

Open Research Online

The Open University's repository of research publications and other research outputs

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

Journal Item

How to cite:

Araya, Yoseph N.; Silvertown, Jonathan; Gowing, David J.; McConway, Kevin J.; Linder, H. Peter and Midgley, Guy (2011). A fundamental, eco-hydrological basis for niche segregation in plant communities. *New Phytologist*, 189(1) pp. 253–258.

For guidance on citations see [FAQs](#).

© 2010 The Authors

Version: Accepted Manuscript

Link(s) to article on publisher's website:

<http://dx.doi.org/doi:10.1111/j.1469-8137.2010.03475.x>

Copyright and Moral Rights for the articles on this site are retained by the individual authors and/or other copyright owners. For more information on Open Research Online's data [policy](#) on reuse of materials please consult the policies page.

oro.open.ac.uk

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

Yoseph N. Araya^{1*}, Jonathan Silvertown¹, David J. Gowing¹, Kevin J. McConway²,
H. Peter Linder³, Guy Midgley⁴

¹ Department of Life Sciences, Open University, Walton Hall, Milton Keynes, MK7 6AA, UK

² Department of Mathematics and Statistics, Open University, Walton Hall, Milton Keynes, MK7 6AA, UK

³ Institute of Systematic Botany, University of Zurich, Switzerland

⁴ Kirstenbosch Research Centre, South African National Biodiversity Institute, Republic of South Africa

Corresponding author: Tel. +44(0)1908655582 Fax. +44(0)1908654167
Y.N.Araya@open.ac.uk

Word count: 4,528

1 SUMMARY

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

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

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

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

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

24 INTRODUCTION

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

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

46 To test how similar the underlying mechanisms structuring the two contrasting
47 communities are, we also compare the trade-off for fynbos species with the equivalent

48 relationship found in an enlarged dataset of nearly 100 species drawn from 18
49 meadow sites in England.

50 **MATERIALS AND METHODS**

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

62 In England, 18 lowland wet meadow sites were studied using between 45 and 821, 1
63 m² quadrats between 1993 and 2001 (Supporting Information, Table S1b). A total of
64 99 species that were sufficiently frequent for hydrological measurement were
65 recorded (Supporting Information, Table S2).

66 Soil water regime within all plots was assessed using hydrological models (Gowing &
67 Youngs, 1997). The models were built from inputs of water-table depth behaviour in
68 the field, topographic variation, soil characteristics and, for meadow sites only,
69 meteorological data. The water-table depth was monitored through an array of tube
70 wells, supported by automatic logging pressure transducers known as 'Divers'

71 (Eijkelkamp). The tube wells were read manually every two weeks, while automatic
72 divers in a sub-sample of wells were set to read every four hours for at least 12
73 months' duration. Topography was surveyed at all quadrat and tube well locations
74 using a total station device (Leica Geosystems TPS300).

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

94 The growing seasons of fynbos and meadows differ, with the former occurring in a

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

102 Niche overlap was computed with pair-wise values of Pianka's index of niche overlap
103 for all combinations of species occurring in 5% or more quadrats at each site (Pianka,
104 1973). Pianka's Index calculates the niche overlap using an index of resource
105 utilization for each pair of species in the assemblage. Niche space at each site was
106 computed in bins of 1 metre.week x 1 metre.week (1 SEV_d x 1 SEV_a respectively),
107 created by sub-dividing the observed SEV range in each site. Then the proportion of
108 each species present in a particular bin relative to all the bins available on the site was
109 calculated and used for Niche overlap analysis. Departures of mean niche overlap for
110 the whole community from random expectation were determined by using a
111 randomization test in Ecosim Version 7.72 (Gotelli & Entsminger, 2007) that
112 randomized the non-zero abundances of species in boxes, but used the observed niche
113 breadths in the randomization and kept zero abundances fixed (that is, algorithm RA4
114 in the notation of Gotelli & Graves, 1996). Ten thousand randomizations were run for
115 each test.

116 In fynbos, we tested for niche segregation across the entire community of plant
117 species found at each of the eight sites and also for the subset of species in each
118 community belonging to the endemic African Restionaceae. This clade of Cape

119 endemics is abundant, species-rich and highly characteristic of fynbos vegetation
120 (Rebello *et al.*, 2006).

121 **RESULTS**

122 <Figure 1>

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

133

134 <Table 1>

135

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

141 p=0.85 respectively).

142 <Figure 2>

143 **DISCUSSION**

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

155 Although the trade-off is identical in the two community types, the sites in which they
156 occur are not and this is reflected in where the two groups of species fall along the
157 trade-off curve (Fig.2). Meadow species are found along the whole curve, but are
158 concentrated around the middle of the line, reflecting the typically moisture-retentive
159 nature of the clay soils on which N. European meadows grow. By contrast, fynbos
160 species are more bi-modally distributed (Fig. 2), reflecting the nature of soils and
161 hydrology in the Cape Floristic Region. Fynbos typically occupies very free-draining
162 soils of quartz sand and can experience long periods of summer drought, hence the
163 concentration of species at the dry, right-hand end of the graph. However, some

164 fynbos soils have permanently high water tables due to groundwater flow from a large
165 sandstone aquifer whilst others have impeded drainage due to the presence of a calcite
166 evaporite pan or the proximity of bedrock and these are waterlogged and occupied by
167 species that lie at the top left end of the graph. Heterogeneity *within* each of the sites
168 is of course the basis of the hydrological niche separation we have found (Table 1).

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

180 Hydrological Niche Segregation occurs in a great variety of vegetation types across
181 the entire spectrum of environments from wet or mesic to arid. Littoral (Grace &
182 Wetzel, 1981) and fen species (Kotowski *et al.*, 2006) segregate under interspecific
183 competition into distinct zones along hydrological gradients. Species in riparian
184 meadows in USA appear to be just as differentially sensitive to water table depth as
185 plants in European wet meadows (Castelli *et al.*, 2000; Dwire *et al.*, 2006); in tallgrass
186 prairie in Kansas, soil water resources are partitioned among coexisting C3 grasses
187 (Nippert & Knapp, 2007) and there is also indirect evidence of this occurring in

188 European experimental grasslands (Verheyen *et al.*, 2008). Partitioning of soil
189 moisture among competing species has been found repeatedly among desert plants
190 (Manning & Barbour, 1988; Nobel, 1997), in Mediterranean shrublands (Filella &
191 Penuelas, 2003) and woodlands (Groom, 2004), in savannah (Weltzin & McPherson,
192 1997; Jackson *et al.*, 1999) and in temperate (Dawson, 1996) and tropical forest
193 (Jackson *et al.*, 1995; Meinzer *et al.*, 1999; Stratton *et al.*, 2000). Tropical trees also
194 differ significantly in their drought tolerance, with consequences for their distribution
195 (Engelbrecht *et al.*, 2007; Baltzer *et al.*, 2008). These examples illustrate the likely
196 generality of HNS in vegetation worldwide.

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

209 Two possible underlying physiological trade-offs, which may not be mutually
210 exclusive, that could be responsible for hydrological niche segregation are 1. the
211 competing demands of water conservation *vs.* carbon acquisition along soil moisture

212 gradients, and 2. the competing demands of light acquisition *vs.* nutrient acquisition
213 along nutrient gradients that are correlated with soil moisture. The first trade-off is a
214 consequence of the fact that plants must regulate water loss through the same
215 apertures (stomata) through which they acquire CO₂ required for growth. In dry
216 conditions stomata must be closed to conserve water, but this occurs at the cost of
217 CO₂ uptake. These conflicting regulatory functions are so fundamental to the water
218 and carbon economies of all plants that it would be surprising if they did not
219 contribute to the physiological trade-off underlying hydrological niche segregation.
220 Water Use Efficiency (WUE) measures the ratio of CO₂ assimilated to stomatal
221 conductance and so ought to vary between species in a systematic manner along soil
222 moisture gradients if this hypothesis is correct (Araya *et al.*, 2010).

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

236 experiments on soil moisture gradients are needed to test these hypotheses.

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

256 **ACKNOWLEDGMENTS**

257 This study was funded by grants from the Leverhulme Trust and the Darwin Initiative
258 (Defra). We are grateful to Cape Nature and Sanparks in the Cape and to the owners
259 of the meadow field sites in England for allowing us to work on their land. We thank

260 Prof. Edward Youngs for assistance with the computation of hydrological models.
261 Deryck deWit gave invaluable assistance in the field in South Africa and Els Dorrat
262 and Raphael Kongor identified fynbos species and prepared vouchers.

REFERENCES

DOI: 10.1111/j.1442-9993.2009.02089.x

- Adler PB, HilleRisLambers J, Levine JM. 2007.** A niche for neutrality. *Ecology Letters* **10**: 95-104.
- Araya YN. 2005.** *Influence of soil-water regime on nitrogen availability and plant competition in wet-meadows.* Open University Milton Keynes.
- Araya YN, Silvertown J, Gowing DJ, McConway KJ, Linder P, Midgley G. 2010.** Variation in $\delta^{13}C$ among species and sexes in the family restionaceae along a fine-scale hydrological gradient. *Austral Ecology* **in press** (doi: 10.1111/j.1442-9993.2009.02089.x).
- Baltzer JL, Davies SJ, Bunyavejchewin S, Noor NSM. 2008.** The role of desiccation tolerance in determining tree species distributions along the malay-thai peninsula. *Functional Ecology* **22**: 221-231.
- Bartelheimer M, Gowing DJ, Silvertown J. 2010.** Explaining hydrological niches: The decisive role of below-ground competition in two closely related *senecio* species. *Journal of Ecology* **98**: 126-136.
- Broad HJ, Hough MN. 1993.** The growing and grazing season in the united kingdom. *Grass and Forage Science* **48**: 26-37.
- Castelli RM, Chambers JC, Tausch RJ. 2000.** Soil-plant relations along a soil-water gradient in great basin riparian meadows. *Wetlands* **20**: 251-266.
- Chesson P. 2000.** Mechanisms of maintenance of species diversity. *Annual Review Of Ecology and Systematics* **31**: 343-366.
- Dawson TE. 1996.** Determining water use by trees and forests from isotopic, energy balance and transpiration analyses: The roles of tree size and hydraulic lift. *Tree Physiology* **16**: 263-272.
- de Aguiar MAM, Baranger M, Baptestini EM, Kaufman L, Bar-Yam Y. 2009.** Global patterns of speciation and diversity. *Nature* **460**: 384-387.
- Dwire KA, Kauffman JB, Baham JE. 2006.** Plant species distribution in relation to water-table depth and soil redox potential in montane riparian meadows. *Wetlands* **26**: 131-146.
- Ellenberg H. 1953.** Physiologisches und ökologisches verhalten derselben pflanzenarten. *Berichte der Deutschen Botanischen Gesellschaft* **65**: 350-361.
- Engelbrecht BMJ, Comita LS, Condit R, Kursar TA, Tyree MT, Turner BL, Hubbell SP. 2007.** Drought sensitivity shapes species distribution patterns in tropical forests. *Nature* **447**: 80-U82.
- Filella I, Penuelas J. 2003.** Partitioning of water and nitrogen in co-occurring mediterranean woody shrub species of different evolutionary history. *Oecologia* **137**: 51-61.
- Gotelli NJ, Entsminger GL 2007.** Ecosim: Null models software for ecology, version 7. In. Jericho: Acquired Intelligence Inc. and Kelsey-Bear.
- Gotelli, N.J. and G.R. Graves 1996.** *Null models in ecology.* Washington, DC: Smithsonian Institution Press.
- Gowing DJ, Spoor G 1998.** The effect of water table depth on the distribution of plant species in lowland wet grassland. In: R. Bailey, P. JoseB. Sherwood eds. *Uk floodplains.* Otley: Westbury, 185-196.
- Gowing DJ, Youngs EG. 1997.** The effect of the hydrology of a thames flood

- meadow on its vegetation. *British Hydrological Society Occasional Paper* **8**: 69-80.
- Grace JB, Wetzel RG. 1981.** Habitat partitioning and competitive displacement in cattails (typha): Experimental field studies. *American Naturalist* **118**: 463-474.
- Groom PK. 2004.** Rooting depth and plant water relations explain species distribution patterns within a sandplain landscape. *Functional Plant Biology* **31**: 423-428.
- Henson IE, Jenson CR, Turner NC. 1989.** Leaf gas exchange and water relations of lupins and wheat. I. Shoot responses to soil water deficits. *Australian Journal Of Plant Physiology* **16**: 401-413.
- Higgins KB, Lamb AJ, van Wilgen BW. 1987.** Root systems of selected plant species in mesic mountain fynbos in the jonkershoek valley, south-western cape province. *South African Journal Of Botany* **53**: 249-257.
- Hubbell SP. 2001.** *The unified neutral theory of biodiversity and biogeography*. Princeton: Princeton University Press.
- IPCC 2007.** Climate change 2007: The physical science basis. Summary for policymakers. In. Geneva: Intergovernmental Panel on Climate Change. 18.
- Jackson PC, Cavelier J, Goldstein G, Meinzer FC, Holbrook NM. 1995.** Partitioning of water resources among plants of a lowland tropical forest. *Oecologia* **101**: 197-203.
- Jackson PC, Meinzer FC, Bustamante M, Goldstein G, Franco A, Rundel PW, Caldas L, Iglar E, Causin F. 1999.** Partitioning of soil water among tree species in a brazilian cerrado ecosystem. *Tree Physiology* **19**: 717-724.
- Kotowski W, Thorig W, van Diggelen R, Wassen MJ. 2006.** Competition as a factor structuring species zonation in riparian fens - a transplantation experiment. *Applied Vegetation Science* **9**: 231-240.
- Manning SJ, Barbour MG. 1988.** Root systems, spatial patterns, and competition for soil moisture between two desert subshrubs. *American Journal of Botany* **75**: 885-893.
- Meinzer FC, Andrade JL, Goldstein G, Holbrook NM, Cavelier J, Wright SJ. 1999.** Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Oecologia* **121**: 293-301.
- Midgley GF, Hannah L, Millar D, Thuiller W, Booth A. 2003.** Developing regional and species-level assessments of climate change impacts on biodiversity in the cape floristic region. *Biological Conservation* **112**: 87-97.
- Nippert JB, Knapp AK. 2007.** Soil water partitioning contributes to species coexistence in tallgrass prairie. *Oikos* **116**: 1017-1029.
- Nobel PS. 1997.** Root distribution and seasonal production in the northwestern sonoran desert for a c-3 subshrub, a c-4 bunchgrass, and a cam leaf succulent. *American Journal of Botany* **84**: 949-955.
- Pickett, STA, Bazzaz, FA. 1978.** Organization of an assemblage of early successional species on a soil moisture gradient. *Ecology* **59**: 1248-1255
- Pianka ER. 1973.** The structure of lizard communities. *Annual Review of Ecology & Systematics* **4**: 53-74.
- Rebello AG, Boucher C, Helme NA, Mucina L, Rutherford MC 2006.** Fynbos biome. In: L. Mucina M. C. Rutherford eds. *The vegetation of south africa, lesotho and swaziland*. Pretoria: South African National Biodiversity Institute.
- Silvertown J. 2004.** Plant coexistence and the niche. *Trends in Ecology & Evolution* **19**: 605-611.
- Silvertown J, Dodd ME, Gowing D, Mountford O. 1999.** Hydrologically-defined

- niches reveal a basis for species-richness in plant communities. *Nature* **400**: 61-63.
- Stratton LC, Goldstein G, Meinzer FC. 2000.** Temporal and spatial partitioning of water resources among eight woody species in a hawaiian dry forest. *Oecologia* **124**: 309-317.
- Terradas J, Penuelas J, Lloret F. 2009.** The fluctuation niche in plants. *International Journal of Ecology* doi:10.1155/2009/959702
- Tilman D. 1988.** *Plant strategies and the dynamics and structure of plant communities*. Princeton, NJ: Princeton University Press.
- Verheyen K, Bulteel H, Palmborg C, Olivie B, Nijs I, Raes D, Muys B. 2008.** Can complementarity in water use help to explain diversity-productivity relationships in experimental grassland plots? *Oecologia* **156**: 351-361.
- Warton DI, Wright IJ, Falster DS, Westoby M. 2006.** Bivariate line-fitting methods for allometry. *Biological Reviews* **81**: 259-291
- Wedin D, Tilman D. 1993.** Competition among grasses along a nitrogen gradient - initial conditions and mechanisms of competition. *Ecological Monographs* **63**: 199-229.
- Weltzin JF, McPherson GR. 1997.** Spatial and temporal soil moisture resource partitioning by trees and grasses in a temperate savanna, arizona, USA. *Oecologia* **112**: 156-164.

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_a) recorded for each monitored quadrat at (a) fynbos sites, South Africa (b) wet meadow sites, UK.

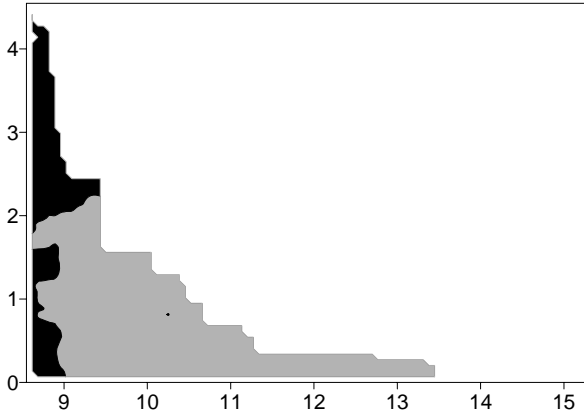
Table 1. Number of species recorded (n) and significance of a test for niche segregation (P) in eight fynbos plant communities. Separate tests were performed for the entire community and for the Restionaceae alone using ECOSIM version 7.7.

Site	All species		Restionaceae only	
	n	P	n	P
Cape Point 1	17	<0.001	8	0.012
Cape Point 2	12	0.12	5	0.842
Jonkershoek	13	0.002	7	0.377
Kogelberg	19	<0.001	10	0.001
New Years Peak	16	<0.001	9	<0.001
Riverlands	20	0.017	12	0.002
Steenbras	13	<0.001	7	0.049
Theewaterskloof	15	<0.001	8	<0.001

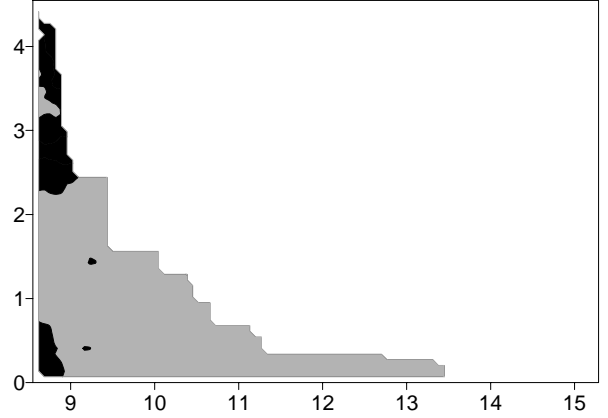
Figure 1. Hydrological niches of the six commonest species of Restionaceae at a typical fynbos site (New Years Peak) in the Western Cape of South Africa. Niche space is defined by two Sum Exceedance Values (SEV_d for soil drying stress and SEV_a for soil aeration stress) and the area of this space available 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 (SEV_d) and soil aeration stress (SEV_a) for a sample of 96 fynbos (filled circles) and 99 meadow species (open circles).

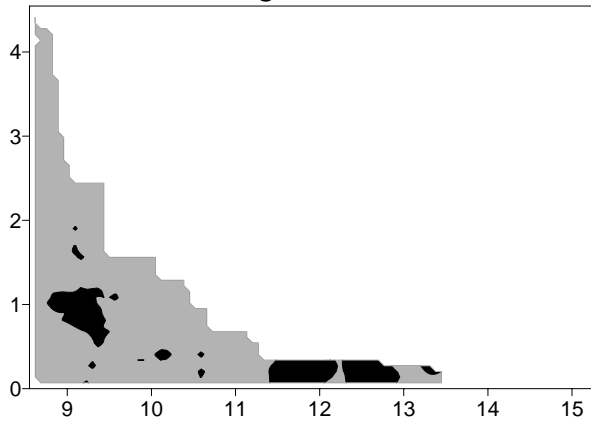
Anthochortus crinalis



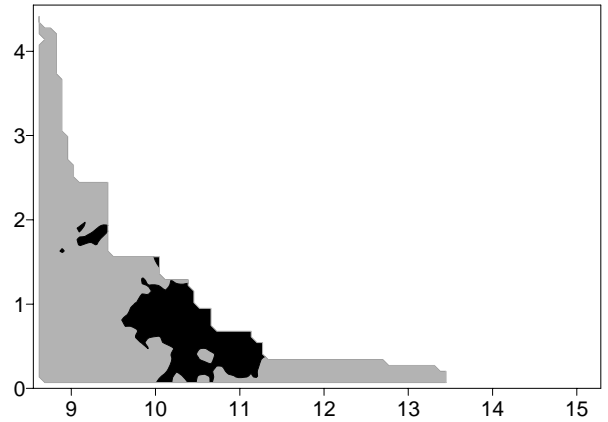
Restio miser



Elegia filacea

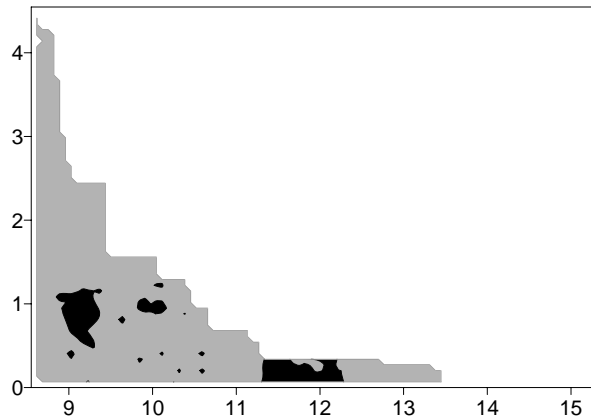


Elegia neesii

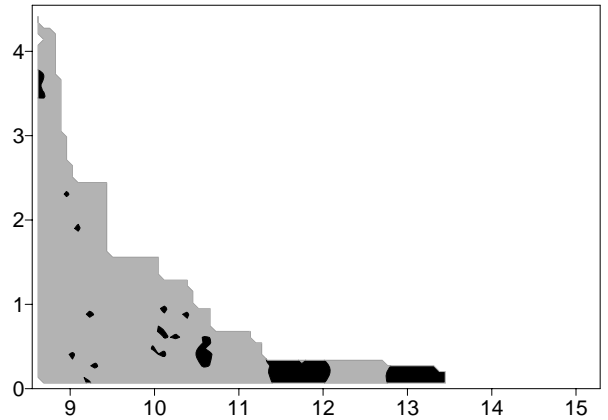


SEV_a (metre.weeks)

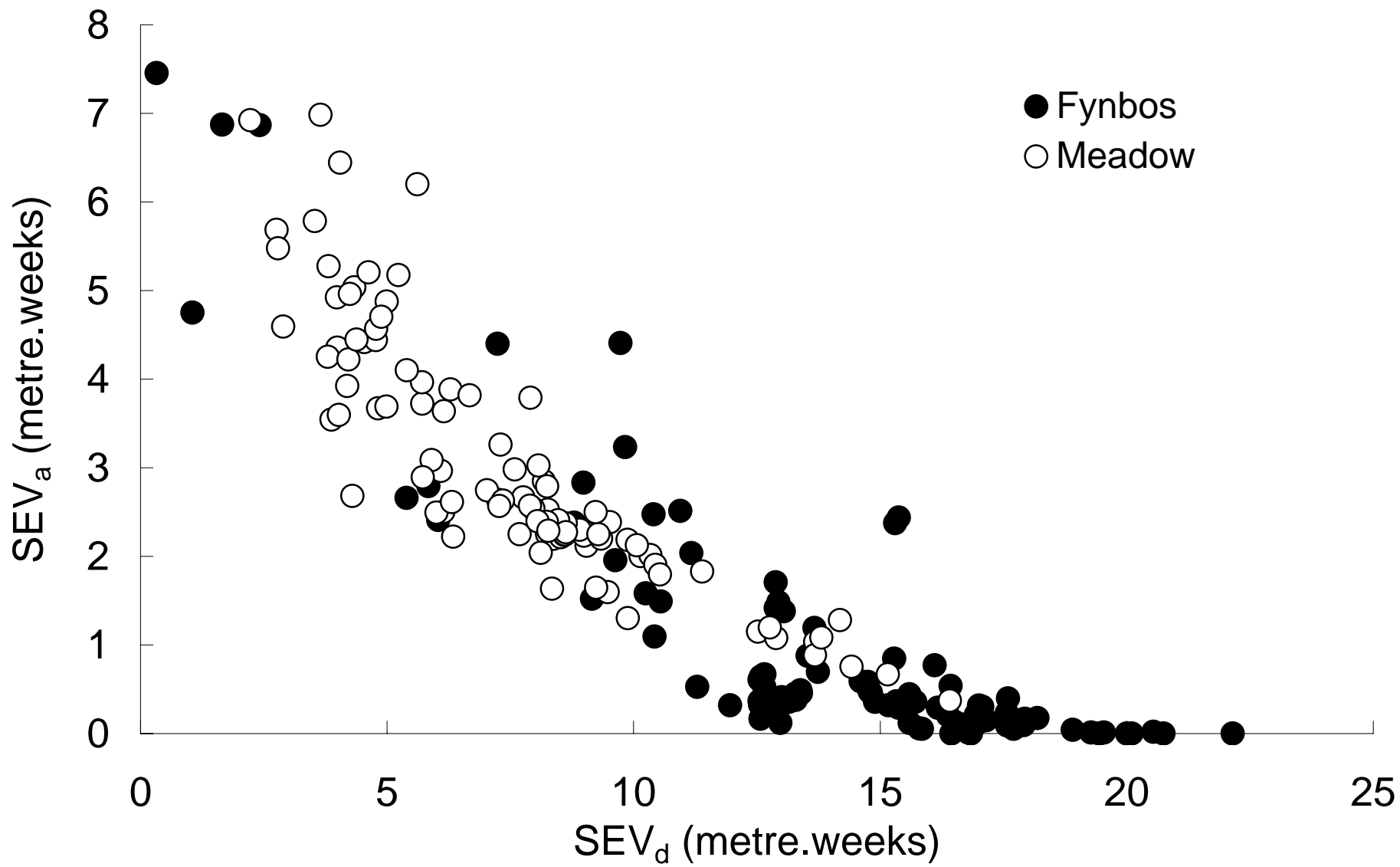
Ischyrolepis curviramis



Restio bolusii



SEV_d (metre.weeks)



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

No.	Site name	Location	Altitude (m a.s.l.)	Quadrats recorded	Species
1	Cape Point 1	S 34.29475 E 18.43853	120	225	28
2	Cape Point 2	S 34.31175 E 18.43168	112	210	27
3	Jonkershoek	S 33.99333 E 18.95290	350	201	29
4	Kogelberg	S 34.27908 E 19.00847	131	200	29
5	New Years Peak	S 33.68881 E 19.10081	1080	235	22
6	Riverlands	S 33.48689 E 18.59536	120	305	65
7	Steenbras	S 34.19436 E 18.87056	350	172	23
8	Theewaterskloof	S 33.98177 E 19.13145	347	200	31

(b) Wet meadow sites, UK

No.	Site name	Location	Altitude /m a.s.l.	Quadrats recorded	Species
-----	-----------	----------	-----------------------	----------------------	---------

1	Belaugh	N 52.70842 E 01.39146	2	69	103
2	Blackthorn	N 51.86601 W 01.08353	61	198	88
3	Broad Dale	N 54.86172 W 03.16216	8	89	71
4	Cricklade	N 51.65011 W 01.86552	79	821	119
5	Dancing Gate	N 54.62340 W 03.17859	70	45	54
6	East Harnham	N 51.05923 W 01.78590	43	90	79
7	Moorlinch	N 51.12001 W 02.87293	4	192	73
8	Mottey Meadows	N 52.71802 W 02.23830	99	215	74
9	Nethercote	N 51.86931 W 01.74722	123	59	84
10	Portholme	N 52.32136 W 00.18500	9	230	78
11	Southlake	N 51.06668 W 02.90904	4	175	76
12	Stonygillfoot	N 54.63177 W 2.11614	233	118	69
13	Tadham	N 51.20124 W 02.83153	2	817	137
14	Upton Ham	N 52.05821 W 02.20559	14	200	46
15	Upwood	N 52.42619 W 00.16158	8	164	96
16	West Sedgemoor	N 51.02799 W 02.91256	5	60	56
17	Westhay	N 51.20000 W 02.77000	3	30	53
18	Wet Moor	N 51.01630 W 02.78830	6	175	54

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 hookeriana

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 festuciformis

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

Goldblatt P, Manning JC. 2000. *Cape Plants. A conspectus of the Cape flora of South Africa.* Pretoria, South Africa: National Botanical Institute.

Stace C. 1997. *New flora of the British Isles.* Cambridge, UK: Cambridge University Press.

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

No.	Site name	SEV_d (Mean \pm SD)	SEV_a (Mean \pm SD)
1	Cape Point	12.34 \pm 0.82	0.23 \pm 0.34
2	Cape Point2	13.14 \pm 0.88	0.29 \pm 0.54
3	Jonkershoek	13.57 \pm 1.13	0.91 \pm 1.04
4	Kogelberg	16.08 \pm 1.21	0.13 \pm 0.32
5	New Years Peak	10.06 \pm 1.21	0.92 \pm 1.30
6	Riverlands	17.73 \pm 2.87	0.11 \pm 0.23
7	Steenbras	1.14 \pm 1.37	4.70 \pm 0.44
8	Theewaterskloof	12.55 \pm 1.45	0.92 \pm 1.06

(b) Wet meadow sites, UK

No.	Site name	SEV_d (Mean \pm SD)	SEV_a (Mean \pm SD)
1	Belaugh	0.02 \pm 0.10	10.63 \pm 3.07

2	Blackthorn	8.99 ± 1.26	3.15 ± 2.48
3	Broad Dale	11.25 ± 1.48	1.27 ± 1.38
4	Cricklade	12.37 ± 5.41	1.24 ± 1.85
5	Dancing Gate	8.11 ± 4.78	4.06 ± 3.39
6	East Harnham	1.49 ± 0.81	4.54 ± 2.05
7	Moorlinch	5.26 ± 0.62	3.84 ± 1.21
8	Mottey Meadows	3.36 ± 0.94	3.40 ± 0.31
9	Nethercote	4.03 ± 3.10	1.99 ± 2.94
10	Portholme	5.90 ± 3.36	3.68 ± 1.83
11	Southlake	7.11 ± 2.16	3.55 ± 0.68
12	Stonygillfoot	16.57 ± 4.41	0.24 ± 0.40
13	Tadham	5.69 ± 2.99	2.58 ± 1.97
14	Upton Ham	7.02 ± 0.87	3.53 ± 1.06
15	Upwood	9.38 ± 1.01	2.36 ± 2.12
16	West Sedgemoor	2.68 ± 1.73	2.61 ± 1.25
17	Westhay	2.75 ± 0.76	7.52 ± 1.49
18	Wet Moor	3.21 ± 2.94	8.04 ± 1.37

Figure S1. Spread of hydrological niche parameters for soil drying stress (SEV_d) and aeration stress (SEV_a) recorded for each monitored quadrat at (a) fynbos sites, South Africa (b) wet meadow sites, UK.

