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1 **Dissecting the hydrological niche: soil moisture, space and lifespan**

2 **Running head:** Dissecting the hydrological niche

3

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14

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18

19 **Summary**

20 **Questions:** Are the communities structured on a hydrological (soil moisture) gradient? Is
21 there spatial segregation into hydrological niches? What is the shape of the hydrological
22 niches of individual species? Controlling for spatial autocorrelation, how much of the
23 spatial structure in the community is due to variation in hydrology? Do annuals and
24 perennials behave alike with respect to questions 1-4?

25 **Locations:** La Mina in Moscosa Farm, Salamanca, Western Spain (*dehesa* community) and
26 Laguna Larga in the Urbión Peaks, Soria, Central-Northern Spain (alpine grassland).

27 **Methods:** The presence of plant species was sampled in two contrasting field sites, for
28 which we also built hydrological models. First we reduced the dimensionality of the plant
29 distribution data (non-metric multidimensional scaling) and measured the correlation
30 between the resulting ordination and the hydrological gradient. Then we defined
31 hydrological niches and tested niche segregation of plant species against null models
32 (Pianka metrics). Finally, we characterised the hydrological niche of each species using
33 Generalised Additive Mixed Models and partitioned the species distribution variance into
34 (a) an hydrological component, (b) a linear trend component and (c) and a spatial
35 component defined through sets of spatial variables (Moran's eigenvector maps).

36 **Results:** Both plant communities were primarily structured along hydrological gradients
37 and spatial segregation into hydrological niches occurred among perennial species, though
38 not among the annuals in the *dehesa* community. *Dehesa* annuals were spatially aggregated
39 in the driest niches. Hydrological variation shaped the responses of 60% of the annual and
40 about 70% of the perennial species in both the *dehesa* meadow and the alpine community.
41 Most responses were either monotonic or hump-shaped. Finally, spatially structured

42 hydrological variation proved to be the main driver of spatially structured species
43 composition in all three cases.

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

50

51 **Key words:** alpine meadow; *dehesa* meadow; determinants of plant community diversity and
52 structure; GAMM regression; Iberian Peninsula; MEM spatial variables; Pianka's index; plant
53 coexistence; RDA models; water table depth.

54

55 **Abbreviations:** AWTD = average water-table depth; GAMM = Generalised Additive Mixed
56 Models; NMDS = non-metric multidimensional scaling; MEM = Moran's eigenvector maps;
57 RDA = Redundancy analysis; SAC = spatial autocorrelation.

58

59 **Nomenclature:** Castroviejo 1986-2012 or (when species are missing) Tutin et al. 1964-1980,
60 except for the species included in Appendix S1.

61

62 ***Introduction***

63 Most plant communities contain mixtures of species that compete for the same essential
64 resources. How competing plants manage to coexist with one another is a long-standing
65 conundrum (Silvertown 2004), but we may at last be nearing a solution. The various
66 mechanisms of coexistence that have been proposed can be divided into two types (Chesson
67 2000): stabilizing mechanisms such as niche segregation, in which the effects of interspecific
68 competition are frequency-dependent, thus protecting species from local extinction when they
69 become rare, and equalizing mechanisms such as the neutral theory (Hubbell 2001), that limit
70 or delay the monopolization of resources by potentially dominant species.

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

79 Examples of stable coexistence achieved through niche segregation and tested in
80 competition models have now begun to accumulate (Adler et al. 2006; Angert et al. 2009;
81 Levine & HilleRisLambers 2009; Adler et al. 2010; Clark et al. 2010). Nonetheless, the
82 ultimate solution to the conundrum of coexistence is likely to be pluralistic because it is widely
83 recognised that the composition of plant communities can be influenced by both stabilizing and
84 equalizing mechanisms to varying degrees (Adler et al. 2007; Stokes & Archer 2010; Chase &

85 Myers 2011; Rosindell et al. 2012; Chase 2014), although stabilizing mechanisms of some kind
86 are essential for indefinite coexistence (Chesson 2000). Wilson (2011) evaluated the 12
87 theories that he believed contain the only distinct mechanisms of plant coexistence and
88 concluded that 5 stabilizing mechanisms and 2 equalizing ones had at least some empirical
89 support. Niche segregation is the best-supported stabilizing mechanism and there is growing
90 field and experimental evidence that soil-moisture gradients are an important niche dimension
91 in many plant communities (Silvertown *et al.* 1999; Araya *et al.* 2011; Markham 2014), as
92 reviewed by Silvertown, Araya & Gowing (2014).

93 While segregation on soil-moisture gradients appears to be ubiquitous across the gamut
94 of plant communities from arid environments through to wetlands (Silvertown et al. 2014), we
95 still do not know what contribution this makes to plant community structure or coexistence. In
96 this paper we introduce a new methodology that makes it possible to answer the first of these
97 questions. We use this methodology to dissect the hydrological niche in two different plant
98 communities and to estimate how much of the spatial variance in plant community structure is
99 due to segregation on a soil-moisture gradient and how much is due to other processes
100 including spatial autocorrelation. Both plant communities are in Spain, one in a wet, sub-alpine
101 environment containing only perennial herbs and the other is a lowland, seasonally dry *dehesa*
102 grassland with a high diversity of both annuals and perennials.

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

108 Our analysis enables us to answer five questions:

- 109 1. Are the communities structured on a hydrological (soil moisture) gradient?
- 110 2. Is there spatial segregation into hydrological niches?
- 111 3. What is the shape of the hydrological niches of individual species?
- 112 4. Controlling for spatial autocorrelation, how much of the spatial structure in the
113 community is due to variation in hydrology?
- 114 5. Do annuals and perennials behave alike with respect to questions 1 - 4?

115

116 ***Materials and methods***

117 ***Sampling design***

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

128 machine (Leica Geosystems TPS800).

129 ***Quantification of the hydrological gradient***

130 We made fortnightly measurements of water-table depth from nine dipwells over a two-
131 year period. A fine-scale topographic map (constructed from the surveyed points) was used to
132 construct a field-scale hydrological models for each of the sites (Gowing & Youngs 1997).
133 This model quantified by interpolation the average water-table depth (AWTD) in each quadrat
134 during the growing season (30 weeks for Moscosa, from mid February to end of September; 20
135 weeks for Urbión, from mid May to mid September). Interpolation was accomplished by
136 regression analysis. Since water-table depth measurements are made from an origin at ground
137 level, low values of AWTD correspond to high levels of oxygen-deficit stress (due to
138 waterlogging); high values of AWTD correspond to high levels of water-deficit stress (due to
139 soil drying) over the growing season.

140 ***Data analysis***

141 Our dissection of the spatial distribution of species in relation to soil-moisture gradients
142 had four steps. First, we used unconstrained non-metric multidimensional scaling (NMDS) to
143 reduce the dimensionality of the plant distribution data without any reference to environmental
144 gradients of any kind. We then tested whether the principal dimensions that result from the
145 NMDS analysis align with the soil-moisture gradient. In the second step, we tested for niche
146 segregation against a null model; in the third step we characterised the hydrological niche of
147 each species using Generalised Additive Mixed Models (GAMMs) while taking spatial
148 autocorrelation into account. Finally, in the fourth step, we partitioned the spatial variance in
149 species distribution into three components, (i) an hydrological component, (ii), a linear trend
150 component, and (iii) a spatial component defined through sets of independent spatial variables

151 constructed using the Moran's eigenvector maps method. A complete, fully referenced,
152 description of the data analysis can be found in Appendix S2.

153 At both sites, we used a two-matrix dataset. For Moscosa, it included a species
154 composition matrix of $n = 196$ sample units \times $p = 123$ species, where each element represented
155 the presence-absence of a species in a sample unit. An environment and spatial matrix of $n =$
156 196 sample units \times $q = 3$ represented the values of AWTD, northing, and easting. The same
157 matrices were used for Urbión, with $n = 172$ sample units and $p = 52$ species.

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

160 **Results**

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

168 For Moscosa, the null hypothesis of random overlap across the hydrological space at a
169 fine scale (thirteen niches) was rejected for the whole community (observed mean = 0.399 <
170 simulated index = 0.410; $p = 0.000$) and for perennials as a group (observed mean = 0.369 <
171 simulated index = 0.383; $p = 0.001$). Hence perennials segregate along the hydrological
172 gradient. Significant GAMM models were fitted for 23 (70% of species with frequency > 5%)

173 perennials (Table S1 in Appendix S3). The average model fit was R^2 (adj.) = 21.3%. Consistent
174 with the observed segregation pattern, monotonic perennial responses were either increasing or
175 decreasing with increasing soil drying (Fig. S1), thus contributing to segregation (compare, for
176 example, *Poa bulbosa* with *Poa trivialis* or *Senecio jacobaea* with *Thapsia villosa* in Fig. S1).
177 The various hump-shaped, or similar, responses (35% of the fitted models) also contribute to
178 segregation (compare, for example, *Briza media*, *Galium verum* and *Echium plantagineum* in
179 Fig. S1). In contrast and as suggested by the unconstrained ordination (Fig. 1), the null
180 hypothesis of random overlap was not rejected for annuals (observed mean = 0.463 > simulated
181 index = 0.448; $p = 0.995$). Hence annuals do not segregate along the hydrological gradient, but
182 rather tend to aggregate at the dry end. Significant GAMM models were fitted for 26 annuals
183 (54%) (Table S2 in Appendix S3), with average model fit R^2 (adj.) = 18.6%. No significant
184 relationships were found for invasive annuals (e.g. *Trifolium dubium*) with relative frequency
185 greater than c.0.9. Consistent with the observed aggregation pattern, most annual responses
186 (60% of the fitted models) are both monotonic (either sigmoid or curvilinear) and increasing
187 with increasing soil drying (Table S3; Fig. S2). This contributes greatly to generate this pattern
188 of species aggregation (compare *Aphanes arvensis*, *Bellardia trixago*, *Brassica barrelieri*,
189 *Galium parisiense*, *Jasione montana*, *Ornithopus perpusillus*, *Trifolium glomeratum* and
190 *Xolantha guttata* in Fig. S2), in spite of 24% of fitted models for annuals being found to
191 display hump-shaped relationships.

192 For Urbi3n, the null hypothesis of random overlap across the hydrological space at a
193 fine scale (seven niches) was rejected for the whole community (observed mean = 0.579 <
194 simulated index = 0.595; $p = 0.010$).). Hence species segregate along the hydrological
195 gradient. Significant GAMM models were fitted for 20 (71% of species with frequency > 5%)
196 species (Table S3 in Appendix S3). The average model fit was R^2 (adj.) = 17.2%. Consistent

197 with the observed segregation pattern, monotonic species responses were either increasing or
198 decreasing with increasing soil drying (Fig. S3), thus contributing to segregation. Hump-
199 shaped responses (25% of the fitted models) also contribute to segregation.

200 Marginal tests (Table 1) show that, for Moscosa, AWTD explains c.18% of multivariate
201 variation in perennials composition and c.16% in annuals composition. Likewise, species
202 composition is strongly spatially structured (c.30% for perennials; c.27% for annuals, as
203 described by MEM spatial variables), with a linear gradient (Table 1; Fig. 5) being responsible
204 for a relatively important part of these spatial structures. Variation partitioning (Fig. 2),
205 however, shows that the unique contribution of the hydrological descriptors to explain
206 composition (fraction [a]) is less than 2% in all three cases, i.e. species composition explained
207 by non-spatially structured hydrological variation is minor. In other words, induced spatial
208 variation (fractions [f] and [g]), which corresponds to spatially structured species composition
209 that is explained by spatially structured hydrological variation, is the strongest element in all
210 three cases. The sum of fractions [f] and [g] amounts to 16.2% of the variance explained in the
211 perennials assemblage and 14.3% in the annuals assemblage. In both cases fraction [g],
212 corresponding to variation in species composition that is associated with the (linear) gradient of
213 slope, is the most important (9.6%). Fraction [f] corresponds to spatially structured variation in
214 species composition that is not associated with linear gradients, but with local topography; this
215 fraction is stronger for perennials (6.6%) than for annuals (4.7%).

216 For the Urbi3n meadow, AWTD explains c.16% of multivariate variation in species
217 composition (Table 1). Likewise, species composition is strongly spatially structured (38.7%),
218 as described by MEM spatial variables). Variance partitioning (Fig. 5) shows that species
219 composition explained by non-spatially structured hydrological variation (fraction [a]) is minor
220 (2.4%). Hence, as in the Moscosa site, induced spatial variation (fractions [f] and [g]), which

221 together add up to 11.9%, represents a strong component). However, in the Urbión site, the
222 spatially structured variation in species composition that is associated with the local
223 topography (fraction [f]) explains 8.1% of adjusted variance and is, therefore, greater than the
224 variation in species composition that is associated with the (linear) gradient of slope (fraction
225 [g]), which represents only 3.8% of adjusted variance

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

232 ***Discussion***

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

243 By analysing the spatial variance in plant community structure, we have been able to
244 answer 5 questions about the hydrological niche, including whether annuals and perennials
245 behave alike. First, we found that both the plant communities that we investigated were
246 structured along hydrological gradients and that their primary axes of variation aligned with
247 Average Water Table Depth (Fig. 1a, b). Average Water Table Depth (AWTD) is measured as
248 a distance below the surface so this measure of hydrological conditions is necessarily highly
249 correlated with fine scale topography. Second, we found that spatial segregation occurred
250 among perennial species, though not among the annuals in the *dehesa* community (Fig. 1a).
251 *Dehesa* annuals as a group were aggregated at the dry end of the hydrological gradient where
252 most fell into just three or four niches (niches 0.50-0.70) out of the 17 that were present.

253 Third, we investigated the shape of species' hydrological niches by fitting GAMS,
254 which showed that species responses were, with very few exceptions, either monotonic
255 (increasing or decreasing along the hydrological gradient) or hump-shaped (between 24-35%
256 of species responses). The important conclusion here is that, contrary to the assumptions of the
257 neutral model, co-occurring species show different responses along soil-moisture gradients.
258 Similar results have now been found in many plant communities (Silvertown et al. 2014).

259 A comparison of the shapes of the species' hydrological niches illuminates the
260 difference in community structure found between perennials and annuals. Since most perennial
261 responses were either monotonic increasing or monotonic decreasing with increasing soil
262 drying (65-75%), this difference created segregation, with hump-shaped responses also
263 contributing to segregation. In contrast, most annuals responses were monotonic increasing
264 with increasing soil drying (62%), thus creating a pattern of overlap and species aggregation.
265 These results suggest that, at least in the *dehesa* community we studied, spatial niche
266 segregation on soil moisture gradients may not be an important mechanism of coexistence in

267 the species-rich sub-community of annuals. Given that rainfall in the area is highly variable
268 from year-to-year (Ceballos et al. 2013), temporal niche segregation (the storage effect), as
269 found among Sonoran desert annuals by Angert *et al.* (2009), is an alternative possibility.

270 Fourth, we partitioned the components of spatial structure in the two plant
271 communities, with complex results (Table 1 and Fig. 2). Among the perennials at Moscosa,
272 18% of the variance in species composition was ascribed to variation in hydrology. For the
273 annuals in Moscosa and for perennials in Urbión, the variance explained was about 16% in
274 both (16.2% and 15.6%, respectively). Nearly all the variance in hydrology that drove species
275 composition was spatially structured, but about 2% of the adjusted variance explaining change
276 in species composition was not. This may simply reflect error in the hydrological models fitted.
277 This spatial structure can be further subdivided into components that correspond to the linear
278 gradients of slope (fraction [g]) and to local topographic variation (fraction [f]). In Moscosa,
279 the gradient of slope (9.6% for both annuals and perennials) was more important than local
280 topography (6.6% for perennials and 4.7% for annuals). In contrast, local topography (8.1%)
281 was more important in Urbión than the gradient of slope (3.8%).

282 Overall, the contributions of hydrologically-correlated spatial variation may appear
283 rather small (16.2% for Moscosa perennials; 14.3% for Moscosa annuals; 11.9% for Urbión),
284 but this was nevertheless the most important driver of spatially structured species composition
285 in the Moscosa data. Spatial structure not correlated with hydrology ([b] + [c] + [e] in Fig.2),
286 amounted to 13.4% for perennials and 12.4% for annuals. By comparison, species composition
287 in the Urbión data was even more strongly spatially structured than in the Moscosa data, and
288 more than a quarter of its spatial variance (26.7%) was not accounted for by hydrology.
289 Nonetheless, we can conclude that hydrology was at least as important as any other single
290 cause of spatial structure because it correlates with the primary axis of variation in Fig.1.

291 Other causes of spatial structure could have included such ecological factors as vegetation
292 pattern created by clonal growth, local variation in soil nutrients, or population processes such
293 as dispersal (Legendre & Legendre 2012).

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

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

313

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323

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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 Figures S1 - S3

Appendix S4. R code

Appendix S5. Moscosa dataset

Appendix S6. Lifespan

Table 1. Marginal tests results from direct RDAs (Redundancy Analysis) 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 Figure 2). *p*-values were obtained by means of 1000 permutations

Source of variation	Model var. (d.f.)	Resid var. (d.f.)	<i>F</i>	<i>p</i>	<i>R</i> 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

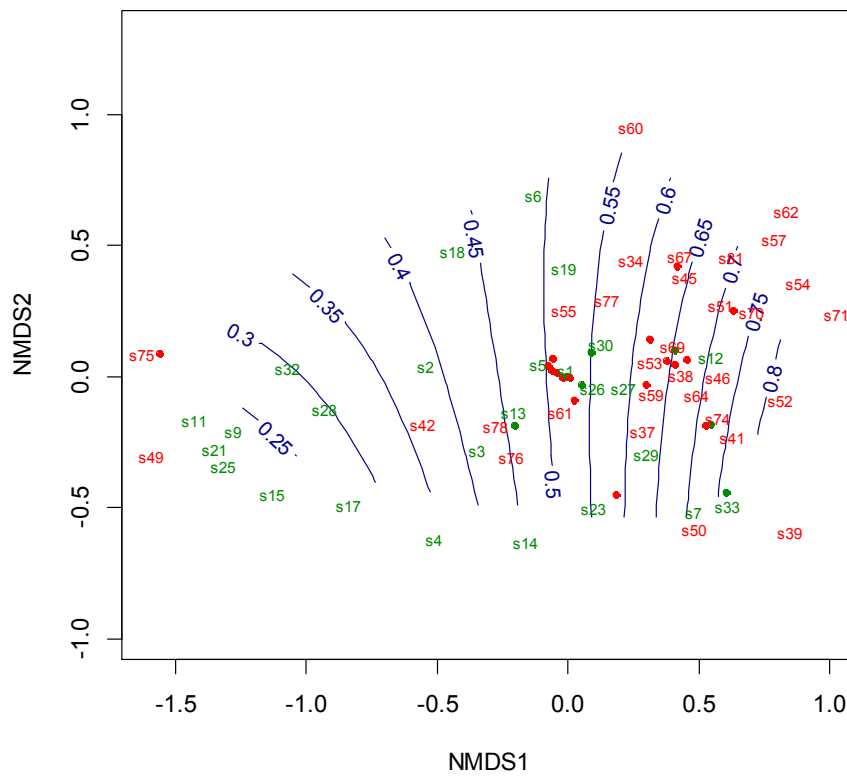
Annuals (Moscosa)

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

(a) NMDS ordination with AWTD trend surface (Moscosa)



(b) NMDS ordination with AWTD trend surface (Urbión)

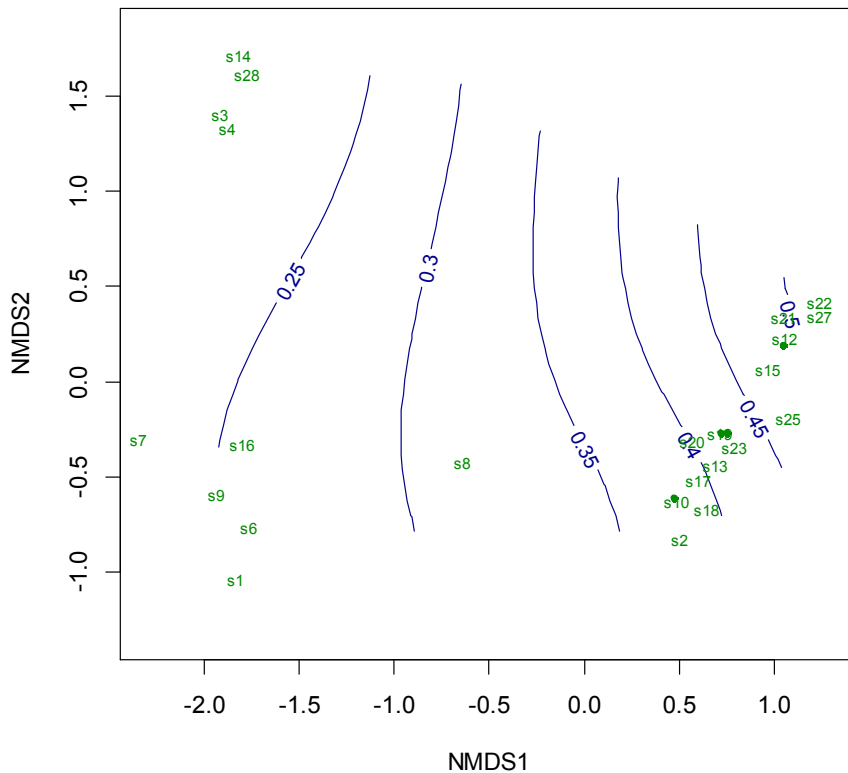


Figure 1. Main species gradients for La Mina meadow in Moscosa Farm (a) and Laguna Larga meadow in the Urbión Peaks (b), as described by non-metric multidimensional scaling (NMDS), in multivariate space (Jaccard measure). Moscosa annuals are indicated in red and perennials in green. Non-metric goodness-of-fit 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 m (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 1.

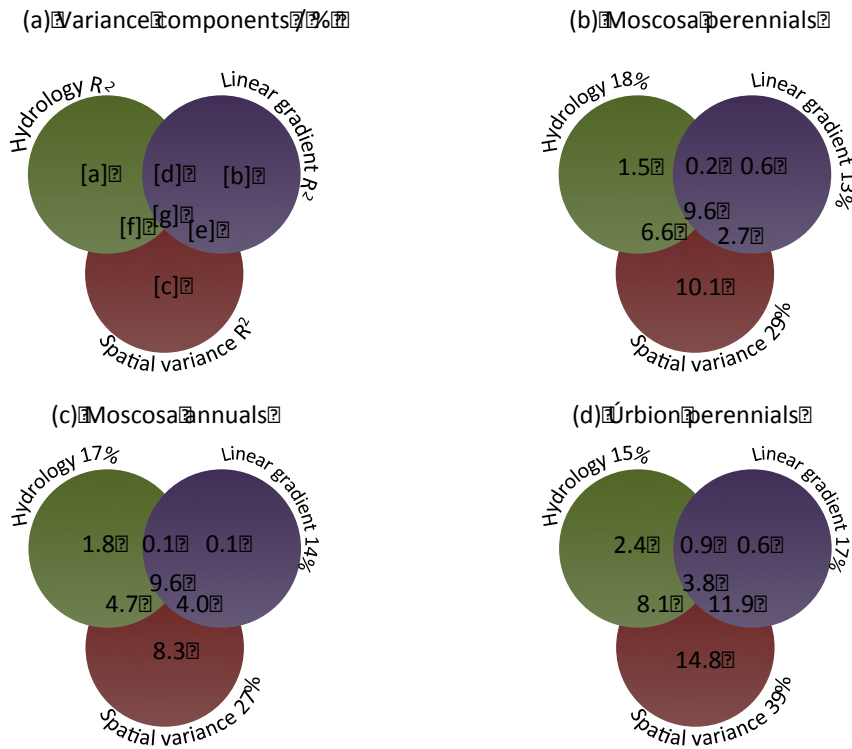


Figure 2. Venn diagrams showing how multivariate variation in species composition was partitioned among a hydrological component, a linear trend component and a spatial component described by MEM variables. Numbers are adjusted R^2 values (%). The hydrological component includes AWTD and its second- 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).