



Dissecting the hydrological niche: soil moisture, space and lifespan

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Keywords

Alpine meadow; *dehesa* meadow; Determinants of plant community diversity and structure; GAMM regression; Iberian Peninsula; MEM spatial variables; Pianka's index; Plant co-existence; RDA models; Water table depth

Abbreviations

AWTD = average water table depth; GAMM = generalised additive mixed models; NMDS = non-metric multidimensional scaling; MEM = Moran's eigenvector maps; RDA = redundancy analysis; SAC = spatial autocorrelation.

Nomenclature

Castroviejo (1986–2012) or (when species are missing) Tutin et al. (1964–1980), except for species included in Appendix S1.

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Introduction

Most plant communities contain mixtures of species that compete for the same essential resources. How competing plants manage to co-exist with one another is a

Abstract

Questions: Are communities structured on a hydrological (soil moisture) gradient? Is there spatial segregation into hydrological niches? What is the shape of the hydrological niches of individual species? Controlling for spatial autocorrelation, how much of the spatial structure in the community is due to variation in hydrology? Do annuals and perennials behave alike with respect to the above questions?

Locations: La Mina in Moscosa Farm, Salamanca, western Spain (*dehesa* community) and Laguna Larga in the Urbión Peaks, Soria, central-northern Spain (alpine grassland).

Methods: The presence of plant species was sampled in two contrasting field sites, for which we also built hydrological models. First, we reduced the dimensionality of the plant distribution data (non-metric multidimensional scaling) and measured the correlation between the resulting ordination and the hydrological gradient. Then we defined hydrological niches and tested niche segregation of plant species against null models (Pianka metrics). Finally, we characterized the hydrological niche of each species using generalised additive mixed models and partitioned the species distribution variance into (1) a hydrological component, (2) a linear trend component and (3) a spatial component, defined through sets of spatial variables (Moran's eigenvector maps).

Results: Both plant communities were primarily structured along hydrological gradients, and spatial segregation into hydrological niches occurred among perennial species, although not among annuals in the *dehesa* community. *Dehesa* annuals were spatially aggregated in the driest niches. Hydrological variation shaped the responses of 60% of the annual and about 70% of the perennial species in both the *dehesa* meadow and the alpine community. Most responses were either monotonic or hump-shaped. Finally, spatially structured hydrological variation proved to be the main driver of spatially structured species composition in all cases.

Conclusions: Linearly (gradient of slope) and topographically (at a fine scale) structured variation in hydrology is the main driver of spatially structured species composition in both communities. Our results support the ecological hypothesis that spatial niche segregation on soil moisture gradients is an important mechanism of co-existence for perennials in both test communities, although not for the species-rich sub-community of annuals in the *dehesa* meadow.

long-standing conundrum (Silvertown 2004), but we may at last be nearing a solution. The various mechanisms of co-existence that have been proposed can be divided into two types (Chesson 2000): stabilizing mechanisms such as niche segregation, in which the effects of interspecific

competition are frequency-dependent, thus protecting species from local extinction when they become rare, and equalizing mechanisms such as the neutral theory (Hubbell 2001), which limit or delay the monopolization of resources by potentially dominant species.

For a decade after the publication of Hubbell's (2001) book, *The Unified Neutral Theory of Biodiversity and Biogeography*, it was often argued that plant communities must be assembled by equalizing mechanisms because the plant niches that would stabilize communities had not been demonstrated (Rosindell et al. 2011). Silvertown (2004) pointed out that an absence of evidence for niche-based co-existence was not evidence of its absence. Purves & Turnbull (2010) showed that the central assumption of neutral theory, which is that species that are different in phenotype will have equal fitness, is only likely to be true in the rarest of circumstances.

Examples of stable co-existence achieved through niche segregation and tested in competition models have now begun to accumulate (Adler et al. 2006, 2010; Angert et al. 2009; Levine & HilleRisLambers 2009; Clark et al. 2010). Nonetheless, the ultimate solution to the conundrum of co-existence is likely to be pluralistic because it is widely recognized that the composition of plant communities can be influenced by both stabilizing and equalizing mechanisms to varying degrees (Adler et al. 2007; Stokes & Archer 2010; Chase & Myers 2011; Rosindell et al. 2012; Chase 2014), although stabilizing mechanisms of some kind are essential for indefinite co-existence (Chesson 2000). Wilson (2011) evaluated the 12 theories that he believed contain the only distinct mechanisms of plant co-existence and concluded that five stabilizing mechanisms and two equalizing ones had at least some empirical support. Niche segregation is the best-supported stabilizing mechanism, and there is growing field and experimental evidence that soil moisture gradients are an important niche dimension in many plant communities (Silvertown et al. 1999; Araya et al. 2011; Markham 2014), as reviewed by Silvertown et al. (2015).

While segregation on soil moisture gradients appears to be ubiquitous across the gamut of plant communities from arid environments through to wetlands (Silvertown et al. 2015), we still do not know what contribution this makes to plant community structure or co-existence. In this paper we introduce a new methodology that makes it possible to answer the first of these questions. We use this methodology to dissect the hydrological niche in two different plant communities and to estimate how much of the spatial variance in plant community structure is due to segregation on a soil moisture gradient and how much is due to other processes, including spatial autocorrelation. Both plant communities are in Spain, one in a wet, sub-alpine environment containing only perennial herbs, and the

other is a lowland seasonally dry *dehesa* grassland with a high diversity of both annuals and perennials.

Annuals and perennials have different regeneration biology, with possible consequences for co-existence (Grubb 1977). Many annuals have life cycles that contain a persistent seed bank, which lends itself to co-existence mediated by temporal niche segregation (Warner & Chesson 1985; Pake & Venable 1996; Angert et al. 2009). This might mean that spatial niche segregation is weaker in annuals than in perennials and so we also test for this.

Our analysis enables us to answer five questions: (1) are the communities structured on a hydrological (soil moisture) gradient; (2) is there spatial segregation into hydrological niches; (3) what is the shape of the hydrological niches of individual species; (4) controlling for spatial autocorrelation, how much of the spatial structure in the community is due to variation in hydrology; and (5) do annuals and perennials behave alike with respect to these questions?

Methods

Sampling design

An Iberian *dehesa* meadow (Eunis habitat type 6310; European Commission 2013) on granite soils was sampled at La Mina in Moscosa Farm (41°8'21.88" N, 6°6'52.33" W; 780 m a.s.l.), Salamanca province, western Spain. A 50 m × 50-m study plot with a 1.8% gradient was sampled (Appendix S1). The presence of plant species was recorded (Spring 2007) in 196 1-m² quadrats placed on a 14 × 14 grid. Similarly, an Iberian alpine meadow on sandstone/conglomerate soils, with a 2.1% gradient, was sampled at Laguna Larga in the Urbión Peaks (42°0'19.50" N, 2°52'2.26" W; 2080 m a.s.l.), Soria province, central-northern Spain, using 172 1-m² quadrats placed regularly. Plant nomenclature followed standard Floras (Tutin et al. 1964–1980; Castroviejo 1986–2012), except for species included in Appendix S1. The spatial variables northing, easting and elevation were measured using a total station machine (Leica Geosystems TPS800).

Quantification of the hydrological gradient

We made fortnightly measurements of water table depth from nine dipwells over a 2-yr period. A fine-scale topographic map (constructed from the surveyed points) was used to construct field-scale hydrological models for each of the sites (Gowing & Youngs 1997). This model quantified by interpolation the average water table depth (AWTD) in each quadrat during the growing season (30 wk for Moscosa, from mid-Feb to end of Sept; 20 wk for Urbión, from mid-May to mid Sept). Interpolation was

accomplished by regression analysis. Since water table depth measurements are made from an origin at ground level, low values of AWTD correspond to high levels of oxygen deficit stress (due to waterlogging); high values of AWTD correspond to high levels of water deficit stress (due to soil drying) over the growing season.

Data analysis

Our dissection of the spatial distribution of species in relation to soil moisture gradients had four steps. First, we used unconstrained NMDS to reduce the dimensionality of the plant distribution data without any reference to environmental gradients of any kind. We then tested whether the principal dimensions that result from the NMDS analysis align with the soil moisture gradient. In the second step, we tested for niche segregation against a null model; in the third step we characterized the hydrological niche of each species using GAMMs while taking spatial autocorrelation into account. Finally, in the fourth step, we partitioned the spatial variance in species distribution into three components, (1) a hydrological component, (2), a linear trend component and (3) a spatial component, defined through sets of independent spatial variables constructed using the Moran's eigenvector maps method. A complete, fully referenced, description of the data analysis can be found in Appendix S2.

At both sites, we used a two-matrix data set. For Moscosa, it included a species composition matrix of $n = 196$ sample units $\times p = 123$ species, where each element represented the presence-absence of a species in a sample unit. An environment and spatial matrix of $n = 196$ sample units $\times q = 3$ represented the values of AWTD, northing and easting. The same matrices were used for Urbión, with $n = 172$ sample units and $p = 52$ species.

Supporting information provides data (Appendices S5, S6) and R coding (Appendix S4) sufficient to replicate the analysis described above.

Results

At Moscosa, we recorded 71 species of annuals and 52 perennials (Appendix S1), but only 81 of the 123 species had a relative frequency >0.05 ; in Urbión, 52 species were found, but only 28 had frequency >0.05 (Appendix S1). Unconstrained ordination (Fig. 1), which here shows the two main species gradients in the meadows without external reference to any environmental variables, shows that the first main species gradient (NMDS1) is, in both cases, strongly associated with the hydrological gradient (as measured by AWTD in m).

For Moscosa, the null hypothesis of random overlap across the hydrological space at a fine scale (13 niches) was

rejected for the whole community (observed mean = 0.399 $<$ simulated index = 0.410; $P = 0.000$) and for perennials as a group (observed mean = 0.369 $<$ simu-

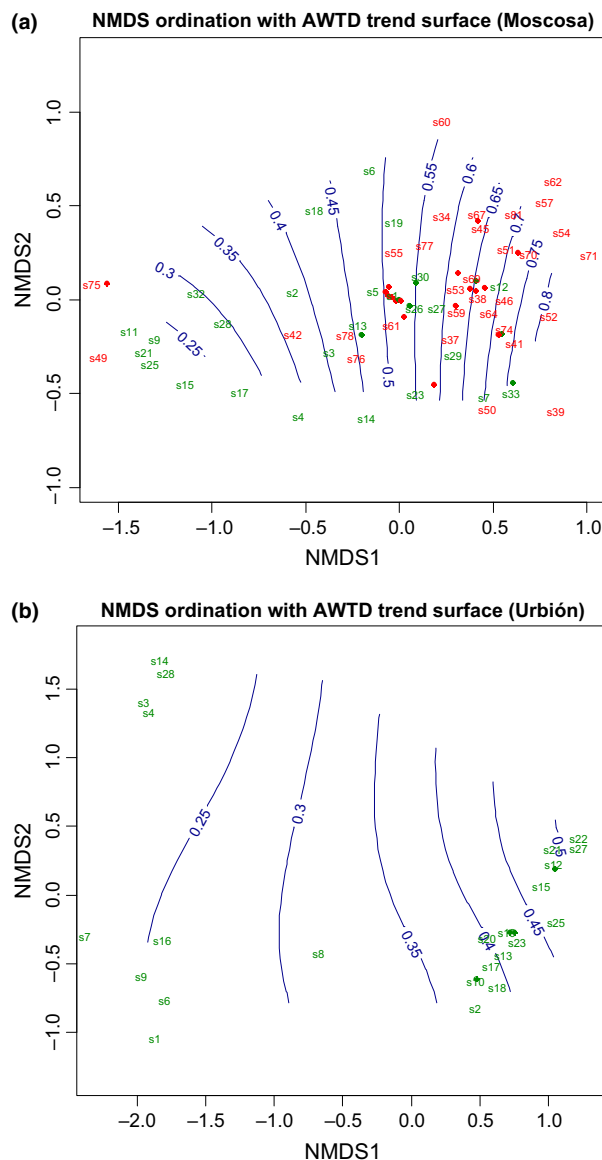


Fig. 1. Main species gradients for La Mina meadow in Moscosa farm (a) and Laguna Larga meadow in the Urbión Peaks (b), as described with NMDS, in multivariate space (Jaccard measure). Moscosa annuals are indicated in red and perennials in green. Non-metric goodness-of-fit of the ordination: $R^2 = 0.967$ (Moscosa) and $R^2 = 0.989$ (Urbión). NMDS is a technique for unconstrained ordination, so the trend surface for AWTD in metres (blue lines) was overlaid onto the species ordination only after the NMDS procedure was concluded. Significance of trend surface: $F = 24.3$, e. d. f. = 2.94, P -value < 0.000 (Moscosa) and $F = 34.1$, e. d. f. = 2.85, P -value < 0.000 (Urbión). In both cases, the hydrological gradient accounts for most of the variation observed in the first ordination axis (NMDS1); the levels of the contours depict the hydrological niches used in this work. Key to species: see Appendix S1.

lated index = 0.383; $P = 0.001$). Hence, perennials segregate along the hydrological gradient. Significant GAMM models were fitted for 23 (70% of species with frequency >5%) perennials (Table S1 in Appendix S3). The average model fit was R^2 (adj.) = 21.3%. Consistent with the observed segregation pattern, monotonic perennial responses were either increasing or decreasing with increasing soil drying (Fig. S1), thus contributing to segregation (compare, e.g. *Poa bulbosa* with *Poa trivialis* or *Senecio jacobaea* with *Thapsia villosa*; Fig. S1). The various hump-shaped, or similar, responses (35% of the fitted models) also contribute to segregation (compare, e.g. *Briza media*, *Galium verum* and *Echium plantagineum*; Fig. S1). In contrast, and as suggested by the unconstrained ordination (Fig. 1), the null hypothesis of random overlap was not rejected for annuals (observed mean = 0.463 >simulated index = 0.448; $P = 0.995$). Hence annuals do not segregate along the hydrological gradient, but rather tend to aggregate at the dry end. Significant GAMM models were fitted for 26 annuals (54%; Table S2 in Appendix S3), with average model fit R^2 (adj.) = 18.6%. No significant relationships were found for invasive annuals (e.g. *Trifolium dubium*) with relative frequency >ca. 0.9. Consistent with the observed aggregation pattern, most annual responses (60% of the fitted models) are both monotonic (either sigmoid or curvilinear) and increasing with increasing soil drying (Table S3, Fig. S2). This contributes greatly to generate this pattern of species aggregation (compare *Aphanes arvensis*, *Bellardia trixago*, *Brassica barrelieri*, *Galium parisiense*, *Jasione montana*, *Ornithopus perpusillus*, *Trifolium glomeratum* and *Xolantha guttata*; Fig. S2), despite 24% of fitted models for annuals displaying hump-shaped relationships.

For Urbión, the null hypothesis of random overlap across the hydrological space at a fine scale (seven niches) was rejected for the whole community (observed mean = 0.579 <simulated index = 0.595; $P = 0.010$). Hence species segregate along the hydrological gradient. Significant GAMM models were fitted for 20 (71% of species with frequency >5%) species (Table S3 in Appendix S3). The average model fit was R^2 (adj.) = 17.2%. Consistent with the observed segregation pattern, monotonic species responses were either increasing or decreasing with increasing soil drying (Fig. S3), thus contributing to segregation. Hump-shaped responses (25% of the fitted models) also contributed to segregation.

Marginal tests (Table 1) show that, for Moscosa, AWTD explains ca. 18% of multivariate variation in perennial composition and ca. 16% in annual composition. Likewise, species composition is strongly spatially structured (ca. 30% for perennials; ca. 27% for annuals, as described by MEM spatial variables), with a linear gradient (Table 1, Fig. 2) being responsible for a relatively important part of

Table 1. Marginal tests results from direct RDAs fitting groups of spatial MEM variables, linear trends and the hydrological descriptor (AWTD) to explain species composition in a *dehesa* meadow at Moscosa Farm and in an alpine meadow at Urbión Peaks, Spain. The response is a Hellinger-transformed presence-absence species matrix in both cases. The hydrological component includes first-, second- and third-degree AWTD terms. The linear trend component is a surface described by the X-Y coordinates. The spatial component comprises sets of MEM spatial variables created specifically for each test (14 variables for the whole community and annuals in Moscosa; 15 for perennials in Moscosa; 18 for the whole community in Urbión); these MEM spatial variables describe spatial structuring. In complex models the amount of variation explained by each component depends on the other components (see Fig. 2). P -values were obtained from 1000 permutations.

Source of Variation	Model Var. (df)	Resid Var. (df)	F	P	R^2 (adj.)
Whole Community (Moscosa)					
Hydrological Descriptor	0.0806 (3)	0.3447 (192)	15.0	0.001	0.177
Linear Trend	0.0631 (2)	0.3622 (193)	16.8	0.001	0.140
Spatial MEM Variables	0.1397 (14)	0.2856 (181)	6.3	0.001	0.277
Perennials (Moscosa)					
Hydrological Descriptor	0.0843 (3)	0.3560 (192)	15.1	0.001	0.179
Linear Trend	0.0615 (2)	0.3788 (193)	15.7	0.001	0.131
Spatial MEM Variables	0.1518 (15)	0.2885 (180)	6.3	0.001	0.290
Annuals (Moscosa)					
Hydrological Descriptor	0.0712 (3)	0.3358 (192)	13.6	0.001	0.162
Linear Trend	0.0596 (2)	0.3474 (193)	16.6	0.001	0.138
Spatial MEM Variables	0.1296 (14)	0.2774 (181)	6.0	0.001	0.266
Whole Community (Urbión)					
Hydrological Descriptor	0.0997 (3)	0.4834 (168)	11.6	0.001	0.156
Linear Trend	0.1057 (2)	0.4775 (169)	18.7	0.001	0.171
Spatial MEM Variables	0.2631 (18)	0.3201 (153)	7.0	0.001	0.387

these spatial structures. Variation partitioning (Fig. 2), however, shows that the unique contribution of the hydrological descriptors to explain composition (fraction [a]) is <2% in all three cases, i.e. species composition explained by non-spatially structured hydrological variation is minor. In other words, induced spatial variation (fractions [f] and [g]), which corresponds to spatially structured species composition that is explained by spatially structured hydrological variation, is the strongest element in all three cases. The sum of fractions [f] and [g] amounts to 16.2% of the variance explained in the perennials assemblage and 14.3% in the annuals assemblage. In both cases, fraction [g], corresponding to variation in species composition that is associated with the (linear) gradient of slope, is the most important (9.6%). Fraction [f] corre-

sponds to spatially structured variation in species composition that is not associated with linear gradients, but with local topography; this fraction is stronger for perennials (6.6%) than for annuals (4.7%).

For the Urbión meadow, AWTD explains ca. 16% of multivariate variation in species composition (Table 1). Likewise, species composition is strongly spatially structured (38.7%), as described by MEM spatial variables. Variance partitioning (Fig. 5) shows that species composition explained by non-spatially structured hydrological variation (fraction [a]) is minor (2.4%). Hence, as in the Moscosa site, induced spatial variation (fractions [f] and [g]), which together amount to 11.9%, represents a strong component. However, in the Urbión site, the spatially structured variation in species composition that is associ-

ated with the local topography (fraction [f]) explains 8.1% of adjusted variance and is, therefore, larger than the variation in species composition that is associated with the (linear) gradient of slope (fraction [g]), which represents only 3.8% of adjusted variance.

Finally, in both meadows, the unique contributions of the MEM spatial variables (fraction [c]), which correspond to spatially structured species composition that is not explained by the hydrological descriptor, but by latent processes, suggests the existence of spatially structured ecological factor(s) other than AWTD driving species composition. This component is stronger in the Urbión site (14.8% of total variance) than for the annuals (8.3%) or the perennials (10.1%) in the Moscosa site.

Discussion

Although soil moisture and local topography are well known influences on plant distribution (Moeslund et al. 2013), we believe that this is the first study to formally decompose plant distribution into spatial components that include the important effect of hydrology. The methods developed by Borcard et al. (1992) and Borcard & Legendre (1994) have been widely used, e.g. to test competing theories regarding dispersal limitation, environmental determinism and neutral models in an American temperate forest (Gilbert & Lechowicz 2004). In Amazonian forests, Tuomisto et al. (2003) found that spatially structured environmental variation was the most important ecological factor explaining plant composition at a regional scale, with dispersal also having some ecological effect, although neutrality was not supported.

By analysing the spatial variance in plant community structure, we have been able to answer five questions about the hydrological niche, including whether annuals and perennials behave alike. First, we found that both plant communities that we investigated were structured along hydrological gradients and that their primary axes of variation aligned with average water table depth (AWTD; Fig. 1a,b). AWTD is measured as a distance below the surface so this measure of hydrological conditions is necessarily highly correlated with fine-scale topography. Second, we found that spatial segregation occurred among perennial species, but not among the annuals in the *dehesa* community (Fig. 1a). *Dehesa* annuals as a group were aggregated at the dry end of the hydrological gradient, where most fell into just three or four niches (niches 0.50–0.70) out of the 17 that were present.

Third, we investigated the shape of species' hydrological niches by fitting GAMS, which showed that species responses were, with very few exceptions, either monotonic (increasing or decreasing along the hydrological gradient) or hump-shaped (between 24–35% of species

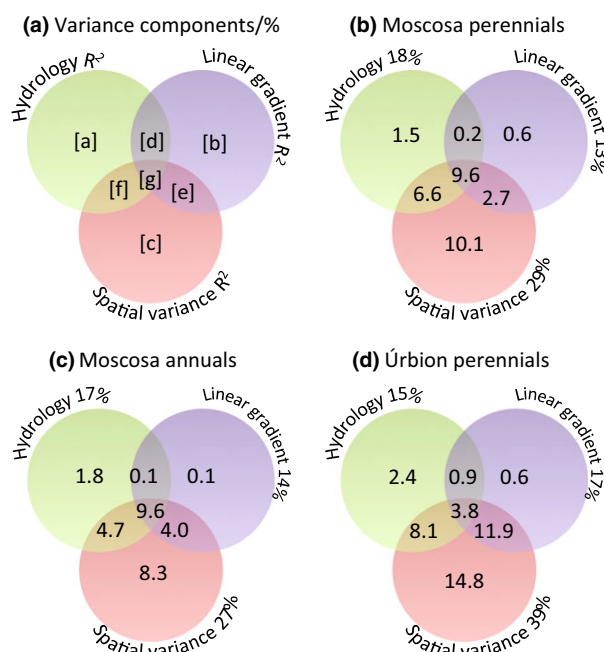


Fig. 2. Venn diagrams showing how multivariate variation in species composition was partitioned among a hydrological component, a linear trend component and a spatial component described with MEM variables. Numbers are adjusted R^2 values (%). The hydrological component includes AWTD and its second- and third-degree terms. The linear trend represents a surface described by the X-Y coordinates. The spatial component comprises sets of MEM spatial variables, selected for each partition specifically. The unique contributions of the hydrological, trend and spatial components are denoted by [a], [b] and [c], respectively. The fractions [f] and [g] correspond to spatially structured biological variation that is explained by the hydrological component, which is also spatially structured (induced spatial variation); fraction [f] is related to local topography at a fine scale; fraction [g] is related to local linear gradients (local gradients of slope). Fraction [d] corresponds to linearly structured hydrological variation. Fraction [e] corresponds to linear variation that is shared by the MEM variables (the MEMs model both purely linear variation and any complex structures present in the data).

responses). The important conclusion here is that, contrary to the assumptions of the neutral model, co-occurring species show different responses along soil moisture gradients. Similar results have now been found in many plant communities (Silvertown et al. 2015).

A comparison of the shapes of the species' hydrological niches illuminates the difference in community structure found between perennials and annuals. Since most perennial responses were either monotonic increasing or monotonic decreasing with increasing soil drying (65–75%), this difference created segregation, with hump-shaped responses also contributing to segregation. In contrast, most annual responses were monotonic increasing with increasing soil drying (62%), thus creating a pattern of overlap and species aggregation. These results suggest that, at least in the *dehesa* community we studied, spatial niche segregation on soil moisture gradients may not be an important mechanism of co-existence in the species-rich sub-community of annuals. Given that rainfall in the area is highly variable from year-to-year (Ceballos et al. 2013), temporal niche segregation (the storage effect), as found among Sonoran desert annuals (Angert et al. 2009), is an alternative possibility.

Fourth, we partitioned the components of spatial structure in the two plant communities, with complex results (Table 1, Fig. 2). Among the perennials at Moscosa, 18% of the variance in species composition was ascribed to variation in hydrology. For the annuals in Moscosa and for perennials in Urbión, the variance explained was about 16% in both (16.2% and 15.6%, respectively). Nearly all the variance in hydrology that drove species composition was spatially structured, but about 2% of the adjusted variance explaining change in species composition was not. This may simply reflect error in the hydrological models fitted. This spatial structure can be further subdivided into components that correspond to the linear gradients of slope (fraction [g]) and to local topographic variation (fraction [f]). In Moscosa, the gradient of slope (9.6% for both annuals and perennials) was more important than local topography (6.6% for perennials and 4.7% for annuals). In contrast, local topography (8.1%) was more important in Urbión than the gradient of slope (3.8%).

Overall, the contributions of hydrologically correlated spatial variation may appear rather small (16.2% for Moscosa perennials; 14.3% for Moscosa annuals; 11.9% for Urbión), but this was nevertheless the most important driver of spatially structured species composition in the Moscosa data. Spatial structure not correlated with hydrology ([b] + [c] + [e] in Fig. 2), amounted to 13.4% for perennials and 12.4% for annuals. By comparison, species composition in the Urbión data was even more strongly spatially structured than in the Moscosa data, and more than a

quarter of its spatial variance (26.7%) was not accounted for by hydrology. Nonetheless, we can conclude that hydrology was at least as important as any other single cause of spatial structure because it correlates with the primary axis of variation in Fig. 1. Other causes of spatial structure could have included ecological factors such as vegetation pattern created by clonal growth, local variation in soil nutrients or population processes such as dispersal (Legendre & Legendre 2012).

Our fifth question was whether annuals behaved differently from perennials, and we found that indeed they did, occupying a distinct zone of niche space at the drier end of the hydrological gradient at Moscosa farm. Elsewhere, annuals have been found to partition a hydrological gradient in vernal pools in California (Bauder 2000), where even different genotypes of a single species occupy different zones of water depth (Linhart & Baker 1973). Niche segregation has also been experimentally demonstrated in several annual communities, although without always identifying the precise nature of the niche axes that are important for this (Sharitz & McCormick 1973; Turnbull et al. 2005; Levine & HilleRisLambers 2009).

Our analysis has demonstrated that niche segregation along soil moisture gradients contributes significantly to community structure, but the results are based on observational data and therefore offer only circumstantial evidence for the importance of the hydrological niche to co-existence (Silvertown 2004). Complementary experimental and theoretical studies are required to quantify what contribution hydrological niche segregation makes to co-existence. We must also be cautious about how the soil moisture gradient influences plant distribution, since soil moisture has direct and indirect effects upon the soil environment for plants. It not only controls water availability, but also – when present in excess – affects oxygen availability, microbial community composition and function, and nutrient availability (Araya et al. 2012). That said, our dissection of the hydrological niche offers a firm statistical justification for exploring the underlying mechanisms and their consequences.

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References

- Adler, P.B., HilleRisLambers, J., Kyriakidis, P.C., Guan, Q.F. & Levine, J.M. 2006. Climate variability has a stabilizing effect on the coexistence of prairie grasses. *Proceedings of the National Academy of Sciences of the United States of America* 103: 12793–12798.
- Adler, P.B., HilleRisLambers, J. & Levine, J.M. 2007. A niche for neutrality. *Ecology Letters* 10: 95–104.
- Adler, P.B., Ellner, S.P. & Levine, J.M. 2010. Coexistence of perennial plants: an embarrassment of niches. *Ecology Letters* 13: 1019–1029.
- Angert, A.L., Huxman, T.E., Chesson, P. & Venable, D.L. 2009. Functional tradeoffs determine species coexistence via the storage effect. *Proceedings of the National Academy of Sciences of the United States of America* 106: 11641–11645.
- Araya, Y.N., Silvertown, J., Gowing, D.J., McConway, K.J., Linder, H.P. & Midgley, G. 2011. A fundamental, eco-hydrological basis for niche segregation in plant communities. *New Phytologist* 189: 253–258.
- Araya, Y.N., Gowing, D.J. & Dise, N. 2012. Does soil nitrogen availability mediate the response of grassland composition to water regime? *Journal of Vegetation Science* 26: 506–517.
- Bauder, E.T. 2000. Inundation effects on small-scale plant distributions in San Diego, California vernal pools. *Aquatic Ecology* 34: 43–61.
- Borcard, D. & Legendre, P. 1994. Environmental control and spatial structure in ecological communities: an example using oribatid mites (Acari, Oribatei). *Environmental and Ecological Statistics* 1: 37–61.
- Borcard, D., Legendre, P. & Drapeau, P. 1992. Partialling out the Spatial Component of Ecological Variation. *Ecology* 73: 1045–1055.
- Castroviejo, S. 1986–2012. *Flora iberica*. Real Jardín Botánico, CSIC, Madrid, ES.
- Ceballos, A., Morán, E. & López, J.A. 2013. Análisis de la variabilidad espaciotemporal de las precipitaciones en el sector español de la cuenca del Duero (1961–2005). *Boletín de la Asociación de Geógrafos Españoles* 61: 235–259.
- Chase, J.M. 2014. Spatial scale resolves the niche versus neutral theory debate. *Journal of Vegetation Science* 25: 319–322.
- Chase, J.M. & Myers, J.A. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society, B-Biological Sciences* 366: 2351–2363.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343–366.
- Clark, J.S., Bell, D., Chu, C.J., Courbaud, B., Dietze, M., Hersh, M., HilleRisLambers, J., Ibanez, I., LaDeau, S., (...) & Wyckoff, P. 2010. High-dimensional coexistence based on individual variation: a synthesis of evidence. *Ecological Monographs* 80: 569–608.
- European Commission, D.E. 2013. *Interpretation manual of European Union habitats. EUR 28*. DG-ENV, Luxemburg, LU.
- Gilbert, B. & Lechowicz, M.J. 2004. Neutrality, niches, and dispersal in a temperate forest understory. *Proceedings of the National Academy of Sciences of the United States of America* 101: 7651–7656.
- Gowing, D. & Youngs, E.G. 1997. The effect of the hydrology of a Thames flood meadow on its vegetation. *British Hydrological Society Occasional Paper* 8: 69–80.
- Grubb, P.J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Reviews of the Cambridge Philosophical Society* 52: 107–145.
- Hubbell, S.P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ, US.
- Legendre, P. & Legendre, L. 2012. *Numerical ecology*, 3rd English Edition. Elsevier Science, Amsterdam, NL.
- Levine, J.M. & HilleRisLambers, J. 2009. The importance of niches for the maintenance of species diversity. *Nature* 461: 254–258.
- Linhart, Y.B. & Baker, I. 1973. Intrapopulation differentiation of physiological response to flooding in a population of *Veronica peregrina* L. *Nature* 242: 275–276.
- Markham, J. 2014. Rare species occupy uncommon niches. *Scientific Reports* 4: 6012.
- Moelsund, J.E., Arge, L., Bøcher, P.K., Dalgaard, T., Odgaard, M.V., Nygaard, B. & Svenning, J.-C. 2013. Topographically controlled soil moisture is the primary driver of local vegetation patterns across a lowland region. *Ecosphere* 4: art91.
- Pake, C.E. & Venable, D.L. 1996. Seed banks in desert annuals: implications for persistence and coexistence in variable environments. *Ecology* 77: 1427–1435.
- Purves, D.W. & Turnbull, L.A. 2010. Different but equal: the implausible assumption at the heart of neutral theory. *Journal of Animal Ecology* 79: 1215–1225.
- Rosindell, J., Hubbell, S.P. & Etienne, R.S. 2011. The unified neutral theory of biodiversity and biogeography at age ten. *Trends in Ecology & Evolution* 26: 340–348.
- Rosindell, J., Hubbell, S.P., He, F., Harmon, L.J. & Etienne, R.S. 2012. The case for ecological neutral theory. *Trends in Ecology & Evolution* 27: 203–208.
- Sharitz, R.R. & McCormick, J.F. 1973. Population dynamics of two competing annual plant species. *Ecology* 54: 723–740.
- Silvertown, J. 2004. Plant coexistence and the niche. *Trends in Ecology & Evolution* 19: 605–611.
- Silvertown, J., Dodd, M.E., Gowing, D.J.G. & Mountford, J.O. 1999. Hydrologically defined niches reveal a basis for species richness in plant communities. *Nature* 400: 61–63.
- Silvertown, J., Araya, Y. & Gowing, D. 2015. Hydrological niches in terrestrial plant communities: a review. *Journal of Ecology* 103: 93–108.

- Stokes, C.J. & Archer, S.R. 2010. Niche differentiation and neutral theory: an integrated perspective on shrub assemblages in a parkland savanna. *Ecology* 91: 1152–1162.
- Tuomisto, H., Ruokolainen, K. & Yli-Halla, M. 2003. Dispersal, environment, and floristic variation of western Amazonian forests. *Science* 299: 241–244.
- Turnbull, L.A., Manley, L. & Rees, M. 2005. Niches, rather than neutrality, structure a grassland pioneer guild. *Proceedings of the Royal Society, B-Biological Sciences* 272: 1357–1364.
- Tutin, T.G., Heywood, V.H., Burges, N.A., Moore, D.M., Valentine, D.H., Walters, S.M. & Webb, D.A. 1964–1980. *Flora Europaea*. Cambridge University Press, Cambridge, UK.
- Warner, R.R. & Chesson, P.L. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *The American Naturalist* 125: 769–787.
- Wilson, J.B. 2011. The twelve theories of co-existence in plant communities: the doubtful, the important and the unexplored. *Journal of Vegetation Science* 22: 184–195.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Sites photographs, full species names and species frequencies.

Appendix S2. Data analysis.

Appendix S3. Generalised additive mixed modelling summaries and Figs S1–S3.

Appendix S4. R code.

Appendix S5. Moscosa data set.

Appendix S6. Lifespan.

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.mk609>.