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1 **TITLE PAGE**

2 **Changes in the frequency of common plant species across linear features in Wales from 1990 to**
3 **2016; implications for potential delivery of ecosystem services**

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21

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27

1 **Changes in the frequency of common plant species across linear features in Wales from 1990 to**
2 **2016; implications for potential delivery of ecosystem services**

3

4 **Abstract**

5 In 2016, 21 1km squares recorded in Wales as part of the Countryside Survey of Great Britain were
6 revisited. One hundred and thirty seven quadrats alongside linear features that had all been
7 recorded in the same place in 1990, 1998 and 2007 were re-found and the plant species
8 compositions recorded. Changes in individual species frequency were analysed and the results
9 summarised by a number of ecosystem services and one disservice whose delivery are linked to
10 functionally important species being present.

11 Results indicated a continuation of a trend toward increased shading and woody cover seen
12 between the first Countryside Survey in 1978 and the last in 2007. Most species showed no
13 significant change in frequency suggesting that the significant directional trend seems only to have
14 impacted a subset of the species present. A greater sample size would be required to capture
15 impacts on a larger number of species including a wider range of Common Standards Monitoring
16 (CSM) positive indicator species that may find refuge on the linear network in lowland Wales. Having
17 grouped species by the ecosystem services they help deliver, we found that injurious weeds (an
18 ecosystem disservice to food production) either declined or remained stable, a greater number of
19 butterfly larval food plants decreased than increased and there was a net decline in potential nectar
20 yield. Consistent with the successional trend, increasing species in these service-providing groups
21 tended to be tall or shade-tolerant herbs and tree species. Decreasing species tended to be short,
22 shade-intolerant forbs.

23

24 **Introduction**

25 Common plants make a disproportionately large contribution to ecosystem functioning and
26 therefore to the delivery of services that benefit humans. In the UK for example, up to five common
27 forage grasses and two *Trifolium* species support our grassland agricultural sector (Gililand *et al.*,
28 2007), one functional group of mosses (*Sphagnum* spp) build our peatlands storing carbon and
29 potentially mitigating downstream flooding (Smart *et al.*, 2010; Holden *et al.*, 2017), 22 common
30 forbs are estimated to provide around 90% of total potential nectar provision (Baude *et al.*, 2016)
31 and common trees and shrubs stabilise our soils, help mitigate noise, air pollution and lowland
32 flooding and provide breeding habitat for many bird species (Rhodes *et al.*, 2015; Smith *et al.*, 2017;

1 Dixon *et al.*, 2016; Chandler *et al.*, 2018). The importance of common species and habitat dominants
2 in influencing the delivery of ecosystem services is predicted by the 'mass:ratio' hypothesis (Grime
3 1998). This has found much subsequent support (Wardle *et al.*, 1999; Smith *et al.*, 2003; Pakeman *et*
4 *al.*, 2011; Smith *et al.*, 2017 and Kershaw and Mallik, 2010 for critical review) and is inevitably also
5 linked to the concept of organisms as 'ecosystem engineers' (Jones *et al.*, 1994). The larger pool of
6 common subordinate plant species, that is species contributing lower biomass but still relatively
7 common across the landscape, are also of importance in supporting different ecosystem functions
8 via a range of mechanisms (Cardinale *et al.*, 2011; Pywell *et al.*, 2015; Carvell *et al.*, 2006). Measuring
9 change in the plant species that dominate Britain by area and by mass focusses on those species
10 likely to be most involved in driving contemporary ecosystem function across the countryside. An
11 exception to this centres on rarer species and the cultural, spiritual and intellectual fulfilment they
12 bring as objects of delight and study. They may also have a role in providing low levels of function
13 but across multiple, complimentary functions (Soliveres *et al.*, 2016). However, understanding the
14 abundance of common species is also relevant to understanding the fortunes of the rarer species
15 because the latter often lose out in competition with common dominants that are favoured by
16 modern land-use regimes (Hodgson 1991; Powney *et al.*, 2014; Smart *et al.*, 2006a; Walker *et al.*,
17 2017). Indeed the results from a wide range of long-term and large-scale studies show how human
18 driving forces have tended to non-randomly filter for different kinds of plants, segregating the
19 declining losers from the increasing winners on the basis of their traits and rarity (Duncan and
20 Young, 2000; Tamis *et al.*, 2005; Walker and Preston, 2006; Sundberg 2014). Across Britain, the
21 Countryside Survey (CS) has been able to describe and quantify these patterns based on a national-
22 scale, stratified random sample of the vegetation (Smart *et al.*, 2002; 2003; 2005; 2006b; Carey *et*
23 *al.*, 2008; Norton *et al.*, 2012). A unique feature of the survey is that it pays particular attention to
24 the plant species composition of linear features comprising hedgerows, the banks of watercourses
25 including ditches, field boundaries and road verges. Analysis of these data has shown how important
26 the linear network is as a reservoir and refuge for functionally important plant biodiversity including
27 common nectar plants (Baude *et al.*, 2016), high conservation value indicator plants (Smart *et al.*,
28 2006a) and Crop Wild Relatives that provide genetic insurance for future crop-breeding in an era
29 when global food security in the face of climate change has risen to the top of the agenda (Jarvis *et*
30 *al.*, 2015). Whilst functioning as refugia for plants not favoured by adjacent land-use, linear features
31 have also been subject to marked successional change that reduce the quality of the refuge for some
32 species and increase it for others. Evidence from Countryside Survey has shown that since 1978 and
33 up to the last survey in 2007 linear features and especially streamsides have seen increased shading
34 and cover of trees and shrubs (Carey *et al.*, 2008). This trend was most evident in England and Wales

1 and has been correlatively linked to increased water quality but also to the suppression of
2 herbaceous species richness as a result of the filtering of shade-intolerant herbs (Smart *et al.*, 2006a;
3 Norton *et al.*, 2016). Since the linear network is best developed in lowland Britain successional
4 changes on linear features have also occurred against a backdrop of intensive land-use, exposure to
5 run-off rich in macronutrients and high atmospheric nitrogen deposition. Yet, since the mid-eighties,
6 management options funded by regionally focussed and then more widespread agri-environment
7 schemes may have ameliorated intensifying factors adjacent to linear features in some places. These
8 schemes have also funded interventions that directly impact linear features in the hope of achieving
9 a wide range of objectives including water course protection, hedgerow management, ecological
10 connectivity and the creation of buffer strips for birds, invertebrates and plants. The signal of agri-
11 environment scheme effects may be present in our results but our objective is not to try to isolate
12 this signal since the sample size is relatively small and we do not currently have access to location-
13 specific information on historical scheme uptake and the duration of options. We return to this
14 briefly in the discussion.

15

16 In this paper we ask whether the trend for increased woody cover and shading on linear features has
17 continued from 1990 to the present. We focus on Wales only. The last GB-wide CS was carried out in
18 2007 but in 2016, 21 of the CS 1 km survey squares in Wales were revisited and their quadrats
19 recorded as part of the Glastir Monitoring & Evaluation Program funded by Welsh Government (Fig.
20 1). These 1 km squares contained 137 linear quadrat locations at which the vegetation has been
21 recorded in the same position in 1990, 1998, 2007 and now in 2016. Our analysis focused on
22 changes in these 137 plots. Those first recorded in 1978 were excluded because of small sample
23 sizes and to serve the exploratory needs of our analysis. They could be included in a future
24 investigation.

25 We summarise the ecological significance of changes in species frequency by grouping individual
26 species according to their potential contribution to various ecosystem services and one disservice
27 across the countryside (Table 1). We did not measure the delivery of each service in the sense of
28 quantifying the benefits realised from the species being present. Our focus was on assembling
29 evidence of changes in abundance of functionally important species assuming that for benefits to be
30 realised the right species need at least to be sufficiently abundant in the regional species pool.
31 Moreover, the delivery of each service is also dependent upon the species being situated in the
32 appropriate habitat. For example, positive Common Standards Monitoring indicators for lowland
33 meadows and upland hay meadows will only contribute to condition assessment when present in
34 existing meadows or grasslands targeted for restoration. However, agri-environment scheme

1 options that aim to achieve maintenance and restoration require a responsive wider species pool.
2 We assume that the success of such options is increased where populations of these indicators
3 persist and can alleviate dispersal limitation. Persistence is often more likely on linear features since
4 these can retain greater diversity than adjacent managed fields (Smart *et al.*, 2002; 2006a).

5 In summary we ask the following questions:

- 6 1. Do changes in the frequency of common plant species indicate an ongoing trend toward
7 greater woody cover and shading on linear features seen across Wales between 1990 and
8 2016?
- 9 2. What are the implications of species frequency changes for ecosystem services delivered by
10 plants on linear features?

11

12 **Methods**

13 *Survey design*

14 The Countryside Survey was established in 1978 with the aim of estimating the stock of common
15 habitat types across Britain and characterising their soils and plant species composition (Wood *et al.*,
16 2017). The sampling design chosen to ensure unbiased yet representative coverage of Britain was
17 based on a random selection of 1km squares stratified by Land Class - a physiographic and climatic
18 classification of 1km squares, correlated with but independent of land-cover and vegetation (Bunce
19 *et al.*, 1996). Subsequent surveys in 1990, 1998 and 2007 were used to quantify changes in soils,
20 vegetation, habitat area and many other attributes over time allowing for adjustments to the sample
21 size and stratification reflecting devolution and the need to report on UK Biodiversity Action Plan
22 Broad and, where possible, Priority Habitats. Detailed methods have been previously documented
23 (Norton *et al.*, 2012; Carey *et al.*, 2008; Smart *et al.*, 2003). Exactly the same field protocols were
24 used for finding and recording quadrats in the 21 CS squares revisited in Wales in 2016 as in previous
25 surveys.

26

27 *Plot types*

28 Linear plots sampled field boundaries (maximum 5 per 1km square), hedgerows (2 per square), road
29 verges (5 per square) and the banks of watercourses including ditches (5 per square). A stratified,
30 random design was used to position plots on their respective features (see Carey *et al.*, 2008 for
31 further details). All linear plots were 1x10m in size with the long axis arranged parallel to the linear

1 feature. Streamside plots were placed next to the channel and then 1m measured up toward the
2 break of slope. Field boundary plots were positioned with one edge adjacent to the first vertical
3 feature defining the edge of the field. Hedgerow plots were aligned with one edge along the central
4 axis of the hedge and road verge plots were positioned along the edge of the road or track and
5 measured 1m into the adjacent vegetation. After being put into position during the first survey,
6 quadrats were recorded in the same position in every year of survey being re-found in each repeat
7 visit using a combination of photographs, sketch maps and in many cases re-finding a small
8 aluminium plate buried at one of the corners of the plot. Surveyors were asked to make a judgement
9 in the field as to whether they found the plot with sufficient accuracy for the data to be treated as a
10 repeat record at the same spatial location as in previous surveys. In total 137 linear plots were
11 available for analysis with each plot having been recorded four times in the same place.

12

13 *Data assembly*

14 Species lists from each plot were arranged as presence/absence data by plot, year and 1km square.
15 A number of taxon amalgamations were implemented for species known to be difficult to separate
16 in the field, for example *Quercus robur* with *Q.petraea*. Nomenclature follows Stace (2010).

17 Changes in frequency across the surveys were analysed at the individual species level. Results were
18 then summarised as counts by groupings of species as follows. All plants analysed were assigned
19 exclusively to one of five growth forms; lianas (*Hedera helix* and *Lonicera periclymenum*), forbs
20 (herbaceous non-graminoids), graminoids (including grasses, sedges and rushes), ferns and woody
21 species (trees, shrubs and dwarf shrubs. *Rubus fruticosus* agg was also included here). These growth
22 forms usefully discriminate later successional species – ferns, lianas and woody species – from early
23 to mid-successional forbs and graminoids. Species were also grouped by average canopy height
24 following the classification used by Grime *et al.* (1995). Species were also assigned to groups that
25 reflected clear and established links to the delivery of ecosystem services and one disservice (Table
26 1).

27

28 *Analysis*

29 For each plant species with greater than 10 recorded occurrences across the four survey years we
30 tested whether it exhibited a linear trend in number of recorded presences (increase or decrease)
31 over time. To determine the significance of the linear trends, a randomisation test was adopted that
32 could both preserve the temporal and spatial structure of the data whilst also incorporating

1 changing detection rates across plant types across years. CS has been repeatedly validated by
2 independent Quality Assurance surveys (Prosser and Wallace, 1992, 1999, 2008). These visit a subset
3 of the quadrats in a sub-sample of CS squares soon after surveyors carry out the 'real' survey. The
4 same team have carried out the QA exercise in every CS maintaining continuity of practice and
5 recording effort. The results have shown that detection rate has varied between surveys and also by
6 broadly defined plant type. Exhaustive analysis of the QA datasets after the 2007 survey showed that
7 most metrics were unaffected by between-survey variation in recording effort however a correction
8 factor was applied to analysis of the mean Ellenberg fertility scores while analysis of changes in
9 individual plant species applied a modification of the Telfer *et al.* (2002) method used for Atlas 2000
10 (Carey *et al.*, 2008; Smart *et al.*, 2008). However, that method involved a correction that took no
11 account of the fact that detection could differ between species groups; for example sedges, forbs or
12 trees and shrubs. The method was also set up for pairs of surveys and not a time series of more than
13 two surveys. Since that time methods for addressing the problem of varying recorder effort have
14 increased in sophistication (Bailey *et al.*, 2014; Isaac *et al.*, 2014). We therefore included varying
15 detection probability between survey year and plant type in our analysis of change in species
16 frequency so that our results were robust to average variation in detection rate specific to each of
17 the four survey years and to the type of plant. Detection rate is simply the proportion of records of a
18 particular plant type - forbs, graminoids or woody species (trees, shrubs, dwarf shrubs and lianas) -
19 found by the QA surveyor that were also found by the CS surveyors. These proportions can be
20 readily calculated for each plot in each random sub-sample of plots visited by both QA and CS
21 surveyors. Since the proportion of the total QA list that was recorded by the CS teams varied
22 between plots the distributions of values were summarised by fitting the parameters of a beta
23 distribution to each QA dataset defined by survey year and plant type (see Fig S1).

24 In the randomisation test the observed regression slope of counts in each year against time was
25 compared against a distribution of regression slopes derived from randomising the presence of each
26 species within each plot and within each 1km square but across years, hence maintaining the
27 structure of the observed data. Detectability was incorporated by including a stochastic process
28 representing whether the randomised presence was recorded or not. Note that the regression
29 slopes were fitted to the total count of each species across occupied plots over time.

30 The randomised distribution of regression slopes for a particular species was generated by the
31 following algorithm:

- 32 1. Extract the total number of years in which the species was present within each quadrat to
33 determine the number of pseudo presences.

- 1 2. Randomly assign these pseudo-presences across the four available years (1990, 1998, 2007,
- 2 2016) but within each plot such. Thus the 1's and 0's from each plot swap years but never
- 3 swap spatial location. Note that if the species was present in every year no random sorting
- 4 was possible for that quadrat. Plots in which the species was never recorded are ignored.
- 5 3. Convert each pseudo-presence into a pseudo-observation by multiplying by a random draw
- 6 from a Bernoulli distribution. The probability in the Bernoulli trial is a random draw from a
- 7 Beta distribution given the fitted parameters for the detection rate relevant to the survey
- 8 year and plant type (Fig S1).
- 9 4. Fit a linear trend to the pseudo-observations generated and store.
- 10 5. Repeat steps 2-4 10,000 times for each species.

11 The probability that the observed slope is significantly larger or smaller than a draw from the null
 12 distribution is calculated as the count of observed slopes that are greater or less than each
 13 randomised slope divided by the total number of randomised slopes.

14 The detection rate (D) is not applied species-specifically as this information is either not available or
 15 sparse for most species, but is applied given the survey year and the plant type to which the species
 16 belongs. The count of randomised presences in any year is therefore reduced to reflect the level of
 17 under-recording quantified by the detection rate for that year and species type. The observed
 18 counts are not adjusted and so end up higher relative to the reduced counts in the randomised data
 19 with which the trend in the observed data is compared. Therefore, the comparison of regression
 20 slopes is corrected for varying recorder effort by down-weighting the randomised data rather than
 21 by having to add pseudo-presences to the observed data. Uncertainty in each detection rate is
 22 introduced by drawing the p for the Bernoulli from the appropriate Beta distribution. So for each
 23 species h in quadrat j in square i in survey year y its pseudo observations were obtained and were
 24 randomly re-assigned to each year with probability,

$$25 \quad I_{hjiy} = D_{hjiy} \cdot T_{hjiy}$$

$$26 \quad D_{hjiy} \sim \text{Bern}(p_{fy})$$

$$27 \quad P_{fy} \sim \text{Beta}(\alpha, \beta)$$

28
 29 where p is drawn from a Beta distribution representing the spread of detection rates for each year y
 30 and each growth form f , T_{hjiy} represents the pseudo-presence/absences generated from step 2 in
 31 the above algorithm and D is a binary draw from the Bernoulli distribution. Parameters for each Beta

1 distribution were fitted using the fitdistrplus R package and the method of moments (Delignette-
2 Muller and Dutang, 2015). See Fig. S1 in Supplementary Material for fitted and observed
3 distributions of detection rate.

4

5 *Contribution to vegetation cover of the species tested*

6 The mass:ratio hypothesis highlights the correlation between biomass and contribution to
7 ecosystem function. While we have no biomass measurements for species in plots a useful indicator
8 of how important the species tested might be in terms of its contribution to standing biomass can be
9 derived by expressing the proportion of total vegetation cover across the linear plots attributable to
10 the species tested. Thus if species that became more or less common, contributed a large
11 percentage of total cover they may have a disproportionate importance in influencing services that
12 are correlated with the amount of vegetation present.

13

14 **Results**

15 *Identity of broad habitats adjacent to the linear features*

16 Linear networks are better developed in the lowland landscapes of Britain and this is clearly
17 reflected in the identity of the broad habitats most commonly found adjacent to the linear plot
18 sample revisited in Wales (Fig. 2). The most common habitat was Improved grassland. Arable land is
19 not extensive in Wales and so was much less common as an adjacent habitat than it would have
20 been in England for example.

21

22 *Changes in species frequency*

23 Of those species that showed significant change in frequency, those increasing were more likely to
24 be trees and those decreasing were more likely to be forbs and grasses (Table 2, Fig. 3). Moreover,
25 shorter species (<10 to 60cm) were more likely to be decreasing while species showing no significant
26 change ranged more widely in height (Table 2, Fig. 4). The tallest species either did not change
27 significantly or increased in frequency (Fig. 4).

28 Forbs were the biggest species group analysed and most did not show any significant change (58 of
29 74 analysed) but in absolute terms the largest number of decreasing species were forbs. The only

1 groups to have no decreasing species but only increasing or stable species were ferns and woody
2 species however these groups of species were small compared to forbs (Fig. 4; Table 2)

3 Among species associated with the potential delivery of ecosystem services and disservices the
4 greatest number of significant changes were reductions in frequency but the majority of species in
5 all groups showed no significant change up or down. Decreasing species included CSM positive
6 indicators (8 of 61 analysed), nectar providing plants (11 of 69), Injurious Weeds (2 out of 5),
7 butterfly larval foodplants (11 of 44) and N fixers (3 of 10) (Table 2; Fig. 5). Increasing species
8 included four species in the CSM positive indicator and Ancient Woodland Indicator (AWI) group
9 (*Blechnum spicant*, *Deschampsia cespitosa*, *Chrysplenium oppositifolium* and *Dryopteris affinis*
10 *agg.*). Increasing butterfly larval foodplants were *Deschampsia flexuosa*, *Hedera helix* *agg.*, *Ilex*
11 *aquifolium* and *Quercus robur/petraea*. Of the N fixing species only *Alnus glutinosa* increased in
12 frequency significantly, consistent with the increased abundance of woody species across the
13 network. No injurious weeds increased significantly. Nine nectar-providing species increased in
14 frequency. These were woody species (*Acer pseudoplatanus*, *Alnus glutinosa*, *Corylus avellana*,
15 *Rubus fruticosus* *agg.*, *Hedera helix* *agg.*) and shade-tolerant or tall herbs (*Galium aparine*, *Geum*
16 *urbanum*, *Chrysplenium oppositifolium* and *Heracleum sphondylium*) (Table 2).

17

18 *Contribution to vegetation cover*

19 The 127 species tested contributed 80% of total plant cover in linear plots in 1990 and 73% in 2016.
20 The significant changes in frequency we detected also appeared to be consistent with changes in
21 total cover. Increasing species occupied 9% of total cover among 1990 plots rising to 20% by 2016.
22 Species that became less frequent also declined from 22% of total cover in 1990 to 11% by 2016. The
23 largest contribution was from species that were frequent enough to be tested but showed no overall
24 significant change over the 26 years (Fig. 6).

25

26 **Discussion**

27 Overall the patterns of changing frequency that we have detected are consistent with the
28 continuation of a successional trend clearly seen in Britain and in particular in Wales from 1978 up
29 until the last CS in 2007 (Carey *et al.*, 2008). Therefore in the last 9 years conditions have continued
30 to become less favourable for mid-successional, shade-intolerant plant species. Two particular
31 groups of shade-intolerant plants are therefore likely to have suffered; a) nutrient-loving species and
32 b) shade-intolerant forbs of less fertile conditions.

1 Nutrient-loving species require ample light to realise the rapid and suppressive growth achievable
2 when macronutrients are freely available. Thus shading reduces their vigour. We see evidence of this
3 in the significantly reduced frequency of the injurious weeds *Cirsium vulgare* and *Rumex obtusifolius*
4 in linear plots from 1990 to 2016 although the other injurious weeds *Cirsium arvense*, *Rumex crispus*
5 and *Senecio jacobaea* showed no significant change in the same period. Species that are less
6 nutrient-demanding but also shade-intolerant include the large pool of short forbs that feature in
7 the CSM positive indicator list. Many CSM positive indicator species are infrequently encountered
8 across Wales because their preferred habitats are relatively rare and because they often have small
9 population sizes and make a small contribution to vegetation cover. Therefore the few CSM positive
10 indicators analysed here are biased toward those more common in the lowlands (Table 2). Species
11 that declined include *Lotus pedunculatus*, *Festuca ovina*, *Hypochoeris radicata* and *Centaurea nigra*
12 but many others did not change significantly such as *Lotus corniculatus*, *Hypericum pulchrum*, *Vicia*
13 *cracca*, *V.sativa* and *Stellaria uliginosa*. Most showed no consistent directional change. Too few CSM
14 positive indicator species were encountered to be able to infer large-scale impacts across such a
15 large and diverse group while many of the habitat specialists in this group are also unlikely to benefit
16 from the refuge or connectivity function of lowland linear features. An exception maybe
17 streamsides. Smart *et al.* (2006a) examined how richness of indicators of unimproved mesotrophic
18 grasslands responded to a spatial gradient of land-use intensity across linear features in lowland
19 Britain. While indicator richness declined on streamsides the rate of decline was slower than
20 adjacent farmland, and streamsides were overall richer in indicator species than field boundaries,
21 road verges and hedgerows. Shading effects interacted with land-use intensity to drive down
22 indicator richness even further but increased shade seemed also able to buffer indicator species
23 against the effects of intensification but only for the small subset of indicators that were shade-
24 tolerant.

25 Given the increase in woody cover, shade-tolerant Ancient Woodland Indicators might have been
26 expected to increase. Most, including *Stellaria holostea*, *Hyaconthoides non-scripta*, and *Oxalis*
27 *acetosella*, showed no evidence of increase. However other shade-tolerators did become more
28 common in linear features in the 26 years including *Hedera helix* agg. and *Geum urbanum*.

29 The importance of linear features as refuge features has also been shown for nectar providing plants
30 and crop wild relatives (Baude *et al.*, 2016; Jarvis *et al.*, 2015). These are also diverse groups of
31 plants so that the shading trend appears to have favoured some but not others. Thus shorter,
32 grassland species such as *Cerastium fontanum*, *Trifolium pratense*, *Cenataurea nigra*, *Hypochoeris*
33 *radicata* and *Lotus pedunculatus* declined while taller nectar-providing species increased including
34 *Heracleum sphondylium*, *Galium aparine*, *Alnus glutinosa*, *Acer pseudoplatanus* and *Rubus fruticosus*

1 agg. While many nectar-providing species showed no change in frequency the net outcome was a
2 reduction in potential nectar production of about 4400 Kg sugar ha⁻¹ year⁻¹ derived crudely as the
3 number of plants species significantly lost or gained weighted by their average potential sugar
4 production (Fig. 7). Two important caveats apply in interpreting this figure. First, the sugar
5 production values are estimates of potential yield. To be realised they obviously require flowering
6 and, for forbs at least, this tends to be reduced under shade and when subject to elevated nitrogen
7 deposition (Phoenix *et al.*, 2012). Second, the nectar production totals do not provide information
8 on when in the growing season each plant is likely to contribute. Plants that flower early and help to
9 fill the spring gap in nectar provision may be critical even if their potential nectar yield is lower than
10 summer-flowering species (Russo *et al.*, 2013).

11 To summarise, the changes in individual species frequency seen over 26 years in an unbiased sub-
12 sample of plots on linear features across Wales indicate a continuation of the trend for increased
13 shading and woody cover seen between 1990 and the last full Countryside Survey in 2007. This trend
14 was also detected across linear features in England but was much less apparent in Scotland (Carey *et*
15 *al.*, 2008). Between 1990 and 2016 in Wales, most species showed no significant change in
16 frequency suggesting that the significant directional trend seems only to have impacted a subset of
17 the species present. A greater sample size would be required to capture impacts on a larger number
18 of species including the many less common CSM positive indicator species that may find partial
19 refuge on the linear network in lowland Wales.

20 By grouping species in terms of the ecosystem services and disservice that they can potentially
21 influence we found that injurious weeds either declined or remained stable, a greater number of
22 butterfly larval food plants decreased than increased and that there was a net decline in potential
23 nectar yield. Consistent with the successional trend, increasing species in these service-providing
24 groups tended to be tall or shade-tolerant herbs and tree species and decreasing species tended to
25 be short, shade-intolerant forbs.

26 A number of further research questions arise from this work. Firstly, to what extent have species
27 changes actually contributed to ecosystem service delivery, especially given the apparent stability
28 among most species? A second question concerns quantifying the longer-term, cumulative effects of
29 over 30 years of agri-environment funding on service-delivering common plants in Wales and the
30 rest of Britain. In Wales the baseline of 1km survey squares established by the Glastor Monitoring &
31 Evaluation Program (GMEP <https://gmep.wales/>) was carefully stratified by uptake of options
32 funded under the Glastir scheme so that in future these data should be able to help address this
33 question. The trend on linear features in Wales toward taller vegetation with greater woody cover is

1 a continuation of one component of a general pattern of homogenisation of plant traits and reduced
2 local species richness seen across Britain from 1978 to 1998 (Smart *et al.*, 2006b). Recently however,
3 analysis of plant and animal records at 10km square and coarser resolutions has indicated a slowing
4 or even reversal of homogenisation and species loss in Britain and parts of Europe (Carvalho *et al.*,
5 2013). The authors hypothesised that this might reflect the widespread and long-term impact of
6 extensification resulting from agri-environment scheme funding. The coarse resolution of their data
7 made it impossible to directly answer this question because they could not differentiate temporal
8 change between habitat types and locations known to have been subject to long-term AES
9 intervention versus locations never in scheme. Building on the legacy of change in CS plots, joint
10 analysis with the GMEP sample alongside emerging data from the National Plant Monitoring
11 Scheme, could allow us to test this hypothesis at the detailed level of habitat, landscape features
12 and associated management options. Such an analysis would require finely-resolved legacy data on
13 past schemes to be assembled.

14 Lastly, the successional trend on linear features may have further facilitated the delivery of other
15 ecosystem services such as flood amelioration, ecological connectivity, carbon storage and
16 watercourse protection. The mechanisms supporting these services are less reliant on individual
17 plant species than changes in vegetation structure attributable to the increasing dominance of
18 woody plant cover. An interesting question centres on the extent to which trade-offs may have
19 arisen for example between those services whose delivery is supported by short forbs versus trees
20 and shrubs.

21

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1 Table 1: Relationships between types of plant species and potential for contributing to the supply of
 2 different ecosystem services. 1. Jarvis *et al.* (2015); 2. Baude *et al.* (2016); 4. Five species notifiable
 3 under the Weeds Act 1959 (<https://www.legislation.gov.uk/ukpga/Eliz2/7-8/54/contents>). 6.
 4 Positive CSM indicators extracted from a full listing across habitats compiled by Walker, K.J for the
 5 NPMS scheme, March 2014, plus Ancient Woodland Indicator species (Kirby 2006, Kimberley *et al.*,
 6 2013); 7. Larval food plants extracted from a phytophagous database originally compiled by Lena
 7 Ward and held at the Biological Records Centre, Wallingford. See Smart *et al.* (2000).

8

COMMON PLANT GROUP	ECOSYSTEM SERVICES
1) Crop Wild Relatives	Genetic insurance for future crop production
2) Potential nectar supply	Pollinator diversity and crop production
3) Nitrogen fixers	Food production and carbon fixation
4) Injurious weeds	Disservice for food production
5) Trees & shrubs	Climate control, soil stabilisation, cultural importance, supporting cultural value of wild bird diversity, carbon storage, flood amelioration
6) CSM & AWI	Positive Common Standards Monitoring indicators (CSM) and Ancient Woodland Indicators (AWI) support cultural biodiversity value and help indicate the status of valued semi-natural habitats
7) Butterfly larval foodplants	Cultural value of biodiversity

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Table 2: Results of an analysis of change in frequency of plant species in linear plots in Wales recorded in the same locations in 1990, 1998, 2007 and 2016. Estimated nectar values for flowering plants were extracted from Baude *et al.* (2016). BL=butterfly larval food plants. CSM & AWI = Positive Common Standards Monitoring indicators or Ancient Woodland Indicator. CWR =Crop Wild Relatives. N_fix=nitrogen fixers. IW=Injurious Weeds. Can_ht = average canopy height in classes (1, <100mm; 2, 101-299mm; 3, 300-599mm; 4, 600-999mm; 5, 1-3m; 6, 3.1-6m; 7, 6.1-15m; 8 >15m). Obs slope = the regression slope of the observed count data versus time. Rand_p the probability that the Obs slope is < than a slope derived from a random shuffling of the species presences between years (see text). Number of plots occupied in each survey year. SIG=empirical two-tailed test of the Rand_p value at the 5% level. Dir; + if observed slope >0, - if <0.

Species name	Estimated nectar (kg sugar ha ⁻¹ yr ⁻¹)	BL	CSM & AWI	IW	CWR	N_fix	Can ht	Obs slope	Rand_p	1990	1998	2007	2016	SIG	Dir
<i>Acer pseudoplatanus</i>	243.75	0	0	0	0	0	8	0.3109	0.0060	4	7	7	13	y	+
<i>Achillea millefolium</i>	603.25	0	1	0	0	0	2	-0.5617	1.0000	35	29	25	20	y	-
<i>Alnus glutinosa</i>	7.07	0	0	0	0	1	8	0.3096	0.0010	2	4	10	9	y	+
<i>Bellis perennis</i>	105.23	0	0	0	0	0	1	-0.2970	0.9870	14	10	8	6	y	-
<i>Blechnum spicant</i>	.	0	1	0	0	0	3	0.3135	0.0010	4	3	9	11	y	+
<i>Centaurea nigra</i>	2569.17	0	1	0	0	0	3	-0.7063	1.0000	31	20	15	12	y	-
<i>Cerastium fontanum</i>	23.26	0	0	0	0	0	1	-0.9122	1.0000	54	40	35	29	y	-
<i>Chrysosplenium oppositifolium</i>	47.79	0	1	0	0	0	2	0.2647	0.0010	5	8	7	13	y	+
<i>Cirsium vulgare</i>	1961.79	1	0	1	0	0	4	-0.3987	0.9990	13	16	12	3	y	-
<i>Corylus avellana</i>	1.7	0	0	0	1	0	6	0.6495	0.0010	11	12	17	28	y	+
<i>Dactylis glomerata</i>	.	1	0	0	1	0	3	-0.6218	1.0000	79	78	63	66	y	-
<i>Deschampsia cespitosa</i>	.	1	1	0	0	0	2	0.3908	0.0010	8	12	13	19	y	+
<i>Deschampsia flexuosa</i>	.	1	1	0	0	0	2	-0.2059	0.9830	11	7	10	4	y	-
<i>Dryopteris affinis</i>	.	0	1	0	0	0	5	0.2548	0.0010	1	1	5	7	y	+
<i>Fagus sylvatica</i>	.	0	0	0	1	0	8	0.4970	0.0010	2	3	10	14	y	+
<i>Festuca ovina agg.</i>	.	1	1	0	1	0	2	-0.4152	0.9990	25	13	12	13	y	-
<i>Fraxinus excelsior</i>	.	0	0	0	1	0	8	0.8053	0.0010	10	17	21	32	y	+
<i>Galium aparine</i>	4.89	0	0	0	0	0	5	0.5135	0.0080	25	46	35	44	y	+

<i>Geum urbanum</i>	1.93	0	0	0	0	0	3	0.2462	0.0090	13	10	16	18	y	+
<i>Hedera helix</i> agg.	705.45	1	0	0	0	0	8	0.3894	0.0080	26	29	36	35	y	+
<i>Heracleum sphondylium</i>	1507.04	0	0	0	0	0	3	0.3947	0.0180	30	28	38	38	y	+
<i>Holcus mollis</i>	.	1	1	0	0	0	2	-0.4125	0.9750	40	32	13	34	y	-
<i>Hypochaeris radicata</i>	101.28	0	1	0	0	0	1	-0.3531	1.0000	17	14	4	10	y	-
<i>Ilex aquifolium</i>	.	1	0	0	0	0	7	0.2172	0.0080	4	7	8	10	y	+
<i>Lolium perenne</i>	.	1	0	0	1	0	3	-0.7003	0.9990	76	69	65	57	y	-
<i>Lotus pedunculatus</i>	8.45	1	1	0	1	1	3	-0.5267	1.0000	19	12	11	4	y	-
<i>Plantago lanceolata</i>	0.37	1	1	0	1	0	1	-0.4092	0.9910	29	22	19	18	y	-
<i>Plantago major</i>	.	1	0	0	0	0	1	-0.6165	1.0000	37	29	23	21	y	-
<i>Quercus robur & petraea</i>	.	1	0	0	0	0	8	0.3023	0.0060	8	8	10	16	y	+
<i>Rubus fruticosus</i> agg.	167.49	0	0	0	0	0	5	0.4488	0.0130	58	50	61	67	y	+
<i>Rumex obtusifolius</i>	.	0	0	1	0	0	3	-0.3677	0.9820	36	24	21	26	y	-
<i>Trifolium pratense</i>	894.26	1	0	0	1	1	2	-0.3050	0.9970	8	13	2	3	y	-
<i>Trifolium repens</i>	803.62	1	0	0	1	1	1	-0.5868	0.9990	57	57	39	46	y	-
<i>Agrostis canina sens.lat.</i>	.	0	1	0	1	0	1	-0.1630	0.9141	14	5	5	9	n	-
<i>Agrostis capillaris</i>	.	1	1	0	1	0	2	-0.1003	0.6713	62	67	68	59	n	-
<i>Agrostis stolonifera</i>	.	0	0	0	0	0	2	0.0422	0.4446	74	85	62	83	n	+
<i>Alopecurus pratensis</i>	.	0	0	0	1	0	2	-0.0713	0.7722	4	7	1	4	n	-
<i>Angelica sylvestris</i>	93.98	0	1	0	0	0	3	0.1063	0.1309	5	5	2	9	n	+
<i>Anthoxanthum odoratum</i>	.	1	0	0	1	0	2	-0.2007	0.8162	45	43	28	44	n	-
<i>Anthriscus sylvestris</i>	150.54	0	0	0	0	0	3	0.2383	0.0919	19	26	20	28	n	+
<i>Apium nodiflorum</i>	.	0	1	0	0	0	3	-0.1399	0.9151	7	9	3	5	n	-
<i>Arrhenatherum elatius</i>	.	1	0	0	1	0	5	0.3274	0.0629	41	38	45	48	n	+
<i>Athyrium filix-femina</i>	.	0	1	0	0	0	5	0.1459	0.1479	12	17	15	17	n	+
<i>Brachypodium sylvaticum</i>	.	1	1	0	0	0	3	-0.0561	0.7133	12	11	9	11	n	-
<i>Bromus hordeaceus</i>	.	0	0	0	1	0	2	-0.1274	0.8641	8	7	8	4	n	-
<i>Cardamine hirsuta/flexuosa</i>	14.26	0	0	0	0	0	2	0.0726	0.3457	15	14	11	18	n	+

<i>Cardamine pratensis</i>	51.14	1	1	0	0	0	2	0.2132	0.0729	6	13	11	13	n	+
<i>Carex hirta</i>	.	0	0	0	0	0	3	0.1921	0.0340	3	8	7	9	n	+
<i>Chamerion angustifolium</i>	335.03	0	0	0	0	0	4	-0.0488	0.7123	4	6	5	3	n	-
<i>Circaea lutetiana</i>	3.28	0	0	0	0	0	2	0.0535	0.3167	6	10	9	8	n	+
<i>Cirsium arvense</i>	80.01	1	0	1	0	0	4	-0.0673	0.6434	32	29	32	29	n	-
<i>Cirsium palustre</i>	4733.31	1	1	0	0	0	4	0.2865	0.0350	19	13	16	26	n	+
<i>Crataegus monogyna</i>	584.18	1	0	0	0	0	7	0.0799	0.2787	20	21	22	22	n	+
<i>Crepis capillaris</i>	59.83	0	1	0	0	0	2	-0.1234	0.8911	6	2	3	2	n	-
<i>Cynosurus cristatus</i>	.	1	0	0	1	0	1	-0.0898	0.6853	25	24	19	24	n	-
<i>Digitalis purpurea</i>	245.6	1	0	0	0	0	4	-0.0825	0.7193	18	19	18	16	n	-
<i>Dryopteris dilatata/carthusiana</i>	.	0	1	0	0	0	3	0.0851	0.2637	14	9	16	14	n	+
<i>Dryopteris filix-mas</i>	.	0	1	0	0	0	5	0.1921	0.0869	13	16	21	17	n	+
<i>Elytrigia repens</i>	.	1	0	0	0	0	3	-0.2158	0.9231	17	17	4	15	n	-
<i>Epilobium hirsutum</i>	50.68	0	1	0	0	0	5	0.0686	0.2767	5	4	10	5	n	+
<i>Epilobium montanum</i>	17.05	0	0	0	0	0	4	0.2244	0.1339	20	28	24	28	n	+
<i>Equisetum arvense</i>	.	0	0	0	0	0	4	0.1102	0.0949	9	4	7	11	n	+
<i>Festuca rubra agg.</i>	.	0	1	0	0	0	2	-0.0442	0.5844	49	62	44	54	n	-
<i>Ficaria verna</i>	0.92	0	0	0	0	0	2	-0.0884	0.8132	7	4	2	5	n	-
<i>Filipendula ulmaria</i>	.	0	1	0	0	0	4	-0.0871	0.7602	22	18	16	20	n	-
<i>Galium palustre</i>	8.28	0	1	0	0	0	4	0.0429	0.3776	12	5	8	12	n	+
<i>Galium saxatile</i>	0.73	0	1	0	0	0	1	-0.1162	0.8342	15	15	14	12	n	-
<i>Geranium robertianum</i>	11.99	0	1	0	0	0	3	0.1234	0.2188	34	39	35	39	n	+
<i>Glechoma hederacea</i>	43.95	0	0	0	0	0	2	0.0772	0.2348	8	11	12	10	n	+
<i>Holcus lanatus</i>	.	1	0	0	1	0	3	-0.3373	0.9321	92	94	86	85	n	-
<i>Hyacinthoides non-scripta</i>	31.24	0	1	0	0	0	2	0.1201	0.0919	6	3	4	9	n	+
<i>Hypericum pulchrum</i>	.	0	1	0	0	0	3	-0.1459	0.9321	8	3	5	3	n	-
<i>Juncus articulatus/acutiflorus</i>	.	0	1	0	0	0	2	0.0086	0.4655	6	8	9	6	n	+
<i>Juncus bufonius sens.lat.</i>	.	0	0	0	0	0	1	0.0594	0.3347	3	11	11	5	n	+

<i>Juncus bulbosus</i>	.	0	1	0	0	0	1	-0.1624	0.9740	5	6	1	2	n	-
<i>Juncus effusus</i>	.	0	1	0	0	0	5	0.2871	0.0320	26	28	32	33	n	+
<i>Juncus inflexus</i>	.	0	0	0	0	0	5	-0.0647	0.6933	10	7	4	9	n	-
<i>Lapsana communis</i>		3.14	0	0	0	0	3	-0.0502	0.6573	12	15	14	11	n	-
<i>Lathyrus pratensis</i>		185.98	1	1	0	1	4	0.0013	0.4715	17	17	14	18	n	+
<i>Lonicera periclymenum</i>		89.64	1	1	0	0	6	0.0785	0.1898	5	8	6	8	n	+
<i>Lotus corniculatus</i>		22.59	1	1	0	1	2	-0.0323	0.5445	11	10	7	11	n	-
<i>Luzula campestris/multiflora</i>	.		0	1	0	0	2	-0.1419	0.8591	20	14	10	17	n	-
<i>Lysimachia nemorum</i>		0.65	0	1	0	0	1	0.0040	0.4426	6	2	5	5	n	+
<i>Mercurialis perennis</i>	.		0	1	0	0	3	0.0422	0.3197	7	11	9	9	n	+
<i>Nardus stricta</i>	.		1	0	0	0	2	0.0323	0.3726	9	12	9	11	n	+
<i>Oenanthe crocata</i>	.		0	1	0	0	4	0.0838	0.1648	11	10	8	14	n	+
<i>Oxalis acetosella</i>		3.76	0	1	0	0	1	0.0838	0.2138	13	11	12	15	n	+
<i>Phleum pratense sens.lat.</i>	.		1	0	0	1	0	-0.1208	0.8212	16	11	9	13	n	-
<i>Poa annua</i>	.		1	0	0	1	0	-0.1815	0.7872	38	48	33	38	n	-
<i>Poa pratensis sens.lat.</i>	.		0	0	0	1	0	-0.3386	0.9481	16	46	10	19	n	-
<i>Poa trivialis</i>	.		1	0	0	1	0	0.0832	0.3746	37	55	24	50	n	+
<i>Polygonum aviculare agg.</i>		2.11	0	1	0	0	4	-0.0284	0.5704	11	5	8	9	n	-
<i>Polypodium vulgare sens.lat.</i>	.		0	1	0	0	2	-0.0277	0.6044	2	5	6	1	n	-
<i>Potentilla anserina</i>		0.09	1	1	0	0	2	0.0825	0.2058	14	14	12	17	n	+
<i>Potentilla erecta</i>		46.83	0	1	0	0	2	-0.1908	0.9341	20	15	13	15	n	-
<i>Potentilla reptans</i>		18.97	1	0	0	0	2	0.1538	0.1119	10	8	9	14	n	+
<i>Potentilla sterilis</i>		6.06	0	1	0	0	1	-0.1261	0.8492	10	8	9	6	n	-
<i>Prunella vulgaris</i>		324.27	0	1	0	0	1	-0.1175	0.8012	14	16	12	12	n	-
<i>Prunus spinosa</i>		258.51	1	0	0	1	0	-0.1776	0.9191	26	28	28	21	n	-
<i>Pteridium aquilinum</i>	.		0	0	0	0	5	0.0601	0.3217	20	20	16	23	n	+
<i>Ranunculus acris</i>		49.66	0	1	0	0	2	0.2759	0.0460	13	18	12	23	n	+
<i>Ranunculus repens</i>		26.39	0	0	0	0	2	0.0073	0.4935	59	61	65	58	n	+

<i>Rumex acetosa</i>	.	1	1	0	0	0	2	-0.1281	0.6953	48	40	37	45	n	-
<i>Rumex acetosella</i>	.	1	1	0	0	0	1	-0.1413	0.9491	7	9	6	4	n	-
<i>Rumex conglomeratus/sanguineus</i>	.	0	0	0	0	0	4	-0.0092	0.5285	1	7	10	0	n	-
<i>Rumex crispus</i>	.	0	0	1	0	0	3	-0.1149	0.7942	10	10	6	8	n	-
<i>Sagina procumbens</i>	.	0	0	0	0	0	1	-0.1459	0.8741	16	12	11	12	n	-
<i>Scorzoneroideis autumnalis</i>	391.29	0	1	0	0	0	1	0.0660	0.3237	4	7	7	6	n	+
<i>Senecio jacobaea</i>	1602.69	0	0	1	0	0	4	-0.1149	0.8721	6	6	2	4	n	-
<i>Silene dioica</i>	101.47	0	1	0	0	0	3	-0.0799	0.7602	17	16	15	15	n	-
<i>Stachys sylvatica</i>	450.74	0	1	0	0	0	3	-0.1036	0.7972	11	10	10	8	n	-
<i>Stellaria graminea</i>	16.25	0	0	0	0	0	2	-0.0713	0.7373	6	7	7	4	n	-
<i>Stellaria holostea</i>	0.01	0	1	0	0	0	3	-0.1947	0.9281	19	16	17	13	n	-
<i>Stellaria media</i>	3.32	0	0	0	0	0	2	-0.0198	0.5395	15	11	15	13	n	-
<i>Stellaria uliginosa</i>	2.49	0	1	0	0	0	1	-0.0759	0.7423	11	8	4	10	n	-
<i>Tamus communis</i>	.	0	1	0	0	0	5	-0.0475	0.7143	8	9	8	7	n	-
<i>Taraxacum agg.</i>	686.23	0	0	0	0	0	2	0.2422	0.1229	53	55	55	60	n	+
<i>Trifolium dubium</i>	.	1	0	0	0	1	1	-0.0026	0.4905	4	7	4	5	n	-
<i>Ulex europaeus</i>	1.11	1	0	0	0	1	5	0.0086	0.4945	6	9	7	7	n	+
<i>Urtica dioica</i>	.	1	0	0	0	0	4	0.3050	0.0819	50	48	50	58	n	+
<i>Veronica chamaedrys</i>	5.06	1	1	0	0	0	1	-0.0865	0.7612	12	16	15	10	n	-
<i>Veronica serpyllifolia</i>	5.46	0	0	0	0	0	1	0.1175	0.1239	4	2	6	6	n	+
<i>Vicia cracca</i>	105.55	1	1	0	1	1	5	-0.0508	0.6813	10	4	5	8	n	-
<i>Vicia sativa</i>	327.02	0	0	0	1	0	4	-0.0026	0.5085	6	10	4	8	n	-
<i>Vicia sepium</i>	75.16	0	1	0	1	1	4	-0.0165	0.6074	10	13	15	9	n	-
<i>Viola riviniana/reichenbiana</i>	20.83	0	1	0	0	0	2	-0.2125	0.9261	26	29	26	21	n	-

Figure 1 Map showing location of Countryside Survey 1km squares surveyed in Wales in 2016.

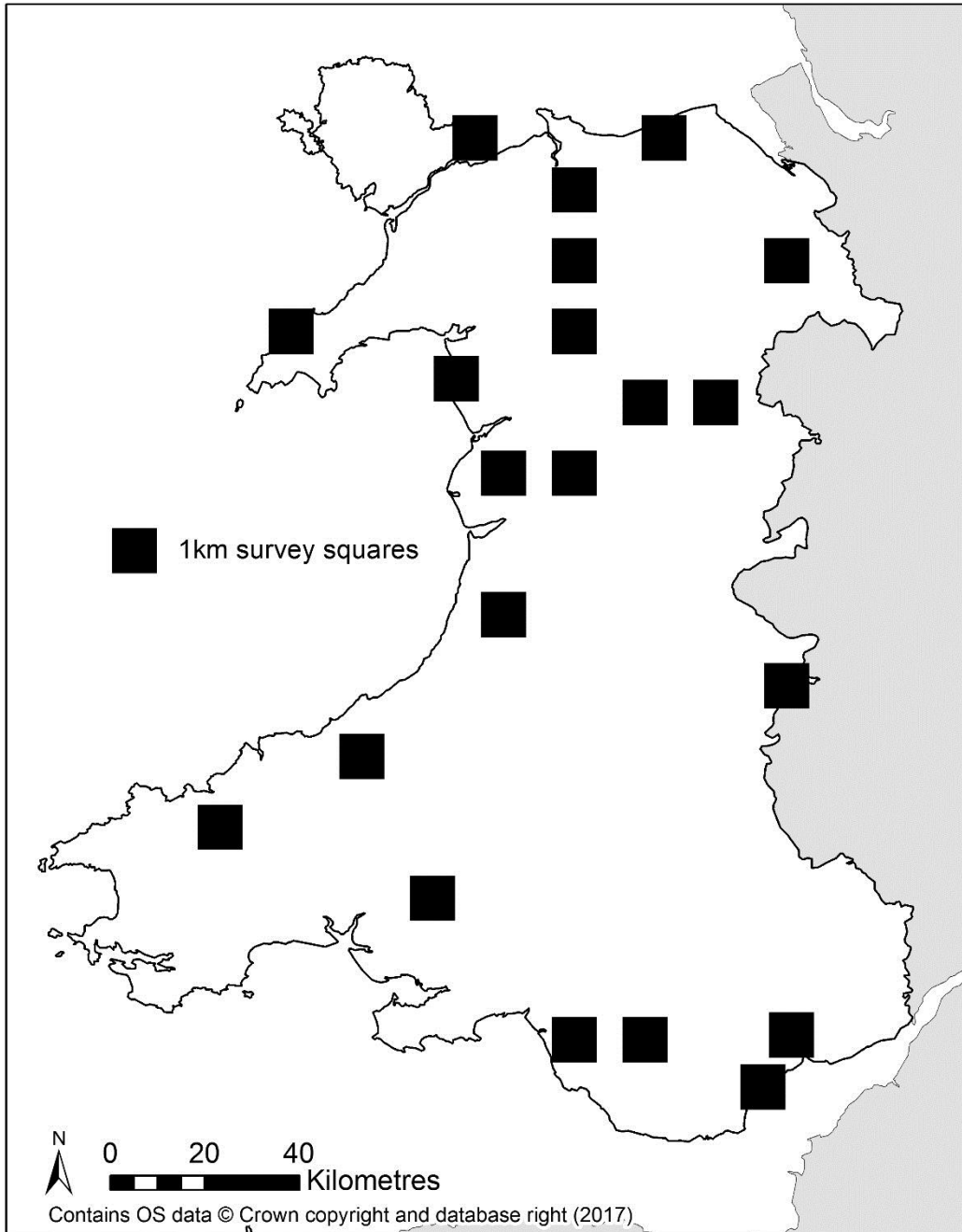


Figure 2: Broad habitats adjacent to the repeat plots when surveyed in 2016. The adjacent habitat is derived from a GIS analysis that assumes a maximum 5m width of each linear feature. Where the feature is >5m then Boundary & linear features is designated as the adjacent habitat.

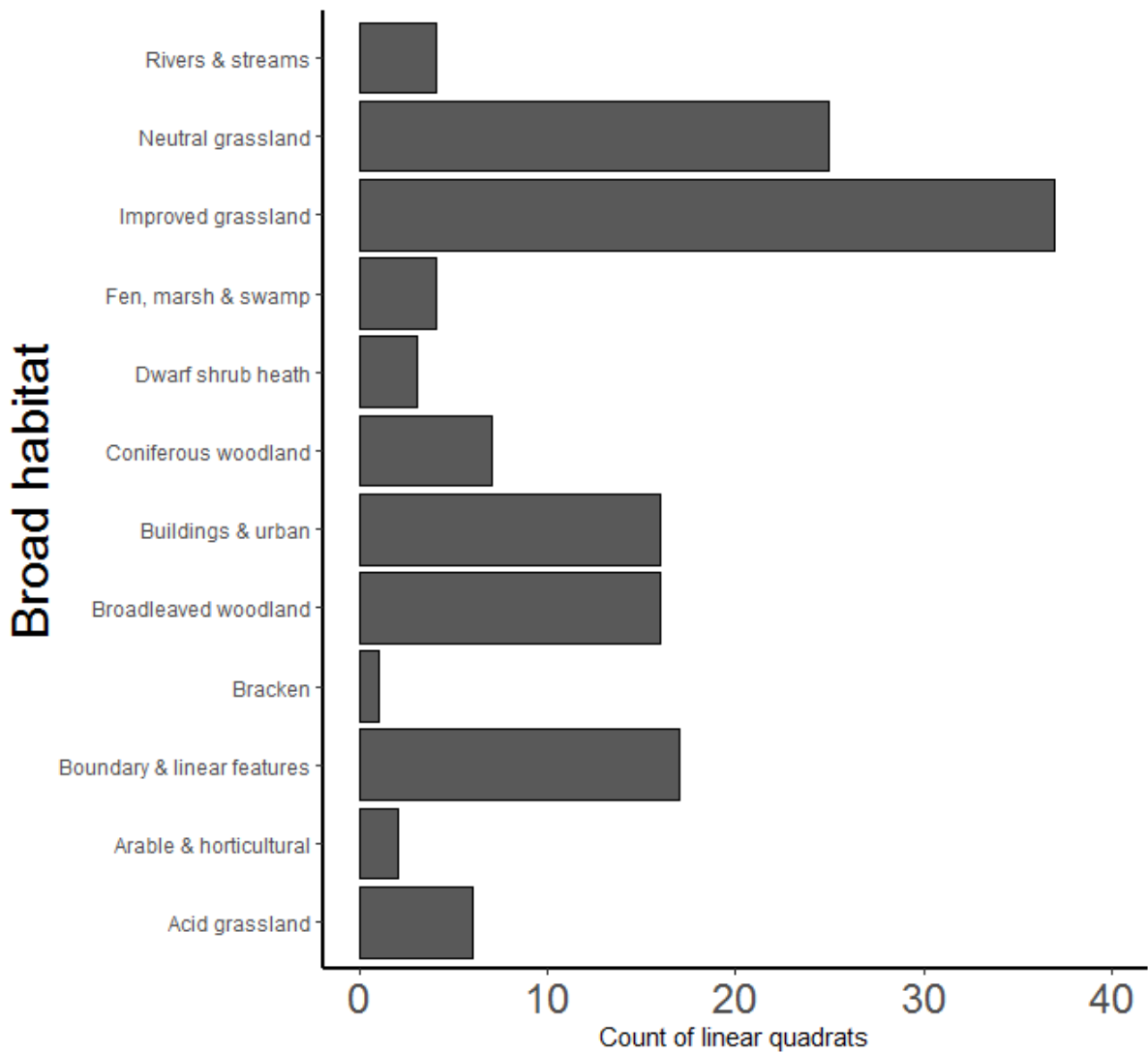


Figure 4: Distribution of average plant heights among decreasing, increasing species and those that showed no significant change between 1990 and 2016 (1 <100mm; 2 101-299mm; 3 300-599mm; 4 600-999mm; 5 1-3m; 6 3.1-6m; 7 6.1-15m; 8 >15m).

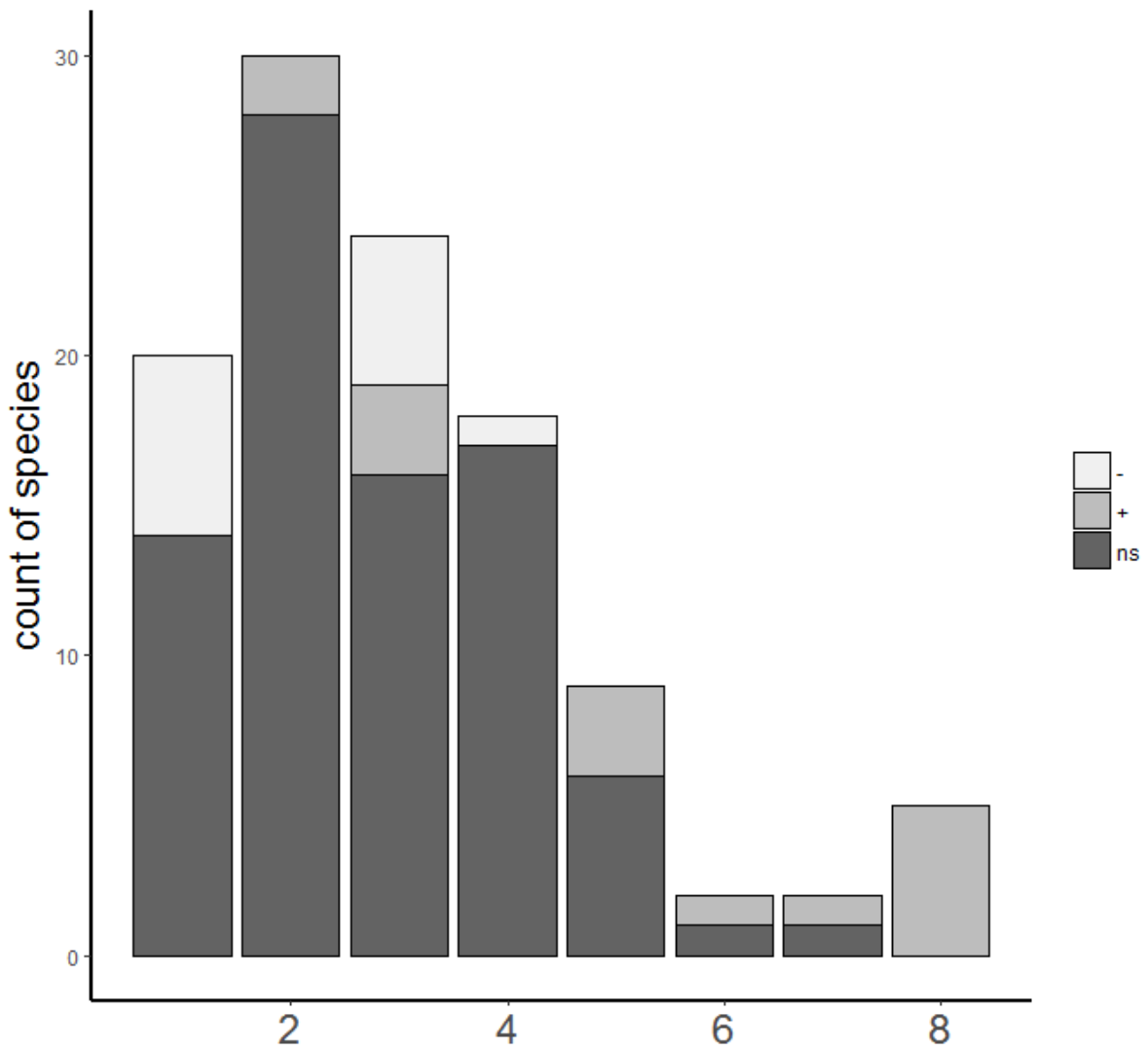


Figure 3: Distribution of growth forms among decreasing, increasing species and those that showed no significant change between 1990 and 2016 (f=forbs, fe=ferns, g=graminoids, w=woody species includes two lianas).

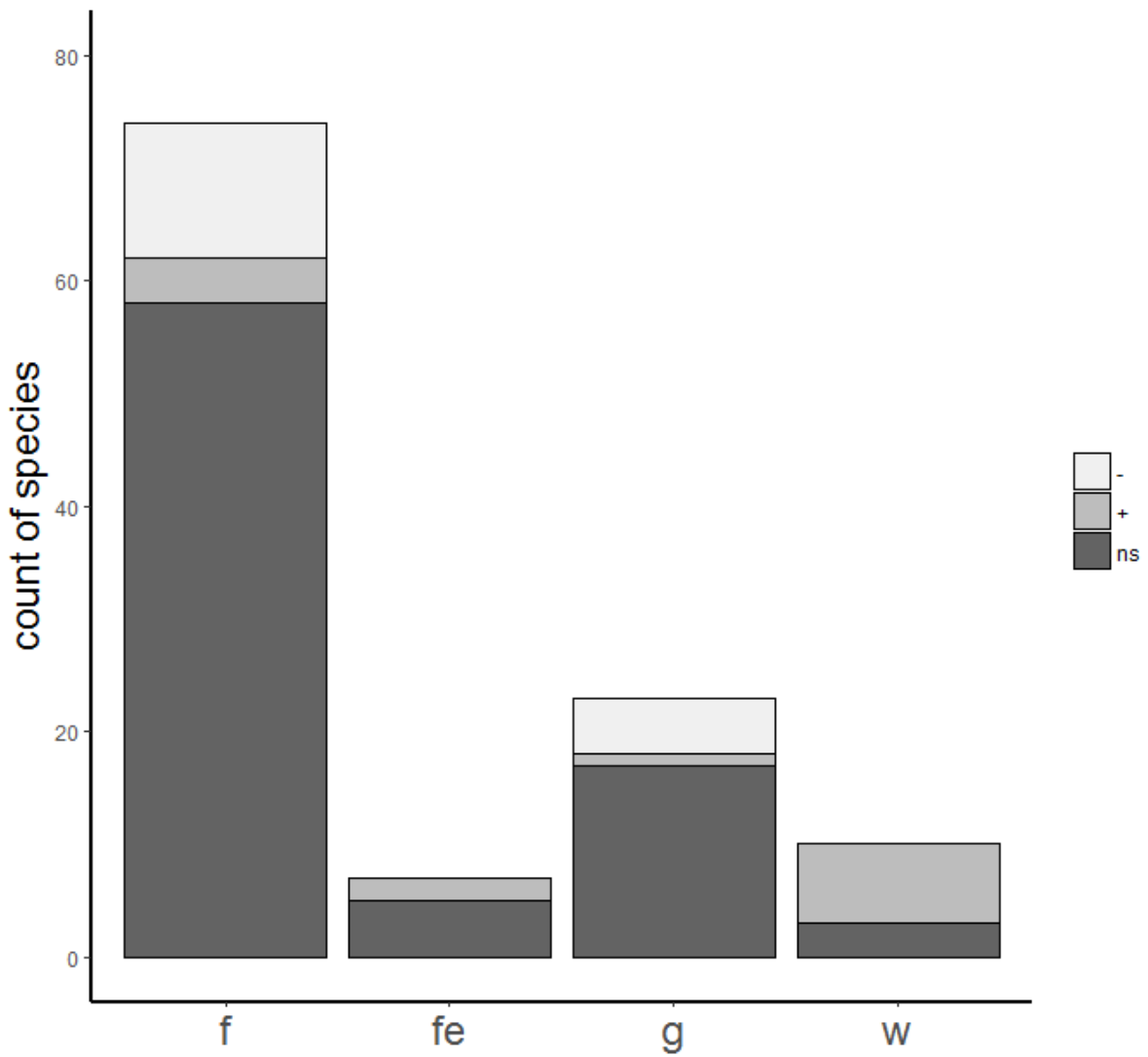


Figure 5: Distribution of service-providing plant groups among decreasing, increasing species and those that showed no significant change between 1990 and 2016 (Butt_larv = butterfly larval foodplants; CSM_AWI= Common Standards Monitoring positive indicators and Ancient Woodland Indicator species; IW= injurious weeds; N_fix=nitrogen fixers).

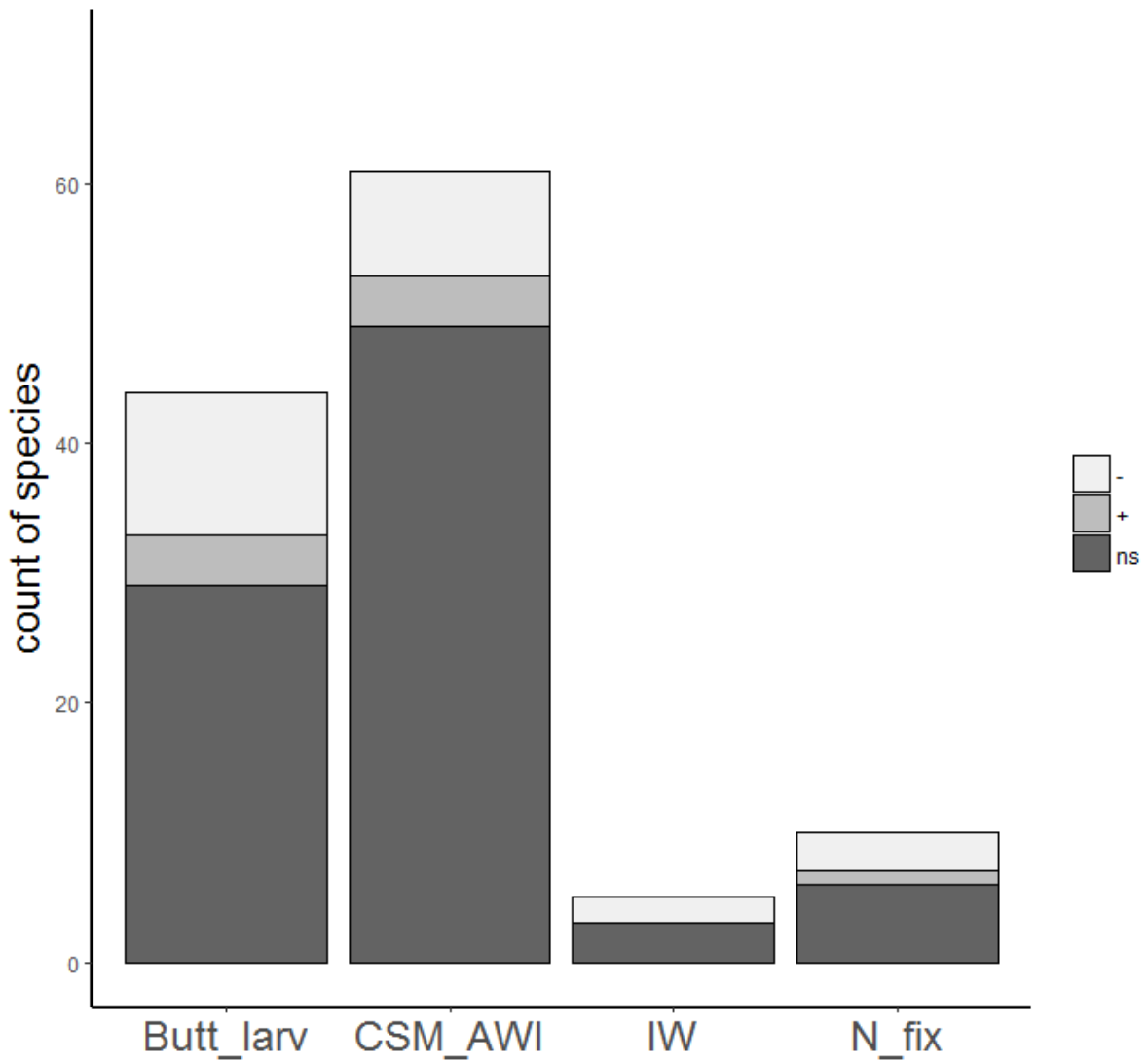


Figure 6: Summed cover of the plant species tested or with too few records to test expressed as a percentage of the total cover of all plant species in the 137 Countryside Survey linear plots in Wales recorded in 1990, 1998, 2007 and 2016.

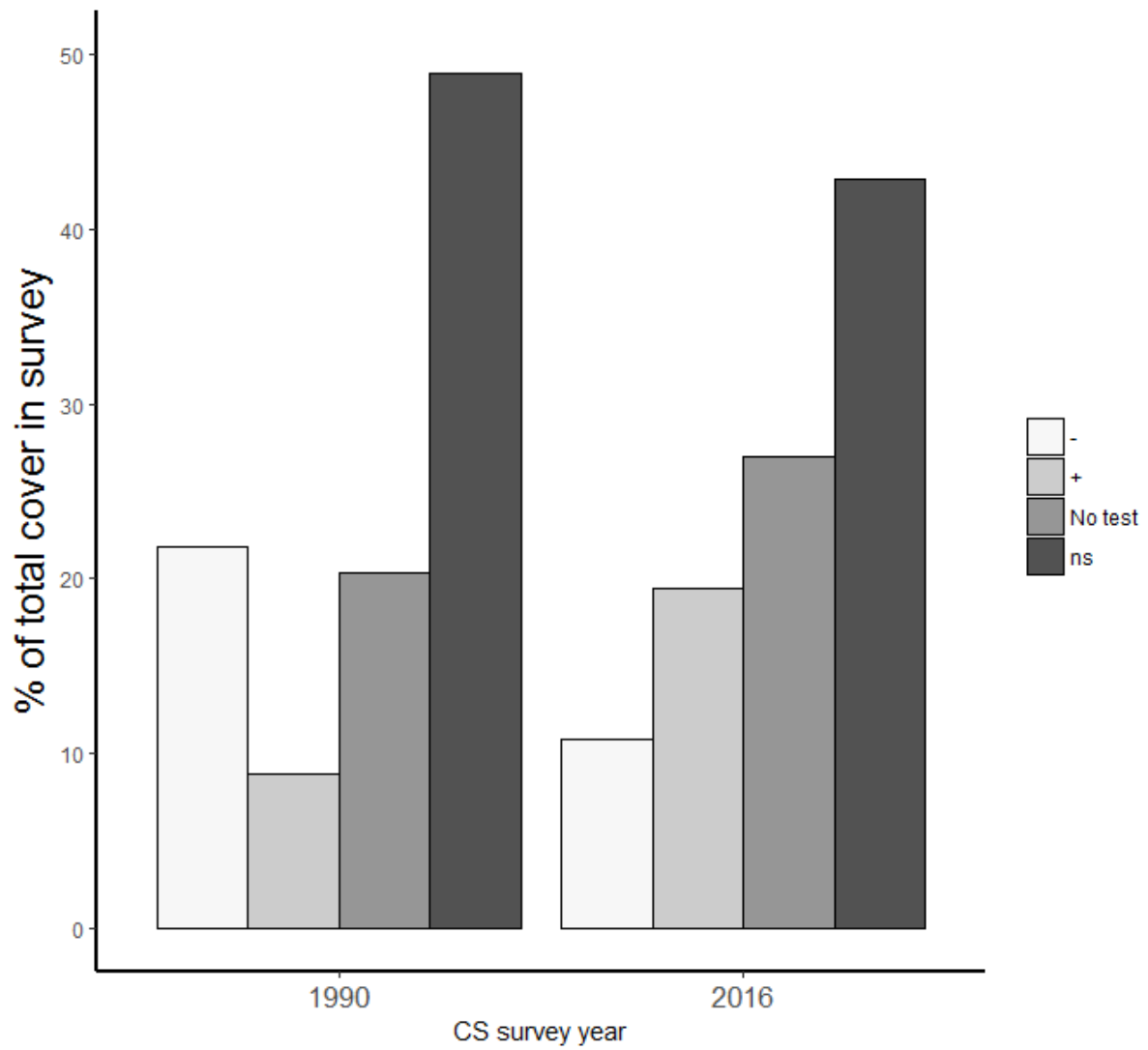


Figure 7: Changes in potential nectar production by growth form (f=forb, w=woody species includes two lianas). Sugar yield was estimated by summing the database values for each plant species given in Baude *et al.*, (2016). These are potential sugar yield values and therefore depend on production of an average number flowers per unit area of plant cover per growing season.

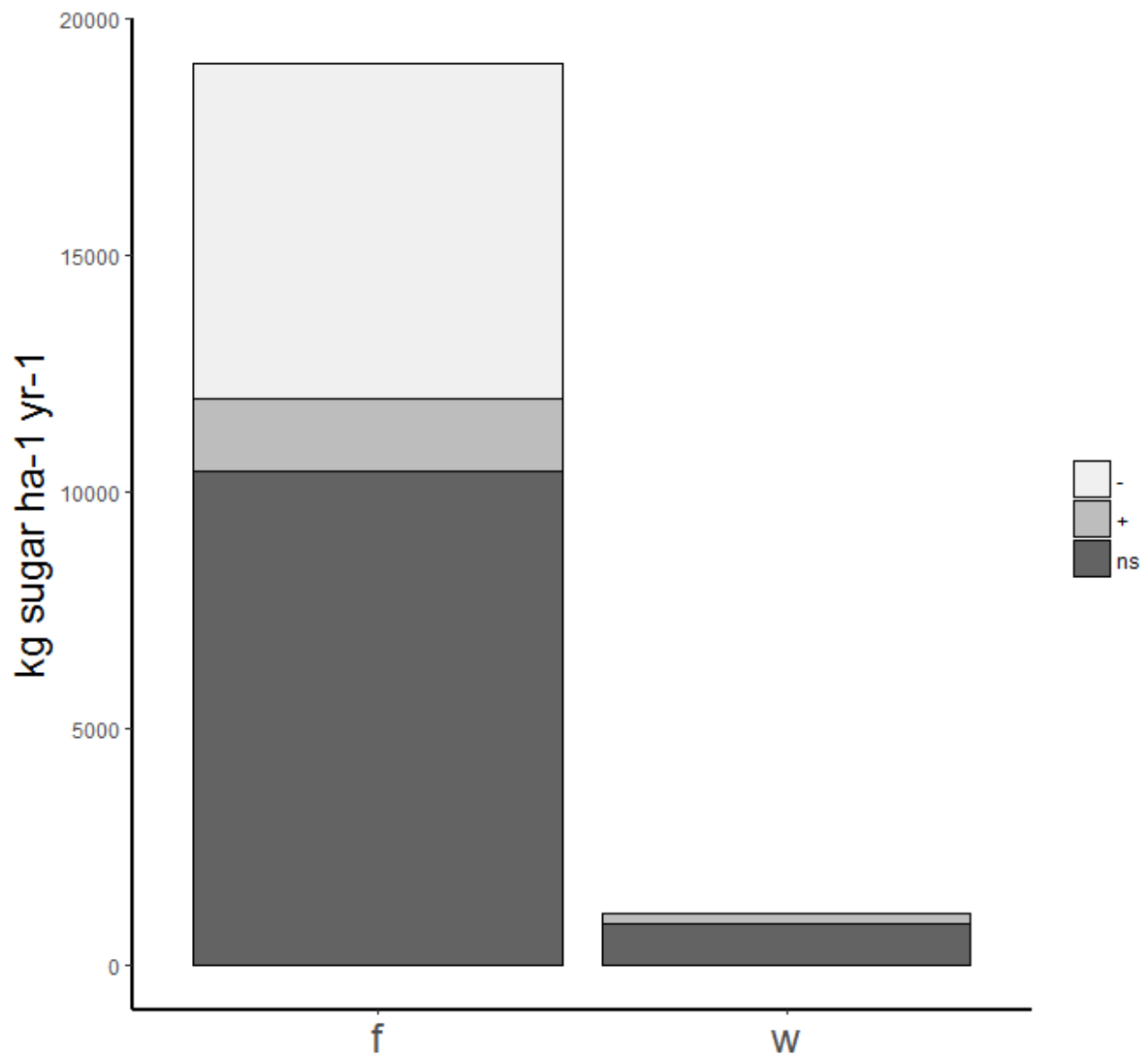


Fig S1: Histograms of detection rate plus a kernel density estimate of predicted values of detection rate given fitted Beta distributions by plant growth form (Gf) where f = forb, g = graminoid, w = woody species, and year of survey (Yr). Detection rate is the proportion of plants species recorded by the QA surveyor that were also recorded by the CS field surveyors.

