Patterns of plant species composition in mesic woodlands are related to a naturally occurring depth-to-groundwater gradient

M.C. Hingee[1], D. Eamus[1], D.W. Krix[1], S. Zolfaghar[1] and B.R. Murray[1,2]

[1] *School of Life Sciences, University of Technology Sydney, PO Box 123, NSW 2007, Australia*
[2] *Corresponding author: Email: Brad.Murray@uts.edu.au, Phone: + 61 2 9514 4075, Fax: + 61 2 9514 4079*

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Abstract: Groundwater-dependent ecosystems (GDEs) are threatened by over-extraction of groundwater for human needs across the world. A fundamental understanding of relationships between naturally occurring gradients in depth-to-groundwater (DGW) across landscapes and the ecological properties of vegetation assemblages is essential for effective management of the impacts of groundwater extraction. Little is known, however, about relationships between DGW and the ecology of mesic woodlands in GDEs. Here, we investigated relationships between a naturally occurring DGW gradient and plant species composition, richness and abundance in mesic *Eucalyptus* woodlands of eastern Australia. Across 16 sites varying in DGW from 2.4 m to 43.7 m, we found that plant species composition varied significantly in relation to DGW, independently of a range of 14 physical and chemical attributes of the environment. Nine understorey species, representing only 7% of the pool of 131 plant species, were identified as contributing to up to 50% of variation in species composition among the study sites. We suggest this dominant pattern driver in the understorey is explained by differential abilities among understorey species in their ability either to tolerate extended dry conditions at deeper DGW sites during periods of low rainfall, or to withstand periodically waterlogged conditions at shallow sites. Plant species richness and total plant abundance (a measure of plant productivity) were not significantly and independently related to DGW or any of the other 14 environmental attributes. Our finding for a direct relationship between DGW and plant species composition provides important reference information on the ecological condition of these mesic woodlands in the absence of groundwater extraction. Such information is vital for setting ecological thresholds that ensure sustainable extraction of groundwater.

Nomenclature: PlantNET (The NSW Plant Information Network System). Royal Botanic Gardens and Domain Trust, Sydney. http://plantnet.rbgsyd.nsw.gov.au

Abbreviations: DGW – Depth-to-GroundWater, GDE – Groundwater-Dependent Ecosystem, HSSGW – Highlands Sandstone Scribbly Gum Woodlands, HSTOF – Highlands Shale Tall Open Forests, NESW – Nepean Enriched Sandstone Woodlands, SCA – Sydney Catchment Authority.

Introduction

Groundwater-dependent ecosystems (GDEs), which must have access to groundwater to maintain their ecological structure and function (Hatton and Evans 1998), are threatened globally by groundwater extraction for human consumption and industry (Murray et al. 2003, Nevill et al. 2010, Brown et al. 2011, Kløve et al. 2014, Eamus et al. 2015). Declines in depth-to-groundwater (DGW) due to extraction can have serious impacts on the ecological properties of vegetation in GDEs, including plant species composition, richness and abundance (Groom et al. 2000, Chen et al. 2006, Sommer and Froend 2014). Worryingly, groundwater is being accessed for human needs at an increasing rate (Konikow and Kendy 2005, Wada et al. 2010). In Australia in particular, utilisation of groundwater for human consumption has increased exponentially in the past 150 years and groundwater is being over-extracted in many catchments (Eamus et al. 2006a, Polglase and Benyon 2009). Given the threats posed to GDEs, it is crucial that all efforts are made to provide a comprehensive understanding of relationships between vegetation properties and DGW, especially in areas that have not yet experienced groundwater extraction. A fundamental, baseline understanding of the role that naturally occurring gradients in DGW play in shaping ecological patterns in plant communities will contribute to the effective management and mitigation of the impacts of groundwater decline (Murray et al. 2006, Jakeman et al. 2016, Mendes et al. 2016).

In riparian forests and in arid and semiarid regions of the world, DGW from the soil surface has extensively been shown to have a strong influence on plant ecophysiology, ecosystem function and vegetation properties (Stromberg et al. 1996, Zhu et al. 2013). In contrast, much less is known about relationships between DGW and ecological properties of vegetation in mesic environments. Yet, in mesic regions, plants are known to access groundwater (Eamus et al. 2006b) and recent work has begun to show that DGW influences plant physiology and productivity (Zolfaghar et al. 2014, 2015). For instance, along naturally occurring DGW gradients in mesic woodlands, areas with shallow DGW have

larger aboveground biomass and net primary productivity than areas where groundwater is much further away from the surface (Zolfaghar et al. 2014). These patterns provide a strong indication that the ecological properties of vegetation in mesic environments will also be related to naturally occurring gradients in DGW (Eamus et al. 2006a).

In this study, we investigated relationships between the ecological properties of mesic woodland vegetation and a naturally occurring DGW gradient of an eastern Australian GDE. Specifically, we addressed the question, do plant species composition, species richness and total plant abundance change in a systematic way in relation to variation in DGW across the landscape? In the study region, DGW ranges from shallow, where groundwater is well within the plant-rooting zone (i.e., < 10 m) and where rainfall can saturate soils, to deep where DGW exceeds 20 m (Canadell et al. 1996, Cook et al. 1998, Benyon et al. 2006, O'Grady et al. 2010). Importantly, there has been no extraction of groundwater for human consumption or industry in the study region (Zolfaghar et al. 2014). A key feature of our approach is that we adopted analytical techniques which allowed us to identify any role played by DGW in shaping the ecological properties of vegetation, independently of a range of other physical and chemical attributes of the environment that could influence vegetation properties.

Methods

Study region and sites

The study region (Fig. 1) was located 100 km south-west of Sydney in Kangaloon (34° 50" 20' S, 150° 56" 74' E) on the Woronora Plateau in eastern Australia. This region has an average annual rainfall of approximately 1067 mm (2000–2012, Bureau of Meteorology station no. 68243). The largest monthly rainfall occurs in the Austral summer (February, average of 186 mm) and the lowest in Austral winter (August, average of 51 mm). Average minimum temperature occurs in July (2.7°C) and average highest temperature in January (24.3°C). The largest maximum daily temperature is 40°C and lowest daily temperature is 5.1°C. Total rainfall was 1561 mm in 2011 and 1188 mm in 2012, which were 46% and 11% larger than the long term average (1067 mm yr^{-1}; 2000–2010). During 2011 and 2012 rainfall was received on more than 415 days. Mean summer and winter temperatures were 16°C and 7°C respectively. Thus the climate of these sites is best described as temperate mesic with warm summers and cool winters. Vapour pressure deficit (VPD) was very low (mean summer and winter VPD were 0.45 and 0.25 kPa, respectively) and generally remained below 1 kPa during 2011 and 2012, considerably lower than normal. Thus the long term annual average (1990–2016) total solar radiation
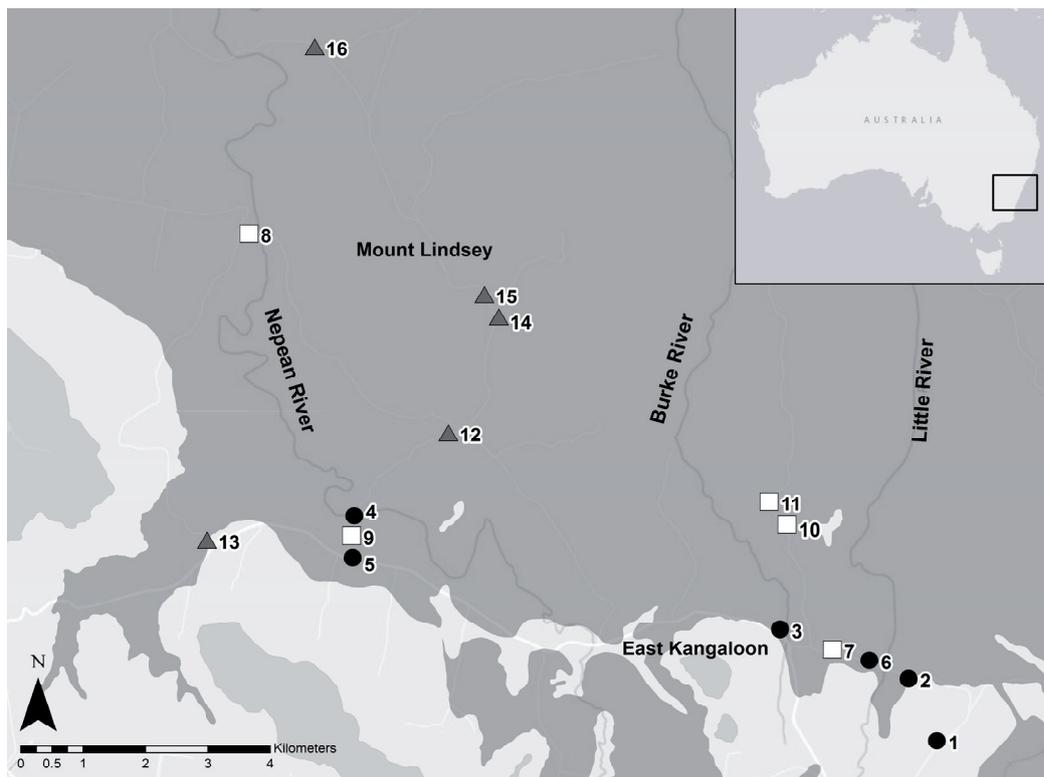
Figure 1. The Kangaloon study region, 100 km south-west of Sydney (34° 50" 20' S, 150° 56" 74' E) in eastern Australia. Depth-to-groundwater 2–10 m at sites 1 to 6 (closed circles), 12–22 m at sites 7 to 11 (open squares), and 27–44 m at sites 12–16 (closed triangles). Dark grey areas = Hawkesbury Sandstone, mid grey areas = Robertson Basalt and light grey areas = Wianamatta Shale. Data provided by the Sydney Catchment Authority.

was 15.7 MJ m^{-2} and the lowest annual mean occurred in 2011 (14.1 MJ m^{-2}) which reflected the cloudy and wet conditions of 2011. In 2010, the annual average total solar radiation was 15.2 MJ m^{-2}, close to the long term mean. It is apparent that 2011 and 2012 were wetter, cooler and more humid than the long-term average values.

Remnant Wianamatta Shale overlies Hawkesbury Sandstone in the region and Tertiary Basalt occurs at higher elevations (Kodela 1990). The surficial geology of the area is dominated by a thick sequence of relatively flat-lying Middle Triassic Hawkesbury Sandstone which constitutes the main 'hard rock' groundwater source for the Sydney Catchment Authority's prospective GW resource to drought-proof Sydney. The Hawkesbury Sandstone is made up of sheet-like to massive interbedded formations of mostly medium to coarse quartz sandstone with occasional to locally numerous, thin interbedded mudrock units. The Hawkesbury Sandstone in the Kangaloon area is partly overlain by the Mittagong Formation and the younger Wianamatta Group (Ashfield Shale). Beneath the Hawkesbury Sandstone are sedimentary rocks of the Narrabeen Group. Recharge is predominantly during large rainfall events which tend to be concentrated in the first 6 months of the year. Estimated rates of recharge are in the region of 3% of annual rainfall. The significant aquifers within the area are porous sandstone beds above a more impervious layer. The main aquifers of the area are within Robertson Basalt and Hawkesbury Sandstone with groundwater in the basalt mainly limited to higher regions of the catchment. Groundwater in the aquifers is recharged by rainfall along ridgelines and discharges in mid-slope areas providing base-flow to several small streams and springs.

Within the study region, the Sydney Catchment Authority (SCA) has in place a series of groundwater monitoring bores. We established a study site within 25 m of every groundwater bore that was located at least 100 m from human disturbances such as roads, walking paths and fire trails (these 16 sites are detailed in Appendix 1). Across all sites, variation in annual rainfall is minimal as the sites are all within 11 km of each other. Each site was 0.1 ha (20 m × 50 m) in area and DGW data for all study sites, which varied from 2.4 m to 43.7 m, were provided by the SCA (Fig. 2, Appendix 1).

Vegetation of the region and plant surveys

Three main vegetation types are found in the region (NPWS 2003), including Nepean Enriched Sandstone Woodlands (NESW), Highlands Sandstone Scribbly Gum Woodlands (HSSGW) and Highlands Shale Tall Open Forests (HSTOF). The vegetation of HSTOF is part of the Southern Highlands Shale Woodlands, an endangered ecological community under the NSW Threatened Species Conservation Act 1995 and a critically endangered ecological community under the Federal Environmental Protection Biodiversity Conservation Act 1999. The vegetation of HSTOF is characterized by an overstorey of *Eucalyptus* species ranging from 25 to 30 m in height, a predominance of midstorey shrubs from the Proteaceae and Fabaceae, and an understorey of scattered rushes, ferns and grasses from the

Poaceae, Lomandraceae and Denstaedtiaceae. The vegetation of NESW is characterized by an overstorey of *Eucalyptus* species ranging from 25 to 35 m in height, a midstorey of shrubs mainly from the Proteaceae, Myrtaceae and Fabaceae, and an understorey of grasses, rushes and herbs from the Cyperaceae, Lomandraceae, Phormiaceae and Poaceae. The canopy of HSSGW is dominated by *Eucalyptus sclerophylla* approximately 15 m in height, and there is a midstorey dominated by shrubs in the Proteaceae and an understorey of grasses, herbs and rushes from the Poaceae, Restionaceae, Cyperaceae and Goodeniaceae.

We performed exhaustive plant surveys across the whole area of each site (20 m × 50 m), recording the presence of all vascular plant species and the abundance of each species (Appendix 2). These woodlands typically do not have a high representation of annuals across the year and are dominated by perennial species (NPWS 2003). Our initial vegetation surveys were conducted between March and July 2012. We then revisited all sites during the following spring and summer and further surveys did not detect any new species. Abundance was measured using counts of individuals 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 15, 20, 30, 40, 50,100, 500, 1000, ≥ 1500 (Sivertsen 2009). For the purposes of the present study, individual trees were defined as single or multi-stemmed woody plants greater (or potentially greater) than 5 m in height; individual shrubs were defined as single or multi-stemmed woody plants between 0.5 and 5 m tall with multiple stems thinner and younger than typical mature tree trunks; and individual groundcover plants were defined as single graminoid, forb, woody, non-woody climbers and ferns up to 0.5 m tall (Pérez-Harguindeguy et al. 2013).
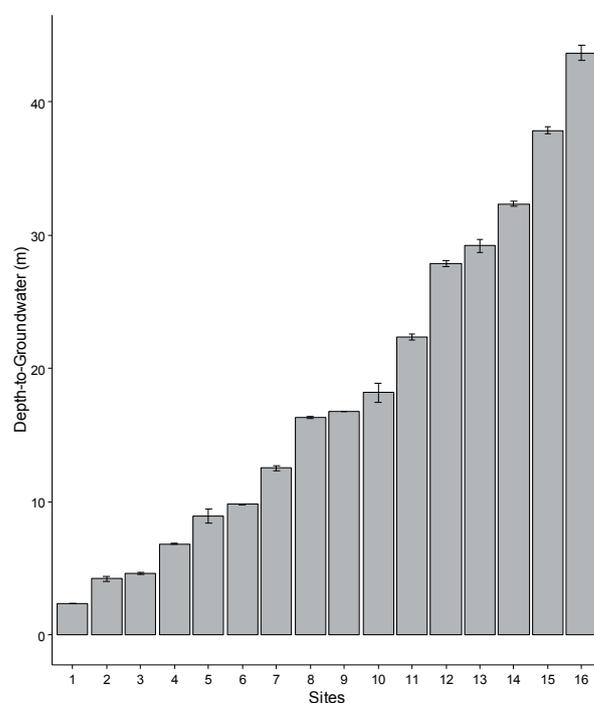
Figure 2. Annual mean depth-to-groundwater (± SE) at each of the study sites in the Kangaloon study region from 2006 to 2012.

Site environmental attributes

We measured a total of 14 environmental attributes at each site (Appendix 3). Soil samples were collected at the same time that the vegetation surveys were performed and subsequently analysed in the laboratory in July and August 2012. Site slope was determined with a hand-held clinometer and reported as degrees from horizontal. Altitude was determined with a hand held GPS (Garmin eTrex H, reported as m above sea level). A shade index (measured between 11:00 a.m. and 1:00 p.m.) was determined as the ratio of the amount of photosynthetically active radiation (PAR, measured in $\mu mol\ m^{-2}\ s^{-1}$) above the canopy (or in a nearby open area) to the amount of PAR measured at 1.5 m beneath the canopy. Three replicate measurements were taken randomly within each site with a Li-Cor PAR sensor (model 250A). A total of 11 soil attributes were measured, with eight to ten soil samples collected along multiple diagonal transects, bulked and mixed thoroughly to obtain a representative sample. Samples were obtained via a stainless steel soil corer (3 cm diameter) to a depth of 10 to 15 cm, after brushing aside any surface leaf litter. In plots where the soil was too rocky or shallow, samples were obtained with a stainless steel trowel. Prior to analyses, bulked soil samples were air dried at ambient laboratory conditions for approximately two weeks. Soil peds were crushed by hand using a mortar and pestle and passed through a mesh (2 mm) screen. Soil pH and electrical conductivity (EC) were determined using a WTW multi-probe (model 3400) on soil extracts with a 1:2 ratio of soil to water after shaking for one hour (Jones 2001). Organic matter content was estimated by loss on ignition (Jones 2001) and field capacity (FC) determined via gravimetric methods (Hillel 1971). Estimates of particle size were determined through a particle size analyser (MALVERN Mastersizer 2000) after pre-treatment of 250 mg soil samples with 2 ml of 0.5% CALGON (sodium polyphosphate) solution for 48 h and in line ultra-sonication for five minutes. Only two fractions were considered, fine fraction (clay) whose particles were < 0.39 μm, and course fraction (sand) whose particles ranged between > 62.5 μm and < 2000 μm. Total nitrogen (N) was analysed on a carbon/nitrogen analyser (LECO Tru-Spec CN-628). Phosphorous (P), potassium (K), magnesium (Mg) and Calcium (Ca) were analysed by inductively coupled plasma mass spectrometry (ICP-MS) after digestion with nitric acid (Krishnamurty et al. 1976).

Statistical analyses

We used canonical correspondence analysis (CCA) to examine variation in plant species composition among the study sites in relation to DGW and the environmental attributes (Ter Braak 1987). A forward-fitting model selection procedure was implemented to determine whether DGW and any of the environmental attributes could significantly and independently explain variation in species composition. The species-by-site dataset was populated with square-root transformed abundance data to reduce any bias due to contributions of highly abundant species and to avoid under-representation of lower abundance species in the analyses (Thorne et al. 1999, Legendre and Gallagher 2001). Redundancy was verified by checking variance inflation factors (VIF) and relationships were tested using Monte Carlo permutation tests (N = 1000).

A similarity percentage analysis (SIMPER) procedure (Clarke 1993) was used to determine those plant species that were major contributors to any observed changes in species composition as a function of DGW. For this analysis, sites where DGW was < 10 m were classed as shallow, sites where DGW was between 12 and 22 m were classed as intermediate, and sites where DGW was between 27 and 44 m were classed as deep (Canadell et al. 1996, Cook et al. 1998, Benyon et al. 2006, O'Grady et al. 2010).

Relationships between DGW and species richness, and DGW and total plant abundance, were examined using generalized linear regression modelling (McCullagh and Nelder 1989). Total plant abundance was measured as the summed abundance across all species within a site and represents an estimate of plant productivity. The response variables richness and total plant abundance were in the form of counts, requiring the use of a Poisson error structure with a log link function in models (Crawley 2007). We included an observation-level random effect term in models to avoid over-dispersion (Bolker et al. 2009). We built minimum adequate models (MAMs) to identify whether any of the explanatory variables (DGW and the environmental attributes) were significantly and independently related to either of the response variables (Quinn and Keough 2002). We first fitted a maximal model for each response variable that included all explanatory variables. We then tested the significance of each explanatory variable when removed from the maximal model. The variable with the lowest non-significant change in deviance was dropped and a reduced model was fitted with all remaining explanatory variables. This procedure was continued until either a subset or none of the explanatory variables was retained. Model comparison using ANOVA was employed to compare the maximal model with the final model to determine via χ^2 tests the overall significance of the final models (Crawley 2007).

To manage any collinearity among the environmental attributes in the multivariate and univariate analyses, six variables (OM, N, Clay, Mg, P and K) that were strongly correlated with each other and with Ca (correlations between < -0.65 and > 0.65; Appendix 4) were excluded from the analysis; Ca was retained in the analysis to represent the suite of excluded correlated attributes (Quinn and Keough 2002). All univariate, multivariate and graphical analyses were performed using R 3.1.3 (R Core Team 2015), with packages stats (R Core Team 2015), vegan (Oksanen et al. 2015) and ggplot2 (Wickham 2009).

Results

We recorded a total of 131 plant species across all study sites (Appendix 2). Among the most widespread, each occurring across 10 or more of the 16 study sites, were four tree species (*Eucalyptus piperita*, *E. sclerophylla*, *E. radiata*, *E. globoidea*), four shrub species (*Banksia spinulosa*, *Lomatia*

silaifolia, *Hakea dactyloides*, *Hibbertia sericea*), and six understorey species (*Entolasia stricta*, *Lomandra longifolia*, *Goodenia bellidifolia*, *Pteridium esculentum*, *Poa sieberiana*, *Dampiera stricta*).

We found that plant species composition varied significantly in relation to DGW ($F_{1,13}$ = 1.41, P < 0.05) and soil Ca ($F_{1,13}$ = 2.26, P < 0.001) across the sites, independently of the other measured environmental attributes (Fig. 3). Nine understorey species, representing only 7% of the pool of all plant species, were identified by SIMPER analysis as contributing to up to 50% of variation in species composition among the sites in relation to DGW. Patterns of abundance variation
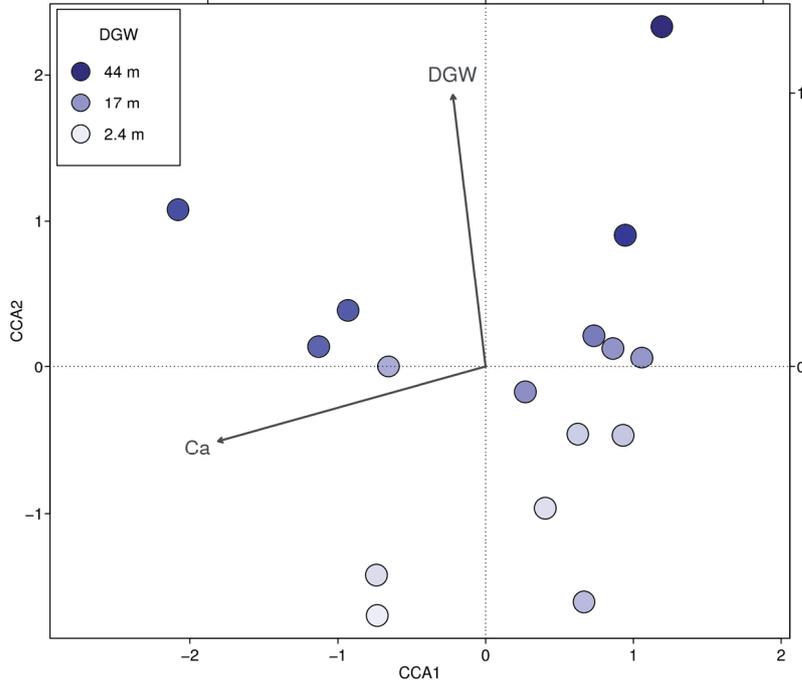
Figure 3. Ordination biplot from canonical correspondence analysis showing relationships between plant species composition and the significant environmental attributes depth-to-groundwater (DGW) and soil calcium content (Ca). Circles are coloured by maximum DGW, shown in the box at top left.
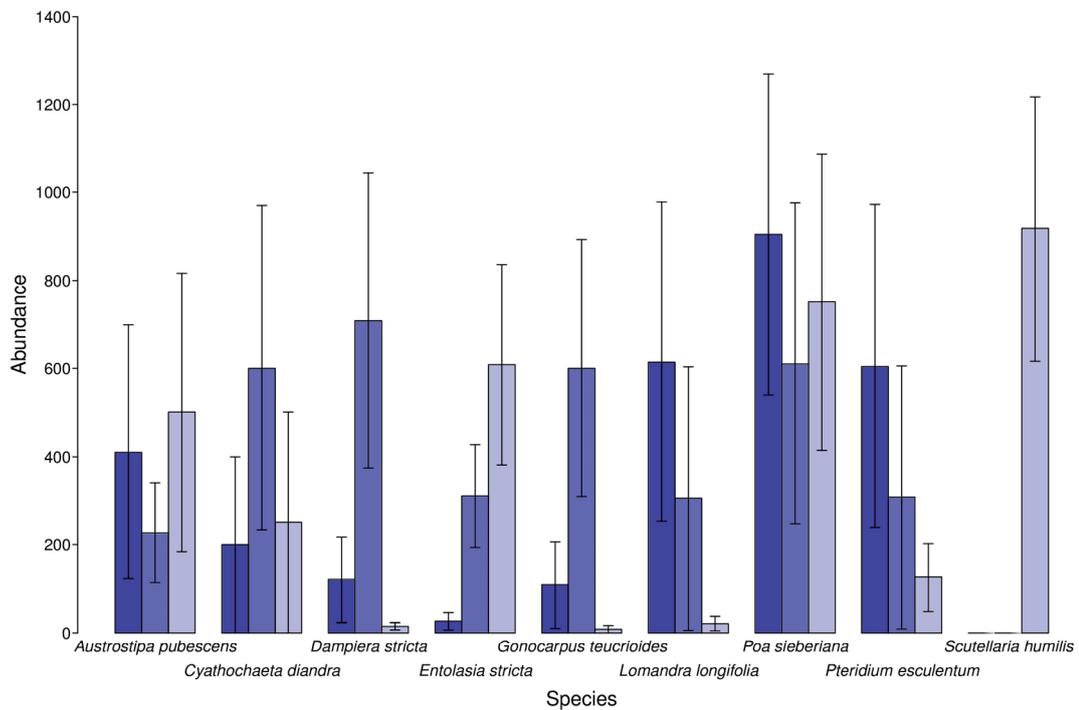
Figure 4. Mean abundances (± SE) of the nine understorey species identified by SIMPER as contributing to 40-50% of variation in plant species composition along the depth-to-groundwater gradient. Depth-to-groundwater < 10 m (light shading), 12–22 m (moderate shading), and 27‒44 m (dark shading).
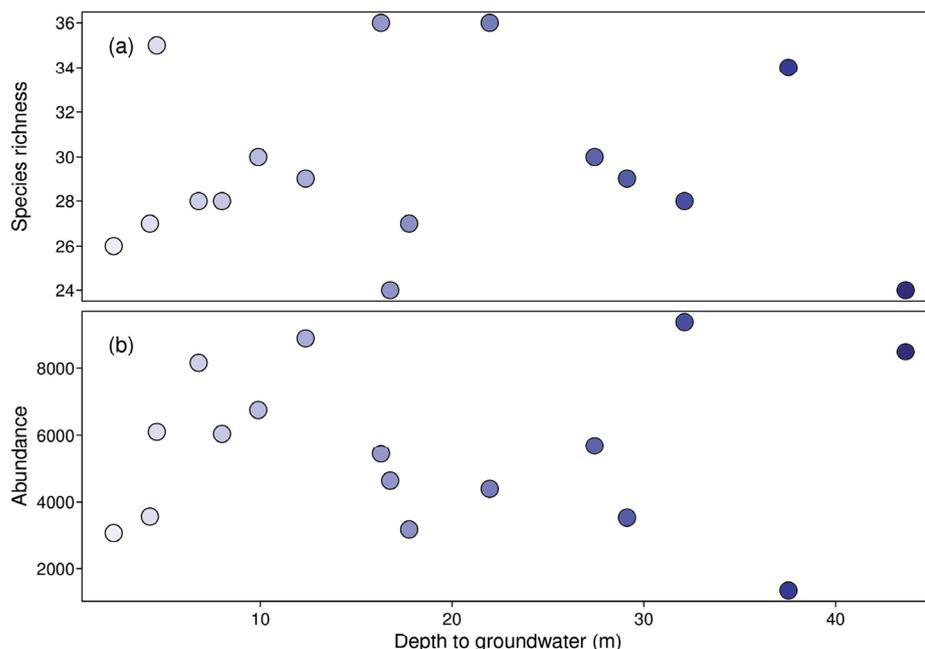
Figure 5.a. Plant species richness (number of species) and **b:** total plant abundance (number of individuals) as a function of DGW across the study sites. Depth-to-groundwater < 10 m (light shading), 12–22 m (moderate shading), and 27¬44 m (dark shading).

across the sites for each of these nine understorey species fell into one of four groups (Fig. 4), providing clear patterns of differentiation of species composition along the DGW gradient: (1) High abundances of the rush *Lomandra longifolia* and the bracken fern *Pteridium esculentum* at depths 27–44 m; (2) High abundances of the multi-stemmed herb *Gonocarpus teucrioides* and the groundcover perennial species *Dampiera stricta* and *Cyathochaeta diandra* at depths between 12 and 22 m; (3) High abundances of the perennial herb *Scutellaria humilis* and the grass *Entolasia stricta* at depths < 10 m; and (4) High abundances of the tussock grass *Poa sieberiana* and the spear grass *Austrostipa pubescens* at the deepest (27–44 m) and shallowest (< 10 m) sections of the gradient.

Across the sites, species richness ranged from 24–36 species and total plant abundance ranged from 1353–9398 individuals (Fig. 5). Our analyses revealed, however, that neither species richness nor total plant abundance varied significantly and independently as a function of DGW or any of the environmental attributes (richness: $\chi^2 = 3.75$, DF = 8, P = 0.88; abundance: $\chi^2 = 1.41$, DF = 8, P = 0.99).

Discussion

This study set out to determine whether plant species composition, richness and abundance varied in a systematic way in relation to a naturally occurring gradient in DGW in mesic woodlands. We found contrasting results for these different vegetation properties. Plant species composition varied significantly as a function of DGW, independently of the other attributes in the multivariate model. In addition, plant species composition was found to vary significantly and independently with soil Ca content, which represented several

other soil attributes in the model. In contrast, however, despite showing site-to-site variation, neither plant species richness nor total plant abundance varied across the landscape in a systematic way in relation to either DGW or any of other measured environmental attributes.

We found that site-to-site variation in the abundance of nine understorey plant species was responsible for significant variation in plant species composition along the DGW gradient. This finding is consistent with the notion that compositional patterns in the understorey are a key driver of variation in plant species composition across landscapes (Specht and Specht 1993, Halpern and Spies 1995). In our study, abundance patterns of the nine understorey species are most likely explained by their differential abilities to tolerate either increasingly dry conditions at deeper DGW sites, and perhaps even the periodically waterlogged conditions at the shallower sites on the DGW gradient. During periods of extended drought at our study sites, for example the millennial drought of 2000–2008, the ecosystem became severely water limited. At sites with shallow groundwater, access to groundwater can mitigate the effects of drought for all species accessing groundwater. At sites with deep DGW, access to groundwater is absent for all species but drought has impacts on shallow rooted species first because the volume of soil explored by shallow rooted species is smaller than the volume explored by deeper roots species. Thus, understorey species at deep sites must be able to tolerate extended dry periods, in contrast to understorey species at shallow sites. Furthermore, soils dry out much faster at deep sites after rainfall than soils at shallow sites (Hingee, unpublished data), such that even during non-drought years, rainwater is available in the soil at deep sites for a shorter period of time for understorey species in

particular. This could be because of periodic flooding occurring at the shallow sites after heavy rainfall which could lead to comparatively more saturated soils. There is also the possibility that soils at the shallow sites maintain higher moisture levels due to hydraulic lift from the capillary fringe located above the water table (Naumberg et al. 2005). At sites with intermediate DGW, shallow rooted species are also affected first as the deeper rooted species maintain connectivity to groundwater for longer.

High abundances of bracken fern (*Pteridium esculentum*) and the rush *Lomandra longifolia* at deep sites indicate that these understorey species are tolerant of dry conditions (Ahmad et al. 2009, ANBG 2012). It is not surprising that a species such as bracken fern is one of the dominant species at the deep sites, as it is an unusual fern that has a high degree of stomatal control of transpiration (Pitman 1989). This means that the stomata are able to tightly regulate transpiration rates when soil water content declines below a threshold (in contrast to anisohydric species that don't regulate transpiration down so readily), while its lignified stipe, rachis and stiff lamina help resist the effects of desiccation (Smith 1985). In addition, bracken fern is well suited to dry soil conditions as it has narrower and more rolled pinnulets with a more dissected frond structure (Thomson 2000). Bracken fern also exhibits extensively spreading mucilaginous rhizomes that serve as efficient water reservoirs (Smith 1985) and the species is capable of storing carbohydrate reserves (McGlone et al. 2005), facilitating growth and transpiration in conditions of low water availability. Carbohydrates are also strongly implicated in refilling of embolised xylem (Brodersen and McElrone 2013), a trait associated with adaptation to drier rather than wetter conditions. These traits allow bracken fern to tolerate dry soils and intermittent drought, which even enables the species to persist at the edge of the semi-arid zones in Australia (Cartledge and Carnahan 1971).

High abundances of the perennial herb *Scutellaria humilis* and the grass *Entolasia stricta* at shallow sites indicate that these species are most likely tolerant of periodic waterlogging. Although there are no quantitative data available about the frequency of waterlogging, our personal observations (M. Hingee, D. Eamus) are that waterlogging was apparent for several months in 2011 and 2012. Indeed, *S. humilis* is particularly abundant in moist habitats including along creek lines and in gullies. In New Zealand, species in the genus *Scutellaria* also commonly occur on the margins of watercourses where frequent flooding occurs (Williams 1992). The comparatively higher abundance of *Dampiera stricta* at sites with intermediate DGW suggests that this species is sensitive to both waterlogged soils and to the dry soils found at DGW deep sites. *Gonocarpus teucrioides* and *Cyathochaeta diandra* demonstrated a similar pattern of abundance variation along the gradient, and although their tolerance of waterlogged or very dry soils remains largely unexplored, the results of this study suggest that their ecophysiological traits might match those of *D. stricta*. Interestingly, the grass species *Poa sieberiana* was abundant across the gradient. The widespread nature of this species across the gradient suggests

that the species is a generalist, able to attain moderate to high abundances across a range of different water availabilities.

We also found a significant relationship between plant species composition and soil Ca, an element representing a suite of highly correlated environmental attributes in the analysis. While this study did not set out to test specific predictions about soil relationships with species composition, our findings are consistent with previous studies which have found that plant species composition varies in relation to a range of soil fertility measures, including soil N, P and K content (Critchley et al. 2002, Marini et al. 2007, Stevens et al. 2011). Indeed, this is why we included the wide range of environmental attributes in our analyses, as it is clearly important to consider other potential environmental correlates of plant species composition when examining the specific role of DGW. Future work that is focused specifically on the role of soil nutrients in shaping the composition of plant assemblages in *Eucalyptus* woodlands could start by developing explicit hypotheses about these soil nutrients.

Across the 2007 to 2012 period in the study region, temporal changes in DGW at all sites were generally less than 5% and always less than 10%. For example, data from Zolfagher (2013) show that at shallow (2.4 m), intermediate (13 m) and deep (37.6 m) sites, DGW varied by less than 0.5 m between 2007 and 2012. Importantly, this shows that temporal variation – both inter-annual and seasonal – in DGW at each site was much smaller than the differences in DGW between sites and that the ranking of DGW across the study sites used in this study did not vary. Thus, our finding for a significant and independent relationship between DGW and species composition across sites is principally due to the landscape gradient in DGW driving vegetation composition. Within each site in this particular study system, it is worth noting that vegetation does not appear to have major impacts that lead to substantial changes in depth to the water table. This is likely because annual rainfall in this mesic study area is relatively high. Between 2008 and 2012 annual rainfall exceeded 1100 mm except in 2009 (848 mm). Recharge rates to aquifers are maintained in most years where water use by vegetation is typically < 50% of annual rainfall (Eamus et al. 2016). During the period 2011 to 2012 annual rates of vegetation water-use were estimated to be about 40% of rainfall (Zolfaghar 2013) and in our mesic study region with tall dense eucalypt forest (tree height 6–14 m; Zolfaghar et al. 2014) recharge was unlikely to have been compromised. This is a principle reason for this aquifer and region being selected as a future commercial bore-field for water extraction to drought-proof Sydney.

Should the Kangaloon study region be developed into a commercial bore-field, with the commencement of groundwater extraction to supplement metropolitan water supplies, declines in DGW may lead to considerable changes in the ecology of the woodlands. Indeed, Triassic fractured Hawkesbury Sandstone aquifers at Kangaloon, our study region, have been identified as prospective water supplies in emergency situations (Ross 2014). In situations where groundwater falls below natural ranges of depths tolerated by the woodlands, the first observable responses, especially where groundwater is close to the soil surface, are often a reduction in the abun-

dance of shallow-rooted plant species (Elmore et al. 2006). For the woodlands in the Kangaloon region, this could potentially lead to the rapid local disappearance of shallow-rooted plant species already in low abundance at shallow sites. In addition, there may be reductions in abundance and potential extirpation of characteristic species at shallow sites such as *Scutellaria humilis* and *Entolasia stricta*. Such declines in abundance and local extinctions of native plant species are often followed by an increase in abundance of exotic plant species (Elmore et al. 2003). Although the native plant assemblages along the DGW gradient in the present study did not differ in species richness among shallow, intermediate and deep sites, exotic plant invasion and local reductions and extirpations of native plant species would undoubtedly combine to reduce native species richness most particularly at the shallow end of the gradient. If the species composition of plant assemblages is altered by exotic plant invasion in addition to groundwater extraction, costly procedures to restore and manage the woodlands may result (Scheffer et al. 2001, van de Koppel et al. 2002). In this context, the findings of our study can be used to guide monitoring efforts during any planned extraction of groundwater to ensure ecological integrity with regard to species composition in the woodlands. There is also the potential for our findings to be used to set ecological thresholds for sustainable groundwater extraction, thereby providing guidance for resource and conservation management.

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Electronic appendices

Appendix 1. Geographic coordinates and depth-to-groundwater for the 16 study sites.

Appendix 2. Study species and their abundances (number of individuals, see Methods for details) at each of the 16 sites.

Appendix 3. Variation in environmental attributes across the 16 study sites.

Appendix 4. Pairwise correlation matrix between environmental attributes