frequently host ferns and crane’s-bills often associated with pavement communities (Parnell & Curtis, 2012; Sterry, 2008; Webb & Scannell, 1983), indicating that the forb assemblages differ from the assemblages in the wider landscape. In addition, the
tendency for wall-adjacent areas to contain relatively high numbers of zoophilous plants indicates their potential as refuges and/or corridors.

Although every effort was made to ensure the consistency in this study, there are nevertheless several important potential sources of error. Only a small number of sites could be surveyed, meaning that the chosen study sites were not homogeneous in terms of elements such as land use and wall age. Moreover, many sites were located near habitats other than the desired grasslands or within mixed habitats. This ultimately became one of the factors precluding any determination of whether the species recorded were typical of meadows and pastures or potential woodland and pavement refugees. Because the field work was carried out in June, only species which are visible during that time would have been recorded; any plants lying dormant in the seed bank would have been entirely overlooked. Additionally, since floral identification often relies on the characteristics of the flower, June-blooming plants may have been more accurately classified. It should also be noted that about half of the surveys took place during a period of unusually warm, dry weather. Plants which would otherwise have been present are likely to have been killed or forced into dormancy by the heat or lack of moisture, especially considering that the sites surveyed later were noticeably dry.

The experimental design for this project was taken from studies of other field boundaries: hedgerows, particularly Corbit, et al. (1999) and Wehling & Diekman (2009). However, as the surveys were being conducted, it was impossible not to notice that one feature of this design may not be sufficient: namely, the quadrat size. The aforementioned hedgerow studies prescribed a quadrat extending 1 m from the wall divided into 0.5 m-wide A and B sections (in addition to the wall itself). Yet at many of the study sites, the entire meter next to the wall appeared to have a markedly different floral composition from the rest of the meadow or pasture, as can be seen in Image 4. If it is true that the area of effect of a dry stone wall extends for an entire meter on either side, this may explain the high degree of similarity between the various A and B sections. However, the fact that they do show some differences suggests that there may be some degree of zonation to a wall’s area of effect, with floral communities becoming more distinct as distance to the wall decreases. If this study’s quadrats were indeed insufficiently large, it does not necessarily mean that the results obtained are invalid. The W section assemblages are still clearly unlike their surroundings, and the species composition of the B sections are still different from areas further from the walls.

Conclusions

There are few specifically designed and systematic investigations into the ecological make-up, functions or biodiversity values of field boundary (dry) stone walls. A modest number of studies have looked at the flora of urban, abandoned buildings or old mortared walls, but none have looked specifically and systematically at the floral characteristics adjacent to field boundary stone walls. This is not because it is difficult or of no value; rather it is an odd oversight on the part of the landscape ecology community.

This study begins to characterize a section of the overall floral ecology of dry stone walls, though it cannot definitively show how they function within the larger ecosystem. The research presented here indicates that field boundary dry stone walls have distinct forb assemblages that differ from the assemblages in the wider
landscape, and as such may act as refuges. Though this study represents one aspect of the ecology of dry stone walls, and how they may function within the agricultural environment, their overall contribution to biodiversity conservation within the landscape ought now to be fully investigated. This research asks more questions than it answers, and this ought to stimulate greater interest and effort in gathering data on these landscape features. Considering their pervasiveness in many landscapes, and in most cases for a considerable period of human and ecological time, it is possible that stone walls could potentially act as refugia for species affected by land use change and climate change, control soil moisture content, and/or augment habitat diversity in agricultural landscapes, especially in exposed locations, through their geological characteristics, their durability and scale, their morphology and style, and/or combinations of all.

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Appendix 1. Total number of each species recorded within each section across the study sites.

| Species                     | A   | B   | W  | Total |
|-----------------------------|-----|-----|----|-------|
| Achillea millefolium        | 428 | 390 | 3  | 821   |
| Agrimonia eupatoria         | 7   | 2   |    | 9     |
| Arum maculatum              | 3   | 2   |    | 5     |
| Asplenium ceterach          | 2   | 37  |    | 39    |
| Asplenium ruta-muraria       | 3   | 3   | 19 | 25    |
| Asplenium scolopendrium     | 7   | 12  | 26 | 45    |
| Asplenium trichomanes       | 2   | 3   | 4  | 9     |
| Athyrium filix-femina       | 4   | 3   |    | 7     |
| Bellis perennis             | 39  | 62  | 380| 481   |
| Calystegia sepium           | 2   | 2   |    | 4     |
| Cardamine hirsuta           | 381 | 480 | 3  | 864   |
| Carlina vulgaris            | 5   | 2   |    | 7     |
| Centaurea nigra             | 147 | 68  |    | 215   |
| Cerastium arvense           | 57  | 113 | 2  | 172   |
| Cerastium fontanum          | 217 | 32  | 2  | 251   |
| Circaea lutetiana           | 70  | 192 | 37 | 299   |
| Cirsium arvense             | 5   | 2   | 3  | 10    |
| Cirsium dissectum           | 9   | 10  | 4  | 23    |
| Cirsium vulgare             | 5   | 4   |    | 9     |
| Conopodium majus            | 15  | 2   |    | 17    |
| Crepis capillaris           | 1   |     |    | 1     |
| Cynoglossum officinale      | 7   | 8   |    | 15    |
| Dactylorhiza fuschii        | 28  | 10  |    | 38    |
| Daucus carota               | 14  | 12  |    | 26    |
| Dryopteris filix-mas        | 2   | 6   | 1  | 9     |
| Epilobium montanum          | 203 | 133 | 2  | 338   |
| Epipactis helleborine       | 1   | 1   |    | 2     |
| Euphrasia arctica           | 186 | 19  |    | 205   |
| Filipendula ulmaria         | 294 | 293 | 46 | 633   |
| Filipendula vulgaris        | 13  | 2   |    | 15    |
| Fragaria vesca              | 67  | 52  | 3  | 122   |
| Galium aparine              | 80  | 152 | 26 | 258   |
| Galium palustre             | 6   |     |    | 6     |
| Galium verum                | 696 | 390 |    | 1086  |
| Geranium robertianum        | 261 | 588 | 146| 995   |
| Geranium rostratumifolium   | 4   | 41  | 32 | 77    |
| Geranium sanguineum         | 294 | 165 | 1  | 460   |
| Geum urbanum                | 41  | 16  |    | 57    |
| Glechoma hederacea          | 86  | 122 | 17 | 225   |
| Gymnadenia conopsea         | 10  | 9   |    | 19    |
| Heracleum sphondylium       | 66  | 36  | 1  | 103   |
| Plant Name                        | A | B | C | Total |
|----------------------------------|---|---|---|-------|
| Hypericum pulchrum               | 74| 60| 1 | 135   |
| Hypochaeris radicata             | 129| 53|   | 182   |
| Lapsana communis                 |   | 2 |   | 2     |
| Lathyrus pratensis               | 123| 51| 3 | 177   |
| Leucanthemum vulgare             | 7 | 2 |   | 9     |
| Linum catharticum               | 20 | 29 | | 49    |
| Lotus corniculatus               | 417| 212| 1 | 630   |
| Medicago lupulina                | 3 |   |   | 3     |
| Melampyrum pratense              | 12| 12 | | 24    |
| Mycelis muralis                  | 7 | 17| 3 | 27    |
| Neottia cordata                  | 2 |   |   | 2     |
| Odontites vernus                 | 53| 16| 1 | 70    |
| Ophrys insectifera               | 1 |   |   | 1     |
| Oxalis acetosa                   | 91| 68| 3 | 162   |
| Pilosella officinarum            | 46| 39 | | 85    |
| Plantago lanceolata              | 203| 24 | | 227   |
| Plantago major                   | 1 |   |   | 1     |
| Polygala vulgaris                | 18| 49 | | 67    |
| Polypodium cambricum             |   | 2 |   | 2     |
| Polypodium vulgare               |   | 2 |   | 2     |
| Potentilla anglica               | 230| 116| 2 | 348   |
| Potentilla anserina              | 188| 101 | | 289   |
| Potentilla erecta                | 2 |   |   | 2     |
| Primula vulgaris                 | 73| 20 | | 93    |
| Pteridium aquilinum              | 156| 189| 28| 373   |
| Ranunculus acris                 | 102| 20 | 1 | 123   |
| Ranunculus repens                | 352| 190| 10| 552   |
| Reynoutria japonica              | 2 | 1 |   | 3     |
| Rhinanthus minor                 | 17|   |   | 17    |
| Rumex acetosa                    | 145| 136 | | 281   |
| Rumex acetosella                 | 49| 133| 1 | 183   |
| Rumex crispus                    | 53| 20 | 1 | 74    |
| Sanicula europaea                | 10| 4 | 1 | 15    |
| Saxifraga hypnoides              | 14| 2 |   | 16    |
| Scorzonoides autumnalis          | 2 |   |   | 2     |
| Senecio jacobaea                 | 19| 14| 3 | 36    |
| Sonchus asper                    | 2 |   |   | 2     |
| Sonchus oleracea                 |   | 3 |   | 3     |
| Stachys sylvatica                | 26| 4 |   | 30    |
| Succisa pratensis                | 483| 370 | | 853   |
| Taraxacum spp.                   | 96| 63| 60| 219   |
| Teucrium scorodonia              | 218| 194| 4 | 416   |
| Thymus drucei                    | 344| 533| 24| 901   |
| Torilis japonica                 | 1 | 11| 1 | 13    |
| Tragopogon pratensis             | 1 | 8 |   | 9     |
| Trifolium pratense               | 101| 43 | | 144   |
| Species                        | Count 1 | Count 2 | Count 3 | Total |
|-------------------------------|---------|---------|---------|-------|
| Trifolium repens              | 1583    | 668     | 1       | 2252  |
| Urtica dioica                 | 55      | 172     | 76      | 303   |
| Valeriana officinalis         | 15      | 7       |         | 22    |
| Veronica arvensis             | 40      | 40      |         | 80    |
| Veronica chamaedrys           | 430     | 385     | 7       | 822   |
| Veronica montana              | 237     | 125     | 1       | 363   |
| Veronica persica              | 6       | 17      | 2       | 25    |
| Veronica serpyllifolia        | 2       |         |         | 2     |
| Vicia sepium                  | 293     | 268     | 23      | 584   |
| Viola riviniana               | 224     | 172     |         | 396   |
| Unidentified 1                | 8       |         |         | 8     |
| Unidentified 2                | 2       |         |         | 2     |
| Unidentified 3                | 34      | 70      | 1       | 105   |
| Unidentified 4                | 2       |         |         | 2     |
| Unidentified 5                | 1       |         |         | 1     |
| Unidentified 6                | 2       |         |         | 2     |
| **Total**                     | 10571   | 8192    | 1060    | 19823 |
Appendix 2. Typical habitat associated with each species. Note that while typical habitat descriptions are taken from Streeter, et al. (2009) to ensure clarity and specificity, a variety of sources were used to corroborate this information (Webb & Scannell, 1983; Parnell & Curtis, 2012; Blamey, et al., 2013; CABI, 2018).

| Species                        | Typical habitat (from Streeter, et al., 2009)                                                                 | Native? |
|-------------------------------|---------------------------------------------------------------------------------------------------------------|---------|
| Achillea millefolium           | All grassland habitats from sea level to 1210 m, lawns, dunes, shingle, waste ground                           | Y       |
| Agrimonia eupatoria            | Rough, grassland, field borders, scrub, hedge banks, roadsides, woodland clearings; lowland to 365 m.        | Y       |
| Arum maculatum                 | Hedgerows, woodlands, coppice, on moist, fertile soils; lowland to 425 m.                                    | Y       |
| Asplenium ceterach             | Basic rocks, limestone pavement, mortared walls.                                                             | Y       |
| Asplenium ruta-muraria          | Crevices in calcareous rocks, scree, limestone pavement; old mortared walls in lowlands.                      | Y       |
| Asplenium scolopendrium        | Damp, shaded habitats: hedge banks, woods, shaded stream sides on base-rich soils, grikies in limestone pavement. | Y       |
| Asplenium trichomanes          | Rocks, cliffs, scree, walls, mine wastes usually on calcareous substrates.                                    | Y       |
| Athyrium filix-femina          | Damp woods, stream sides, ditches, damp rocky habitats, on well-drained acid soils                           | Y       |
| Bellis perennis                | Familiar plant of lawns, pastures, roadside verges; also characteristic of grazed, mown, trampled grasslands, dune slacks, stream sides, upland flushes. To 915 m. | Y       |
| Calystegia sepium              | Hedgerows, scrub, wood margins, fen carr, riverbanks, waste ground, gardens.                                 | Y       |
| Cardamine hirsuta              | Garden weed; rocks and scree, especially on limestone. To 1190 m.                                           | Y       |
| Carlina vulgaris               | Dry calcareous grassland, coastal cliffs, dunes; to 455m.                                                   | Y       |
| Centaurea nigra                | Rough grassland, meadows, pastures, roadsides, sea cliffs, waste ground; to 580 m.                           | Y       |
| Cirsium arvense                | Well-drained permanent grassland, hedge banks, road verges, sand-dunes, on calcareous to slightly acid sandy soils; lowland to 300 m. | Y       |
| Cerastium fontanum             | Meadows, pastures, montane grassland, cultivated soils, road verges, sand-dunes, shingle; to 1220 m.        | Y       |
| Circaea lutetiana              | Woodlands, hedgerows, stream banks; also a garden weed                                                       | Y       |
| Cirsium arvense                | Pastures, meadows, rough grassland, roadsides, waste ground, on fertile soils; to 845 m.                    | Y       |
| Cirsium dissectum              | Fen meadows, wet pastures, flushes, wet heaths, on wet, mildly acid or calcareous peat; to 500 m.             | Y       |
| Cirsium vulgare                | Common weed of pastures, rough grassland, roadsides, waste ground, on fertile, base-rich soils               | Y       |
**Conopodium majus**

Open woodlands, rough grassland, grass heaths, upland hay meadows, hedge banks, on mildly acid soils, to 700 m.

**Crepis capillaris**

Grassland, roadsides, heaths, waste ground, old walls; to 445 m.

**Cynoglossum officinale**

Wood margins, rough open grassland, on dry, well-drained soils, coastal dunes, shingle; to 400 m.

**Dactylorhiza fuskii**

Neutral and calcareous grasslands, roadsides, open woodlands, marshes, fens, dune slacks, quarries, embankments; to 530 m.

**Daucus carota**

Broken turf, rough grassland, roadsides, waste ground, on dry calcareous soils.

**Dryopteris filix-mas**

Woods, hedge banks, ditches, stream banks, rocky hillsides, scree; also walls and gardens.

**Epilobium montanum**

Woodland, waste ground, walls, hedge banks, ditches; also a garden weed. To 845 m.

**Epipactis helleborine**

Woods, hedge banks, roadsides, dune slacks, limestone pavement, on mildly acid to calcareous soils.

**Euphrasia arctica**

Damp hay meadows, pastures, roadsides.

**Falloppia japonica**

Roadsides, railways, riverbanks, waste ground.

**Filipendula ulmaria**

Marshes, fens, wet woods, ditches; river, stream and lake margins; wet alpine meadows, rock ledges. To 880 m.

**Filipendula vulgaris**

Dry calcareous grassland; to 365 m.

**Fragaria vesca**

Woodlands, scrub, hedge banks, rough grassland, on base-rich soils; to 640 m.

**Galium aparine**

Hedgerows, cultivated ground, scrub, banks of streams and rivers, scree, shingle beaches, waste ground, on fertile soils

**Galium palustre**

Marshes, fens, wet woodlands, edges of ponds, lakes, streams and ditches; to 825 m.

**Galium verum**

Dry calcareous grassland, hay meadows, hedge banks, dunes, machair, cliff tops, verges; to 780 m.

**Geranium robertianum**

Woodlands, hedge banks, scree, limestone pavement, old walls, coastal shingle, avoiding the most acid soils and preferring shaded habitats.

**Geranium rotundifolium**

Usually dry hedge banks, wall tops; occasionally an arable weed on both sandy and calcareous soils.

**Geranium sanguineum**

Limestone rocks, coastal cliffs, open woodland, scree, grassland; also fixed calcareous coastal sand-dunes. To c. 370 m.

**Geum urbanum**

Shaded areas, woodlands, scrub, hedgerows, roadsides, gardens, on base-rich soils; lowland to
| Species                          | Habitat Description                                                                                      | Altitude (m) |
|---------------------------------|---------------------------------------------------------------------------------------------------------|--------------|
| *Glechoma hederacea*            | Woodland rides, scrub, hedgerows, permanent grassland, waste ground, shaded gardens, on calcareous or heavy soils; to 465 m. | 450 m.      |
| *Gymnadenia conopsea*           | Dry calcareous grassland                                                                                |              |
| *Heracleum sphondylium*         | Hedgerows, roadside verges, woodland clearings, rough grassland.                                        | Y            |
| *Hypericum pulchrum*            | Grassy heaths, commons, woodland clearings, rides, on well-drained acid soils; to 82 m.                  | Y            |
| *Hypochaeris radicata*          | Pastures, meadows, lawns, grass heaths, roadsides, dunes, on mildly acid soils.                           | Y            |
| *Lapsana communis*              | Disturbed and shaded habitats, hedgerows, roadsides, walls, wood borders, gardens, waste ground.           | Y            |
| *Lathyrus pratensis*            | Dry grassland, coastal cliffs, dunes, waste ground, roadside verges, railway banks, on neutral or calcareous soils; to 845 m. | Y            |
| *Leucanthemum vulgare*          | Grassy heaths, commons, woodland clearings, rides, on well-drained acid soils; to 82 m.                  | Y            |
| *Linum catharticum*             | Grazed calcareous grassland, mires, flushes, limestone cliffs, calcareous dunes; to 840 m.                | Y            |
| *Lotus corniculatus*            | Calcareous grassland, meadows, hill pastures, grass heaths, cliffs, shingle, sand-dunes; to 915 m.        | Y            |
| *Medicago lupulina*             | Short calcareous grassland, well-drained soils, road verges, lawns; lowland to 440 m.                    | Y            |
| *Melampyrum pratense*           | Heathy woodlands, moorlands, on acid soils; scrub, hedgerows, woodlands, on calcareous soils.              | Y            |
| *Mycelis muralis*               | Shaded hedge banks, calcareous woods, rocks, walls, grikes in limestone pavement; to 500 m.               | Y            |
| *Neottia cordata*               | Damp, shaded acid habitats; to 1065 m.                                                                  | Y            |
| *Odonites vernus*               | Rough grassland, tracksides, arable fields, waste ground, sandy shores, salt marshes.                   | Y            |
| *Ophrys insectifera*            | Shady woodland, scrub, on dry calcareous soils; to 390 m. In Ireland, occurs in fens, calcareous flushes. | Y            |
| *Oxalis acetosella*             | Shaded woodlands, hedgerows, banks, rough upland grassland, grikes in limestone pavement; to 1160 m.     | Y            |
| *Pilosella officinarum*         | Short turf, grass heaths, dunes, banks, walls, cliffs, on dry sandy or calcareous soils; to 915 m.        | Y            |
| *Plantago lanceolata*           | Common on meadows, pastures, grass heaths, verges, maritime and dune grassland, cliffs; to 790 m.        | Y            |
| *Plantago major*                | Common plant of disturbed ground, paths, tracks, gateways, gardens, cultivated ground generally; tolerant of trampling. To 625 m. | Y            |
| *Polygala vulgaris*             | Short calcareous grassland, heaths, commons, sand-dunes; to 730 m.                                     | Y            |
| *Polypodium cambricum*          | Well-drained base-rich rocks, limestone cliffs, old mortared walls, quarries.                            | Y            |

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| **Polypodium vulgare** | Hedge banks, walls, rock outcrops, on well-drained acid soils; also occurs as an epiphyte in W Britain. | Y |
| **Potentilla anglica** | Field borders, woodland clearings, hedge banks, grass heaths, on well-drained acid soils | Y |
| **Potentilla anserina** | Roadside, farm tracks, gateways, waste ground, abandoned arable land, dunes, upper levels of salt marshes. | Y |
| **Potentilla erecta** | Grassland, heaths, moors, bogs, fens, open woodland, hedge banks, usually on mildly acid soils, to 1040 m. | Y |
| **Primula vulgaris** | Woodland clearings, coppice, hedge banks, old grassland, especially on heavy soils. | Y |
| **Prunella vulgaris** | Permanent grasslands, meadows, pastures, lawns, waste ground, on neutral or calcareous soils; to 845 m. | Y |
| **Pteridium aquilinum** | Moorland, hill pasture, heathlands, deciduous woodland, on well-drained acid (rarely basic) soils. Particularly dominant and aggressive on deep loams and abandoned agricultural land. | Y |
| **Ranunculus acris** | Damp pastures and meadows, road verges, upland rock ledges. | Y |
| **Ranunculus repens** | Damp grassland, marshes, fens, woodland clearings and rides, pond and lake margins, and as arable weed. | Y |
| **Rhinanthus minor** | Partial parasite of nutrient-poor calcareous grassland; to 1065 m. | Y |
| **Rumex acetosa** | Grassland, woodland rides, roadside verges, riverbanks, coastal shingle, mountain ledges; to 1215 m. | Y |
| **Rumex acetosella** | Acid grassland, heaths, commons, on well-drained sandy soils; to 1050 m. | Y |
| **Rumex crispus** | Cultivated soils, waste places, roadsides, hedge banks, water margins, to 845 m. | Y |
| **Sanicula europaea** | Deciduous woodland, hedge banks, on calcareous or base-rich soils; lowland to 500 m. | Y |
| **Saxifraga hypnoides** | Sides of mountain streams, cliffs, scree, rocky slopes; rarely on sand-dunes. To 1215 m. | Y |
| **Scorzoneroides autumnalis** | Meadows, pastures, grass heaths, roadsides, scree, salt marshes, dunes; to 975 m. | Y |
| **Senecio jacobaea** | Rough grassland, rabbit-grazed pasture, scrub, woodland rides, waste ground, roadsides, sand-dunes; to 670 m. | Y |
| **Sonchus asper** | Rough grassland, roadside verges, gardens, arable fields, coastal habitats, waste places. | Y |
| **Sonchus oleraceus** | Common weed of gardens, arable lands, roadsides, disturbed ground, on fertile soils | Y |
| **Stachys sylvatica** | Hedge banks, woodlands, shaded gardens; to 500 m. | Y |
| **Succisa pratensis** | Wet meadows, marshes, fens, wet heathland, woodland rides, on mildly acid soils; also chalk and limestone grassland. To 970 m. | Y |

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| Species                     | Habitat Description                                                                 | Range |
|----------------------------|-------------------------------------------------------------------------------------|-------|
| *Teucrium scorodonia*      | Woodlands, rough grassland, hedgerows, scrub, heaths, rocky hillsides, limestone pavement, sand-dunes, shingle; to 550 m. | Y     |
| *Thymus drucei*            | Close-grazed permanent grassland, maritime and mountain heaths, cliffs, limestone pavement, mature sand-dunes, on dry calcareous or acid soils. | Y     |
| *Torilis japonica*         | Hedgerows, road verges, woodland margins, rough grassland; to 410 m.                | Y     |
| *Tragopogon pratensis*     | Subsp. *pratensis* on dry grassland, roadsides, waste ground. Subsp. *minor* similar, but also rough grassland, sand-dunes; to 365 m. | Y     |
| *Trifolium pratense*       | Pastures, meadows, rough grassland, verges.                                        | Y     |
| *Trifolium repens*         | Meadows, pastures, calcareous grassland, lawns, tracks; to 800 m.                  | Y     |
| *Urtica dioica*            | Woodlands, fens, ditches, riverbanks, stream sides, areas associated with habitation on fertile or enriched soils; to 850 m. | Y     |
| *Valeriana officinalis*    | Marshes, fens, alpine meadows, wet woods; also rough grassland on dry calcareous soils | Y     |
| *Veronica arvensis*        | Dry, open areas, including arable fields, open grassland (ant-hills), sand-dunes, walls, banks, paths; to 820 m. | Y     |
| *Veronica chamaedrys*      | Familiar plant of hedge banks, verges, wood borders, rough grassland, upland scree, on well-drained or calcareous soils; to 750 m. | Y     |
| *Veronica montana*         | Well established in damp woodlands, coppice, hedge banks, on loamy, sandy soils; to 435 m. | Y     |
| *Veronica persica*         | Arable fields, gardens, waste ground, on fertile soils.                             | N     |
| *Veronica serpyllifolia*   | Short grassland, commons, woodland rides, rock ledges, weed of gardens, on damp acid soils. | Y     |
| *Vicia sepium*             | Hedge banks, woodland clearings, scrub, rough grassland; to 820 m.                | Y     |
| *Viola riviniana*          | Woodland, hedge banks, downland, grass heaths, old pasture, mountain grassland; to 1020 m. | Y     |