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A fundamental, eco-hydrological basis for niche segregation in plant communities

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SUMMARY

- Ecologists still puzzle about how plant species manage to coexist with one another while competing for the same essential resources. The classic answer for animal communities is that species occupy different niches, but how plants do this is more difficult to detect. We previously found niche segregation along fine-scale hydrological gradients in European wet meadows and proposed that the mechanism might be a general one especially in communities which experience seasonal saturation.

- We quantified hydrological niches of 96 species from eight fynbos communities in the biodiversity hotspot of the Cape Floristic Region, South Africa and 99 species from 18 lowland wet meadow communities in the UK. Niche overlap was computed for all combination of species.

- Despite the extreme functional and phylogenetic differences between the fynbos and wet meadow communities, an identical trade-off (i.e. specialisation of species towards tolerance of aeration and or drying stress) is found to cause segregation along fine-scale hydrological gradients.

- This study confirms not only the predicted generality of hydrological niche segregation, but also emphasizes its importance for structuring plant communities. Eco-hydrological niche segregation will have implications for conservation in habitats that face changing hydrology caused by water abstraction and climate change.

Keywords: fynbos, hydrological gradient, niche segregation, Sum Exceedance Values, trade-off, wet meadow
INTRODUCTION

The fundamental question of how competing plant species manage to coexist with one another to form stable, diverse communities is a problem that continues to vex community ecology. The issue has lacked resolution for so long that it has often recently been claimed that neutral models that assume the ecological equivalence of all species cannot currently be rejected and that stabilizing mechanisms are unimportant (Hubbell, 2001; de Aguiar et al., 2009). For neutral models to be rejected, the existence of mechanisms that stabilize communities through niche segregation must be established (Chesson, 2000; Adler et al., 2007). Many such mechanisms have been proposed and more than one may function simultaneously in particular plant communities, but one of the potentially most general mechanisms invokes niche segregation along fine-scale hydrological gradients (Silvertown, 2004).

We have previously shown that segregation on hydrological gradients occurs in European wet meadows and that specialization of species into distinct niches is due to a trade-off between tolerance of aeration stress and tolerance of drying stress (Silvertown et al., 1999). The trade-off was shown to apply across species drawn from the two largest clades in the phylogeny of the angiosperms (monocots and eudicots) and was therefore predicted to be a fundamental constraint likely to affect the ecology of plants more generally (Silvertown et al., 1999). Here, we test this prediction by quantifying the hydrological niches of plants in fynbos plant communities in the Cape of South Africa, which are floristically, functionally, and phylogenetically distinct from European wet meadows.

To test how similar the underlying mechanisms structuring the two contrasting communities are, we also compare the trade-off for fynbos species with the equivalent
relationship found in an enlarged dataset of nearly 100 species drawn from 18 meadow sites in England.

**MATERIALS AND METHODS**

We quantified hydrological niches in eight fynbos plant communities selected to represent much of the diversity in this vegetation type in the Western Cape, from lowland (120m) to montane (1,080m) (Supporting Information, Table S1). Permanent plots about 50m X 50m (exact size varied with the topography of the site) were established at each of the eight sites and between 200 and 305, 1 m² quadrats, placed on a grid 3-5 m apart, were surveyed for the presence/absence of Angiosperm species between 2005 and 2008 (Supporting Information, Table S1a). A total of 96 species that were sufficiently frequent for hydrological measurement were recorded. Voucher specimens of all Cape plants recorded were lodged at Compton Herbarium, South African National Biodiversity Institute or at the Stellenbosch University Herbarium. A full list of species is given in Supporting Information, Table S2.

In England, 18 lowland wet meadow sites were studied using between 45 and 821, 1 m² quadrats between 1993 and 2001 (Supporting Information, Table S1b). A total of 99 species that were sufficiently frequent for hydrological measurement were recorded (Supporting Information, Table S2).

Soil water regime within all plots was assessed using hydrological models (Gowing & Youngs, 1997). The models were built from inputs of water-table depth behaviour in the field, topographic variation, soil characteristics and, for meadow sites only, meteorological data. The water-table depth was monitored through an array of tube wells, supported by automatic logging pressure transducers known as ‘Divers’
The tube wells were read manually every two weeks, while automatic divers in a sub-sample of wells were set to read every four hours for at least 12 months’ duration. Topography was surveyed at all quadrat and tube well locations using a total station device (Leica Geosystems TPS300).

Using the hydrological monitoring from tube wells and Divers, the water-table depths for each quadrat location were then obtained via the hydrological model. These water-table depths were then summarized and interpreted through the concept of Sum Exceedance Values (SEV) for aeration and water stress (Gowing & Spoor, 1998). The SEV method relies on two threshold depths uniquely calculated for a particular site. The first threshold defines the water-table depth at which the zone of densest rooting (taken to be 0-100 mm depth; Higgins et al., 1987) begins to become waterlogged (air filled pore space <10 % of total soil volume), and the second defines when drying of the surface soil becomes detectable by plants. The waterlogging threshold was calculated from the soil moisture release curve as the depth that gives 10% air-filled porosity. The soil drying threshold was calculated using Richard’s equation (Gowing & Spoor, 1998) as the depth that gives 50 cm (5 kPa) tension at the soil surface, i.e. where plants start to show effects of water stress (Henson et al., 1989). The thresholds varied between 15 - 20 cm for aeration stress and 45-48 cm for drying stress in our study sites. For each threshold, the SEV represents the degree to which water tables exceed it i.e. SEV$_a$ for aeration stress and SEV$_d$ for soil drying. The extent of the exceedance and its duration throughout the growing season is then cumulated to obtain the respective SEV. The range of SEV’s encountered in our sites is given in Supporting Information, Table S3.

The growing seasons of fynbos and meadows differ, with the former occurring in a
Southern Mediterranean climate and the latter in a Northern temperate one. We measured SEVs for fynbos communities over a twelve month season, but SEVs for meadows were measured only over the 7 month growing season characteristic of grassland vegetation in England (Broad & Hough, 1993). In order to compare SEVs values, that are measured in metre-weeks, for species in the two community types on the same temporal scale, we scaled-up SEV measurements for meadows to their 12-month equivalent values.

Niche overlap was computed with pair-wise values of Pianka's index of niche overlap for all combinations of species occurring in 5% or more quadrats at each site (Pianka, 1973). Pianka's Index calculates the niche overlap using an index of resource utilization for each pair of species in the assemblage. Niche space at each site was computed in bins of 1 metre.week x 1 metre.week (1 SEV_d x 1 SEV_a respectively), created by sub-dividing the observed SEV range in each site. Then the proportion of each species present in a particular bin relative to all the bins available on the site was calculated and used for Niche overlap analysis. Departures of mean niche overlap for the whole community from random expectation were determined by using a randomization test in Ecosim Version 7.72 (Gotelli & Entsminger, 2007) that randomized the non-zero abundances of species in boxes, but used the observed niche breadths in the randomization and kept zero abundances fixed (that is, algorithm RA4 in the notation of Gotelli & Graves, 1996). Ten thousand randomizations were run for each test.

In fynbos, we tested for niche segregation across the entire community of plant species found at each of the eight sites and also for the subset of species in each community belonging to the endemic African Restionaceae. This clade of Cape
endemics is abundant, species-rich and highly characteristic of fynbos vegetation (Rebelo et al., 2006).

RESULTS

The hydrological niche space defined by the two SEV axes was approximately lower-triangular in shape (grey areas in Fig. 1). This shape means in our dataset there are no points in the upper right sector of the diagram (Supporting Information Figure S1), where plants get exposed to high levels of drought as well as aeration stress. Such points can occur in soils with very low porosity, i.e. soils which contain too little air to allow oxygen diffusion even when dry enough to induce a drought response in plants. However, fynbos and meadow soils have high porosity which means the two stresses tend not to occur simultaneously. Tests at the eight fynbos sites show niche segregation to be significant for the whole community at seven sites and also for the Restionaceae alone at six (Table 1).

Fynbos species (n = 96) showed the expected trade-off between SEV_d and SEV_a (Fig. 2), and this did not differ significantly from the sample of 99 meadow species. We used SMATR (Warton et al., 2006) to compare standardised major axis fit lines after power transforming both SEV_d and SEV_a data (power 2/3) to achieve linearity. The results show the slope and elevation of the two regression lines are similar (p= 0.6 and
p=0.85 respectively).

<Figure 2>

**DISCUSSION**

We have shown that fynbos plants segregate along fine-scale hydrological gradients (Table 1). Although fynbos is a fire-regenerating heathland ecosystem entirely unlike wet meadows and despite the extreme differences in evolutionary history and geography between the plants of northern hemisphere wet meadows and southern hemisphere fynbos, an identical trade-off occurs in both (Fig.2). The curve represents tolerance of aeration stress at its left hand end and tolerance of drying stress at its right hand end. This demonstrates that the same physiological constraints may cause niche segregation on hydrological gradients in these two very different communities and confirms the predicted generality of hydrological niche segregation. It now seems very likely that this kind of niche segregation plays an important role in coexistence in a wide variety of other vegetation types too.

Although the trade-off is identical in the two community types, the sites in which they occur are not and this is reflected in where the two groups of species fall along the trade-off curve (Fig.2). Meadow species are found along the whole curve, but are concentrated around the middle of the line, reflecting the typically moisture-retentive nature of the clay soils on which N. European meadows grow. By contrast, fynbos species are more bi-modally distributed (Fig. 2), reflecting the nature of soils and hydrology in the Cape Floristic Region. Fynbos typically occupies very free-draining soils of quartz sand and can experience long periods of summer drought, hence the concentration of species at the dry, right-hand end of the graph. However, some
fynbos soils have permanently high water tables due to groundwater flow from a large sandstone aquifer whilst others have impeded drainage due to the presence of a calcite evaporite pan or the proximity of bedrock and these are waterlogged and occupied by species that lie at the top left end of the graph. Heterogeneity *within* each of the sites is of course the basis of the hydrological niche separation we have found (Table 1).

How general is hydrological niche segregation in other plant communities? The evidence is scattered and has yet to be fully reviewed. We define hydrological niche segregation (HNS) as 1. partitioning of space on fine-scale soil moisture gradients (fine-scale being defined as a distance sufficiently small for species to compete for the same resources), or 2. partitioning of water as a resource through different strategies of water acquisition such as different phenologies or different rooting depths. Mechanisms 1 and 2 are not as different from each other as they may appear because the horizontal and the depth distribution of water are not independent of each other and these vary over time. An advantage of using sum exceedance values as we have done is that it captures all three components of soil moisture variation in space, depth and time to deal with fluctuation niche (Terradas *et al.*, 2009).

Hydrological Niche Segregation occurs in a great variety of vegetation types across the entire spectrum of environments from wet or mesic to arid. Littoral (Grace & Wetzel, 1981) and fen species (Kotowski *et al.*, 2006) segregate under interspecific competition into distinct zones along hydrological gradients. Species in riparian meadows in USA appear to be just as differentially sensitive to water table depth as plants in European wet meadows (Castelli *et al.*, 2000; Dwire *et al.*, 2006); in tallgrass prairie in Kansas, soil water resources are partitioned among coexisting C3 grasses (Nippert & Knapp, 2007) and there is also indirect evidence of this occurring in
European experimental grasslands (Verheyen et al., 2008). Partitioning of soil moisture among competing species has been found repeatedly among desert plants (Manning & Barbour, 1988; Nobel, 1997), in Mediterranean shrublands (Filella & Penuelas, 2003) and woodlands (Groom, 2004), in savannah (Weltzin & McPherson, 1997; Jackson et al., 1999) and in temperate (Dawson, 1996) and tropical forest (Jackson et al., 1995; Meinzer et al., 1999; Stratton et al., 2000). Tropical trees also differ significantly in their drought tolerance, with consequences for their distribution (Engelbrecht et al., 2007; Baltzer et al., 2008). These examples illustrate the likely generality of HNS in vegetation worldwide.

That a single, common trade-off governs niche segregation in communities that are as ecologically different from one another as the species in wet meadows and fynbos strongly implies that the underlying mechanism is physiologically fundamental to plants. As yet, we do not know what the mechanism is, but it must involve resource acquisition because interspecific competition for resources shapes hydrological niches. Species that overlap broadly in their fundamental hydrological niche when growing without interspecific competition are typically confined to significantly narrower niches that overlap less when the species compete with one another on soil moisture gradients (Ellenberg, 1953, Pickett & Bazzaz, 1978). Mesocosm experiments also show that root competition can lead to hydrological niche segregation between congeneric species (Bartelheimer et al., 2010), implicating the importance of below-ground limiting resources (nutrients).

Two possible underlying physiological trade-offs, which may not be mutually exclusive, that could be responsible for hydrological niche segregation are 1. the competing demands of water conservation vs. carbon acquisition along soil moisture
gradients, and 2. the competing demands of light acquisition vs. nutrient acquisition along nutrient gradients that are correlated with soil moisture. The first trade-off is a consequence of the fact that plants must regulate water loss through the same apertures (stomata) through which they acquire CO₂ required for growth. In dry conditions stomata must be closed to conserve water, but this occurs at the cost of CO₂ uptake. These conflicting regulatory functions are so fundamental to the water and carbon economies of all plants that it would be surprising if they did not contribute to the physiological trade-off underlying hydrological niche segregation.

Water Use Efficiency (WUE) measures the ratio of CO₂ assimilated to stomatal conductance and so ought to vary between species in a systematic manner along soil moisture gradients if this hypothesis is correct (Araya et al., 2010).

The second mechanism would necessarily be more complicated because it involves a correlation between nutrient availability and soil moisture, rather than a trade-off caused by soil moisture directly. Nitrogen availability varies along soil moisture gradients with a maximum in mesic soils and minima in waterlogged and very dry conditions (Araya, 2005) because N mineralization is limited by anoxia in waterlogged soil and by lack of water in dry conditions. Thus, a complex gradient of N availability can be associated with a simple (linear) soil moisture gradient. By its very existence, a nutrient gradient produces opposing selective forces upon plants, because different resources will limit plant growth at either end (Tilman, 1988; Wedin & Tilman, 1993). Nutrients will limit growth where these are scarce, while light will limit growth where nutrients are plentiful. Plants must allocate resources to roots to compete successfully for nutrients, but to shoots to compete for light and thus a nutrient gradient engenders a trade-off that forces plants to specialize. Further
experiments on soil moisture gradients are needed to test these hypotheses.

The finding of niche segregation along fine-scale hydrological gradients in fynbos plant communities confirms the predicted generality of the phenomenon, which is now deepened by the discovery that plants belonging to disparate communities in the Northern and Southern hemispheres are constrained by an identical trade-off between hydrological niche axes. This provides an excellent basis for investigating the ecohydrology of other plant communities, other plant functional types, and for studies at even finer spatial scales. These results emphasize the importance of soil moisture and hydrology for structuring plant communities generally and this has implications for the conservation of plant communities that face changing hydrology caused by water abstraction and climate change. Under projected anthropogenic climate change scenarios, both changing temperature and precipitation (IPCC, 2007) are likely to alter hydrological regimes at fine scales. Current niche-based bioclimatic models that project plant species response to climate change do not account for fine-scale soil moisture as an explanatory variable (Midgley et al., 2003). This study provides a potential basis for remedying this shortcoming both through permitting the production of fine scale projections of soil moisture conditions relevant to plant performance, and potentially allowing their use in projecting impacts on species persistence at the sub-landscape scale. The development of such methods could also be applied to risk assessments of water abstraction impacts on species richness.

**ACKNOWLEDGMENTS**

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DOI: 10.1111/j.1442-9993.2009.02089.x


Gowing DJ, Youngs EG. 1997. The effect of the hydrology of a thames flood


**Silvertown J, Dodd ME, Gowing D, Mountford O. 1999.** Hydrologically-defined


**SUPPORTING INFORMATION**

**Table S1.** Location and details of study sites and number of species recorded at (a) fynbos sites, South Africa (b) wet meadow sites, UK.  

**Table S2.** List of species in (a) fynbos in South Africa and (b) wet meadows in England. Names follow (Goldblatt & Manning 2000) and (Stace 1997), respectively.  
Fynbos specimens that could not be identified to species were given codes as surrogate names.

**Table S3.** Values of hydrological niche parameters for soil drying stress (SEV\(_d\)) and aeration stress (SEV\(_a\)) recorded at (a) fynbos sites, South Africa (b) wet meadow sites, UK.

**Figure S1.** Spread of hydrological niche parameters for soil drying stress (SEV\(_d\)) and
aeration stress (SEV<sub>a</sub>) recorded for each monitored quadrat at (a) fynbos sites, South Africa (b) wet meadow sites, UK.
Table 1. Number of species recorded (n) and significance of a test for niche segregation (P) in eight fynbos plant communities. Separate tests were performed for the entire community and for the Restionaceae alone using ECOSIM version 7.7.

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<th>Restionaceae only</th>
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<td></td>
<td>n</td>
<td>P</td>
<td>n</td>
<td>P</td>
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<td>&lt;0.001</td>
<td>8</td>
<td>0.012</td>
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<tr>
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Figure 1. Hydrological niches of the six commonest species of Restionaceae at a typical fynbos site (New Years Peak) in the Western Cape of South Africa. Niche space is defined by two Sum Exceedance Values (SEV$_d$ for soil drying stress and SEV$_a$ for soil aeration stress) and the area of this space available for colonization is shaded grey. Black areas show the region of niche space in which the named species is recorded at a significantly higher frequency than random expectation (P < 0.05), calculated using inverse-distance weighted interpolations from 10 records per grid node.
**Figure 2.** Trade-off between Sum Exceedance Value niche parameters of soil drying stress ($\text{SEV}_d$) and soil aeration stress ($\text{SEV}_a$) for a sample of 96 fynbos (filled circles) and 99 meadow species (open circles).
**SUPPORTING INFORMATION**

**Table S1.** Location and details of study sites and number of species recorded at (a) fynbos sites, South Africa (b) wet meadow sites, UK.

(a) Fynbos sites, South Africa

<table>
<thead>
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<th>Quadrats recorded</th>
<th>Species</th>
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(b) Wet meadow sites, UK

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</table>
Table S2. List of species in (a) fynbos in South Africa and (b) wet meadows in England. Names follow (Goldblatt & Manning 2000) and (Stace 1997), respectively. Fynbos specimens that could not be identified to species were given codes as surrogate names.

(a) Fynbos species

**Asphodelaceae**

*Bulbinella nutans* *turfosicola*

**Asteraceae**

*Anthanasia rugulosa*

*Stoebe plumosa*

**Bruniaceae**

*Berzelia abrotanoides*

**Cyperaceae**

*Cyperaceae J*

*Cyperaceae 1 T*

*Cyperaceae 2 T*

*Cyperaceae CP1*

*Cyperaceae CP2*
Cyperaceae K

Ficinea indica

Ficinea nigrescence

Tetraria ferruginea

**Droseraceae**

Drosera sp. CP1

Drosera sp. CP2

Drosera sp. S

Drosera sp. K

**Ericaceae**

Erica bruniales

Erica gnaphaloides

Erica hispidula

Erica imbricata

Erica lasciva Salisbury

Erica multumbellifera

Erica muscosa

Erica nudiflora

Erica parviflora
*Erica sp. CP1*

*Erica sp. CP2*

*Erica spumosa*

**Iridaceae**

*Aristia capitata*

**Lauraceae**

*Cassytha ciliolata*

**Oxalidaceae**

*Oxalis sp. T*

*Oxalis sp. CP2*

*Oxalis sp. CP1*

**Penaeaceae**

*Pennaea mucronata*

**Poaceae**

*Ehrharta setacea setacea*

*Pennisetum macrourum*

*Pentaschistis curvifolia*

**Poaceae T**

**Poaceae S**
Pseudopentameris caespitosa

Tribolium uniolae

Proteaceae

Diastella divaricata

Leucadendron coniferum

Leucadendron corybosum

Leucadendron lanigereum lanigereum

Leucodendron sp. K

Spatalla mollis

Restionaceae

Anthochortus crinalis

Anthochortus laxiflorus

Calopsis hyalina

Calopsis viminea

Cannomois cf. acuminata

Chondropetalum nudum

Elegia asperiflora

Elegia caespitosa

Elegia coleura
Elegia cuspidata

Elegia filacea

Elegia hookerania

Elegia juncea

Elegia neesi

Elegia thyrsifera

Hypodiscus albo-aristatus

Hypodiscus aristatus

Hypodiscus willdenowia

Ischyrolepis capensis

Ischyrolepis cincinnata

Ischyrolepis curviramus

Ischyrolepis macer

Ischyrolepis monanthos

Ischyrolepis tenuissima

Mastersiella digitata

Platycaulus callistichus

Restio bifidus

Restio bifurcus
Restio dodii  dodii

Restio festicuformis

Restio filiformis

Restio miser

Restio pedicellatus

Restio quinquefarius

Restio bolusii

Restio triticeus

Staberoha cernua

Staberoha distachyos

Thamnochortus fruticosus

Thamnochortus punctatus

Willdenowia arescens

Willdenowia sulcata

Rhamnaceae

Phyllica imberbis

Rosaceae

Cliffortia filifolia

Cliffortia subsetacea
Rutaceae

*Diosma aspalathoides*

(b) Wet meadow species

Amblystegiaceae

*Calliergon cuspidatum*

Apiaceae

*Heracleum sphondylium*

*Oenanthe fistulosa*

*Silaum silaus*

Asteraceae

*Achillea millefolium*

*Bellis perennis*

*Centaurea nigra*

*Leucanthemum vulgare*

*Cirsium arvense*

*Cirsium palustre*

*Hypochoeris radicata*

*Leontodon autumnalis*
Leontodon hispidus

Leontodon saxatilis

Senecio aquaticus

Taraxacum sect. vulgaria

Tragopogon pratensis

**Boraginaceae**

Myosotis laxa caespitosa

Myosotis discolor

**Brachytheciaceae**

Brachythecium rutabulum

Rhynchostegium confertum

Eurhynchium praelongum

**Brassicaceae**

Cardamine pratensis

**Caryophyllaceae**

Cerastium fontanum

Lychnis flos-cuculi

Stellaria graminea

**Cyperaceae**
Carex acuta

Carex acutiformis

Carex disticha

Carex flacca

Carex hirta

Carex nigra

Carex panicea

Carex riparia

Eleocharis palustris

Dipsacaceae

Succisa pratensis

Equisetaceae

Equisetum palustre

Fabaceae

Lathyrus pratensis

Lotus corniculatus

Lotus pedunculatus

Trifolium dubium

Trifolium pratense
Trifolium repens

Vicia cracca

Juncaceae

Juncus acutiflorus

Juncus articulatus

Juncus effusus

Juncus inflexus

Luzula campestris

Lamiaceae

Prunella vulgaris

Ophioglossaceae

Ophioglossum vulgatum

Plantaginaceae

Plantago lanceolata

Poaceae

Elytrigia repens

Agrostis stolonifera

Agrostis capillaris

Alopecurus geniculatus
Alopecurus pratensis

Anthoxanthum odoratum

Arrhenatherum elatius

Briza media

Bromus commutatus

Bromus hordeaceus hordeaceus

Bromus racemosus

Cynosurus cristatus

Dactylis glomerata

Deschampsia cespitosa cespitosa

Festuca arundinacea

Festuca pratensis

Festuca rubra

Glyceria fluitans

Glyceria maxima

Holcus lanatus

Hordeum secalinum

Lolium perenne

Phalaris arundinacea
Phleum pratense

Poa pratensis

Poa humilis

Poa trivialis

Trisetum flavescens

**Polygonaceae**

Persicaria amphibia

Rumex acetosa

Rumex crispus

**Primulaceae**

Lysimachia nummularia

Primula veris

**Ranunculaceae**

Caltha palustris

Ranunculus acris

Ranunculus bulbosus

Ranunculus flammula

Ranunculus repens

Thalictrum flavum
Rosaceae

Filipendula ulmaria

Potentilla anserina

Potentilla reptans

Sanguisorba officinalis

Rubiaceae

Galium palustre

Galium verum

Scrophulariaceae

Rhinanthus minor

Veronica serpyllifolia serpyllifolia


**Table S3.** Values of hydrological niche parameters for soil drying stress (SEV$_{d}$) and aeration stress (SEV$_{a}$) recorded at (a) fynbos sites, South Africa (b) wet meadow sites, UK.

(a) Fynbos sites, South Africa

<table>
<thead>
<tr>
<th>No.</th>
<th>Site name</th>
<th>SEV$_{d}$ (Mean ± SD)</th>
<th>SEV$_{a}$ (Mean ± SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Cape Point</td>
<td>12.34 ± 0.82</td>
<td>0.23 ± 0.34</td>
</tr>
<tr>
<td>2</td>
<td>Cape Point2</td>
<td>13.14 ± 0.88</td>
<td>0.29 ± 0.54</td>
</tr>
<tr>
<td>3</td>
<td>Jonkershoek</td>
<td>13.57 ± 1.13</td>
<td>0.91 ± 1.04</td>
</tr>
<tr>
<td>4</td>
<td>Kogelberg</td>
<td>16.08 ± 1.21</td>
<td>0.13 ± 0.32</td>
</tr>
<tr>
<td>5</td>
<td>New Years Peak</td>
<td>10.06 ± 1.21</td>
<td>0.92 ± 1.30</td>
</tr>
<tr>
<td>6</td>
<td>Riverlands</td>
<td>17.73 ± 2.87</td>
<td>0.11 ± 0.23</td>
</tr>
<tr>
<td>7</td>
<td>Steenbras</td>
<td>1.14 ± 1.37</td>
<td>4.70 ± 0.44</td>
</tr>
<tr>
<td>8</td>
<td>Theewaterskloof</td>
<td>12.55 ± 1.45</td>
<td>0.92 ± 1.06</td>
</tr>
</tbody>
</table>

(b) Wet meadow sites, UK

<table>
<thead>
<tr>
<th>No.</th>
<th>Site name</th>
<th>SEV$_{d}$ (Mean ± SD)</th>
<th>SEV$_{a}$ (Mean ± SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Belaugh</td>
<td>0.02 ± 0.10</td>
<td>10.63 ± 3.07</td>
</tr>
<tr>
<td></td>
<td>Location</td>
<td>Value 1 ± SD</td>
<td>Value 2 ± SD</td>
</tr>
<tr>
<td>---</td>
<td>------------------</td>
<td>-------------</td>
<td>-------------</td>
</tr>
<tr>
<td>2</td>
<td>Blackthorn</td>
<td>8.99 ± 1.26</td>
<td>3.15 ± 2.48</td>
</tr>
<tr>
<td>3</td>
<td>Broad Dale</td>
<td>11.25 ± 1.48</td>
<td>1.27 ± 1.38</td>
</tr>
<tr>
<td>4</td>
<td>Cricklade</td>
<td>12.37 ± 5.41</td>
<td>1.24 ± 1.85</td>
</tr>
<tr>
<td>5</td>
<td>Dancing Gate</td>
<td>8.11 ± 4.78</td>
<td>4.06 ± 3.39</td>
</tr>
<tr>
<td>6</td>
<td>East Harnham</td>
<td>1.49 ± 0.81</td>
<td>4.54 ± 2.05</td>
</tr>
<tr>
<td>7</td>
<td>Moorlinch</td>
<td>5.26 ± 0.62</td>
<td>3.84 ± 1.21</td>
</tr>
<tr>
<td>8</td>
<td>Mottey Meadows</td>
<td>3.36 ± 0.94</td>
<td>3.40 ± 0.31</td>
</tr>
<tr>
<td>9</td>
<td>Nethercote</td>
<td>4.03 ± 3.10</td>
<td>1.99 ± 2.94</td>
</tr>
<tr>
<td>10</td>
<td>Portholme</td>
<td>5.90 ± 3.36</td>
<td>3.68 ± 1.83</td>
</tr>
<tr>
<td>11</td>
<td>Southlake</td>
<td>7.11 ± 2.16</td>
<td>3.55 ± 0.68</td>
</tr>
<tr>
<td>12</td>
<td>Stonygillfoot</td>
<td>16.57 ± 4.41</td>
<td>0.24 ± 0.40</td>
</tr>
<tr>
<td>13</td>
<td>Tadham</td>
<td>5.69 ± 2.99</td>
<td>2.58 ± 1.97</td>
</tr>
<tr>
<td>14</td>
<td>Upton Ham</td>
<td>7.02 ± 0.87</td>
<td>3.53 ± 1.06</td>
</tr>
<tr>
<td>15</td>
<td>Upwood</td>
<td>9.38 ± 1.01</td>
<td>2.36 ± 2.12</td>
</tr>
<tr>
<td>16</td>
<td>West Sedgemoor</td>
<td>2.68 ± 1.73</td>
<td>2.61 ± 1.25</td>
</tr>
<tr>
<td>17</td>
<td>Westhay</td>
<td>2.75 ± 0.76</td>
<td>7.52 ± 1.49</td>
</tr>
<tr>
<td>18</td>
<td>Wet Moor</td>
<td>3.21 ± 2.94</td>
<td>8.04 ± 1.37</td>
</tr>
</tbody>
</table>
Figure S1. Spread of hydrological niche parameters for soil drying stress (SEVₐ) and aeration stress (SEVₐ) recorded for each monitored quadrat at (a) fynbos sites, South Africa (b) wet meadow sites, UK.