

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

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Summary

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- Ecologists still puzzle over 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 determine. 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 that experience seasonal saturation.
- We quantified the 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 combinations of species.
- Despite the extreme functional and phylogenetic differences between the fynbos and wet meadow communities, an identical trade-off (i.e. specialization of species towards tolerance of aeration and/or drying stress) was found to cause segregation along fine-scale hydrological gradients.
- This study not only confirms 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.

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. However 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 a result of 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 tested 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 compared the trade-off for fynbos species with the equivalent relationship found in an enlarged data set 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 (120 m) to montane (1080 m) (Supporting Information, Table S1). Permanent plots *c.* 50 m × 50 m (the 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 (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 Table S2.

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

The 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' (Eijkkelkamp, Giesbeek, the Netherlands). The tube wells were read manually every 2 wk, while automatic divers in a subsample of wells were set to read every 4 h for at least 12 months' duration. The topography was surveyed at all quadrat and tube well locations using a total station device (Leica Geosystems TPS300, Heerbrugg, Switzerland).

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 using the concept of sum exceedance values (SEVs) 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, that is, where plants start to show effects of water stress (Henson *et al.*, 1989). The thresholds varied between 15 and 20 cm for aeration stress and between 45 and 48 cm for drying stress in our study sites. For each threshold, the SEV represents the degree to which water tables exceed it, that is, 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 SEVs encountered in our sites is given in 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 12-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, which are measured in metre-weeks (m.wk), 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 m.wk × 1 m.wk (1 SEV_d × 1 SEV_a, respectively), created by subdividing 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 using a randomization test in ECOSIM version 7.72 (Gotelli & Entsminger, 2007) that randomized the nonzero 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 (Rebello *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 that in our data set there are no points in the upper right sector of the diagram (Fig. 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, that is, soils that 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 that the two stresses tend not to occur simultaneously. Tests at the eight fynbos sites showed 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 standardized major axis fit lines after power-transforming both SEV_d and SEV_a data (power $2/3$) to achieve linearity. The results

showed that the slope and elevation of the two regression lines were similar ($P = 0.6$ and $P = 0.85$, respectively).

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 was found to occur 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.

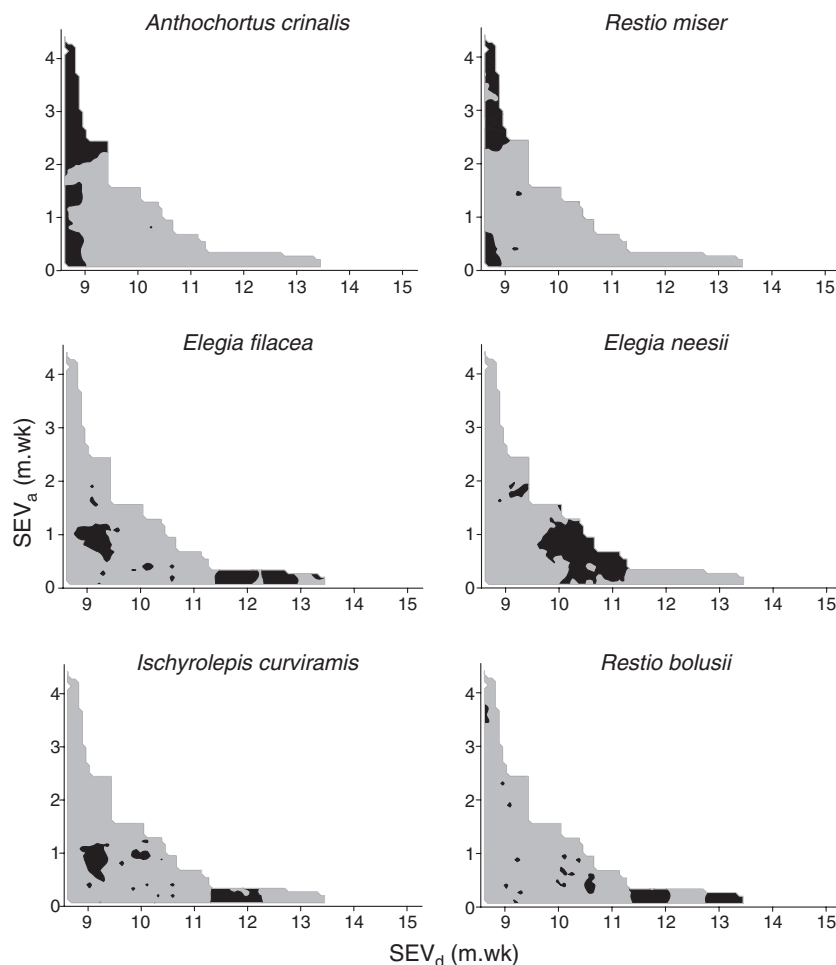
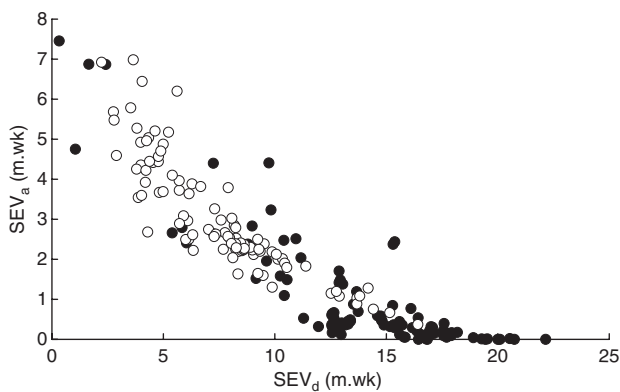


Fig. 1 Hydrological niches of the six commonest species of Restionaceae at a typical fynbos site (New Years Peak) in the Western Cape of South Africa. Niche space is defined by two sum exceedance values (SEV_d for soil drying stress and SEV_a for soil aeration stress) and the area of this space available 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.

Table 1 Number of species recorded (*n*) and significance of a test for niche segregation (*P*) in eight fynbos plant communities

Site	All species		Restionaceae only	
	<i>n</i>	<i>P</i>	<i>n</i>	<i>P</i>
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

Bold values indicate statistical significance. Separate tests were performed for the entire community and for the Restionaceae alone using ECOSIM version 7.7.

**Fig. 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).

Although the trade-offs are 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 Northern European meadows grow. By contrast, fynbos species are more bimodally 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 as a result of groundwater flow from a large sandstone aquifer while others have impeded drainage as a result of 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 distributions of water are not independent of each other and these vary over time. An advantage of using SEVs as we have done is that this method captures all three components of soil moisture variation in space, depth and time to deal with the fluctuation niche (Terradas *et al.*, 2009).

HNS 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 the 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 world-wide.

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), suggesting 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 the competing demands of water conservation vs carbon acquisition along soil moisture gradients, and 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 (N) 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 strengthened 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 eco-hydrology of other plant communities and 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 changing 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 by permitting the production of fine-scale projections of soil moisture conditions relevant to plant performance, and by 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.

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Supporting Information

Additional supporting information may be found in the online version of this article.

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

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

Table S2 List of species in (a) the fynbos in South Africa and (b) the wet meadows in England

Table S3 Values of hydrological niche parameters for soil drying stress (sum exceedance value for soil drying (SEV_d)) and aeration stress (SEV_a) recorded at (a) the fynbos sites, South Africa and (b) the wet meadow sites, UK

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