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ABSTRACT

Banksia (Proteaceae) woodlands are one of a number of groundwater dependent ecosystems in southwestern Western Australia that are threatened by groundwater abstraction. In addition to this threat is an ongoing decline in regional water tables due to a drying climate. We used ecological resilience theory to analyse and interpret a long-term vegetation monitoring dataset from a site that has experienced an abstraction-induced acute groundwater drawdown in the late 1980s and early 1990's. Despite reduced plant abundance, all dominant over- and understorey species were still found on all transect plots in which they were recorded pre-drawdown. This suggests a notional resilience and a strong likelihood of recovery, in the event that pre-drawdown ecohydrological habitat conditions were to return. However, since the drawdown event, the regional water table continued to decline, with the vegetation responding through progressive and uni-directional change in abundance and composition. The change in composition was primarily manifested as a shift towards non-woody, shallow-rooted species not dependent on specific hydrological conditions. This slow, progressive change in hydrology associated with reduced rainfall and land use changes has continued to force a transition in the floristics towards an alternative ecohydrological state. Despite the absence of an acute drawdown event, the same progressive floristic response was also observed at two reference sites that were not under the immediate influence of production bores. The challenge for adaptive water resource management will be to enhance the capacity for resilience in these groundwater-dependent ecosystems in a drying environment through appropriate regulation of groundwater abstraction.

INTRODUCTION

Groundwater-dependent plant (phreatophytic) communities are a common feature of low-rainfall regions of the world, where they are supported by shallow groundwater aquifers (Elmore *et al.*, 2008, Naumburg *et al.*, 2005). Because of the scale, complexity and generally large number of species that make up natural communities, the term 'groundwater-dependent community' does not imply that all species making up such a community are dependent on groundwater (Eamus *et al.*, 2006). If a community supports easily-identifiable groundwater-dependent species (usually larger, woody species), it is often inferred from the presence of those species that the community is groundwater-dependent (Eamus*, et al.*, 2006). However, such a community can consist, for instance, of herbaceous and grass species relying on recent precipitation, as well as deep-rooted species that, in the absence of rainfall, rely directly on groundwater. Microhabitat features and local topography are additional important factors in determining community composition. Upland species, for instance, are more inclined to tolerate water stress than lower-lying, obligate phreatophytic species which tend to be more sensitive to changes in groundwater regimes (Camporeale *et al.*, 2006). This complex, dynamic character of groundwater-dependent plant communities imparts a resilience to changes in environmental conditions, including fluctuating groundwater levels.

The concept of ecological resilience is founded on the theory that the natural state of a system is one of change rather than of equilibrium (Holling, 1973). This is especially applicable to plant communities which, primarily due to their lack of mobility, have adapted to varying degrees of recurrent disturbances or 'perturbations' whilst still retaining the same self-organized processes and structures (defined as 'alternative stable states'; Gunderson, 2000; Holling, 1986). Although groundwater-dependent communities are adapted to natural fluctuations in groundwater levels, an extra-ordinary or sudden drawdown may exceed the resilience or adaptive capacity of the system, forcing it into an alternative stable state with consequent loss of the ecological character (*sensu* Ramsar Convention, 2005) of the original or previous state. In this paper, we use the term 'ecohydrological state' to represent various 'alternative (stable) states' of groundwater-dependent plant communities. These ecohydrological states are characterized primarily by their groundwater requirements, but also by community composition, function and ecological character.

Impacts from groundwater drawdown range from gradual changes in plant community structure to sudden and extensive vegetation deaths (*e.g.*, Groom *et al.*, 2000a). The latter is especially undesirable where the perturbation is a consequence of poor environmental management practices, and even more so when superimposed on the anthropogenic perturbation are multiple, more or less uncontrollable natural perturbations (climate change being the best example). Understanding the nature of the resilience of natural communities, particularly ones dependent on resources for which there are competing demands, is fundamental to the effective adaptive management of such ecological communities (see for instance, Allison and Hobbs, 2004, Gunderson, 1999, Nelson *et al.*, 2007, Sharma and Craig, 1989).

We present in this paper a case study from the Swan Coastal Plain, Western Australia. In 1985 increased summer abstraction of groundwater from a well-field located within groundwater-dependent *Banksia* woodland caused rapid drawdown of the groundwater table, resulting in the death of up to 80% of all *Banksia* trees within the vicinity of the well-field (Groom *et al.*, 2000a). Subsequently, a vegetation monitoring program was implemented in order to study and monitor the effects of groundwater abstraction on the extant groundwater-dependent woodlands. A vegetation transect was established within close proximity to an abstraction bore referred to as 'P50', located within a newly established well-field ~ 25 km north of the original tree deaths. Vegetation monitoring of this transect commenced in 1988, one year prior to commencement of abstraction. At the time, depth to groundwater at the site was approximately 2.5 m. In summer 1991 (two years after commencement of pumping), extensive tree deaths surrounding the abstraction bore were observed following several days of high summer temperatures (Groom *et al.*, 2000a). Groom *et al.* (2000a) initially assessed and described the floristic changes that have occurred within the P50 transect. They found that deep-rooted shrub and tree species (phreatophytes) were most affected by the drawdown. Over the same period of time, no significant declines in over- or understorey species had occurred at a comparable site that was not directly influenced by groundwater abstraction, suggesting that the vegetation impacts at P50 were primarily caused by the sudden drawdown event, exacerbated by the extreme weather conditions at the time.

By 2005 (some 15 years after the drawdown event), the vegetation of the site superficially appeared to have recovered and yet the depth to groundwater had increased to 7.5 m. Little is known about the nature of this 'recovery' in terms of composition, function and groundwater requirements, factors that would define the resilience of this groundwater-dependent community. Hence, the aim of the current study was to assess the resilience of *Banksia* woodland communities by testing the following null-hypotheses:

(1) Floristic composition has not changed significantly over time, and by 2005, floristic composition was little different from pre-drawdown composition in 1988;

(2) The plant community has fully 'recovered', and has not undergone a transition to an alternative ecohydrological state (*sensu* Holling, 1973).

Interpretation of these long-term data poses the inherent complication that the post-drawdown, 'recovery' phase of the vegetation community at P50 coincided with a regional trend of declining rainfall (and concomitantly, groundwater levels). In an attempt to untangle these two factors, two additional null-hypotheses were tested:

(3) P50 temporal floristic changes are comparable to other vegetation transects in the region that have been subject to the same long-term drying trend, but have not been subjected to groundwater abstraction;

(4) Hydrological drivers (groundwater regimes and climatic factors) do not explain observed floristic changes.

79　In the case of $H_{0(4)}$ being rejected, we sought to ascertain the relative importance of
80　individual, or combinations of, hydrological drivers that best explained the floristic changes.

81　 METHODS

82　*Study area and vegetation monitoring*

83　The climate of the Swan Coastal Plain is warm Mediterranean with five to six dry months per
84　year, extending roughly from mid October to the end of March. The average rainfall in the
85　Perth region is ~750 mm year^{-1}, falling mainly in winter. However, there have been extended
86　periods of below-average rainfall during the late 1970's and since the early 1990s. In
87　addition, and of relevance to this study, Perth experienced a series of extreme temperature
88　days in the summer months of 1990-91 and 1993-4 (>40°C), coupled with low winter
89　rainfall.

90　 The vegetation transect in question lies within the Pinjar well-field on the northern Swan
91　Coastal Plain (Figure 1). It was set up in 1988 next to the groundwater abstraction bore
92　known as P50 (31°37′21″S, 115°49′11″E). Surrounding vegetation is classified as '*Banksia
93　woodland*', a groundwater-dependent community dominated by an overstorey of Slender
94　*Banksia* (*Banksia attenuata*), Menzies' *Banksia* (*B. menziesii*) and Holly-leaf *Banksia* (*B.
95　ilicifolia*), and a typical sclerophyllous sandplain heath understorey consisting of various
96　shrubs from the Myrtaceae, Fabaceae and Epacaridaceae families. Non-native *Pinus pinaster*
97　plantations and horticultural land also lie in the vicinity of the transect. The site lies on the
98　geomorphic unit locally known as the 'Bassendean dunes' which consists of deep, leached
99　Pleistocene quartz sands with very low water-holding capacity (McArthur and Betteney,
100　1960). The superficial sediments of this dune system, together with the younger, more
101　calcareous and higher formations that lie to the west (the Spearwood and Quindalup dunes),
102　support the vast regional aquifer known as the Gnangara groundwater mound. The Gnangara
103　mound is Perth's most important freshwater resource, supplying up to 60% of its drinking
104　water. Increasing demands on this resource, coupled with declining winter rainfall, has
105　resulted in a dramatic lowering of the regional groundwater table over the last few years, with
106　measurable consequences for the numerous groundwater-dependent ecosystems (wetlands,
107　caves, mound springs, as well as phreatophytic vegetation) sustained by the aquifer
108　(Department of Environment, 2005).

109　 The P50 transect starts 50 m from the abstraction bore, is 40 m wide x 200 m long, and is
110　well within the estimated distance from the bore that would be influenced by groundwater
111　abstraction (Groom *et al.*, 2000a). All of the Gnangara mound monitoring transects were set
112　out so as to maximize the coverage from the dune crest to a swamp or depression.
113　Understorey plant abundances were recorded in 4 m x 4 m quadrats located at regular
114　intervals within two parallel 20 m x 20 m overstorey plots. Within each overstorey plot, the
115　abundances, number of dead and alive trees and the diameter at breast height for each species
116　were recorded. The overall vigour of each tree was based on a visual assessment of canopy
117　condition (leaf chlorosis, canopy fullness, branch dieback and epicormic sprouting) and was
118　then categorized into one of the following: healthy, stressed or dead. Vegetation monitoring

119   has occurred in 1988 (pre-pumping), 1993, 1996, 1999, 2002, 2004 and 2005. Because of
120   reported tree deaths in summer 1991, an additional, unscheduled assessment of the overstorey
121   was conducted in the following spring of that year. Monitoring always took place in spring,
122   between October and November, when maximum soil moisture was expected.

123   Comparison sites were selected on the basis that they had available both long-term
124   vegetation and hydrological data. Further criteria included location on the same
125   geomorphological setting (*i.e.* on Bassendean sands) with the same vegetation complexes.
126   Finally, the sites were to have experienced the same regional trend in groundwater decline as
127   P50, but no groundwater pumping in the immediate vicinity. The two chosen sites were
128   'Neaves'(31°42′S, 115°53′E), ~8.5 km south of P50 and closest production bore one km
129   away, and Yeal (31°29′S, 115°45′E), ~16 km north of P50 and closest production bore 14.7
130   km away (Figure 1). As for P50, both sites have been regularly monitored as part of the
131   Department of Water's long-term vegetation monitoring program of the Gnangara mound. As
132   the three transects were not always monitored in the same years, years used in the analyses
133   described below were 1987, 1990, 1993, 1996, 1999, 2002 and 2005 for Neaves, and 1987,
134   1990, 1993, 1996, 2002 and 2005 for Yeal. For Neaves, overstorey plots were not surveyed in
135   2005, but were in 2008.

136   The fire history of the three sites was assessed by examining and comparing historical
137   Landsat images obtained from the Western Australian Department of Environment and
138   Conservation (DEC) for fire scars in the areas of interest. Pests and diseases can also impact
139   on site flora. On the Gnangara mound only *Phytophthora cinnamomi* (a fungal pathogen that
140   causes root-rot disease symptoms) can influence vegetation composition at the community
141   scale (see for instance Hill *et al*., 1994). Recent surveys conducted by DEC do not indicate
142   the presence of significant dieback symptoms that would account for the floristic patterns
143   observed at any of the three study sites (Kinloch and Wilson, 2009).

144   *Data analyses*

145   Entire-transect (*i.e.* data pooled from ten 20x20 m overstorey quadrats and, nested within
146   these, twenty 4x4 m understorey quadrats) vegetation abundance data were compiled for each
147   of the survey years in order to assess multi-temporal changes in community composition. The
148   pooling of the data was justified due to the flat nature of the transect (overall slope of only
149   0.15%). Community water requirements were inferred by allocating individual species to two
150   functional classification schemes:

151   (1) Havel hydrological habitat preference categories

152   Havel (1968) reported that many Swan Coastal Plain species inhabiting damplands and
153   swamps were able to tolerate periods of waterlogging and excessive wetness, while others
154   were able to tolerate moist (but not waterlogged) sites fringing these depressions. These
155   species have proven to be highly susceptible to non-seasonal decreases in soil moisture
156   availability (Havel, 1968). The Havel categories employed in this study include (A) tree and
157   shrub species tolerant of excessive wetness; (B) tree and shrub species of optimum moist
158   sites, but intolerant of extremes in moisture conditions; (C) tree and shrub species with wide

159 tolerances, but with maximum development on dry sites; and (D) tree and shrub species
160 without clear cut site preference.

161 Hydrological habitat preferences of species for which there were no Havel categories were
162 determined by considering where individual species were found in relation to topography and
163 groundwater depths based on ~17 transects on the Gnangara mound over ~30 years of
164 monitoring.

165 (2) Dodd *et al.* (1984) and Pate *et al.* (1984) rooting pattern categories

166 These include: Types 1 and 2 - rooting patterns which are largely fibrous and adventitious in
167 origin (usually annual monocotyledons); Type 3 - Tap-rooted plants; Type 4 - the vertical and
168 horizontal root morphology that occurs predominately in woody genera, 4a shallow roots, 4b
169 deep roots; Type 5 - Root systems with only shallow horizontal main roots; Type 6 - A highly
170 infrequent though present type with stout woody roots with branches neither predominately
171 vertical nor horizontal. Only Type 3 and Type 4b patterns contain species that are deep
172 rooted (> 2 m rooting depth), and thus have the potential to be phreatophytic.

173 Where abundance data were available, species were further classified into life history
174 traits (annual, perennial), life-form (tree, shrub, herb/grass) and endemicity (native or exotic).

175 The Neaves and Yeal data sets were subjected to the same treatment as described above
176 for P50. This includes the pooling of entire transect data which enabled multivariate analyses
177 to be applied uniformly to all three data sets and thus general patterns of floristic change
178 across sites to be detected. Although Neaves and Yeal had greater slopes (3.4% and 5.9%
179 respectively) than P50 (0.15%), the ranges in groundwater depths over time were comparable
180 across sites, and all three sites had species representative of all Havel water tolerance and
181 rooting depth categories.

182 Historical hydrological data (groundwater levels and pumping regimes) were obtained
183 from the Western Australian Department of Water and the Water Corporation of Western
184 Australia. Climate data were obtained from the Australian Bureau of Meteorology (data
185 interpolated to the P50 coordinates). Hydrological and climate data were compiled and
186 analysed for the relevant vegetation survey years (as indicated above). In order to be able to
187 compare complete seasons, rather than annual figures, 'winter' was calculated from 1st May
188 to 31st October of the survey year, and 'summer' from 1st November of the previous year to
189 the 30th April of the survey year.

190 Temporal change in species composition at P50 (and at the comparison sites, Neaves
191 and Yeal) was assessed by initially computing a distance matrix among observations (*i.e.* the
192 7 survey years) based on Ln(y+1)-transformed species abundance data using the Bray-Curtis
193 dissimilarity coefficient. A Principal Coordinate Analysis (PCoA) was then conducted on this
194 matrix to produce an ordination plot of the time series. Pearson's correlations of
195 (transformed) species abundances with the first two PCoA-axes were conducted and overlaid
196 on the ordination. The relative significance of floristic changes over time was assessed by
197 considering the proportion of variability in the data set explained by the first two ordination

198 axes. This represents an advantage over non-metric multidimensional scaling (NMDS) where
199 relative significance of the ordination must be assessed from a goodness-of-fit ('stress') value
200 which is relative only, and can vary depending on which software program is used (Legendre
201 and Legendre, 1998). The SIMPER function in the Primer (v. 6.1) package was used to
202 ascertain the contribution of each species to the average dissimilarities between the
203 monitoring years.

204   In order to judge whether the P50 vegetation has undergone changes in ecological
205 character (equating to ecohydrological states) over time, temporal variations in community
206 water requirements, life history traits, life-form, endemicity groupings (as described above),
207 and biodiversity (Shannon-Wiener Diversity H′($\log_{10}$)) were computed and compared.

208   The association between hydrological and climate variables with changes in
209 community composition was assessed by first overlaying Pearson's correlations of these
210 variables with the first two PCoA-axes. Because we had a very large number of hydrological
211 variables (many of which were auto-correlated), we selected only those with the highest
212 correlations for further analysis. Selected hydrological data were initially transformed
213 ($\log_{10}(x+1)$) and then standardized (by range to 0-1). We then proceeded to decompose the
214 variation in the floristic data set in order to assess the independent and joint effects of the
215 hydrological and climate variables (Anderson and Gribble, 1998, Liu, 1997). Because of the
216 afore-mentioned collinearity of the environmental variables, only those with acceptable
217 collinearity statistics (R^2s, Variance Inflation Factor and tolerances) were used in the
218 analysis. This involved the following steps: (1) a redundancy analysis (RDA) was performed
219 on Hellinger-transformed plant abundances using all selected environmental variables as
220 explanatory variables (this gives the total amount of variation explained by all environmental
221 variables); (2) a series of partial RDAs were run on each individual environmental variable
222 using the remaining variables together as covariables, and the other way around, with and
223 without covariables, until all combinations of variables and covariables have been exhausted.
224 The significance of each of the fractions was tested using Monte Carlo permutation (999
225 permutations). All of these analyses were performed in XLStat version 2009.2.1
226 (Addinsoft®). The results of these analyses were organized in a table and presented as a
227 Venn diagram.

228

229   RESULTS

230 *Climate, fire and hydrological history*

231 The region experienced variable total annual rainfall between 1966 and 2008, ranging from
232 513.7 mm in 2006 to 1021.8 mm in 1967. A distinct declining trend in the 5-year average
233 rainfall was only obvious from 1994 onwards (Figure 2). Maximum summer temperatures, on
234 the other hand, were above average from 1994 onwards, with the exception of the low-
235 rainfall year 2006. Winter 1990 experienced the lowest rainfall over the displayed time series
236 (only 481.6 mm; Figure 2), and although maximum temperatures of the following summer
237 were near-average, two heat waves occurred immediately prior to the observed tree deaths.

238 One was between 29th and 31st January 1991 (40°C – 45.5 °C), the other between 19th and
239 23rd February 1991 (36°C – 46 °C). During this period, groundwater had continued to be
240 pumped, and the first tree deaths were observed by the end of February (Groom *et al.*,
241 2000a).

242   Groundwater levels at the P50 site declined throughout the monitoring period (1975 –
243 2005) (Figure 3). Although the decline has been more or less gradual, two more severe
244 drawdowns occurred, one between September 1988 and March 1989 (drop of 2.02 m), and
245 the other between July 1990 and January 1991 (drop of 2.83 m). These declines coincided
246 with groundwater pumping (Figure 3). Thereafter groundwater recovered (although
247 monitoring was not continuous) to similar levels as those of three nearby bores (PVEG1-3).
248 From the summer of 1998 onwards, however, water levels at the P50 bore were consistently
249 lower than that of the three adjacent bores. The overall decline in groundwater at P50
250 between 1988 and 2005 was ~5.4 meters, compared with ~4.4 meters at Yeal and ~1.7 meters
251 at Neaves.

252   There was an absence of intense, frequent fires during the history of monitoring at all
253 three study sites.

254 *Multi-temporal changes in community composition*

255 PCoA ordinations for the P50 transect and for the comparison sites, Neaves and Yeal (Figure
256 4), all display the typical 'arch effect' that occurs when community composition changes
257 progressively along an environmental gradient (Legendre and Legendre, 1998). Figure 4a
258 shows Pearson's correlations of environmental variables with PCoA axes F1 and F2, and
259 demonstrates that for all three transects, early monitoring years were associated with higher
260 rainfall and smaller groundwater depths, while later years were associated with the reverse as
261 well as higher mean maximum summer temperature (see also Tables 1-3). Figure 4c shows
262 correlations of plant species with the PCoA axes. These have been coded into Havel (1968)
263 hydrological habitat preference categories and show that at the P50 transect there has been a
264 shift from species with mixed water tolerances in the earlier years to species belonging
265 predominantly to category D (species without clear-cut site preferences) in the later years
266 (see Table 1 for species names and correlation coefficients). At the two comparison sites this
267 shift is less pronounced, although the dominant trend is towards less species of the Havel A
268 and B categories (wetter habitats) to more of the C and D (drier, upland) categories. One
269 species belonging to the Havel A category, the tree *Melaleuca preissiana*, is associated with
270 later monitoring years at the Neaves and Yeal transects (although non-significant at Neaves;
271 see Tables 2 and 3). Figure 6 however shows that although more *M. preissiana* were present
272 in the overstorey plots in 2008 than in 1987, more than half of these were stressed. At Yeal
273 nearly all the *M. preissiana* present in 2005 were stressed (Figure 6).

274   Floristic changes in terms of rooting morphology were less clear-cut than those of the
275 hydrological habitat preference categories because most plants (shrubs and trees), particularly
276 those at P50 and Yeal, were of either 4A (woody genera/shallow roots) or 4B (woody
277 genera/deep roots) type. There is a trend though of plants having a 4A type rooting pattern to

278   be more strongly associated with the early monitoring years, especially at P50 (Table 1).
279   There were no evident patterns in floristic changes in terms of life form (Table 1).

280   Despite acute drawdown in 1989 at P50, vegetation composition between 1988 and
281   1993 was still (statistically) more similar than between 1988 and any of the later years
282   (Figure 4). This is shown more clearly (and without the distortion of an arch effect) in Figure
283   5 as the Bray-Curtis distances plotted over time. The magnitude of floristic change was
284   similar at all three transects between 1987/88 and 1990/93 (15.5%, 15.5% and 15.8% for P50,
285   Neaves and Yeal respectively). Similar magnitudes of change continued to occur at P50 from
286   survey year to survey year, culminating in 2005 (the last survey year) with 44.1%
287   dissimilarity relative to 1988. At the Neaves transect, dissimilarities between survey years
288   were more erratic, but also culminated in a 43.7% dissimilarity with 1987 (Figure 5). Yeal,
289   the transect furthest away from a production bore, displayed a comparatively small floristic
290   dissimilarity between 1987 and 2005 of 25.9%. At all three transects the greatest floristic
291   change took place between 1999 and 2002 (between 1996 and 2002 at Yeal), with some
292   indication of recovery in 2005 (reflected by a smaller Bray-Curtis dissimilarity). The
293   immediate floristic response to drawdown at P50 (as revealed by the SIMPER analysis of the
294   combined under- and overstorey data between 1988 and 1993) constituted a significant
295   decline in all tree species, but particularly in the highly groundwater-dependent (Groom,
296   2004; Zencich *et al.*, 2002) *Banksia ilicifolia* (1988: 220 trees, 1993: 59 trees) which
297   contributed almost 18% to the overall floristic dissimilarity between 1988 and 1993. *B.*
298   *attenuata* declined from 236 to 165 trees (7.9% contribution to dissimilarity) and *B. menziesii*
299   from 130 to 95 trees (3.9% contribution to dissimilarity). Not only did overall abundances
300   decline, but vigour of the surviving trees deteriorated markedly (Figure 6). Of the remaining
301   45 *B. ilicifolia* in the overstorey plots in 1991(from a total of 199 in 1988), only 11 were
302   healthy. For *B. attenuata*, 125 out of 132 surviving trees in 1991 were 'stressed', and only 7
303   healthy, and of a total of 69 surviving *B. menziesii*, 68 were 'stressed'. Similar tree declines
304   and deterioration of vigour was not observed over the same period at Neaves and Yeal
305   (Figure 6). However, by 2005/2008, all overstorey species, including those at the comparison
306   sites, contained large proportions of stressed individuals.

307   Understorey species that declined markedly between 1988 and 1993 were *Hibbertia*
308   *subvaginata*, *Verticordia drummondii*, *Hibbertia* sp. Gnangara, *Petrophile linearis*,
309   *Leucopogon sprengelioides*, *Melaleuca seriata*, *Leucopogon conostephioides* and
310   *Hypocalymma angustifolium*. This group of species is of mixed water tolerance and rooting
311   pattern categories and continued to decline in abundances until 2005. One herbaceous
312   species (considered to grow best at moist sites), *Actinotus glomeratus*, increased markedly in
313   abundance between 1988 and 1993 (from 78 to 214 plants, contributing 15% to the overall
314   dissimilarity), but decreased again between 1993 and 1996 (to 122), and during the last
315   survey in 2005, only ten plants were recorded. The greatest contribution (40.9%) to the
316   floristic change of 18.5% (Figure 5) between 1999 and 2002 was from a decline of *Melaleuca*
317   *seriata* (1999: 686 individuals; 2002: 394 individuals)*,* a shallow-rooted species which grows
318   optimally in moist conditions. *Verticordia nitens, Hypocalymma angustifolium, Verticordia*
319   *drummondii, Hibbertia sp*. Gnangara*, Leucopogon conostephioides* and *Actinotus glomeratus*

320 also suffered large declines between the two survey years. On the other hand, all overstorey
321 species increased slightly in abundances over this period (Figure 6).

322 *Multi-temporal changes in ecological character*

323 Although overall species abundances at P50 have distinctly declined over time, there was no
324 marked decline in species diversity (Shannon's H' [$\log_{10}$]). (Figure 7). Only two species have
325 been lost from the transect (*Astartea fascicularis* and *Hibbertia spicata*, both present in low
326 numbers until 1996) and three have been gained (*Anigozanthos humilis*, *Beaufortia elegans*
327 and *Phyllangium paradoxum*, present from 1993, 1996 and 1993 respectively). Furthermore,
328 even though abundances of most species have declined, these still remained present in most
329 of the plots in which they were originally found in 1988.

330 The proportions of individuals belonging to the various rooting categories have also
331 not changed much over time (Figure 8). Only by 2005 have the proportions of the rooting
332 categories 4A and 4B declined in favour of categories 1, 2 and 5. Likewise, the proportions of
333 individuals belonging to the various water tolerance classes have not changed much over
334 time, apart from a slight increase in the proportion of Havel class D individuals in 2004 and
335 2005 (at the expense of Havel class A and B individuals). In terms of life history traits, there
336 was a decreasing trend in the proportions of trees and shrubs, in favour of herbs (although the
337 latter make up a very small proportion of total plant individuals; Figure 8). Weed species
338 were primarily recorded as percentage cover or presence/absence and therefore could not be
339 included in these analyses. In 2005, the following weeds were observed: *Briza maxima*,
340 *Ehrharta calycina*, *Gladiolus caryophyllaceus*, *Hypochaeris glabra*, *Ursinia anthemoides*,
341 and *Wahlenbergia capensis*. However percent coverage of these were very low in the
342 individual plots (ranging from <0.1 to 0.5%).

343 *Hydrological and climatic influence on floristic patterns*

344 Above analyses suggest that both declining rainfall (and associated climatic variables) and
345 increasing depth to groundwater (and associated hydrological variables) influenced observed
346 floristic changes at P50. It was not possible to separate the variation in the floristic data
347 between the climatic and hydrological variables (*i.e.* two groups) due to the strong multi-
348 collinearity between the two data sets. Examination of the multicollinearity statistics resulted
349 in the retention of three of the original 36 environmental variables. These were: the 3-year
350 mean highest groundwater level (to serve as a surrogate for 'depth to groundwater'), the 3-
351 year mean rainfall (to serve as a surrogate for 'rainfall') and the 3-year mean maximum
352 summer temperature (to serve as a surrogate for 'temperature'). The ordination resulting from
353 the tb-RDA (transformation-based RDA; Legendre and Gallagher, 2001) using 'depth to
354 groundwater', 'rainfall' and 'temperature' as explanatory variables, accounted for 92.2% of
355 total variation ($\lambda = 0.871$, $p < 0.05$). It shows the plant species strongly aligned with the F1
356 axis, the 'depth to groundwater' vector (Figure 9). The list of plant species, arranged in order
357 of their appearance on the F1 axis is given in Table 4. The two locally 'extinct' species
358 *Astartea fascicularis* and *Hibbertia spicata* were restricted to early survey years which are

359 associated with shallower depths to groundwater, lower maximum summer temperatures and
360 higher rainfall (Figure 9).

361   Decomposition of the variation in the floristic data set amongst the three variables
362 (depth to groundwater, rainfall and temperature) required one tb-RDA (Figure 9) and twelve
363 partial tb-RDAs. The resulting Venn diagram (Figure 10) shows that each of the three
364 components significantly explains the floristic variation over time when the other two are
365 incorporated as covariables (eigenvalues (λ) of 0.672 (p< 0.0001), 0.456 (p< 0.05) and 0.587
366 (p< 0.01) for depth to groundwater, rainfall and temperature respectively). However, the
367 explained fraction that could be attributed purely to individual components (*i.e.* without
368 covariables) was not significant for any of the components (although depth to groundwater
369 was close: λ= 0.187, *p*= 0.057). The explanatory fraction shared by the three components
370 (35%) was greater than the effects of the individual components or combinations of two
371 individual components (Figure 10). The negative fraction of explained variation shared by
372 depth to groundwater and rainfall (-1.9%) indicates that the two components individually
373 explain a slightly greater proportion of the floristic variation than their combined effect does
374 (when temperature is not taken into consideration). The total variation explained by the three
375 environmental variables was 87.1% (*p*= 0.027), leaving an unexplained fraction of 12.9%
376 (Figure 10).

377

378   DISCUSSION

379 It is clear that there has been a progressive, directional change in floristic composition
380 between 1988 and 2005 at the P50 transect. However, the same change was also observed at
381 the two reference transects, Neaves and Yeal, which are not under the immediate influence of
382 production bores. It is therefore fair to assume that these general patterns are attributable
383 predominantly to the on-going decline in the regional groundwater table due to reduced
384 rainfall and land use changes (*e.g.* plantation forestry), and only secondarily to groundwater
385 abstraction. Moreover, the magnitude of floristic change between the pre-drawdown year
386 1988 (1987 for Neaves and Yeal) and 1993 was very similar for all three sites (all ~15%).
387 The data provide evidence, however, that pumping (which has resulted in a greater magnitude
388 and rate of groundwater decline at P50) may have nevertheless altered the pathway of
389 floristic change to one of a threshold response followed by recruitment/regrowth and then
390 further progressive change similar to the reference sites.

391   First, the transects closest to production bores experienced the greatest overall floristic
392 changes (44% at both P50 and Neaves, 500 m and 1 km from the nearest abstraction bores
393 respectively; 26% at Yeal, 14.7 km from the nearest bore) (Figure 5). That Yeal has
394 undergone less floristic change than Neaves over the same time period despite experiencing a
395 greater decline in groundwater depth (~4.4 meters *versus* ~1.7 meters at Neaves), suggests
396 there may be some perching of water above the recorded water table or greater retention of
397 soil water due to differences in stratigraphic retention characteristics.

Second, the effect of the acute drawdown events of 1989 and 1991 is evident in the overstorey species (all phreatophytes) plots of P50 but absent at the reference sites (Neaves and Yeal). The abundances of those tree species whose populations had collapsed in 1991 at P50 had not recovered by 2005. In contrast, tree species at the reference sites tended to respond to declining groundwater levels with deteriorating vigour rather than markedly decreased abundances. This gradual loss of condition in persistent individuals was also observed on the Swan Coastal Plain by Groom *et al.* (2001) in their assessment of long-term changes in vigour of *Banksia* and *Melaleuca* species. Canopy decline in this earlier study was most noticeable in species typical of shallow depths to groundwater (Havel A) that had experienced a low rate of drawdown. One may assume that the hydrological changes (lower rates of progressive groundwater decline) observed in such situations are approaching tolerance limits but remain below species thresholds and within their capacity to physiologically adapt.

Third, the shift from a plant community with mixed Havel water tolerances (equivalent representation of classes A, B, C and D) to a greater dominance of species without clear-cut site preferences (Havel D) was most pronounced at P50. It appears that at P50, not only have the abundances of vulnerable species (Havel A) declined significantly with increasing groundwater depth, but the abundance of other indicator classes specific to a site hydrology (Havel B and C) have also declined. This gradual reduction in (inferred) foliage cover and therefore transpirational loss from the site may represent optimization of the vegetation in response to altered hydrological conditions (Caylor *et al.*, 2008, Eagleson, 1982, Eagleson and Segarra, 1985). We therefore reject our first null hypothesis; floristic composition at P50 has changed significantly from a community with no dominance of any particular water tolerance category to one dominated by 'plastic' species (*sensu* Bradshaw, 1965) with no specific hydrological habitat preference.

The above discussion suggests that the vegetation at P50 has displayed a notional resilience to the hydrological changes observed. Whilst recruitment and regrowth after the early perturbations in water source availability (rapid drawdown due to pumping) suggests resilience to such events, ongoing progressive change in floristics (associated with lower rates of groundwater drawdown) implies the vegetation has not attained a 'stable' floristic endpoint equivalent to what existed prior to the hydrologic disturbance.   In the context of stable state theory, it therefore appears unlikely that the vegetation has shifted to an alternative ecohydrological state which usually occurs as a consequence of having surpassed an ecological threshold (Holling, 1973). Holling's (1973) descriptions of ecological threshold imply a certain irreversibility, however in open systems where reinvasion is possible, full recovery is likely, provided the necessary environmental conditions return and persist after the threshold response. Indicator species of all water tolerance classes except Havel class D dramatically declined in abundance immediately after the drawdowns of 1989 and 1991 (threshold response through mortality) and displayed limited recovery in the years that followed because of ongoing groundwater drawdown (although at lower rates). In spite of the initial threshold response, none of the previously dominant species were lost. Of the two shrub species that have been lost from the transect, *Astartea fascicularis* was only ever

440 present in very low numbers, while *Hibbertia spicata* is a declared taxa (Priority 3, 'poorly
441 known') which, given it does not appear to have any specific water preferences (*i.e.* Havel
442 D), may have perished due to other reasons. In addition, although Havel A, B and C type
443 species' abundances declined, diversity only declined slightly (and recovered after 2002 in
444 spite of a further drastic decline in overall plant abundance; Figure 7). There were some
445 changes in the relative proportions of individuals belonging to the various water tolerance,
446 rooting morphology and life history classes (Figure 8), however these changes were small.
447 More importantly, all species (apart from the two afore-mentioned) were still found on all
448 transect plots in which they were recorded pre-drawdown. These arguments suggest that the
449 system had retained its intrinsic ecological character and, if groundwater levels would have
450 recovered, there would have been scope for floristic recovery. In essence, the plant
451 community can be regarded as being in the process of re-organizing itself in an effort to
452 retain the 'same function, identity and feedbacks', which is the definition of 'resilience' given
453 by Walker *et al.* (2004). However, ongoing change in the hydrological habitat has prevented
454 recovery to a stable state equivalent to the pre-drawdown condition. Although, the vegetation
455 at P50 has displayed a notional resilience to the rapid drawdown events, we must
456 nevertheless reject our second null hypothesis based on the significant vegetation
457 dissimilarity relative to the original state.

458   Of relevance is that environmental conditions did not recover and floristic change
459 continued on a trajectory until 2005. In this sense, our third null hypothesis must be accepted
460 because multi-temporal changes at P50 were very similar to those in the region that have
461 been subject to the same long-term drying trend, but have not been subjected to groundwater
462 abstraction in their immediate vicinity. The continuation of this uni-directional change
463 suggests an alternative state has not (yet?) been attained and the community can be described
464 as being in transition (Westoby *et al.*, 1989). Alternatively, it signals the nearing of a
465 threshold, and the possibility, perhaps inevitability, of crossing the boundary and entering
466 into another domain of attraction over time. Critical here is that if the trajectory of
467 environmental change is faster than vegetation adaptability (*e.g.* by extending deep roots to
468 follow a receding capillary zone), recovery through a successional trajectory back to an
469 equivalent (or at least 'desirable') ecohydrological state may not be possible. The key,
470 therefore, is to identify the relative importance of the individual hydrological and climatic
471 components that are driving the observed changes.

472   At all three sites, shallower groundwater depths, higher rainfall and lower maximum
473 summer temperatures were associated with the 'earlier' monitoring years, and the opposite
474 with the 'later' monitoring years (Figure 4): this is a reflection of the climatic and hydrologic
475 trend on the entire Swan Coastal Plain since the early 1970's (Yesertener, 2008).
476 Groundwater depth, rainfall and temperature significantly explained observed floristic
477 changes at P50 (Figure 9). We can therefore reject our last null hypothesis ($H_{0(4)}$). The fact
478 that none of these three drivers on their own significantly explained the floristic variation,
479 suggests that all three components were synergistically implicated in the observed changes.
480 For example, if the drawdown had occurred (say primarily from pumping), but summer
481 temperatures would not have been as extreme, and winter rainfall 'average', vegetation

482   response may have been milder, perhaps negating a threshold response. That temperature
483   (and the combination of groundwater depth/temperature) explained a larger proportion of the
484   floristic variation than rainfall (or the combination groundwater depth/rainfall) is perhaps not
485   surprising given this is a phreatophytic community where plants are either directly or
486   indirectly (*e.g.* hydraulic lift, (Dawson, 1993, Horton and Hart, 1998) dependent on
487   groundwater when rainfall is scarce. The persistence of the phreatophytic community at P50
488   will be determined by the community's resilience to ongoing drying of the environment.

489   Ecological resilience is in reality not as clearly defined as the seemingly emphatic
490   hypotheses formulated in this paper may suggest. The purpose of analyzing these datasets in
491   the light of resilience theory is to be able to apply adaptive management principles to all
492   remnant groundwater-dependent vegetation on the Swan Coastal Plain. One difficulty is that
493   much of the resilience literature, especially that relating to plant ecology, has focused on
494   'surprising' and 'discontinuous' perturbations (*sensu* Holling, 1973) such as fire or disease,
495   while the literature on on-going, progressive perturbations remains scarce (although with
496   advent of climate change this can be expected to change). In this case study of phreatophyte
497   response, a slow, progressive change in hydrology has clearly overridden the sharp
498   drawdown perturbation; despite a minor shift in vegetation characteristics a *Banksia*
499   woodland community persists at P50 and continues to respond like the reference sites.
500   Resilience, however, may be site-specific rather than species-specific (Meinzer, 1927). This
501   stems from historical adaptation to seasonal as well as cyclic fluctuating groundwater levels.
502   For example, the development of dimorphic root morphology where a species possesses both
503   superficial lateral roots and deeply penetrating tap roots is one such adaptation (Dawson and
504   Pate, 1996). Zencich *et al.* (2002) have shown that *Banksia* trees on the Gnangara mound
505   preferentially used shallow soil moisture if it was available and switched to groundwater as
506   shallow layers became dry. Moist, aerated soil layers left behind by falling water tables
507   facilitate root proliferation with depth (Naumburg et al., 2005). Leaf and branch drop in
508   plants experiencing water stress, whilst a direct impact of drought, may at the same time
509   facilitate plant survival because the plant's water needs are reduced (Horton and Hart, 1998,
510   Naumburg *et al.*, 2005). Once further water stress thresholds are surpassed, deaths of
511   individual plants occur. This 'thinning out' of the site (which has been observed at P50 and
512   other locations on the Gnangara mound) may allow the persistence of the survivors as well as
513   slow further groundwater decline. These and other characteristics that make up the resilience
514   of phreatophytic plant communities suggest that they have the capacity to absorb change
515   without dramatic alteration. This resilience is nevertheless limited. Phreatophytic
516   communities sustained by the shallow Gnangara aquifer may well be able to recover from
517   acute drawdown events, however, their resilience to long term drying will be compromised if
518   the rate of groundwater decline exceeds potential root reach, growth rate, or physiological
519   tolerance. The challenge for adaptive water resource management will be to enhance the
520   capacity for resilience in these groundwater-dependent ecosystems in a changing
521   environment through appropriate regulation of groundwater abstraction.

522

523   Acknowledgements

529

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TABLES

Table 1. Plant species and environmental variables displayed in Figure 4 (P50 transect). Life form: S= shrub, H= herb, T= tree. Havel class and root type categories are explained in the text. Columns 'F1' and 'F2' display correlations with PCoA axes F1 and F2 (*= p<0.05; **= at least p<0.01).
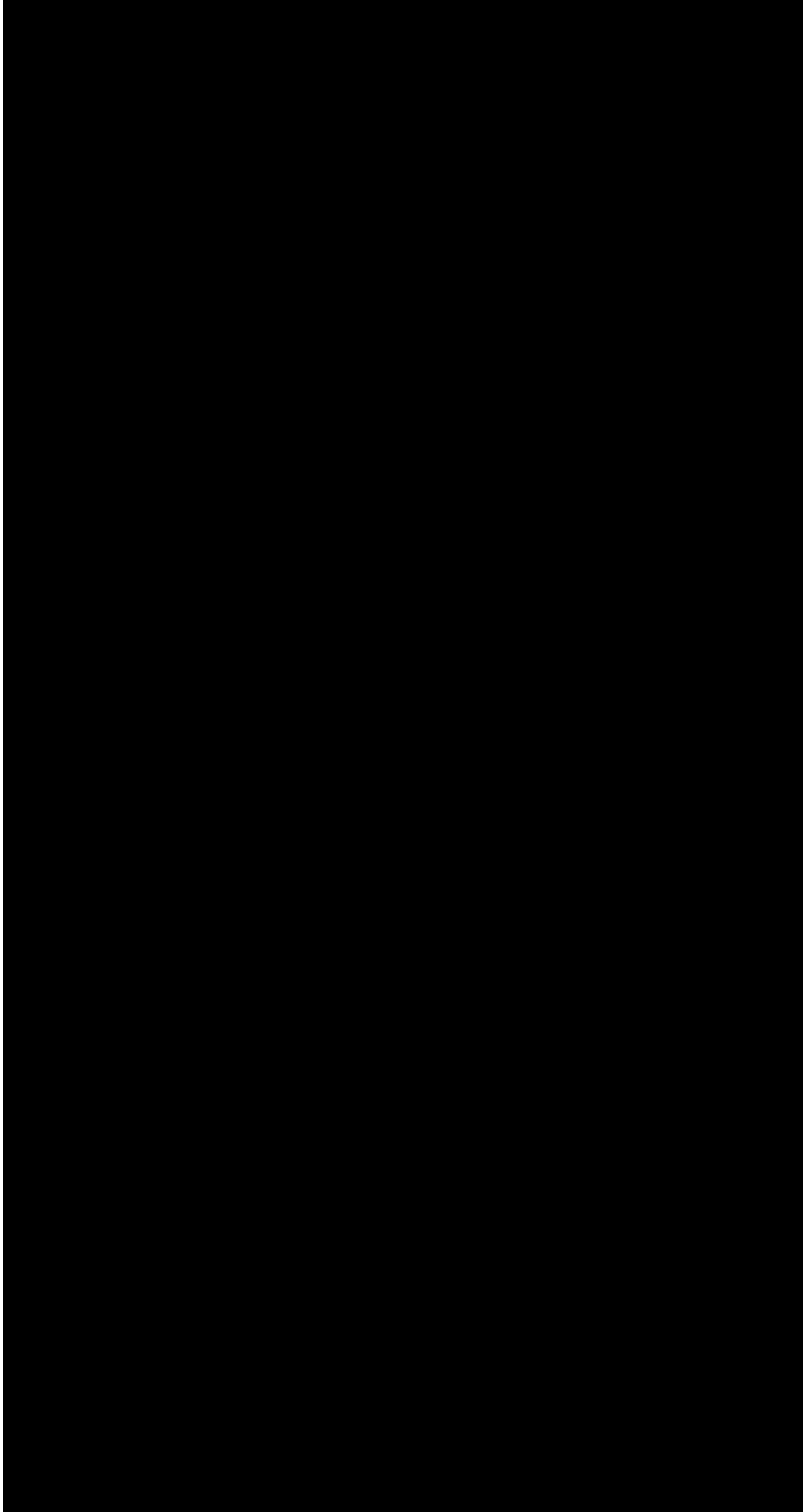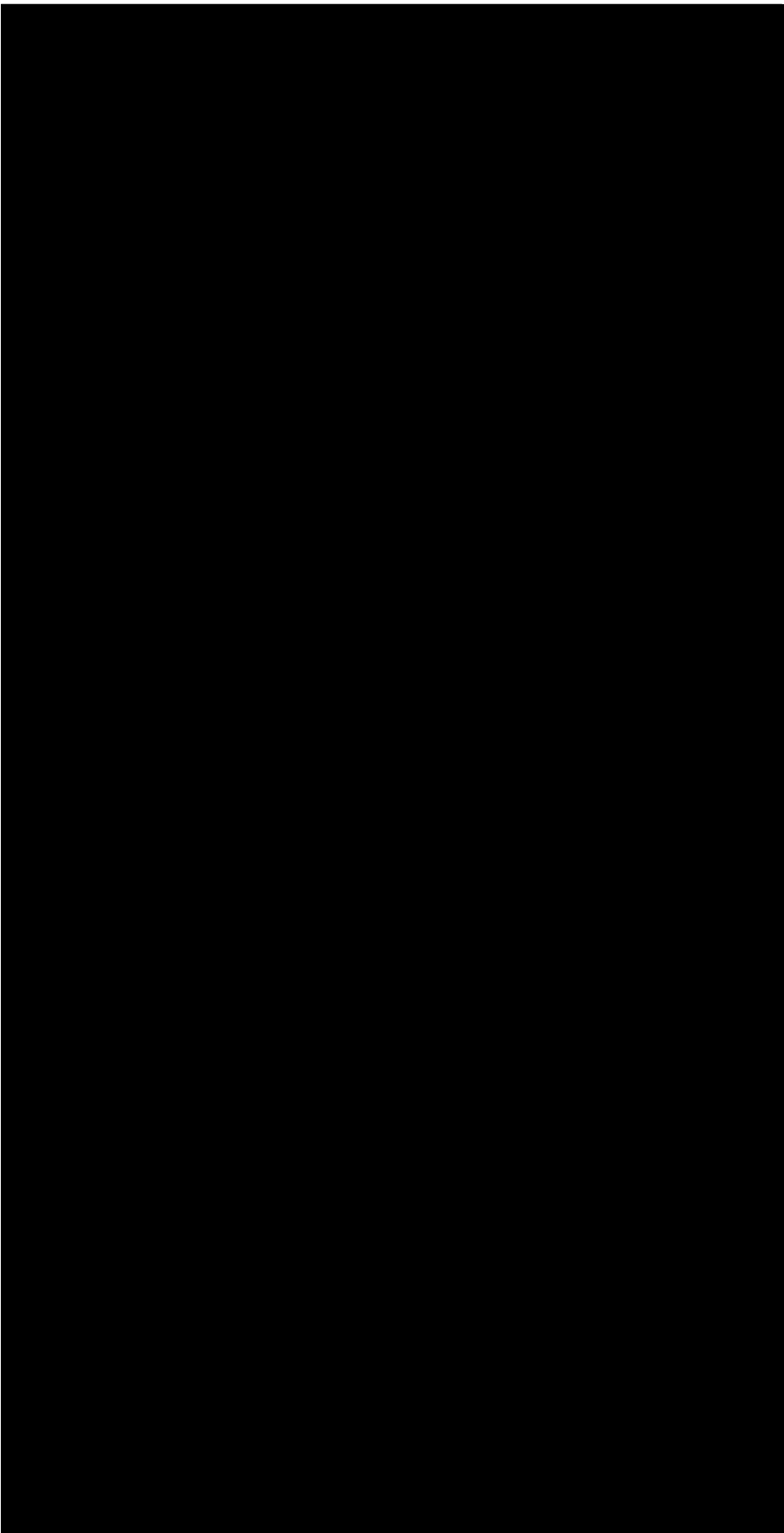
667   Table 2. Plant species and environmental variables displayed in Figure 4 (Neaves transect).
668   Life form: S= shrub, H= herb, T= tree. Exotic species depicted with '#'. Havel class and root
669   type categories are explained in the text. Columns 'F1' and 'F2' display correlations with
670   PCoA axes F1 and F2 (*= p<0.05; **= at least p<0.01).

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Table 3. Plant species and environmental variables displayed in Figure 4 (Yeal transect). Life form: S= shrub, H= herb, T= tree. Havel class and root type categories are explained in the text. Columns 'F1' and 'F2' display correlations with PCoA axes F1 and F2 (*= p<0.05; **= at least p<0.01).

Species (Yeal)	Life form	Havel class	Root type	F1	F2
Acacia stenoptera	S	C?	6?	**0.976****	-0.175
Bossiaea eriocarpa	S	D	4B	**0.963****	-0.058
Leucopogon polymorphus	S	C	6	**0.959****	0.165
Scholtzia involucrata	S	C	4B	**0.956****	0.152
Acacia huegelii	S	D?	4A	**0.953****	0.103
Adenanthos cygnorum	S	B	4B	**0.951****	-0.223
Corynotheca micrantha	S	B?	1	**0.943****	0.010
Oxylobium capitatum	S	?	?	**0.941****	-0.195
Calothamnus sanguineus	S	C	4B	**0.916****	0.177
Gompholobium tomentosum	S	D?	4A	**0.910****	0.339
Leucopogon propinquus	S	C	6	**0.908***	-0.373
Croninia kingiana	S	C	?	**0.899***	-0.228
Andersonia lehmanniana	S	C?	6	**0.890***	0.226
Hibbertia subvaginata	S	D	4A	**0.885***	0.426
Conostephium pendulum	S	D	1	**0.850***	0.182
Banksia ilicifolia	T	B	4B	**0.847***	0.164
Leucopogon conostephioides	S	C	6	**0.839***	-0.439
Verticordia nitens	S	B	4B	**0.828***	-0.081
Eucalyptus rudis	T	A	4B	0.640	0.540
Nuytsia floribunda	T	D	4B	0.353	-0.056
Eucalyptus todtiana	T	C?	4B	0.223	0.782
Melaleuca preissiana	T	A	4A	**-0.884***	0.178
Acacia saligna	S	C?	4B?	**-0.868***	-0.190
Banksia attenuata	T	C	4B	-0.434	-0.319
Banksia menziesii	T	C	4B	-0.296	-0.582
Environmental variables					
20 Mean no of rain days last 10 years				**0.970****	0.124
26 Mean Winter rainfall over last 10 years				**0.963****	-0.130
30 Mean duration of recharge over last 3 years				**0.941****	-0.253
29 Mean duration of recharge over last 2 years				**0.899***	-0.281
10 Mean summer rainfall over last 10 years				**0.876***	-0.257
31 Mean recharge ratel over last 5 years				**0.830***	-0.115
9 Mean summer rainfall over last 5 years				**-0.926****	0.333
4 Lowest WL present year				**-0.879***	0.202
5 Mean lowest WL over last 2 years				**-0.864***	0.265
1 Mean highest WL over last 2 years				**-0.856***	0.179
0 Highest WL present year				**-0.850***	0.177
2 Mean highest WL over last 3 years				**-0.849***	0.241
3 Mean highest WL over last 5 years				**-0.841***	0.304
6 Mean lowest WL over last 3 years				**-0.840***	0.302
34 Mean max. summer temp last 10 years				**-0.822***	0.441
33 Mean max. summer temp 3 years ago				**-0.820***	0.378
21 Duration of drawdown				**-0.816***	0.316

723 Table 4. RDA scores of plant species at the P50 transect shown in Figure 9. They are
724 arranged according to their F1 scores (largest to smallest) which can also be regarded as their
725 dependency on depth to groundwater, and to a lesser extent rainfall.

| Species	F1	F2
Hibbertia spicata	0.452	0.104
Astartea fascicularis	0.399	-0.115
Leucopogon sprengelioides	0.284	0.103
Actinotus glomeratus	0.262	0.062
Euchilopsis linearis	0.262	0.021
Acacia pulchella	0.254	-0.014
Verticordia drummondii	0.246	0.032
Acacia barbinervis	0.199	0.041
Comesperma calymega	0.198	-0.086
Banksia ilicifolia	0.191	0.083
Hibbertia subvaginata	0.188	0.083
Leucopogon conostephioides	0.174	0.027
Jacksonia floribunda	0.166	0.037
Philotheca spicata	0.157	0.083
Petrophile linearis	0.150	0.018
Calytrix flavescens	0.129	-0.018
Regelia ciliata	0.119	0.012
Hypocalymma angustifolium	0.103	0.020
Verticordia nitens	0.081	-0.008
Scholtzia involucrata	0.069	0.052
Banksia menziesii	0.058	0.029
Tricoryne elatior	0.054	0.022
Melaleuca seriata	0.045	0.012
Adenanthos cygnorum	0.031	-0.098
Banksia attenuata	0.031	0.015
Conostephium pendulum	0.016	0.000
Hibbertia sp. Gnangara	0.009	-0.031
Xanthorrhoea preissii	0.006	0.002
Stylidium repens	-0.003	-0.022
Eucalyptus todtiana	-0.014	-0.008
Bossiaea eriocarpa	-0.036	-0.004
Daviesia physodes	-0.040	-0.229
Platytheca galioides	-0.064	0.023
Monotaxis occidentalis	-0.077	0.054
Conostylis juncea	-0.093	0.037
Stylidium brunonianum	-0.102	0.005
Dampiera linearis	-0.135	0.013
Nuytsia floribunda	-0.142	0.044
Gonocarpus cordiger	-0.200	0.020
Ursinia anthemoides	-0.207	0.235
Acacia huegelii	-0.218	-0.121
Anigozanthos humilis	-0.265	0.031
Beaufortia elegans	-0.340	-0.050
Phyllangium paradoxum	-0.356	0.238
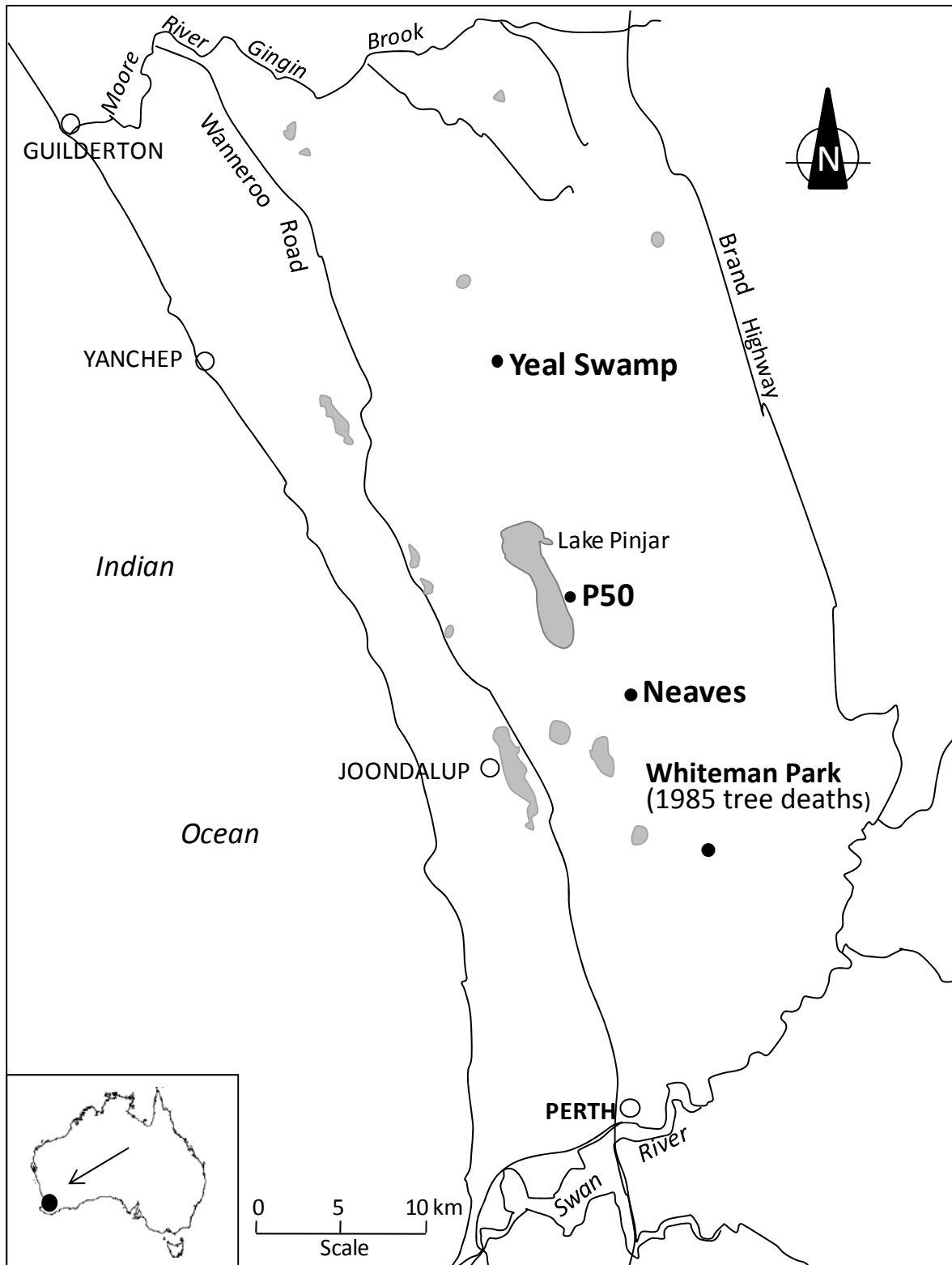
Figure 1. Northern Swan Coastal Plain (under which lies the Gnangara aquifer), Western Australia, showing the location of the P50 transect, and the comparison sites, Neaves and Yeal Swamp. Some of the wetlands that occur on the plain are shown as shaded grey areas.
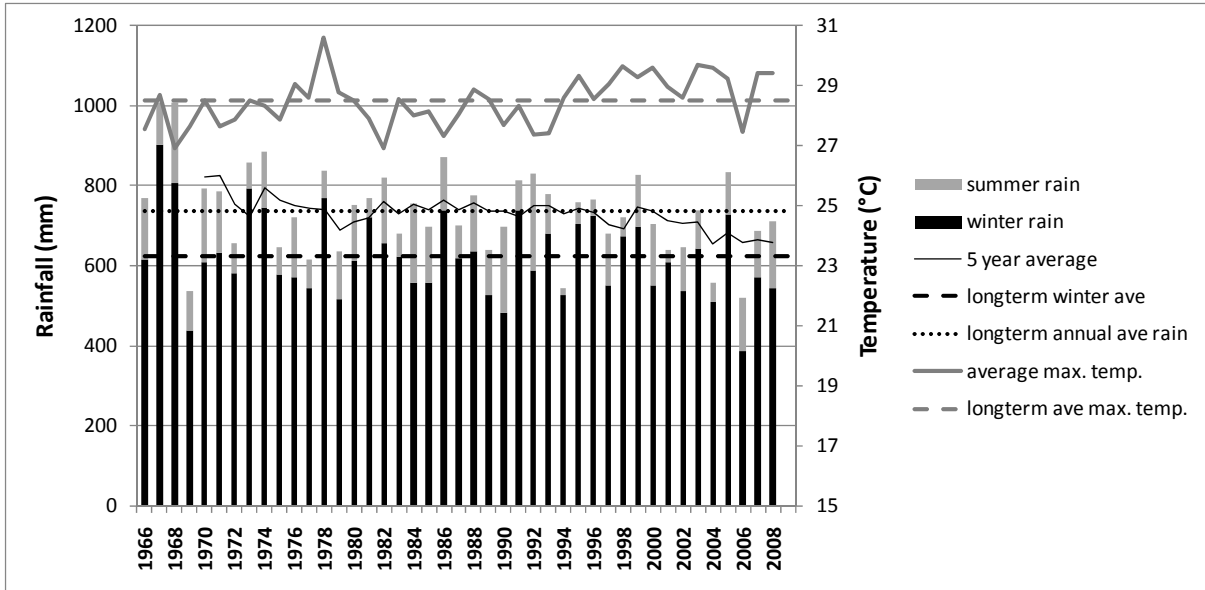
Figure 2. Summary of climate data (Australian Bureau of Meteorology) for the P50 site on the northern Swan Coastal Plain. 'Winter' was calculated from 1st May to 31st October of the year indicated, and summer from 1st November of the previous year to the 30th April of the current year indicated.
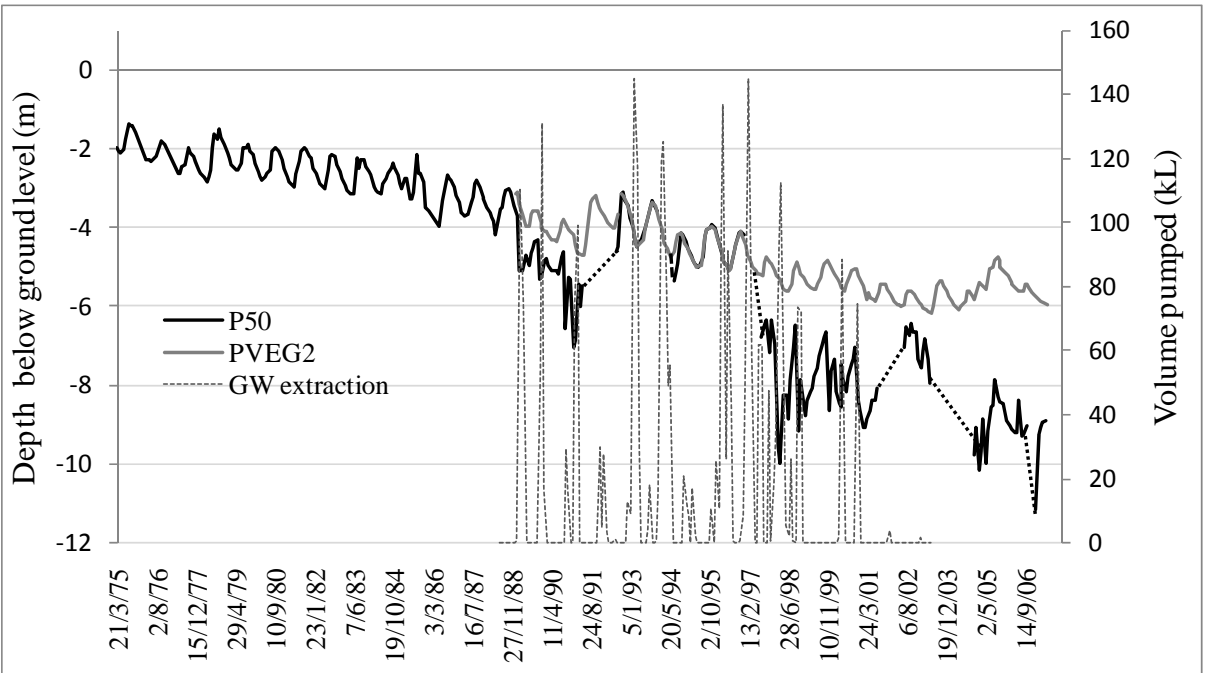
Figure 3. Monthly groundwater levels for the P50 production bore and the closest monitoring bore to it (PVEG2). Dashed lines indicate monitoring gaps.
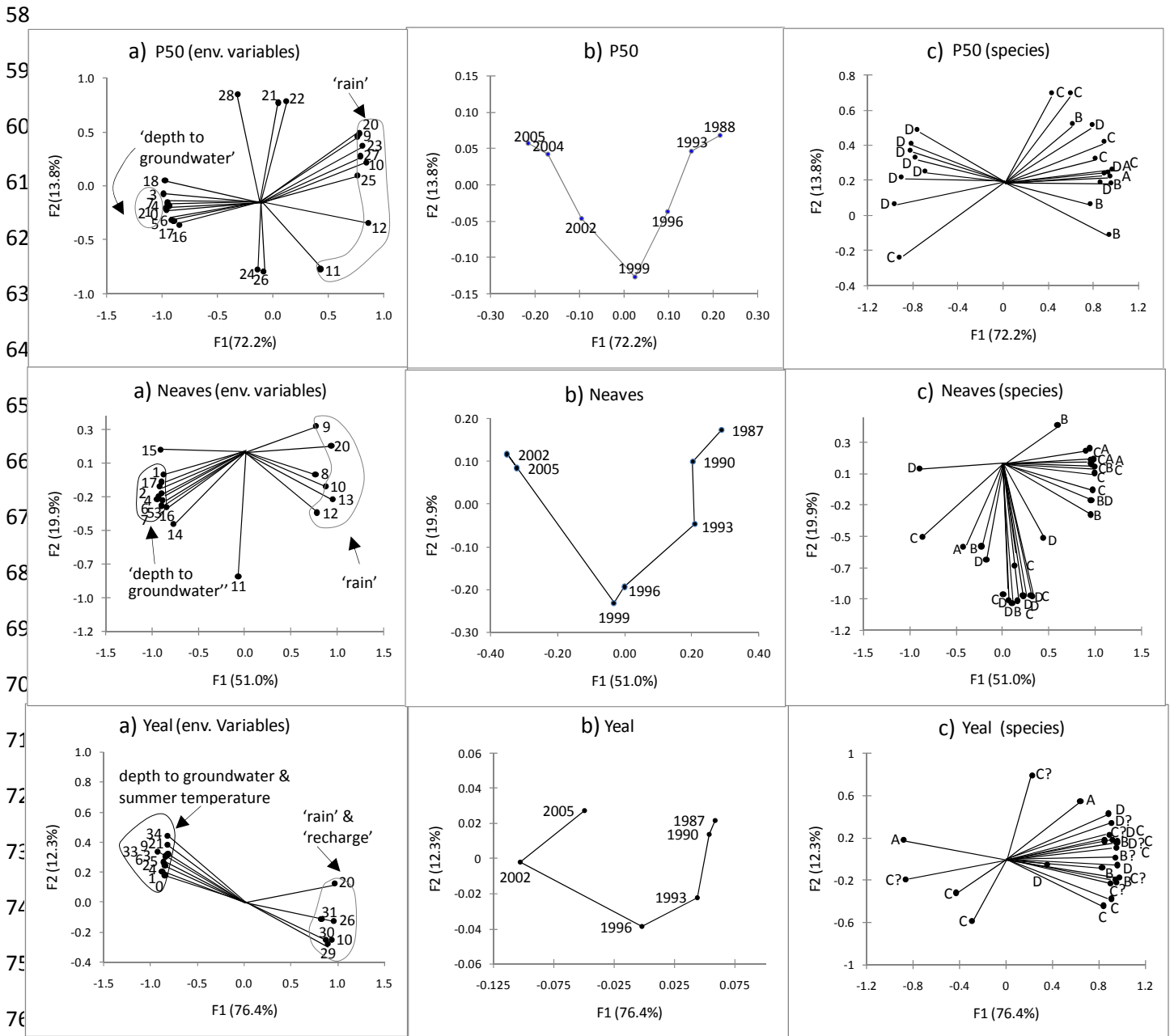
Figure 4. Principal Coordinate Analysis (PCoA) ordinations of vegetation abundance data of the P50 transect from 1988 to 2005, and of the Neaves and Yeal transects for comparison. Directions of maximum correlations of environmental variables (number codes explained in Tables 1-3) and plant species with the PCoA axes are shown as separate graphs left (a) and right (c) of the PCoA ordinations. Letters are Havel water tolerance categories: A = species of wet sites, B= species of moist sites, C= species of dry sites, D= species with no clear preferences. Only indicator species (generally with correlations > 0.90 with F1; see Tables 1-3) are shown. Principal coordinate axes were scaled (x 8) in order to improve the clarity of the graph.
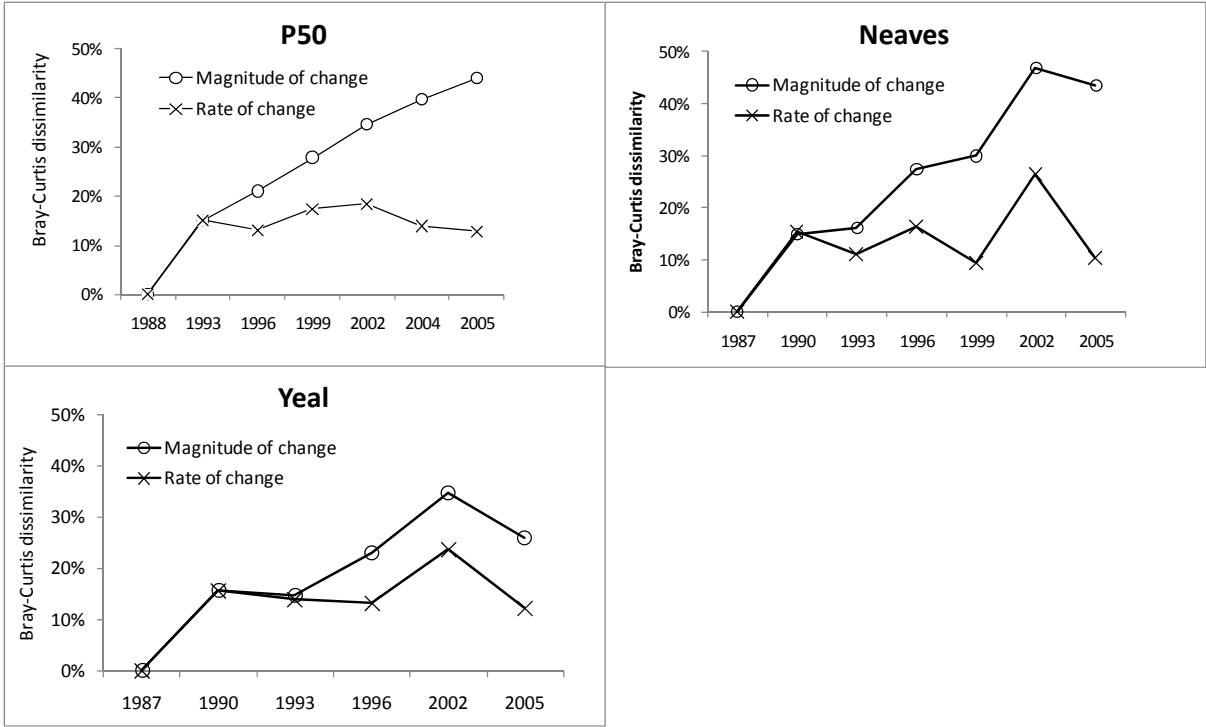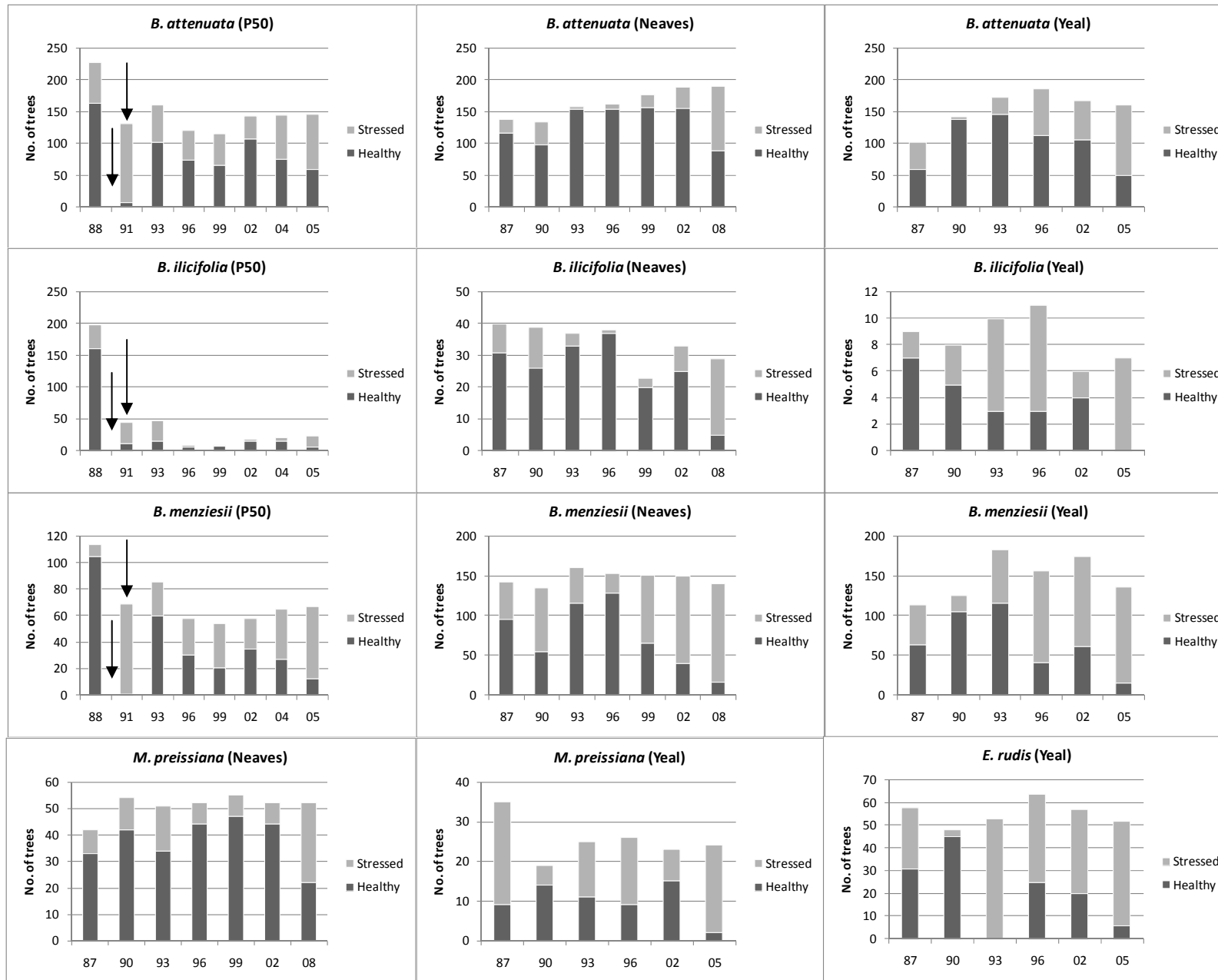
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101 Figure 5. Percentage change (Bray-Curtis dissimilarity) in vegetation composition from the
102 base year (= magnitude of change) and from monitoring year to monitoring year (= rate of
103 change) for the P50 transect, and for the Neaves and Yeal transcects for comparison.

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Figure 6. Temporal changes in abundance and vigour of dominant overstorey species at the P50 transect and the comparison transects, Neaves and Yeal. Black arrows show where the groundwater drawdown has occurred.

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Plant diversity

Shannon diversity (H')

Chart: Total no. of individuals (bars) with Shannon diversity (line) for years 88, 93, 96, 99, 02, 04, 05. Left axis: Total no. of individuals (0–4000). Right axis: Diversity (0–1.4).
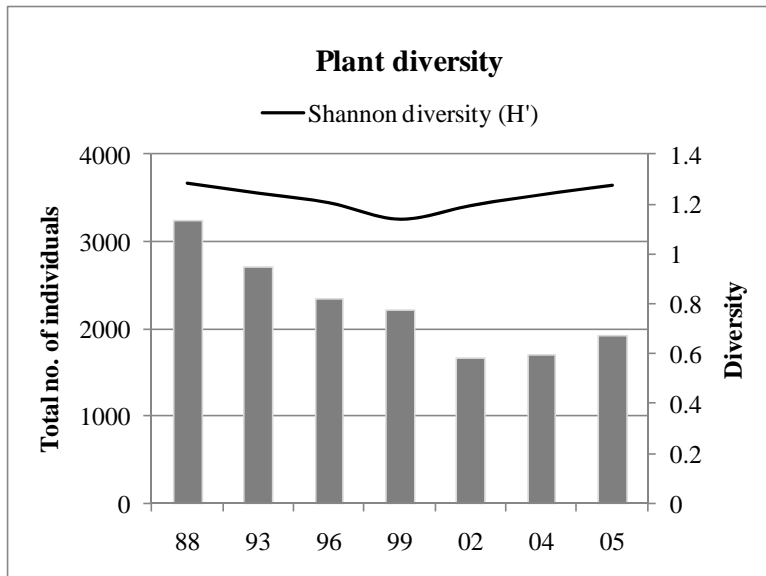
144 Figure 7. Total number of plant individuals at the P50 transect over time, with Shannon
145 diversity index (solid line) overlain.

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Chart: Havel water tolerance classes — Proportion of individuals (0–100%) for years 88, 93, 96, 99, 02, 04, 05. Legend: d, c, b, a.

Chart: Rooting classes — Proportion of individuals (0–100%) for years 88, 93, 96, 99, 02, 04, 05. Legend: 6, 5, 4B, 4A, 3, 2, 1.

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Chart: Life history: form — Proportion of individuals (0–100%) for years 88, 93, 96, 99, 02, 04, 05. Legend: Tree, Shrub, Herb.
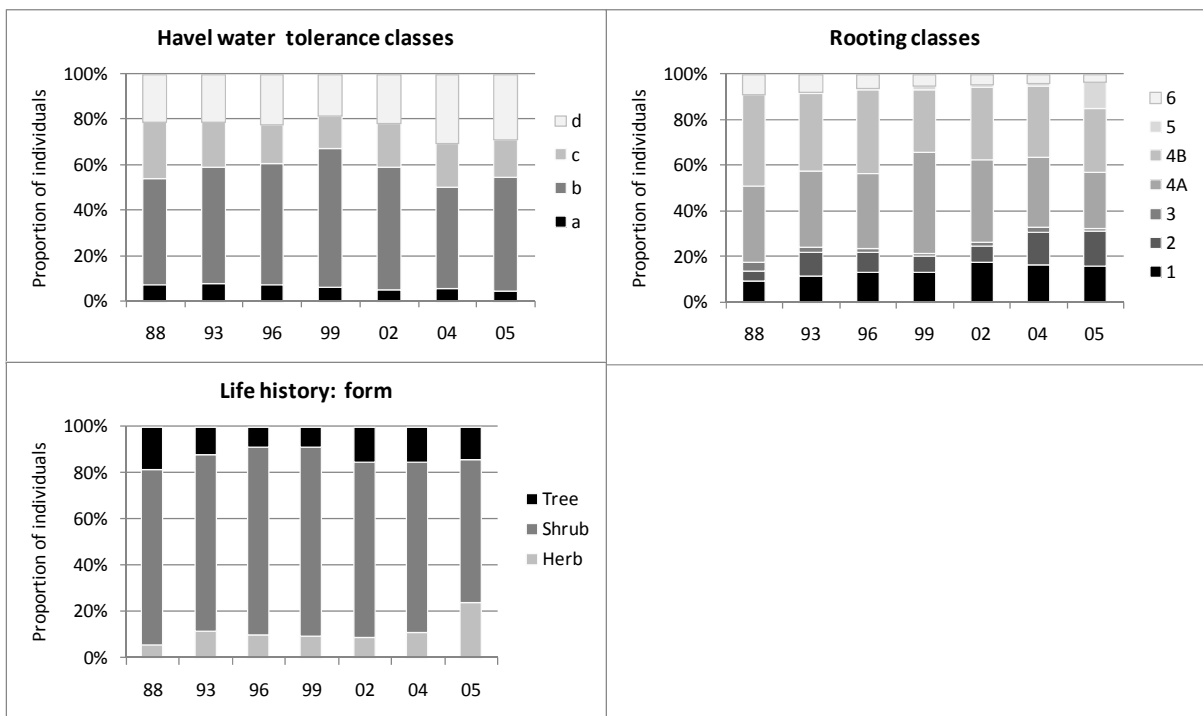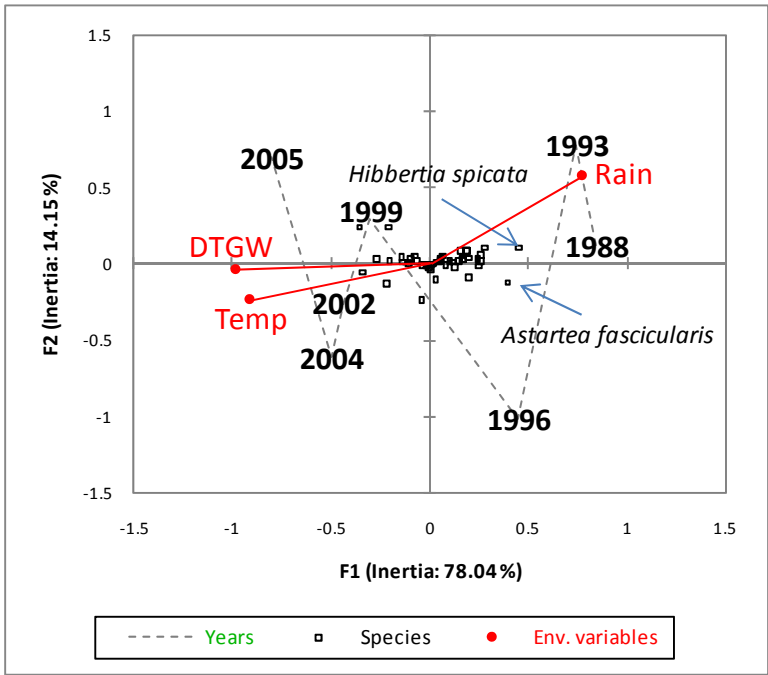
159 Figure 8. Proportions of life history traits, water tolerance classess and rooting categories of
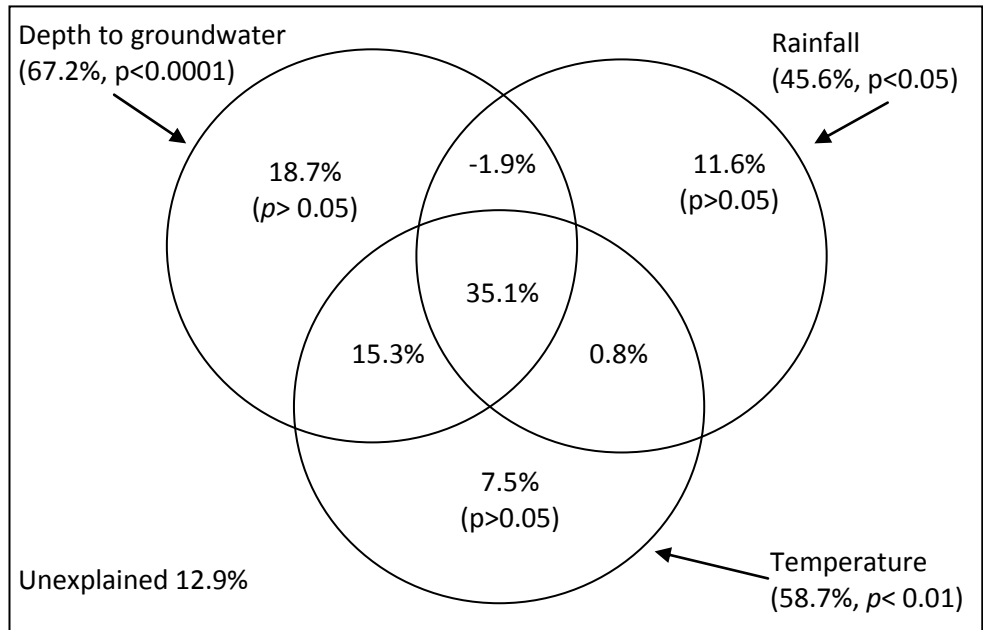160 the P50 transect vegetation community over time.

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Figure 9. tb-RDA ordination triplot of vegetation abundance data of the P50 transect from
1988 to 2005. Inertia is the amount of variation explained.

Figure 10. Venn diagram showing the partitioning of the variation in the multi-temporal P50
floristic data set explained by three environmental variables, depth to groundwater, rainfall
and temperature. The percentages explained variation were calculated by multiplying the
eigenvalues obtained from twelve partial RDA's by 100; the significance values were
calculated by Monte Carlo permutation (999 permutations). The intersections of the circles
depict shared explained variation. These do not have any associated significance values
because they were computed from the other fractions.