Quantifying soil hydrology to explain the development of vegetation at an ex-arable wetland restoration site

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ABSTRACT

Wetland restoration frequently sets well-defined vegetation targets, but where restoration occurs on highly degraded land such targets are often not practical and setting looser targets, in combination with establishing surveillance methods to track developing wetland habitats under an ‘open-ended’ approach to restoration, may be more appropriate. Water regime and soil structure are known to influence the distribution and composition of developing wetland vegetation, and may be quantified using Sum Exceedence Values (SEV), calculated using the position of the water table and knowledge of soil stress thresholds. Use of SEV to explain patterns in naturally colonizing vegetation on restored, ex-arable land was tested at Wicken Fen (UK). Analysis of values from ten locations showed that soil structure was highly heterogeneous. Five locations had shallow aeration stress thresholds and so had the potential to support diverse wetland assemblages. Deep aeration stress thresholds at other locations precluded the establishment of a diverse wetland flora, but identified areas where species-poor wetland assemblages may develop. SEV was found to be a useful tool for the surveillance of sites where restoration targets are not specified in detail at the outset and may help predict likely habitat outcomes at sites using an open-ended restoration approach.

Keywords: natural regeneration; soil stress thresholds; Sum Exceedence Value; Wicken Fen

INTRODUCTION

Wetland restoration projects regularly set targets to establish specific vegetation assemblages for which hydrological and substrate requirements appear to be well understood. Despite this, restoration projects frequently do not achieve their stated aims (Klimkowska et al. 2007; Desrochers et al. 2008; Moreno-Mateos et al. 2012), because in many cases historical damage to wetland structure and function is, at least partially, irreversible (Okruszko 1995; Zedler and Kercher 2005; Rey-Benayas et al. 2009). This in turn suggests that the abiotic and biotic starting conditions at many wetland restoration sites may be novel and that setting looser targets would be more appropriate for the likely novel outcomes (Seastedt et al. 2008; Hughes et al. 2012). There is also an increasing appreciation that ecosystems are in non-equilibrium states (Mori 2011) and that over longer time-scales (10^1-10^2 years), restoration projects may need to be less prescriptive and to involve less interventionist approaches (Higgs & Rousch 2011). However, it is a considerable challenge to know how to articulate restoration targets and then monitor restoration achievement against this backdrop of greater uncertainty.

One possibility is to modify our way of conceiving of targets so that they become more open-ended, with targets less fixed in space and time, and to develop new surveillance methods that complement this alternative approach (Hughes et al. 2011). An open-ended approach to setting restoration targets has been adopted at a wetland restoration project (the Wicken Fen Vision project) bordering Wicken Fen National Nature Reserve (NNR) in the UK.

On the NNR, there is a statutory requirement to maintain the well documented, semi-natural alkaline fen vegetation communities which dominate on the undrained peats that underlie the site. In the UK, conserving these often small remnants of semi-natural wetland habitats usually involves highly prescriptive management practices based on an understanding of the relationships between the vegetation and the underlying soil hydrology. In some cases (e.g. semi-natural floodplain meadow communities), these complex relationships have been elucidated using the Sum Exceedence Value (SEV) approach (Sieben 1965; Gowing and Spoor 1998). The SEV model utilises the position of the water table and knowledge of soil porosity to describe the water regime of individual locations (Gowing et al. 1997). This knowledge is then applied to prescribe tailored hydrological regimes that conserve the vegetation target, with some success (Gowing et al 2002).

On the adjacent restoration land of the Wicken Fen Vision, the alkaline fen peats comprising the restoration site have experienced prolonged (>60 years) drainage and ploughing (Stroh 2012a). As a result, it is not feasible to expect the establishment of semi-natural fen-type vegetation associated with the relatively intact and undrained soils found at Wicken Fen NNR, because the pre-conditions of restoration are so unlike the conditions that gave rise to these communities (Colston 2003, Hughes et al. 2005). These novel conditions and longer-term uncertainties in water availability have led to the adoption of an open-ended approach to setting restoration targets (Hughes et al. 2011). In practice this means that a very broad restoration target has been set as ‘a changing mosaic of wetland habitats’ where the likely component vegetation types are also broadly labelled with no particular species assemblages specified (for example ‘wet grassland’).

The location and type of broad habitats that develop across the project land will to a large extent depend upon i) contemporary soil structure as a legacy of duration and intensity of past arable use, and ii) the evolving relationships between different soil structures, hydrology and vegetation. Because targets for open-ended restoration projects tend to be framed in terms of achieving dynamic rather than static habitat outcomes they require novel surveillance approaches that can track the changing nature of these evolving relationships. In this paper we test the efficacy of using the SEV approach as a surveillance tool for tracking developing habitats rather than as a way of defining prescriptions for maintaining specified vegetation targets in chosen locations. We use the Wicken Fen Vision project as a case study for this work.

MATERIAL AND METHODS

Study Site

The study site, owned by the National Trust (a Non Governmental Organisation), comprised Wicken Fen NNR and the Wicken Fen Vision and was situated 25 kilometres north of Cambridge, UK (52°18’24N, 0°16’51E). Wicken Fen NNR is designated under UK and European legislation for its species-rich relic-fen flora and fauna, with vegetation managed on a three year “cut and gather” rotation (Friday 1997). Land within the Wicken Fen Vision has been allowed to regenerate naturally following cessation of arable farming, and is managed with minimal intervention using free-roaming large herbivores and partial hydrological manipulation (Colston 2003) with no attempt to restore specific NNR fen vegetation assemblages. Four fields that were in arable farming for different periods of time prior to restoration were selected for sampling within the Wicken Fen Vision area (see Table 1). An additional field was sampled within the undrained peat soils of Wicken Fen NNR so that a comparison could be made between 'intact' and 'degraded' peat soils. Average annual rainfall for the area is 530mm, but is exceeded by average annual potential evapotranspiration (594mm) from April to September (McCartney & de la Hera 2004). This places constraints on the development of wetland and a mosaic of both wet and dry habitats has developed. This study was carried out from March 2008 to September 2010.

Soil hydrology

In order to calculate SEV values it is necessary to have data on both water table levels and soil porosity. The study was conducted in five fields in locations adjacent to dipwells set up as part of the water table monitoring network for the Wicken Fen Vision project. One of the fields was situated within the NNR, and the remaining four fields were on ex-arable land (Figure 1). The full range of soil types, hydrological regimes and vegetation assemblages across the Wicken Fen Vision (ca.900 hectares) is not represented in the study because it is restricted to water table monitoring sites. Nevertheless, the five fields sampled include a wide range of physical site types, land-use histories and length of time under conversion from arable agriculture (Table 1).

Each of the five fields was ditch-bounded and had two dipwells recording the hourly water table depth for the three years of the study; one in the field centre and one close to a ditch edge, giving a total of ten field positions for the study. Each dipwell consisted of 60 mm slotted PVC triple layer geoscreen and a 650 micron geosock, with a cap at the base of the dipwell. Water levels were measured using Eijkelkamp Mini-Divers plus a Baro-Diver to compensate for atmospheric pressure and cross-checked with monthly manual dip data. All data were corrected to give water table values in metres below ground level. Hourly dipwell data for each of the ten positions were aggregated to give a weekly mean water table depth for the growing seasons of 2008, 2009 and 2010 (March to September inclusive). Water tables measured in the wells are representative of water tables in the root zone and respond rapidly to rainfall events in both ex-arable and undrained fen areas within the study site (Lewis 2010).

In order to calculate soil porosity at each field position, three undisturbed soil cores measuring 5cm in diameter and 5cm depth were extracted beside each of the ten dipwells after digging down to a mid-point depth of 10cm below the soil surface, which is taken as the densest rooting zone for herbaceous species (Gowing et al. 2002). Cores were saturated in water for 5 days, weighed and placed on a sand table whose tension was decreased at ten set levels. The cores were weighed every 5 days before being oven-dried, (following Barber et al. 2004) and soil moisture release curves were plotted.

Stress thresholds

Aeration thresholds were defined as the depth to which the water table had to fall in order for ten percent of the total soil pore space to be air-filled (Whalley et al. 2000). This is considered equivalent to the depth of the water table required to aerate the rooting zone (taken as the top 10cm of the soil profile). The aeration threshold for each core was calculated from the soil moisture release curves. This curve displays the relationship between water content and water potential for each individual soil sample, allowing precise examination of the interaction between soil, vegetation and water at an individual location (Dumortier 1991). After log transformation of the data, a fixed linear regression was performed on each curve, and the regression equation used to calculate the tension at the point at which 10% of the soil sample's pore space was occupied by air. In five of the ten locations, one of the three cores produced an extreme value and so the median aeration threshold value was selected to represent each field position. The soil drought thresholds used were standardised for each location at 50 cm water table depth following Davis & Gowing (1999).

Sum Exceedence Values

The aeration SEV (referred to as SEVa and presented in units of metre.weeks) for each year was calculated by subtracting the mean water table depth from the aeration threshold depth for each week and cumulating this value from March – September inclusive at each of the ten field positions. Calculation of SEV was restricted to this 'growing season' because this is when plants are most susceptible to changes in the oxygen status of the rooting zone (Gowing et al. 2002). When the aeration threshold value was >30cm, the cumulated weekly SEVa value was capped at 30cm since the soil is saturated above this threshold. The soil drought SEV (referred to as SEVd and presented in units of metre.weeks) was calculated by subtracting the soil drought threshold depth (50 cm) from the mean water table depth for each week from March – September inclusive. Weekly exceedence of the soil drought stress threshold was limited to 40cm below the threshold value (i.e. 90cm), as once the water table falls below this critical depth it is contributing virtually no moisture to the rooting zone (Gowing et al. 2005). The number of weeks that the aeration and drought thresholds were exceeded throughout the growing season was totalled for each year of the study in order to give a measure of stress duration. SEVa and SEVd values were plotted against each other for each of the ten field positions in order to characterise the hydrological niche of each field position.

Soil organic matter

In order to characterise peat degradation resulting from drainage and arable use, soil Loss on Ignition (LOI) values were calculated following Littlewood et al. (2006) for soil cores taken at each of the 10 field positions using a 2.5cm diameter and 5cm depth auger after digging down to a depth of 10 cm. The auger thus removed a core from 10-15cms depth.

Vegetation

Vegetation was recorded in the summers of 2008, 2009 and 2010 at each of the ten field positions within two 2m x 2m fixed quadrats next to each dipwell. All plant species were identified (nomenclature follows Stace 2010) and cover/abundance recorded as % cover values. Cover values were averaged across the three years of the study for each species in each quadrat to capture average species values for the period for which SEV was calculated.

A Detrended Canonical Correspondence Analysis (DCCA) ordination by segments was performed using Canoco for Windows 4.5 (ter Braak & Ŝmilauer 2002) to aid interpretation of the relationships between species data, LOI, SEV scores and duration values at each field position. Data were log (x+1) transformed to prevent high values from disproportionately influencing the ordination, and rare species were downweighted as they may also have an excessive influence on the analysis (ter Braak & Ŝmilauer 2002).

RESULTS

Soil stress thresholds

Aeration thresholds, SEVa and SEVd values, and the duration of threshold exceedence for each field position are presented in Table 2. The soil aeration thresholds relating to water table depth ranged from exceptionally well aerated (19.23 cm) for undrained peat soils within the NNR to very poorly aerated and structurally damaged (>90cm) soils for some ex-arable positions. Aeration stress thresholds were surpassed for more than 50% of the growing season at field positions 1 (ditch), 2 (ditch) and 3 (centre), although the SEVa was relatively low for field position 1 (ditch) compared to 2 (ditch) and 3 (centre) due in part to the shallower aeration threshold. Soil drought thresholds were surpassed for >50% of the growing season at all ex-arable locations apart from field 2 (ditch and centre), with the highest SEVd at field positions 4 (ditch) and 4 (centre). The lowest SEVd values were recorded from field positions 2 (ditch) and 2 (centre).

The interpretation of threshold exceedence for aeration and drought stress in relation to observed water table depths for all field positions is shown in figure 2. The gap between the aeration threshold and the drought threshold in each figure represents suitable growing conditions for many wet grassland plants. There is a substantially wider gap between aeration and drought thresholds for undrained peat (field 1(ditch and centre)) compared to all ex-arable soils except for field 2 (centre). Field 3 (centre) and field 4 (ditch and centre) show a drought stress threshold depth that is shallower than the aeration stress threshold depth. This is a result of very compact soils with very little pore space. In such circumstances, plants can suffer from lack of air (waterlogging) in the rootzone and lack of moisture (drought) simultaneously because the soil is ineffective at supplying either.

Vegetation in relation to soil variables

The DCCA ordination (figure 3) displayed a separation of field positions 1 (ditch and centre) and 2 (ditch and centre) from all other field positions along Axis 1. Axis 1 explained 27.1% of the total species variability and axis 2 a further 6.2%. The first axis was strongly correlated with the species-environment data, explaining 49.9% of the variability (eigenvalue = 0.721; length of gradient = 4.198) and represents a gradient of tolerance to drought stress. It is positively correlated with the number of weeks (duration) of drought stressed soil conditions during the growing season and, more weakly, with the soil aeration stress threshold depth, and negatively correlated with both LOI and weekly duration of aeration stress. LOI was positively correlated and weekly duration of aeration stress and soil aeration threshold were negatively correlated with axis 2, which explained a further 13.4% of the species-environment relationship (eigenvalue 0.164; length of gradient = 1.875). Axis 1 showed a clear gradient of moisture tolerant (e.g. *Phragmites australis; Mentha aquatic; Valeriana officinalis*) through to moisture intolerant species (e.g. *Convolvulus arvensis; Picris echioides; Arrhenatherum elatius*), corresponding to the hydrological conditions recorded at the field positions and the LOI values, reflecting degradation of the peat soils. Species associated with low aeration threshold values and high LOI were positioned at the top of axis 2 and correspond to vegetation typical of undrained species-rich fens (e.g. *Eleocharis quinqueflora*, *Cirsium dissectum*, *Dactylorhiza incarnata*, *Carex lepidocarpa*). Species to the bottom of axis 2 were associated with prolonged aeration stress and were typical of species-poor tall-herb fen (e.g. *Phalaris arundinacea, Epilobium hirsutum, Eupatorium cannabinum*).

Fields 1 and 2 include the species most typical of fens but their separation along axis 2 reflects the impact of even a short period of drainage and arable use (6 years) on plant species assemblages. Of the ex-arable field positions, only field 2 (ditch and centre) demonstrated strong affinities to wetland vegetation, although field 5 (centre) did support some species associated with species-poor wet grassland (e.g. *Carex riparia, Agrostis stolonifera, Juncus inflexus*) despite severe drought conditions during the growing season. Such species, once established in the sward, are able to persist and tolerate a wide range of edaphic conditions, and are likely to reflect hydrological conditions at the field position pre-2008. The remaining ex-arable field positions were associated with species-poor, dry grassland vegetation assemblages (e.g. *Cirsium arvense, Arrhenatherum elatius, Galium aparine*). A characterisation of hydrologically defined niche spaces for vegetation development (defined by SEVa and SEVd) (Figure 4) again shows a clear separation between field positions 1 (the NNR) and 2 and the more recently converted ex-arable positions (fields 3 to 5) along the SEVd axis. Within fields 1 and 2, there is a separation between field 2(ditch) and the other three positions along the SEVa axis.

DISCUSSION

The soils that were sampled in this study demonstrated considerable heterogeneity within the Wicken Fen Vision project area as well as a contrast between soils undergoing restoration and soils sampled within the NNR. Aeration thresholds ranged from ~20 cm in the undisturbed fibrous peat soils of the undrained NNR to ~100 cm in some drained and highly compacted remnant peat soils within ex-arable areas. Aeration threshold values of ~40 cm reflect well structured soils which are able to aerate whilst still holding freely available water, whereas values of >60 cm reflect soils that have to dry substantially before aeration is achieved because of a lack of structural pores (Henson et al. 1989).

The soil aeration stress thresholds for ex-arable field positions 2 (ditch and centre), 3 (ditch), and 5 (ditch and centre) are typical of reasonably well structured soils capable, under suitable water table regimes, of supporting a diverse range of wetland plant species. However, the SEVd values for field positions 3 (ditch) and 5 (ditch and centre) are very high, surpassing their soil drought stress thresholds for 65%, 70% and 58% of the growing season respectively. This hydrological regime makes it very difficult for a diverse wetland vegetation to establish, whereas field positions 2 (ditch and centre) surpassed drought stress thresholds for only 15% and 33% respectively of the growing season and supported a reasonably diverse wetland plant community. A substantial decrease in the SEVd at field positions 3 (ditch) and 5 (ditch and centre) through water level management could promote conditions suitable for the eventual establishment of relatively species-rich wetland vegetation assemblages, depending on the availability of viable propagules (Stroh et al, 2012a). The remainder of the ex-arable field positions, based on their deep aeration stress thresholds, would not be capable of supporting species-rich wetland vegetation assemblages even if a diverse propagule source were available and hydrological conditions were to be altered. However, these areas have the potential to support species-poor vegetation assemblages capable of tolerating long periods of waterlogging, such as *Phragmites australis*-dominated reed bed.

The deepest soil aeration stress thresholds, reflecting the greatest compaction of surface soils, were found in the centres of field positions 3 and 4 which have experienced the longest history of arable agriculture. They also have the lowest soil organic matter measured as LOI values. In contrast, the ditch positions in fields 3 and 4 have comparatively shallower aeration thresholds and higher LOI values which are likely to be the result of both historic ditch drainage management practices and the presence of uncropped headlands around each field, adjacent to the ditches. Fenland ditch management has traditionally involved the regular removal of ditch silts and emergent vegetation and their subsequent deposition on the field margin (Blomqvist et al. 2003), giving rise to an often more organic and less compacted area of soil around field margins.

Species associated with field position 5 (centre) comprised wide-leaved (>5mm) sedges able to survive prolonged periods of waterlogging (*Carex riparia*) alongside herbs associated with wetland drawdown zone vegetation (*Veronica catenata*; *Ranunculus sceleratus*) and species which, once established in the sward, are tolerant of a wide range of water regimes (*Juncus inflexus*) (Grime et al. 2007). The relatively shallow soil aeration threshold at field 5 is likely to be a result of historical land management. Aerial photographs dating from the early 1940s show that much of field 5 regularly held standing water, and the locality falls within a topographical depression (LiDAR data © Environment Agency 2007). Drainage was never as effective in this area and it experienced continuous flooding from 1930-1940 when it was used for duck shooting (Ennion 1942).

The wetland vegetation recorded from Wicken Fen NNR (field 1 positions) was associated with low values of both SEVa and SEVd throughout the growing season. This regime, combined with well structured soils and the absence of historical arable farming or prolonged land drainage, has resulted in suitable growing conditions for a wide range of wetland plants (e.g. *Hydrocotyle vulgaris; Carex lepidocarpa; Dactylorhiza incarnata; Cirsium dissectum; Eleocharis quinqueflora*). This is in contrast to ex-arable field position 2 (ditch), where a comparatively high SEVa has produced a wetland vegetation assemblage containing species which are able to tolerate prolonged periods of waterlogging (e.g. *Phragmites australis)* alongside species-poor tall-herb fen (e.g. *Eupatorium cannabinum; Epilobium hirsutum;*

Carex otrubae). Two additional factors operating at the site level may explain this disparity in vegetation assemblages. Even short periods of ploughing and drainage have been shown to eliminate most of the species associated with semi-natural fens from the seed bank and standing vegetation (e.g. Bakker et al. 1996; Matus et al. 2003; Stroh et al. 2012a). In addition, different management regimes are used at the two locations, with vegetation within the NNR (field 1) cut and baled on a three-year rotation and vegetation in the ex-arable field 2 extensively grazed by free-roaming Konik and highland cattle (Colston 2003). Summer mowing has been shown to influence the abundance and composition of fen vegetation (Godwin 1941), and can reduce the abundance of tall-herb species in such plant communities (Rodwell 1995; Middleton et al. 2006).

Soil aeration conditions in conjunction with water table fluctuation regimes act as important environmental filters on the potential for the successful germination and establishment of propagules which are either present in the soil seed bank or are naturally dispersed to the sites via a range of vectors from *ex-situ* sources (Gowing & Spoor 1998; Leyer 2005; Stroh et al. 2012b). In this study, use of the SEV approach to characterise soil aeration conditions through time has been useful in the surveillance and explanation of vegetation developing under an open-ended approach to restoration. It could also be used to predict the likely locations and extent, and thus the practicality, of the broadly-defined wetland habitat targets typical of an open-ended approach. This is a novel use of the method which has previously been used to understand and prescribe management practices for established semi-natural wetland vegetation types.

CONCLUSIONS

Our study has shown that SEVs (calculated using data on soil structure and water table fluctuations) can be used as a tool for the interpretation of contemporary wetland plant species assemblages that have developed through natural regeneration on ex-arable land. Land use histories have also been shown to play an important role in determining variations in contemporary soil structure, lending support to the idea that restoration outcomes are often strongly context-specific through local soil conditions (Eviner and Hawkes 2008). Many studies of ex-arable land show nutrient enrichment to be an important form of soil degradation (Manchester et al. 1999), but our study would suggest that damaged soil structure, through its effects on the aeration and drought stress experienced through the growing season, is also critical in determining wetland restoration outcomes.

In practice, once soil stress thresholds have been calculated, quantifying hydrological regimes using SEVs allows a site manager to integrate information on soil structure and on vegetation assemblages each growing season as long as water tables and vegetation continue to be monitored. SEVs have the potential to provide a sensitive tool for understanding vegetation development because they capture temporal as well as spatial dimensions of variation in soil moisture conditions. In this regard they appear to provide a good surveillance tool for interpreting the range of (sometimes novel) vegetation assemblages forming across open-ended restoration projects.

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	Field 1	Field 2	Field 3	Field 4	Field 5
Duration in arable	not applicable - undrained NNR	ca.10 years	ca.65 years	ca.90 years	ca.60 years
Duration in restoration	not applicable - undrained NNR	60 years	15 years	6 years	6 years
Soil profile (ditch)	Fibrous black peat (0cm-30cm)	Dry, dark grey humified peat and occasional mineral silts (0cm-85cm)	Dark brown humified peat, occasional shell fragments (0cm-50cm)	Black silty humified peat (0cm-40cm)	Black, crumbly degraded peat (0cm-40cm
	Calcareous shell marl (31cm-50cm)	Light grey stiff clay (86cm -150cm)	Brownish-yellow peaty silt (46cm-100cm)	Reddish brown, sandy silt (41cm-65cm)	Black silty peat (41cm-80cm)
	Fibrous black peat (51cm-250cm)		Light grey silty clay (101-150cm)	Greenish-grey stiff clay (66cm-150cm)	Organic detritus mud (80cm-140cm)
					Light grey stiff clay (141cm-200cm)
Soil profile (field centre)	Fibrous black peat (0cm-15cm)	Dry, dark grey humified peat and occasional mineral silts (0cm-85cm)	Dark brown humified peat (0cm-35m)	Dark red brown to near-black humified peat (0cm-40cm)	Dark brown humified peat (0cm-55cm)
	Calcareous shell marl (16cm-25cm)	Light grey stiff clay (86cm-150cm)	Light brown sandy silt loam (36cm-70cm)	Olive grey clay (41cm-100cm)	Light grey marl paste (56cm-75cm)
	Fibrous black peat (26cm-250cm)		Light grey stiff clay (71cm-150cm)	Grey clay (101cm-150cm)	Light grey stiff clay (76cm-150cm)
Loss on Ignition (%)	Field centre = 48.3; Ditch = 62.7	Field centre = 36.1 Ditch = 46.6	Field centre = 13.5 Ditch = 18.0	Field centre = 19.1 Ditch = 31.5	Field centre = 26.3 Ditch = 37.8
Mean Water Table depth (field centre)	Growing season = -29 cm Winter = -17 cm	Growing season = -47 cm Winter = -29 cm	Growing season = -59 cm Winter = -29 cm	Growing season = -72 cm Winter = -47 cm	Growing season = -69 cm Winter = -52 cm
Mean Water Table depth (ditch)	Growing season = -25 cm Winter = -16cm	Growing season = -31 cm Winter = -11cm	Growing season = -61 cm Winter = -37cm	Growing season = -74 cm Winter = -71cm	Growing season = -57 cm Winter = -51cm

Table 1: Soil and water table measurements for sampled locations. Soil profile values are taken from Morgan (2005), Lewis (unpublished report) and Stone (unpublished report). Soil Loss On Ignition (LOI) values were measured as a part of this study.

site	aeration threshold (cm)	SEVa (metre.weeks)	SEVd (metre.weeks)	wet duration (weeks)	dry duration (weeks)
field 1 (ditch)	21.17	2.18	1.22	15.33	7
field 2 (ditch)	47.02	5.84	0.51	25.33	4.67
field 3 (ditch)	27.64	0.3	5.31	4.33	20
field 4 (ditch)	61.51	0.3	7.52	0.33	29.33
field 5 (ditch)	40.63	2.5	4.57	11	21.67
field 1 (centre)	19.23	2.12	1.69	13.33	7.67
field 2 (centre)	23.7	1.67	0.51	13.33	10.33
field 3 (centre)	95.18	6.66	4.45	24.67	17
field 4 (centre)	100.38	6.75	7.45	3	26.67
field 5 (centre)	48.6	2.61	7.18	12.33	18

Table 2: Soil aeration thresholds and water regimes (as defined by the SEVs) for sampled locations Aeration threshold and SEVs are mean values (2008-10). Dry threshold (not included in the table) standardised at 50cm depth for each field position in each year. Duration refers to the mean number of weeks that a threshold was exceeded during the study period (2008-2010).

Figure 1 Map of Wicken Fen NNR and the Wicken Fen Vision project showing the location of field sites used in this study.

Figure 2. Visual representations of the exceedence of aeration thresholds (dark grey dotted area) and drought thresholds (light grey plain area) for each field position throughout the growing season (March-September) from 2008-2010. Solid horizontal lines represent the soil aeration threshold and the soil drought threshold values. Broken horizontal lines represent the

capped exceedence value for soil aeration and drought thresholds. Joined dots with a connecting line represent the mean weekly fluctuation of the water table.

Figure 3. Differences in vegetation composition across the ten field positions within the study site. The plot shows samples and species on an unconstrained ordination diagram produced by Detrended Canonical Correspondence Analysis (DCCA). Sample labels follow the ten field positions where F1d=Field 1 (ditch); F1c=Field 1 (centre); F2d=Field 2 (ditch); F2c=Field 2 (centre); F3d=Field 3 (ditch); F3c=Field 3 (centre); F4d=Field 4 (ditch); F4c=Field 4 (centre); F5d=Field 5 (ditch); F5c=Field 5 (centre). Axis 1 explained 27.1% and Axis 2 explained 6.2% of the total species variability. Abbreviations: agro sto=*Agrostis stolonifera;* alop myu=*Alopecurus myursuroides;* alop pra=*Alopecurus pratensis;* ange syl=*Angelica sylvestris;* anis ste=*Anisantha sterillis;* arrh ela=*Arrhenatherum elatius;* brom com=*Bromus commutatus;* brom hor=*Bromus hordeaceus;* cala can=*Calamagrostis canescens;* caly sep=*Calystegia sepium;* care fla=*Carex flacca;* care hir=*Carex hirta;* care hos=*Carex hostiana;* care lep=*Carex lepidocarpa;* care obt=*Carex otrubae;* care pan=*Carex panacea;* care rip=*Carex riparia;* cent nig=*Centaurea nigra;* cirs arv=*Cirsium arvense;* cirs dis=*Cirsium dissectum;* cirs pal=*Cirsium palustre;* cirs vul=*Cirsium vulgare;* clad mar=*Cladium mariscus;* conv arv=*Convalaria arvensis;* dact glo=*Dactylis glomerata;* dact inc=*Dactylorhiza incarnate;* desc ces=*Deschampsia cespitosa;* eleo pal=*Eleocharis palustris;* eleo qui=*Eleocharis quinqueflora;* elyt rep=*Elytrigia repens;* epil hir=*Epilobium hirsutum;* epil par=*Epilobium parviflora;* epil tet=*Epilobium tetragonum;* equi arv=*Equisetum arvensis;* eupa can=*Eupatorium canabinum;* fest rub=*Festuca rubra;* fill ulm=*Fillipendula ulmaria;* gali pal=*Galium palustre;* gali uli=*Galium uliginosum;* gera dis=*Geranium dissectum;* hera sph=*Heracleum sphondylium;* holc lan=*Holcus lanatus;* hydr vul=*Hydrocotyle vulgaris;* junc art=*Juncus articulates;* junc inf=*Juncus inflexus;* junc sub=*Juncus subnodulosus;* loli

per=*Lolium perenne;* lysi vul=*Lysimachia vulgaris;* malv syl=*Malva sylvestris;* ment aqu=*Mentha aquatic;* moli cae=*Molinea caerulea;* pers amp=*Persicaria amphibian;* pers mac=*Persicara maculosa;* phal aru=*Phalaris arundinacea;* phra aus=*Phragmites australis;* picr ech=*Picris echioides;* plan maj=*Plantago major;* poa ann=*Poa annua;* poa tri=*Poa trivialis;* ranu sce=*Ranunculus sceleratus;* rume cri=*Rumex crispus;* rume hyd=*Rumex hydrolapathum;* sina arv=*Sinapis arvensis;* sonc asp=*Sonchus asper;* stac pal=*Stachys palustris;* succ pra=*Succisa pratensis;* symp off=*Symphytum officinale;* thal fla=*Thalictrum flavum;* tusi far=*Tussilago farfara;* urti dio=*Urtica dioica;* vale off=*Valeriana officinalis;* vero cat=*Veronica catenata;* vero per=*Veronica persica*

Figure 4: Visual interpretation of the hydrological niche for each of the ten sampled field positions created by plotting mean SEVa (aeration stress) against SEVd (drought stress) for each field position for the period 2008-2010. SEV is shown as metre.weeks. Low stress at the sampled position is represented by low SEVa and SEVd. High stress due to waterlogging is represented by high SEVa and low SEVd. High stress due to drought is represented by low SEVa and high SEVd. Strong fluctuations in the water regime produced a high SEVa and SEVd.

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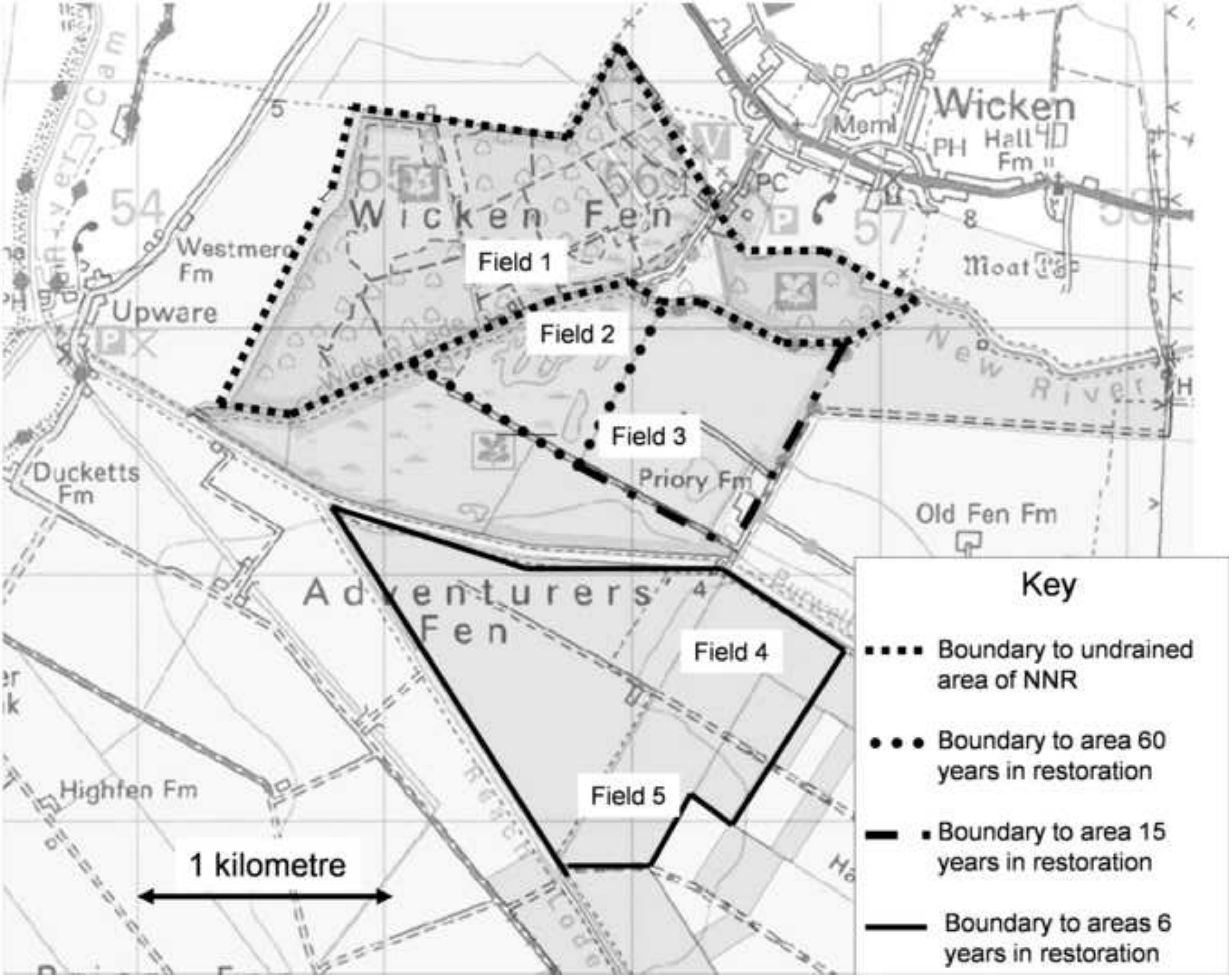

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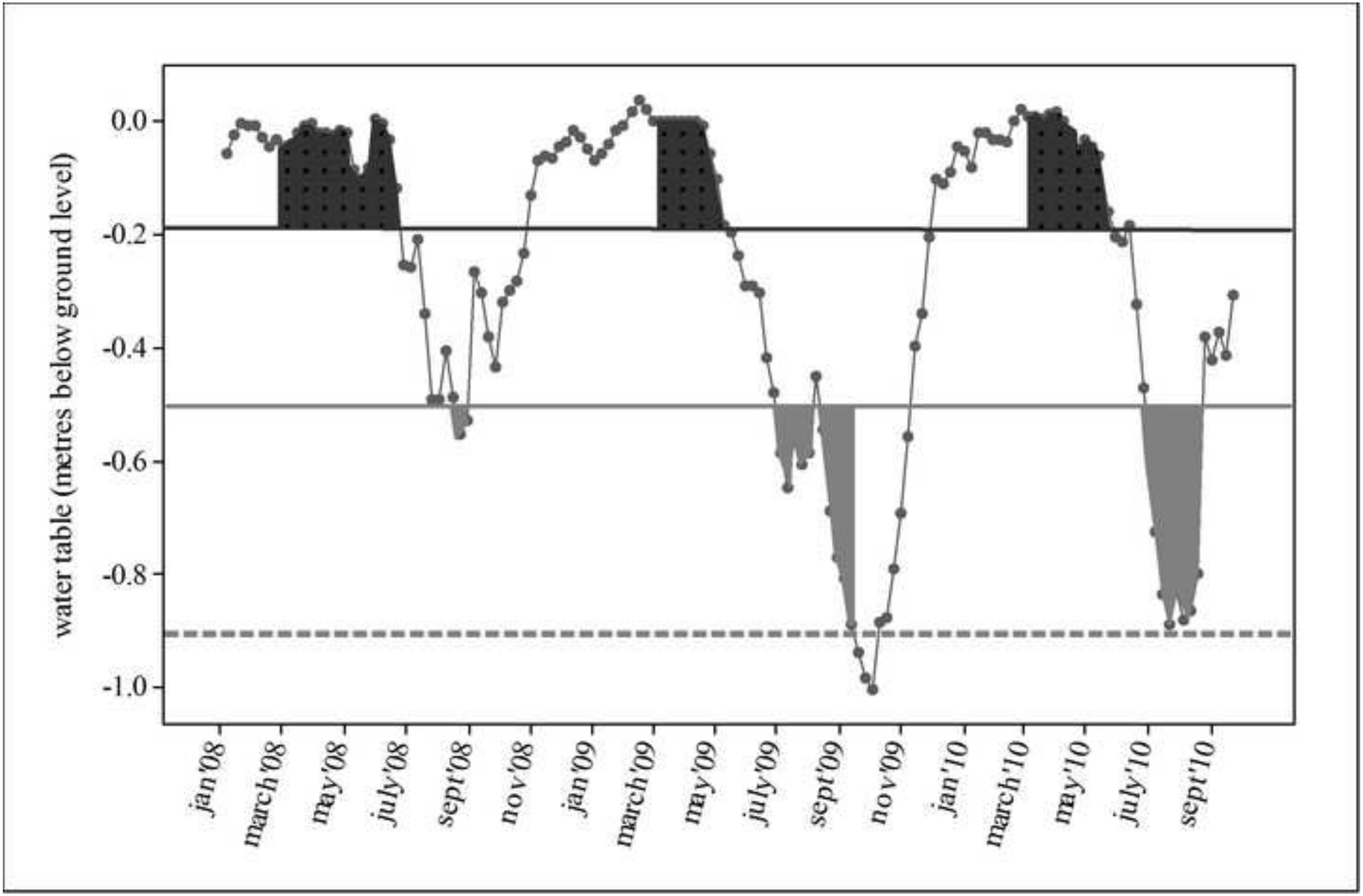

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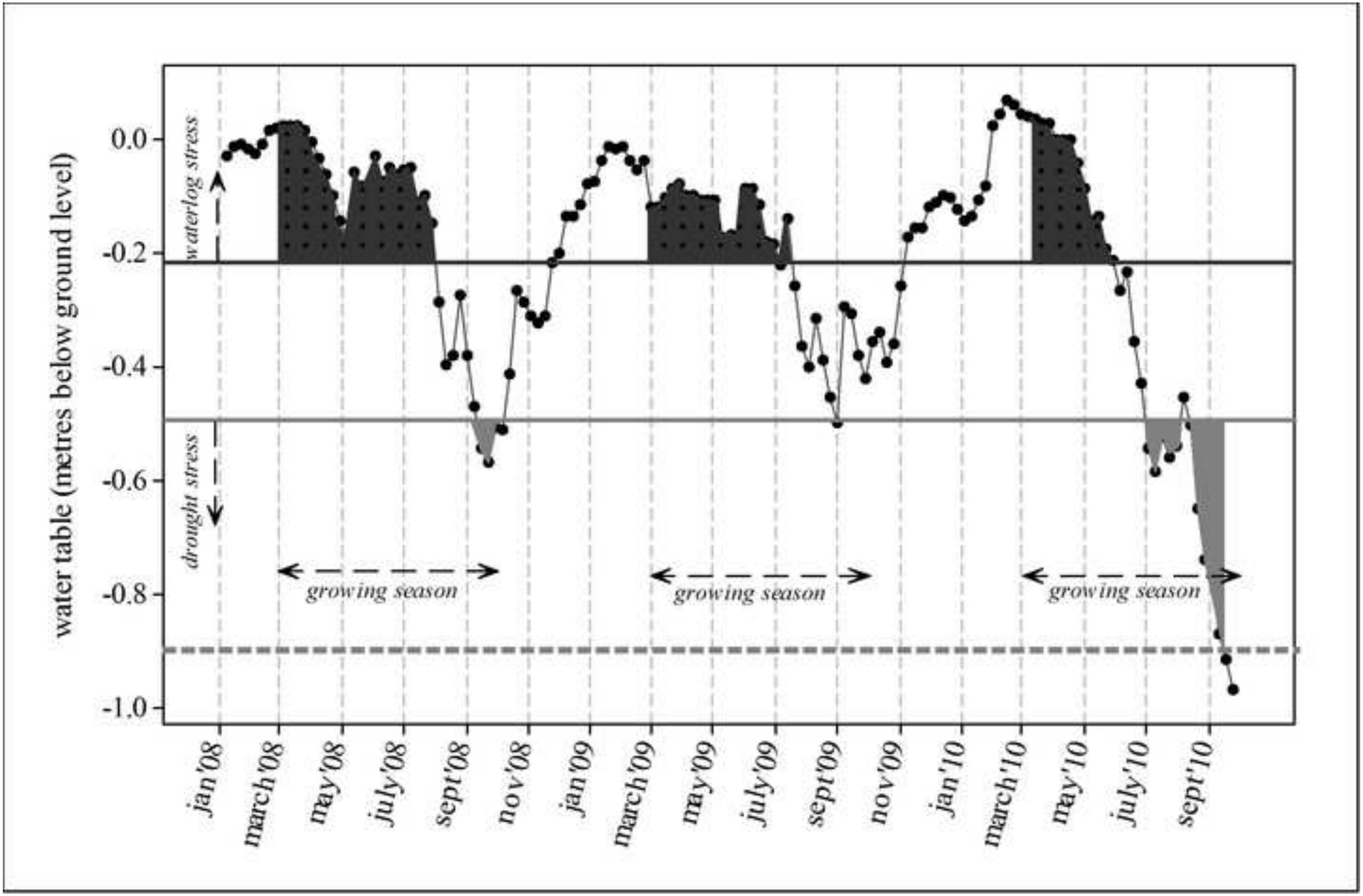

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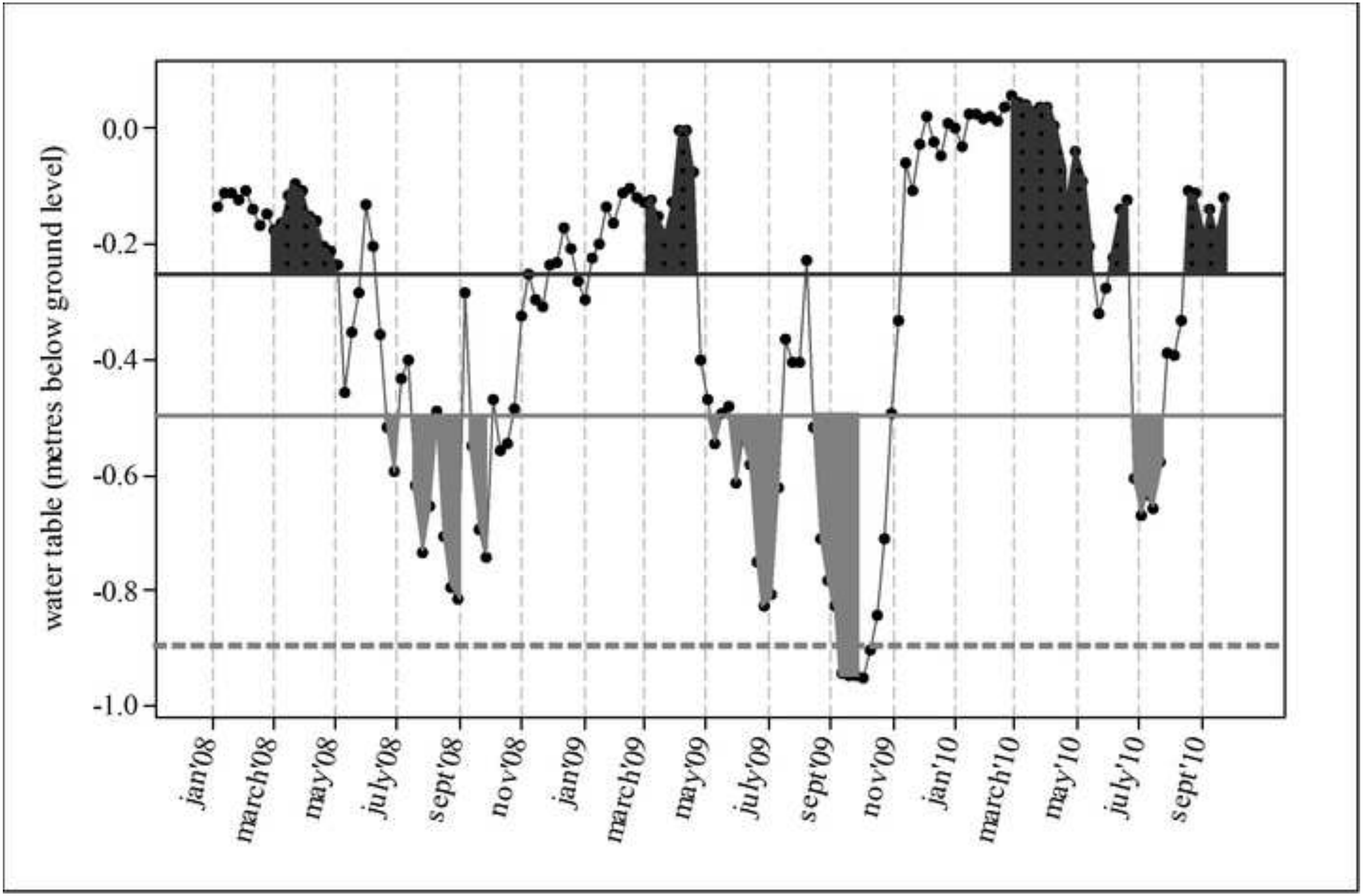

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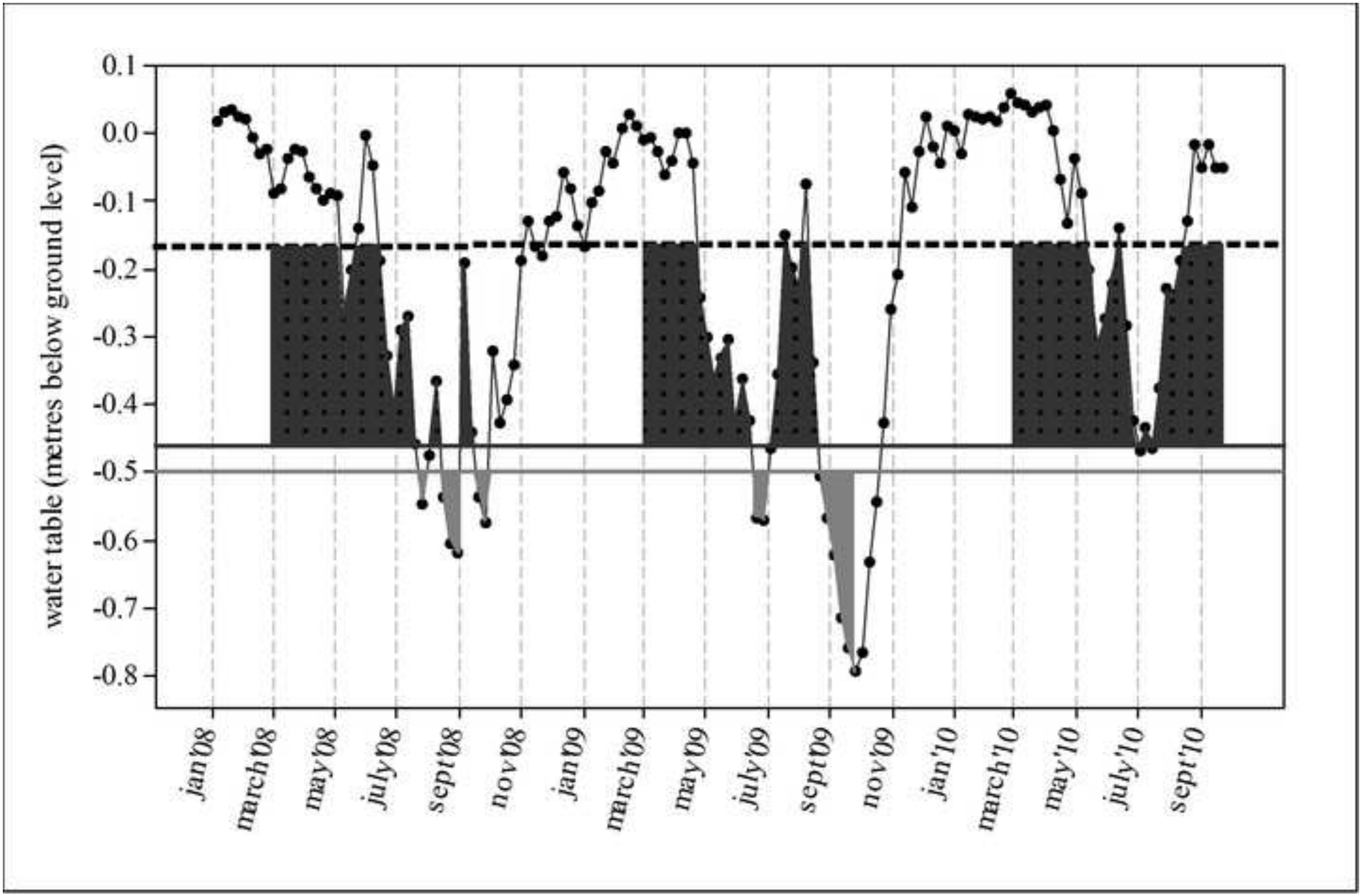

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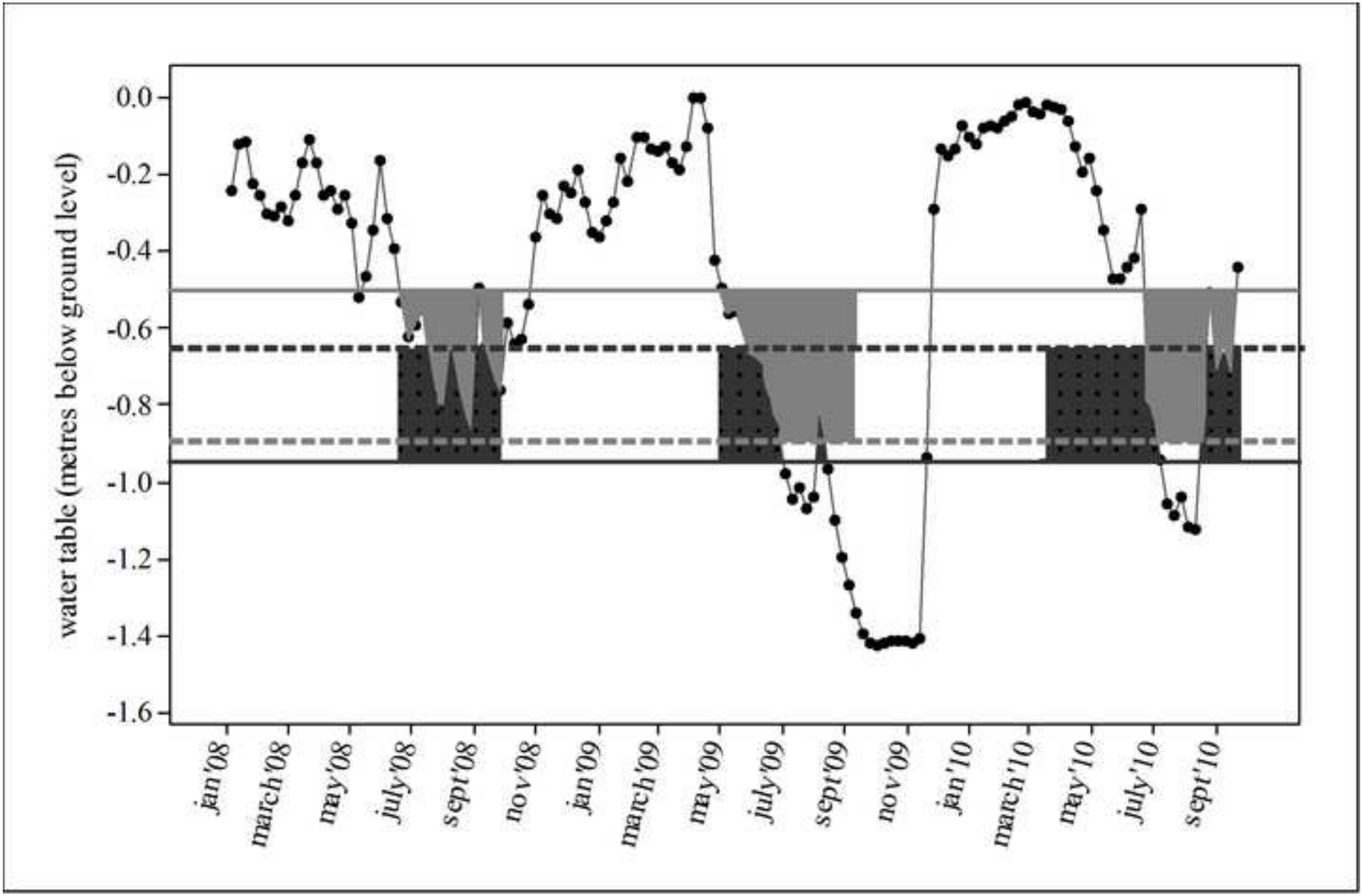

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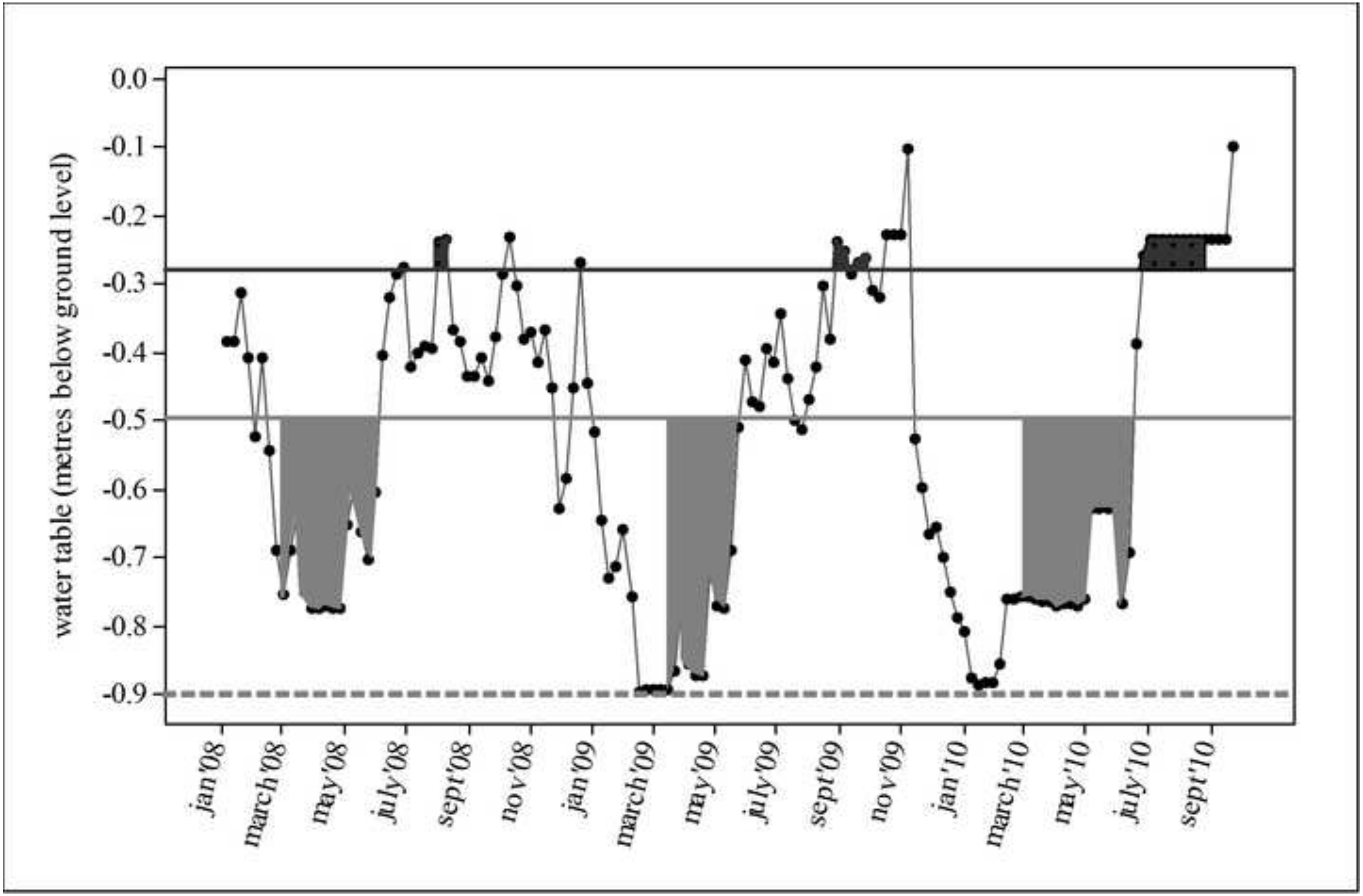

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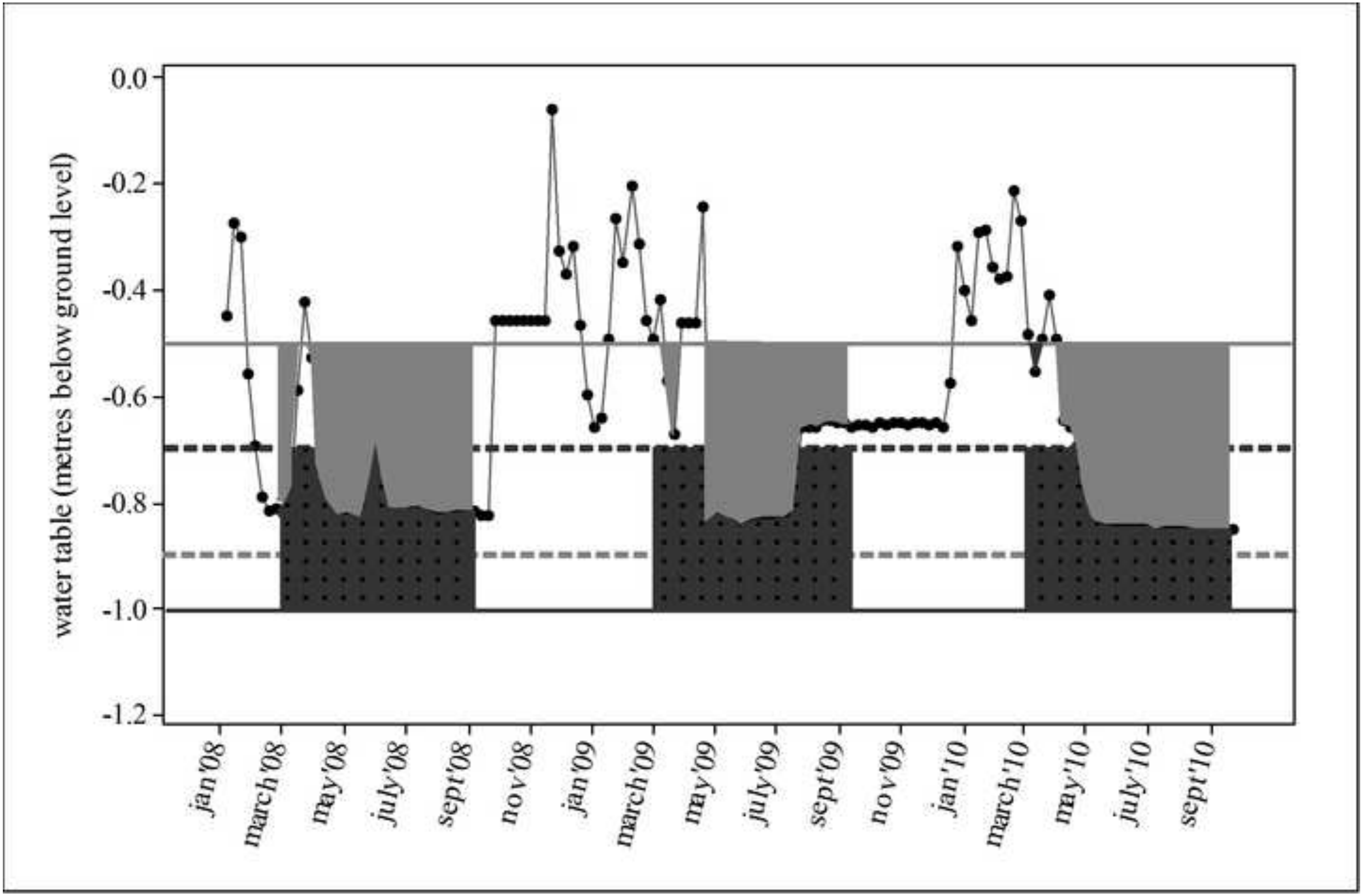

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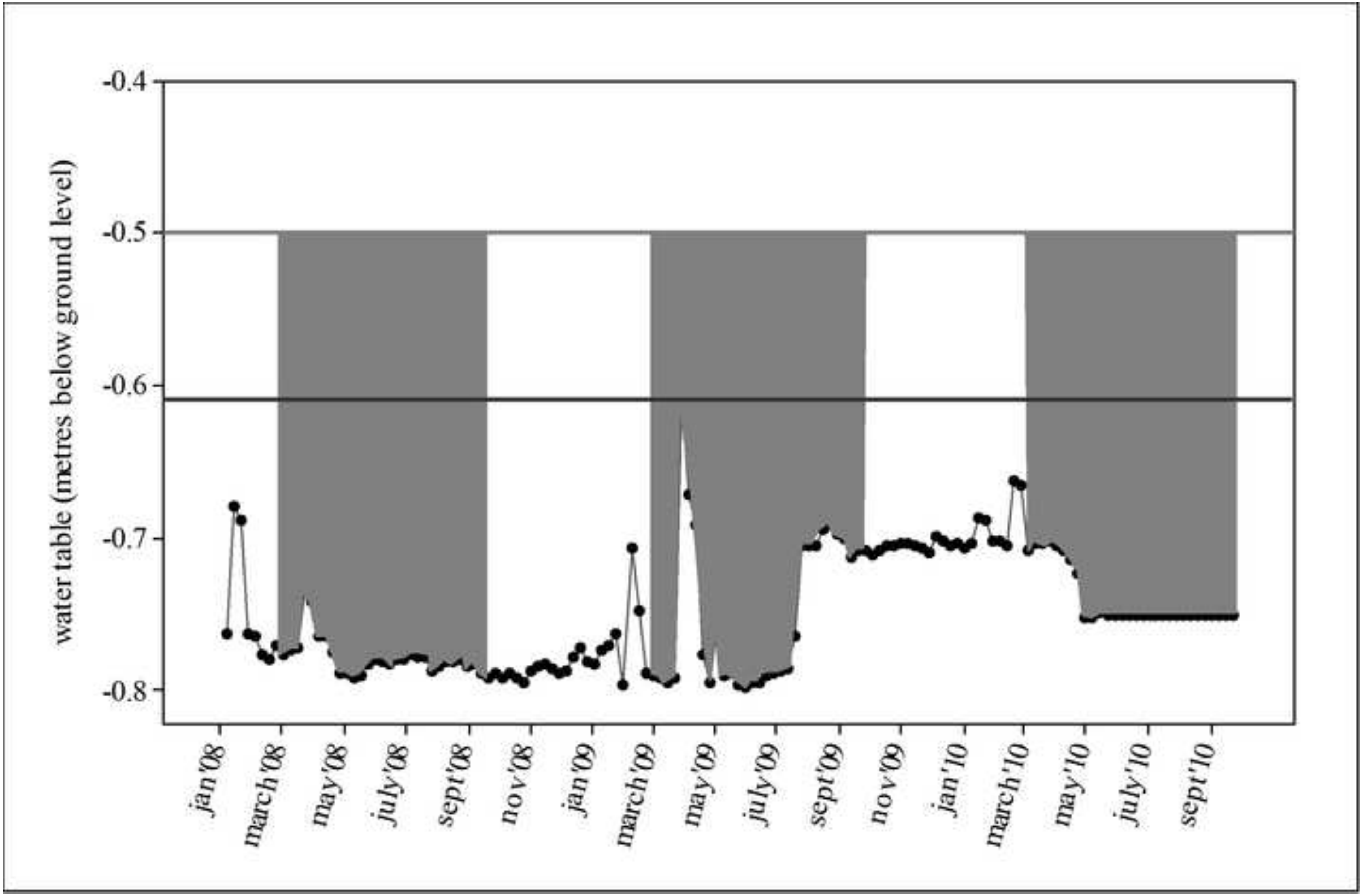

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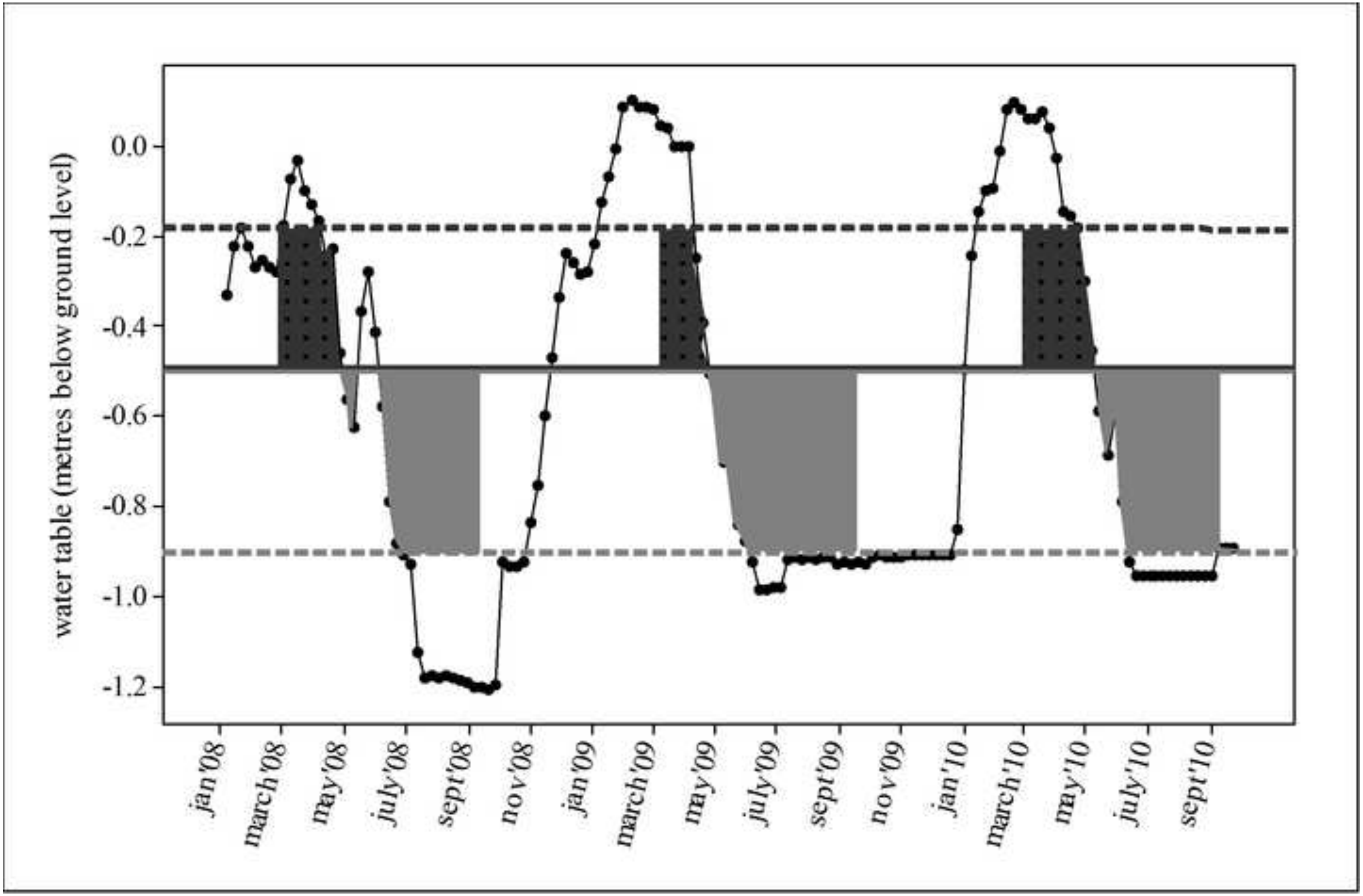

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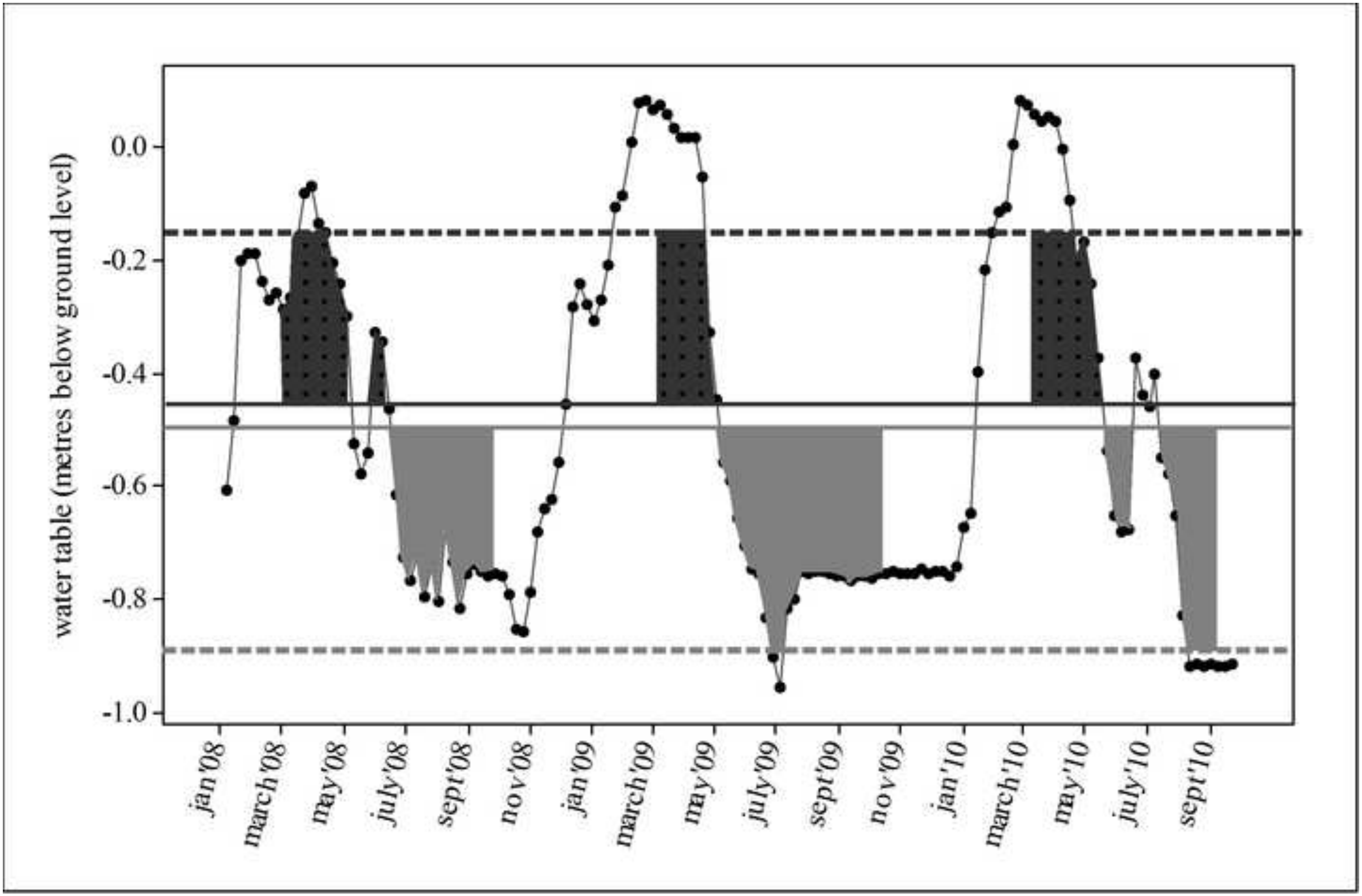

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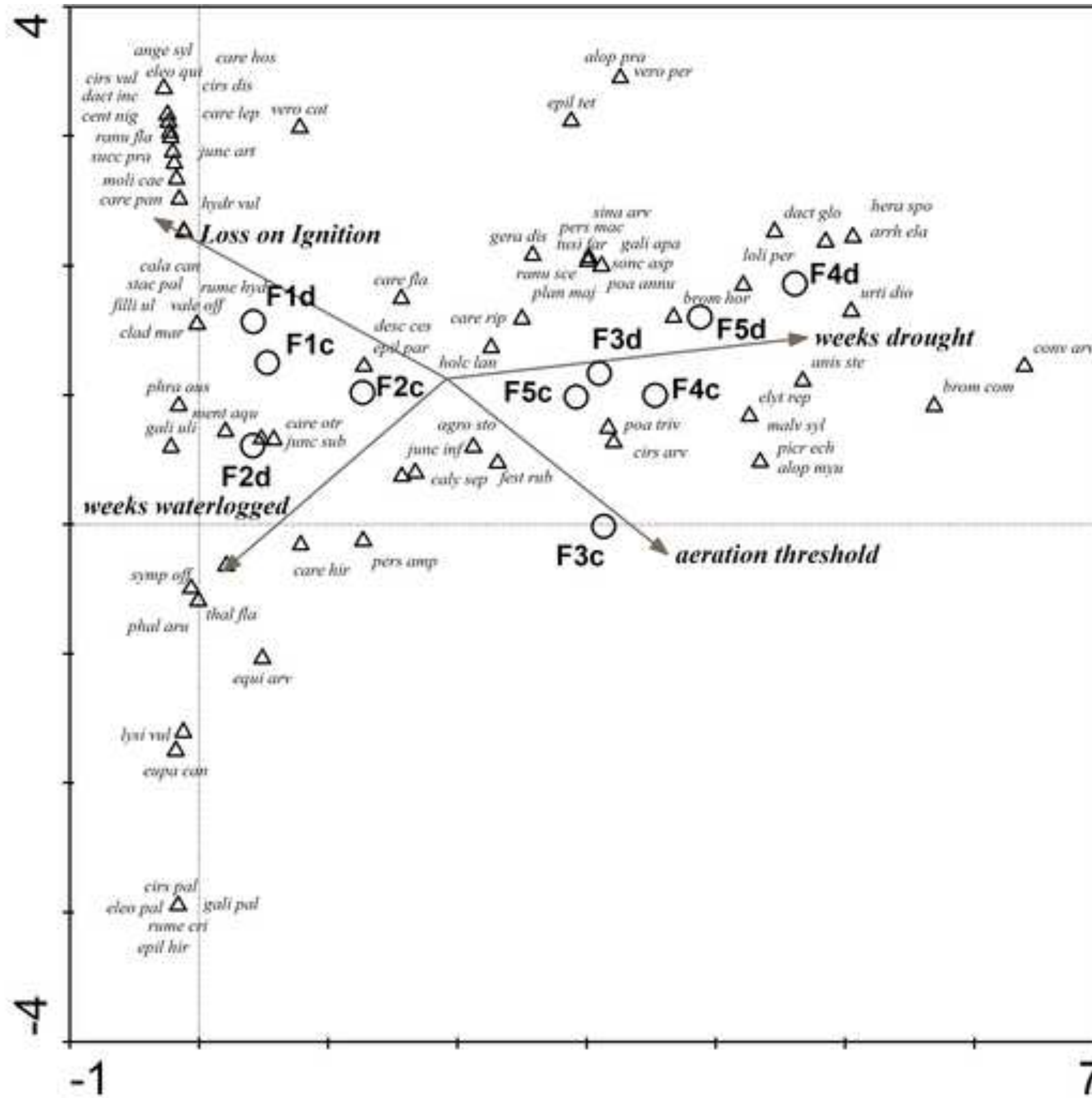

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