

## Current status of the rare British endemic *Gentianella amarella* subsp. *occidentalis*, Dune Gentian (Gentianaceae)

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### Abstract

*Gentianella amarella* subsp. *occidentalis*, Dune Gentian, is a rare annual of dune slacks endemic to Western Britain. Its current status was compared to historic records. A maximum of 2250 plants were found in ten subpopulations in four sites in 2019-2020. It was not refound in three sites and 15 subpopulations. It is assessed as IUCN threat category 'Endangered'. Its primary vegetation type is SD14d *Salix repens* - *Campylium stellatum* dune slack *Festuca rubra* subcommunity, within which it favours short, open structure on dry, low nutrient soils. Conservation requires managing and creating its niche in the dune slacks.

**Keywords:** Dune slack; Endangered; England; IUCN threat criteria; Wales.

### Introduction

*Gentianella amarella* subsp. *occidentalis* T.C.G. Rich & McVeigh, Dune Gentian, is a small, summer annual of dune slacks endemic to South Wales and North Devon in Western Britain (Rich & McVeigh, 2019; Stace, 2019; Figs. 1 & 2). Historically referred to as *Gentianella uliginosa* (Willd.) Börner in Britain, it was recently recognised as a morphologically distinct taxon related to the biennial *G. amarella* subsp. *amarella* (Rich *et al.*, 2018). A short video showing the plant and its habitat prior to the work reported here is given by Rich (2019).

Rich & McVeigh (2019) noted Dune Gentian had been recorded from seven sites in four vice-counties (North Devon, Glamorgan, Carmarthenshire and Pembrokeshire) and gave its IUCN threat category as 'Vulnerable'. Following concern that it was declining, a comprehensive survey of all its sites in 2019-2020 was undertaken, its IUCN threat category re-assessed, the habitat described and recommendations made for its conservation. The results are summarised here; fuller details are given in Evans (2020).

### Methods

Historical data on its distribution, abundance and habitat were compiled from herbaria (**ABD, BIRM, BM, CGE, HDD, K, LTR, NMW, OXF, RNG**), literature, the BSBI Distribution Database (<https://database.bsbi.org/>, accessed January 2019), Aderyn/LERC Wales (accessed January 2019) and data held by Natural Resources Wales. The population counts from the last 50 years presented in the figures have been compiled from Vaughan *et al.* (1972), Elias (1981), Youngson (1986), Jones

(1992, 1993, 1994), Kay & John (1995), Rich (2004), Dockerty (2010), the BSBI database and our personal observations.



**Figure 1. *Gentianella amarella* subsp. *occidentalis*.**



**Figure 2: Sites from which *Gentianella amarella* ssp. *occidentalis* has been recorded. Basemap © Google maps**

L. Evans with the help of M. Breeds, N. Ferris, R. Harding, T.C.G. Rich and J. Woodman searched all sites except for one subpopulation in August and September 2019, and most of the Welsh sites were searched again in August and September 2020 including the missing subpopulation. Populations were counted by careful searching, and taking care to distinguish plants from *G. amarella* subsp. *amarella* with which it often grows (Rich & McVeigh, 2019). Hybrids reported as *G. amarella* x *uliginosa* are no longer accepted and most such plants are depauperate subsp. *amarella* (Rich & McVeigh, 2019).

IUCN (2001, 2019) threat categories were determined by assessing the site and population data against the IUCN criteria, using the highest recent population count where two counts were available. Estimates of extent and occupancy were calculated using MAGIC maps (DEFRA, 2013).

Vegetation data were recorded using 2 x 2 m quadrats following the NVC protocol but also with percentage cover (Rodwell, 2000, 2006). Additional quadrats from surrounding dune slacks and slopes approximately 1 m altitude above and below the *Gentianella* population were recorded to provide comparative data. NVC community types were allocated using the floristic tables and keys in Rodwell (2000) and 'MAVIS' software (Smart, 2000).

Ellenberg indicator values (Hill *et al.*, 2004) were calculated for each quadrat in MAVIS. Mean values were calculated by combining quadrat data at, below and above the level of the target species; these values were analysed using one-way ANOVA to determine which variables differed significantly. Ellenberg values for each

population were compared to those derived from the 'standard' associated NVC community data from Rodwell (2000); as the NVC tables give Domin scores, percentage cover required by MAVIS was calculated by taking the median Domin value from the cited range and calculating  $(\text{Domin})^{2.6}/4$  to correct for underestimation of the means (Currall, 1987).

Vascular plant nomenclature follows Stace (2019). NVC types follow Rodwell (2006).

## Results

### *Population sizes*

#### 1. Braunton Burrows (v.c.4)

It was first collected at Braunton Burrows in 1843 but was only rediscovered recently (Holyoak, 1999). It been recorded as widely distributed in five slacks but never in quantity; Holyoak (1999) recorded 'over 130 plants', BSBI records mention 'several plants' and an unpublished Natural England report from 2012 states 'half a dozen plants'. In 2019, a total of 43 plants were found in four slacks, again all in small quantity (Table 1) including two new subpopulations. It was not refound in three historic subpopulations (one slack was suitable but two were not) giving a total of seven locations within the Burrows.

#### 2. Northam Burrows (v.c.4)

It was only recorded once at Northam Burrows in 1882 (Rich, 1996). No plants were found in 2019 or on three previous searches by T. Rich 2004-2008. Northam Burrows is now a golf course and only one small slack remains with generally unsuitable habitat.

#### 3. Oxwich Bay (v.c.41)

It was first recorded at Oxwich in 1927 and subpopulations have been recorded at up to seven slacks (Lousley, 1950; Kay, 1973; Elias, 1981; Table 1). The recent population data traced are summarised in Fig. 3. Jones (1994) noted populations recorded by Morgan (1988) in three slacks had gone by 1993. In the early 1990s, the large population in Slack 21 was nearly destroyed by construction of a dune scrape (Q.O.N. Kay, pers. comm. 1995); it has taken over 20 years for this population to recover.

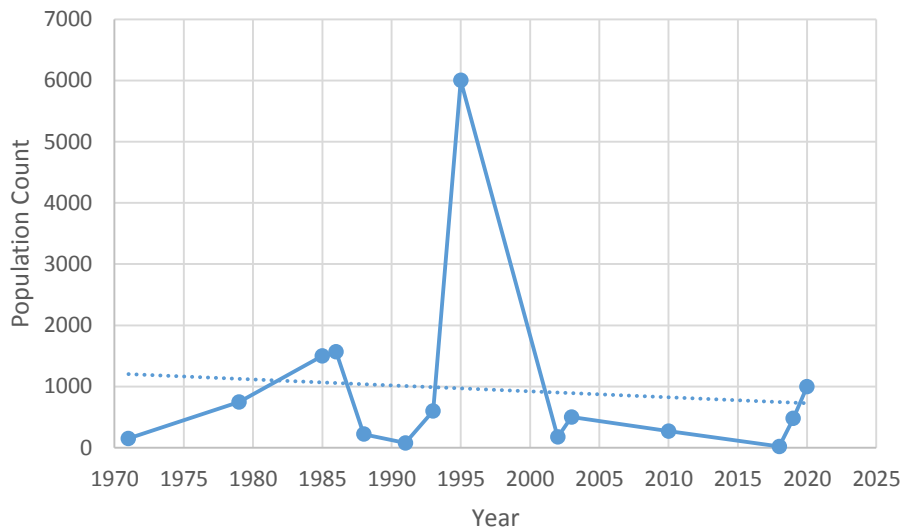
In 2019, one good population of 478 plants was found on the scraped edges of Slack 21, with a few isolated plants in the centre. In 2020, 998 plants were present (Table 1). The six slacks with historic records now all have coarse vegetation or scrub and no plants were found in them.

#### 4. Whiteford Burrows (v.c.41)

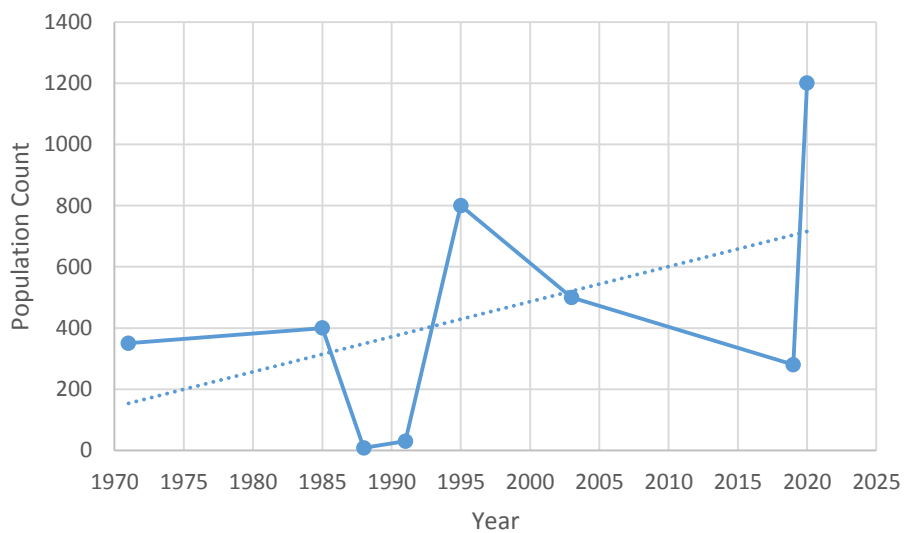
It was first recorded at Whiteford in 1934 and has been recorded in at least seven widely distributed slacks (Lousley, 1950; Kay, 1973; Table 1). In 2019, 280 plants were found in four slacks, with over two-thirds of the population in Slack 19. Slacks 7 and 9, which had records of several hundred plants in 2003-2004, had only several dozen plants despite having suitable habitat at the time of survey. At Slack 60 where it was recorded as 'occasional' in 2015, one diminutive plant was found. In 2020, a total of c.1200 plants were found in Slacks 9 and 19, the latter again with the largest subpopulation. Many of the slacks on the east side of the dunes with records from



the 1970s have scrubbed over with *Salix* spp. and *Betula pubescens*. The recent population data traced are summarised in Fig. 4.



**Figure 3. Population counts of *Gentianella amarella* subsp. *occidentalis* at Oxwich. A trend line (dotted) is also given.**



**Figure 4. Population counts of *Gentianella amarella* subsp. *occidentalis* at Whiteford. A trend line (dotted) is also given.**

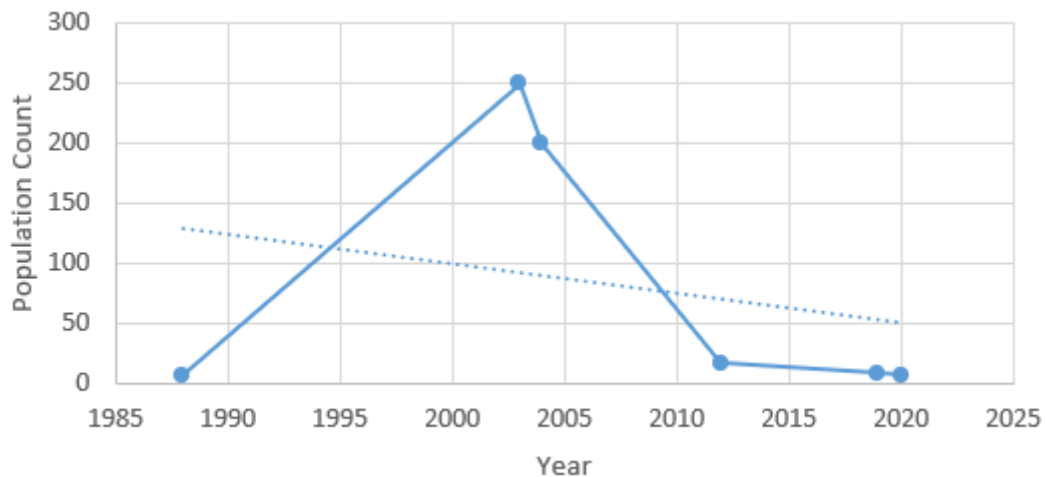
#### 5. Pendine Burrows (v.c.44)

It was first recorded at Pendine in 1944 (Vaughan *et al.*, 1972) and has occurred in two locations, on tractor ruts in a slack and beside a test track. A possible third subpopulation at SN284072 (Jones, 1993) has not been confirmed and no plants were found there in 2020. It was last recorded in 1992 when seed was collected and no plants were reported in 1993 (Jones, 1994).

In 2019 and 2020, no plants were found; the slack has become unsuitable with coarse slack vegetation (though there had been some recent scrub clearance) and the test track has only a modicum of suitable slack vegetation.

#### 6. Pembrey Burrows (v.c.44)

It was first recorded at Pembrey in 1961 and has been recorded at three locations. The recent population data traced are summarised in Fig. 5. In 2019, only nine plants were found in an area of short turf, which had seven plants in 2020 (Table 1). It was not re-located on a trackway where previously noted as 'occasional' and where suitable habitat was present, or the helipad where it was frequent in 2003 but was dominated by coarse vegetation in 2019.



**Figure 5. Population counts of *Gentianella amarella* subsp. *occidentalis* at Pembrey. A trend line (dotted) is also given.**

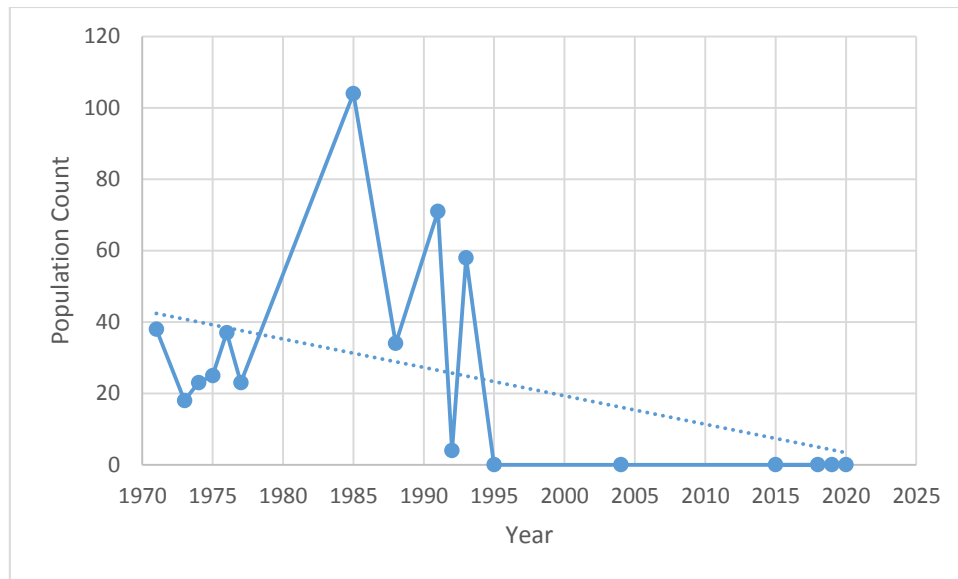
#### 7. Penally Burrows, Tenby (v.c.45)

It was first recorded at Penally in 1923 and was recorded in damp sandy pastures and a dune slack; the former may have been destroyed by construction of the golf course in 1946 and by 1950 and 1971 was restricted to one slack (Pugsley, 1924; Lousley, 1950; Vaughan *et al.*, 1972). A population of 58 plants was recorded in 1993 (Jones 1994) and it was last recorded in 1994. The population data traced are summarised in Fig. 6.

No plants were found in five visits 2004-2020. The slack from where it was most recorded has become dominated by rank grass and scrub, although parts of the slack had been partially scraped off in *c.*2016 in a possible attempt to restore the habitat. Grass and scrub cuttings seem to have been regularly dumped by the slack for many years which may have contributed to the changes in the vegetation.

Population fluctuations are difficult to estimate based on historical data and our survey results, but some indication of fluctuations are shown in Figs. 3-6. In 2020 in Welsh sites there were nearly three times as many plants as in 2019 showing some fluctuations from year to year (Table 1). Jones (1999) also noted that it appears to be sensitive to climatic conditions and may disappear or occur in low numbers during wet and cool summers and can reappear in abundance in warm years.

In summary, in 2019-2020 a maximum total of *c.*2250 plants were recorded in four sites in ten subpopulations and it was not recorded in three former sites or 15 subpopulations (Table 1).



**Figure 6. Population counts of *Gentianella amarella* subsp. *occidentalis* at Penally. A trend line (dotted) is also given.**

#### *IUCN threat category*

IUCN (2001) Criterion A considers a reduction in population sizes. This is difficult to quantify as the historical records are mainly sporadic, site specific and incomplete. Our population counts varied threefold between 2019 and 2020, which is consistent with the peaks and troughs historically recorded at individual sites (Figs. 3-6). Youngson (1986) estimated the Welsh populations as 2064 plants. An estimate of the Welsh populations 1991-1993 from the combined data in Jones (1992, 1993, 1994) is 215+ plants. Kay and John (1995) gave estimates of the Welsh populations as 4000-8000 plants at Oxwich, 600-1000 plants at Whiteford and 40+ plants at Pendine, suggesting (using mid-range values) a population of c.6840 (we have some concerns about the accuracy of these estimates, though it may have been an exceptional year). However, it is clear that all sites in South Wales have lost subpopulations and a significant ten year decline seems very likely (Figs. 3-6; Table 1). It is difficult to assess trends at Braunton from the fragmentary data.

IUCN (2001) Criterion B1 considers the geographic range. The extent of occurrence is defined as the smallest imaginary boundary drawn between all known sites (IUCN, 2001, 2019). A degree of subjectivity was involved in estimating extent; a generous boundary gave an extent of 1100 km<sup>2</sup> while a frugal boundary gave an extent of 130 km<sup>2</sup>; both figures place it between 100 km<sup>2</sup> - 5000 km<sup>2</sup> which equates to the 'Endangered' category. The population is highly fragmented and is currently known from four sites. It is subject to continued decline based on (i) a reduction in extent of occurrence as a result of being lost from the Penally and Pendine sites in recent years; (ii) a decline in area of occupancy as a result of being lost from the Penally and Pendine sites; (iii) decline in quality of suitable habitat, particularly as a result of scrub encroachment on sites across South Wales; and (iv) a decline in the number of subpopulations, particularly at Oxwich and Whiteford, qualifying it as 'Endangered'.

**Table 1. Population counts of *Gentianella amarella* subsp. *occidentalis* for all sites surveyed 2019-2020.**

| <b>Site</b>             | <b>Subpopulation</b>     | <b>No. plants 2019</b> | <b>No. plants 2020</b> | <b>Maximum total per site</b> |
|-------------------------|--------------------------|------------------------|------------------------|-------------------------------|
| Braunton Burrows        | Beach Head Slack         | 3                      | -                      |                               |
|                         | Beach Head Slack north a | 0                      | -                      |                               |
|                         | Beach Head Slack north b | 0                      | -                      |                               |
|                         | Bush grass Slack         | 0                      | -                      |                               |
|                         | Partridge Slack          | 21                     | -                      |                               |
|                         | Pebble Slack             | 6                      | -                      |                               |
|                         | Pine Slack               | 13                     | -                      |                               |
|                         |                          |                        |                        | 43                            |
| Northam Burrows         | Northam Burrows          | 0                      | -                      |                               |
|                         |                          |                        |                        | 0                             |
| Oxwich                  | Slack 11/Near Slack 9    | 0                      | 0                      |                               |
|                         | Slack 16/18              | 0                      | 0                      |                               |
|                         | Slack 20                 | 0                      | 0                      |                               |
|                         | Slack 21 (new scrape)    | 478                    | 998                    |                               |
|                         | SW of Slack 21           | 0                      | 0                      |                               |
|                         | Slack 31                 | 0                      | 0                      |                               |
|                         | Slack 39                 | 0                      | 0                      |                               |
|                         |                          |                        |                        | 998                           |
| Pembrey                 | Helipad                  | 0                      | -                      |                               |
|                         | South of targets         | 9                      | 7                      |                               |
|                         | Targets by track         | 0                      | -                      |                               |
|                         |                          |                        |                        | 9                             |
| Penally Burrows         | Golf course Slack        | 0                      | 0                      |                               |
|                         |                          |                        |                        | 0                             |
| Pendine                 | Slack C9                 | 0                      | 0                      |                               |
|                         | Slack E4                 | -                      | 0                      |                               |
|                         |                          |                        |                        | 0                             |
| Whiteford               | Slack 7                  | 54                     | 0                      |                               |
|                         | Slack 9                  | 23                     | c.100                  |                               |
|                         | Slack 19                 | 202                    | c.1100                 |                               |
|                         | Slacks 20-28             | 0                      | 0                      |                               |
|                         | Slack 43                 | 0                      | 0                      |                               |
|                         | Slack 60                 | 1                      | 0                      |                               |
|                         | Slack 94                 | 0                      | 0                      |                               |
|                         |                          |                        |                        | c.1200                        |
| Maximum total all sites | 28 sites                 |                        |                        | c.2250                        |

IUCN (2001) Criterion B2 also considers the geographic range using area of occupancy, defined as the area of suitable habitat from which the taxon is currently



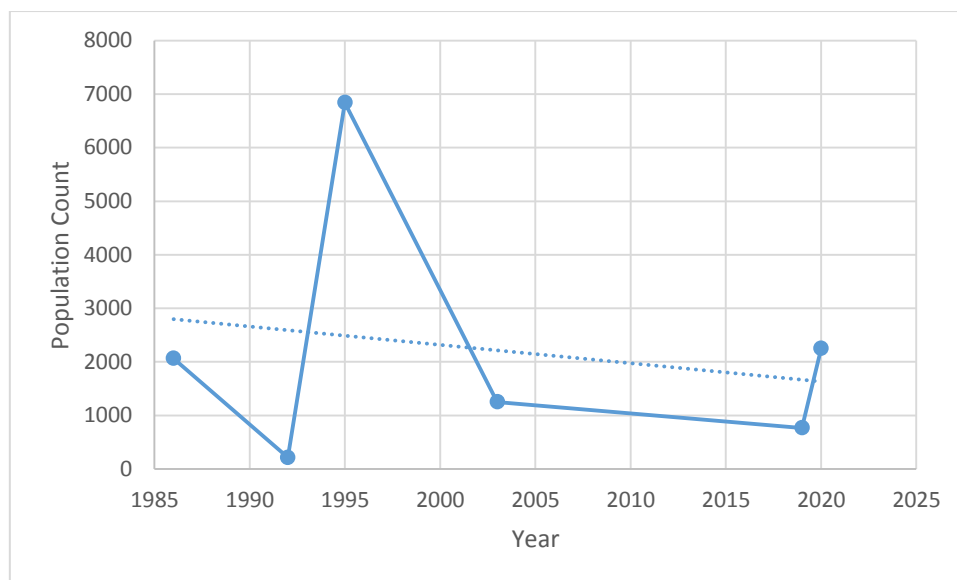
known (IUCN, 2001, 2019). The area of occupancy was measured as 9.24 km<sup>2</sup> by measuring the area of the sand dune systems at its current four sites. When combined with a continued decline in (i) extent of occurrence; (ii) area of occupancy; (iii) quality of habitat; and (iv) number of subpopulations, this qualifies as 'Endangered'.

IUCN (2001) Criterion C considers the population sizes coupled with decline. With only c. 2250 plants recorded in 2019-2020, it is classified as 'Endangered', the threshold for which is fewer than 2500 individuals coupled with an observed or projected population decline. Given the loss of the plant from several sites and numerous subpopulations and the declines indicated in Figs. 3, 5 and 6, it seems likely that losses of significant magnitude have taken place in recent decades.

IUCN (2001) Criterion D deals with very small or restricted population sizes. A maximum population size of c. 2250 plants qualifies it as 'Vulnerable' in this category.

IUCN (2001) Criterion E concerns population projections and the likelihood of extinction in the wild. Fig. 7 shows the overall population sizes in South Wales where comparable data across sites is available. As this is based on only six data points and there is some uncertainty over the Kay & John (1995) population estimates it requires cautious interpretation. There is little evidence of a general decline over the last 30 years but it is clear individual sites and subpopulations are declining or have disappeared (as above). There is not enough data to predict when, in the absence of conservation measures, it could become extinct.

Based on our data, under Criteria A, B and C, *G. amarella* subsp. *occidentalis* clearly qualifies as IUCN (2001) threat category 'Endangered'.



**Figure 7. Total population counts of *Gentianella amarella* subsp. *occidentalis* from Welsh sites only. A trend line (dotted) is given.**

### *Vegetation*

The species associated with *G. amarella* subsp. *occidentalis* at constancies of V, IV and III (cf. Rodwell, 2006, i.e. occurring in more than 40% of the quadrats,) are summarised in Table 2; another 12 species were recorded at constancy II and 49 species at constancy I. The vegetation was short (average vegetation height 3.4 cm

± 1.62 cm s.d., range 1-7 cm), open (average cover of 93.3% ± 8.76% s.d., range 75-100%) and species-rich (average number of species per quadrat of 25.9 ± 4.22 s.d., range 16-33 species). The associated species included a few short-lived plants like *G. amarella* subsp. *amarella* and *Linum catharticum* which occur in the open gaps between the perennials.

During the surveys it was noticed that there may be a pattern of stratification within the slacks; small colonies and some isolated plants of *G. amarella* subsp. *occidentalis* occurred at the lowest points in a number of dune slacks where frequent associates included *Epipactis palustris*, *Hydrocotyle vulgaris*, *Lysimachia tenella* and *Pulicaria dysenterica*. The more extensive colonies occurred in marginally drier areas with species more associated with dune slopes including *Hypochaeris radicata*, *Rhinanthus minor* and *Rubus caesius*.

In terms of British Plant Communities (Rodwell, 2000), the data indicated that in South Wales *G. amarella* subsp. *occidentalis* occurs in the SD14d *Salix repens*-*Campyllum stellatum* dune slack *Festuca rubra* subcommunity. At Braunton Burrows it occurred in the grassier, older and drier dune slacks with an affinity to both SD14d and to SD16 *Salix repens*-*Holcus lanatus* community which had low *Salix repens* cover and could not be clearly allocated to a subcommunity.

As *G. amarella* subsp. *occidentalis* is a summer annual, plants must occupy a narrow niche within the dune slack where plants can germinate, establish, flower and fruit within a temporally variable habitat whose major variable is water table. The ecological factors were therefore characterised further using Ellenberg indicator values for the quadrats (Hill *et al.*, 2004; Table 3). Moisture levels lay between 'moist site' and 'damp site' on the Ellenberg scale. 'Nitrogen', a proxy for soil fertility, indicated the quadrats were located on 'more or less infertile sites'. Light values fell between the definitions 'plant generally in well-lit places, but also occurring in partial shade' and 'light-loving plant rarely found where illumination in summer is less than 40%', but as no plants were found in former sites which were now shaded by scrub, light is obviously important overall. Reaction values, a measure of soil pH, were between 'moderately acid soils' and 'weakly acid to weakly basic'. There was no indication of any saline influence in the vegetation in which it occurred.

By comparing Ellenberg values for quadrats with *G. amarella* subsp. *occidentalis* with quadrats without it from adjacent vegetation at altitudes *c.* 1 m above and below, the key factors were indicated to be Moisture ( $F = 5.47$ ;  $p = 0.01$ ) and Nitrogen ( $F = 13.56$ ;  $p = 0.0001$ ), both well known to be important factors for controlling the occurrence of dune slack vegetation (Rodwell, 2000). Light ( $F = 1.43$ ;  $p = 0.26$ ) and Reaction ( $F = 0.55$ ;  $p = 0.58$ ) values were not significantly different between vegetation supporting *G. amarella* subsp. *occidentalis* and adjacent vegetation without it.

The Ellenberg values were also compared against the values calculated for the 'standard' SD14d *Salix repens*-*Campyllum stellatum* dune slack *Festuca rubra* subcommunity and the SD16 *Salix repens*-*Holcus lanatus* community (Rodwell, 2000; Table 3). The Moisture value for the *G. amarella* subsp. *occidentalis* quadrats was 0.9 points lower than the SD14d standard sub-community (Table 3), suggesting that it occurs in areas that are atypically dry, and lies much closer to that of SD16 than SD14d, with SD16 being associated with older and drier dune slacks as at Braunton (Rodwell, 2000). There is much less variability in Nitrogen values than for moisture (Table 3), which is to be expected in a sand dune system low in available nutrients

(Grootjans *et al.*, 1998), though *G. amarella* subsp. *occidentalis* lies over half a point lower than the standard SD14d community and almost a point lower than the SD16 standard community with which it more closely aligns on Moisture value. The Light and Reaction values are very similar (Table 3).

**Table 2. Species associated with *Gentianella amarella* subsp. *occidentalis* in 16 quadrats (5 at Braunton, 5 at Oxwich, 2 at Pembrey and 4 at Whiteford).**

| Species  | Constancy |
|--|-----------|
| <i>Gentianella amarella</i> subsp. <i>occidentalis</i> | V         |
| <i>Carex flacca</i>                                    | V         |
| <i>Festuca rubra</i>                                   | V         |
| <i>Gentianella amarella</i> subsp. <i>amarella</i>     | V         |
| <i>Leontodon saxatilis</i>                             | V         |
| <i>Linum catharticum</i>                               | V         |
| <i>Lotus corniculatus</i>                              | V         |
| <i>Prunella vulgaris</i>                               | V         |
| <i>Salix repens</i>                                    | V         |
| <i>Equisetum variegatum</i>                            | IV        |
| <i>Euphrasia</i> spp.                                  | IV        |
| <i>Hydrocotyle vulgaris</i>                            | IV        |
| <i>Leontodon hispidus</i>                              | IV        |
| <i>Agrostis stolonifera</i>                            | III       |
| <i>Carex viridula</i>                                  | III       |
| <i>Danthonia decumbens</i>                             | III       |
| <i>Epipactis palustris</i>                             | III       |
| <i>Holcus lanatus</i>                                  | III       |
| <i>Homalothecium lutescens</i>                         | III       |
| <i>Lysimachia tenella</i>                              | III       |
| <i>Mentha aquatica</i>                                 | III       |
| <i>Polygala vulgaris</i>                               | III       |
| <i>Pulicaria dysenterica</i>                           | III       |
| <i>Ranunculus flammula</i>                             | III       |
| <i>Rubus caesius</i>                                   | III       |
| <i>Trifolium pratense</i>                              | III       |
| <i>Trifolium repens</i>                                | III       |

## Discussion

The total world population of *G. amarella* subsp. *occidentalis* comprised only c.2250 plants in 2019-2020. It occurred in only ten subpopulations in four sites. Whilst declines are difficult to quantify due to varied historical recording, the data suggests that it has declined in both populations and sites since the 1970s and it was not refound in three sites and 15 subpopulations. The decline noted by Jones (1994) has continued with the loss of the Penally and Pembrey sites, and it must now be regarded as IUCN (2001) threat category 'Endangered'.

**Table 3. Ellenberg indicator values (Hill *et al.*, 2004) of *Gentianella amarella* subsp. *occidentalis* quadrats compared with those for SD14d *Salix repens-Campyllum stellatum* dune slack *Festuca rubra* subcommunity and SD16 *Salix repens-Holcus lanatus* community.**

| <b>Ellenberg Indicator</b> | <b>Mean value (<math>\pm</math> SD) subsp. <i>occidentalis</i> quadrats</b> | <b>Mean value for SD14d community</b> | <b>Mean value for SD16 community</b> |
|----------------------------|---|---------------------------------------|--------------------------------------|
| Moisture                   | 6.03 ( $\pm$ 0.64)  | 6.9                                   | 6.2                                  |
| Nitrogen                   | 3.16 ( $\pm$ 0.30)  | 3.7                                   | 4.0                                  |
| Light                      | 7.52 ( $\pm$ 0.17)  | 7.5                                   | 7.4                                  |
| Reaction                   | 6.11 ( $\pm$ 0.17)  | 6.3                                   | 6.3                                  |

The decline has occurred despite it having had statutory protection (as *Gentianella uliginosa* auct. angl.) for years. It is protected under Schedule 8 of the Wildlife and Countryside Act 1981 as amended, is a Section 41 Species of Principal Importance under the Natural Environment and Rural Communities Act 2006 in England, a Section 7 Species of Principal Importance in Wales under the Environment (Wales) Act 2016 in Wales and a Red Data Book species (Wigginton, 1999). The decline has also occurred despite it being listed as a feature in the SSSI schedules for all of its recent sites (Braunton Burrows SSSI, Oxwich Bay SSSI, Whiteford Burrows, Landimore Marsh and Broughton Bay SSSI, Pembrey Coast SSSI, Laugharne-Pendine Burrows SSSI and Lydstep Head to Tenby Burrows SSSI; it was probably long gone before Northam Burrows SSSI was designated). Furthermore, the Whiteford and Oxwich populations are within National Nature Reserves, the Braunton Burrows population is within a Biosphere Reserve, and the Whiteford, Pembrey, and Pendine Burrows sites are within the Carmarthen Bay Dunes Special Areas of Conservation. Such designations may have provided general protection to the sites (though the Oxwich population was nearly destroyed by scraping its slack in the early 1990s), but have not maintained the specific ecological niche it requires.

A refocus on maintaining and creating appropriate growth conditions is clearly required so the habitats have been characterised. The vegetation analysis showed the primary ecological niche is the SD14d *Salix repens-Campyllum stellatum* dune slack *Festuca rubra* subcommunity. This species-rich vegetation type occurs in slacks of moderate age that are neither newly formed nor long-established and shares many of its characteristics with species-rich fens (Rodwell, 2000; Proctor, 2013). It is an uncommon community - in Wales only occurring extensively at ten sites - which supports 18 rare or scarce plants including dune slack specialities such as *Liparis loeselii* and *Teucrium scordium* (Rhind & Jones, 1999; Rodwell, 2000; Blackstock *et al.*, 2010).

However, whilst both the soil Moisture and Nitrogen Ellenberg values are important in determining its niche, they do not seem to be entirely typical of SD14d vegetation. Whilst the gentian requires reasonable levels of moisture, as would be expected from a dune slack species (Grootjans *et al.*, 2004), the Ellenberg values indicate it favours slightly drier soils than 'typical' SD14d; with some of the largest subpopulations occurring within drier slacks or towards the edge of mechanical scrapes. This may account for the similarities to the SD16 community, which tends

to occur in drier slacks further along the successional sequence (Rodwell, 2000). A 'grassy look' to the sward is used to describe both SD14d and SD16 which is typical of many of the communities surveyed, but the low *Salix repens* scrub which typifies SD16 and to a lesser extent SD14 is not a feature of the *G. amarella* subsp. *occidentalis* niche in which the mean vegetation height was only 3.4 cm.

Soil fertility seems to be a major factor and it favours areas that are less fertile than are typical of the communities. As it favours nutrient-poor soils, it is possible that atmospheric nitrogen deposition may have had a long-term impact on some sites. Nitrogen deposition in dune slacks is thought to have a limited effect on the vegetation (Jones *et al.*, 2004), though studies at Braunton Burrows showed that dune vegetation responds to increased nitrogen levels (Willis, 1963). Nutrient enrichment also results from the accumulation of organic matter associated with sand-dune succession (Olf *et al.*, 1993) or accumulation of biomass from a lack of grazing.

Local factors within the vegetation may also play a role in determining the gentian's niche. Many of the populations surveyed occurred near trackways, paths or where mechanical groundwork had been undertaken and it clearly prefers open ground. Such ground disturbance is usually favourable to annuals (Kleyer, 1999), such as *G. amarella* subsp. *occidentalis*, and should be considered as part of future management.

Longer term, management is also key to maintaining populations and its niche. Rabbit grazing was evident at all extant populations and the close-cropped sward that they produce is important to maintaining the open vegetation. Where rabbit numbers have been reduced in the past, for example by myxomatosis at Braunton, there has been a marked decline in the richness of dune vegetation (Breeds & Rogers, 1998). However, rabbits are only likely to be able to maintain suitable conditions when used in conjunction with other grazing animals that are more effective at removing coarser vegetation (Rhind & Jones, 2009; Ausden, 2007). Lack of management has resulted in *Salix* and *Betula* scrub encroachment and many South Wales slacks are now in the latter successional stages, and accounts for declines such as at Oxwich. Maintaining the present vegetation and niche around the largest remaining populations at Oxwich and Whiteford is thus critical. Habitat restoration is also required and should focus on areas where *G. amarella* subsp. *occidentalis* was recently known to occur or slacks near to existing populations. There is a clear need for experimental management work to be undertaken under field conditions as has been done for *Liparis loeselii* which appears to occupy a similar niche (Jones, 1998; Carrington *et al.* 2010).

At a landscape scale, the dune slack habitats are created by natural processes, progressing over periods of 20-60 years from pioneer slacks to mature slacks before being lost to succession (Grootjans *et al.*, 2002, 2004). The Dune Gentian and other rare plants are dependent on this dynamic system allowing maintenance of metapopulations, but dune systems have become less dynamic in the last 60-70 years as a result of changes in both climate and management (Pye *et al.*, 2013) and it is uncertain that the processes will continue to create adequate suitable habitat in the future. Species-rich dune slack communities can be both maintained and re-established through judicious management (Sýkora *et al.*, 2004). The 'Sands of LIFE' project (Natural Resources Wales, 2021) aims to recreate natural movement in and rejuvenate habitats in ten Welsh dunes sites 2018-2022 including the Pembrey,

Pendine and Whiteford sites, which may indirectly benefit *G. amarella* subsp. *occidentalis* in the long term which is not specifically included in the project.

*Gentianella amarella* subsp. *occidentalis* has no obvious adaptation to seed dispersal and the life of its seed bank (cf. Jones, 1999) is unknown, so local seed reintroductions could be considered should populations continue to decline. Five small seed collections are held in the Millennium Seed Bank from Oxwich (1967, 1992), Penally (1992), Pendine (1992) and Pembrey (1974) (S. Miles, pers. comm. 2021) and new collections from Braunton and Whiteford would be a priority to collect. Although *Gentianella* taxa are notoriously difficult to grow from seed, possibly due to a dependency on specific vesicular-arbuscular mycorrhizae, T. Rich was able to grow one collection of *G. amarella* subsp. *occidentalis* (collected under licence) from Oxwich to fruit set using the sand from the dune slack so it may be possible to bulk up seed stocks for reintroduction and management programmes.

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