



Piosphere contribution to landscape heterogeneity: a case study of remote-sensed woody cover in a high elephant density landscape

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Vegetation gradients developing around water sources (i.e. piospheres) are important features of arid and semi-arid ecosystems. Studied extensively in pastoral areas, piospheres have rarely been investigated in areas hosting rich herbivore diversity. We studied piospheres in woody cover assessed through remote-sensing in Hwange National Park, Zimbabwe, which has one of the world's largest elephant populations. As no preferred statistical model for piosphere studies has emerged, we first contrasted results from ordinary least-square (OLS) regressions on raw data with those from other statistical models (OLS on aggregated data and simultaneous autoregressive models on raw data), and selected the most parsimonious, unbiased, model to study the influence of artificial and natural waterholes, and the abundance of elephants, others browsers, and grazers on piospheres. OLS models provided unbiased parameter estimates, despite the strong spatial autocorrelation present in woody cover data, whereas other statistical models had important drawbacks. Using an OLS framework we showed that despite an important negative non-linear mean effect, distance-to-water was a poor predictor of woody cover at any location. Woody cover was on average more reduced in the vicinity of water at artificial waterholes than at natural waterholes. Elephant abundance was not consistently associated with lower woody cover, and poorly explained woody cover heterogeneity, as did all other herbivore-related variables. Our study indicates that piospheres may develop differently in pastoral and protected areas, suggesting the importance of herbivore diversity in ecosystem functioning. Our results also show that heterogeneity in woody cover persists within piospheres, calling for further investigation on the origin and role of this heterogeneity in the maintenance of ecological processes and biodiversity within these key-areas of the landscape.

Herbivore foraging affects various aspects of vegetation dynamics (Huntly 1991). Recent attention has particularly focused on understanding herbivore influence on the spatial heterogeneity of vegetation (Adler et al. 2001). At the landscape scale, radial gradients in vegetation characteristics developing around concentrated resource areas (saline, resting sites, waterholes etc.) provide particularly striking evidence of herbivore influence on vegetation patterns (Coughenour 1991). Such model systems have been particularly well-studied in semi-arid pastoral and commercial rangelands, where the term piosphere was coined to describe vegetation gradients developing around permanent water supplies (Lange 1969, Thrash and Derry 1999). For instance, many studies conducted in grazed areas show that grazing may allow for the dominance of shrubs or trees and cause bush encroachment near water, ultimately leading to land degradation (Pickup et al. 1994). However, little is known about the development of piosphere gradients in ecosystems with a diverse community of herbivores, particularly where browsers may prevent the development of woody cover otherwise facilitated by grazing. A striking

example comes from concerns that African elephants *Loxodonta africana* may outweigh any other effects and create piospheres within which woody cover would be dramatically reduced (O'Connor et al. 2007). Indeed, elephant impact on vegetation structure is higher in the vicinity of water (Conybeare 1991, Ben-Shahar 1993), but no comprehensive assessment of woody cover at the landscape scale has been conducted. Investigating piosphere effects associated with natural herbivore communities is vital to understand the functioning of ecosystems, particularly at a time when water provision policies in protected areas are under heavy criticism in the face of a paradigm shift from conservation of large herbivores to more general conservation of biodiversity and ecosystem heterogeneity (Gaylard et al. 2003).

Vegetation heterogeneity within piospheres has rarely been investigated (Jafari et al. 2008), as the general interest has so far been concentrated on the mean effects of distance-to-water (Thrash and Derry 1999). However there is a growing recognition that heterogeneity affects most ecological processes. Both an accurate assessment of the strength

(effect size) and of the predictive power (R^2) of the relationships between vegetation parameters and distance-to-water is thus required for a successful understanding and management of piospheres, a key area of arid and semi-arid landscapes.

Investigation of piosphere effects has commonly relied on the analysis of aggregated data, averaged across classes of increasing distance-to-water (Lind et al. 2003, Washington-Allen et al. 2004). Although aggregation of data “smooths out most spatial patterns resulting from processes other than grazing” (Pickup et al. 1994: p. 505), regressions on aggregated data may provide biased parameter estimates and artificially increase the coefficient of determination, suggesting that distance to water has a higher predictive power than is statistically defensible. An alternative is to use standard regressions on raw data, taking into account the full variability of the studied variables (Todd 2006). However, although by definition concerned with spatial structure, no studies on piospheres have accounted for spatial autocorrelation, although the role of the latter is under scrutiny (Legendre and Legendre 1998, Haining 2003, Dormann et al. 2007). This issue requires further study as it might become particularly acute with the increasing use of full-coverage, high resolution data from remote sensing (Pickup et al. 1994, Lind et al. 2003, Washington-Allen et al. 2004, Jafari et al. 2008).

Here, we applied ordinary least-square (OLS) models to raw or aggregated data, and simultaneous autoregressive (SAR) models explicitly taking into account spatial autocorrelation, to study piosphere influence on woody cover in Hwange National Park, Zimbabwe. This park relies on artificial surface water to maintain high abundances of large

herbivores, and hosts one of the world’s largest elephant populations (Blanc et al. 2007). We used remote-sensed data for woody cover to provide full-coverage spatial data, and assessed vegetation heterogeneity at the landscape scale. Using the most consistent model in parameter estimation in the face of spatial autocorrelation, we investigated the relationship between piospheres and herbivore abundances. We discuss methodological issues associated with the study of piospheres and highlight how our results emphasize the need for a better understanding of the origin and role of the heterogeneity which persists within piospheres.

Methods

Study area

Hwange National Park (hereafter HNP) is located at the northwestern border of Zimbabwe, covering 15 000 km² of dystrophic wooded savannas. For this work we distinguished 3 major vegetation types, characterized by their dominant species, each of which has distinct sensitivity to elephant foraging. *Baikiaea plurijuga* is unpalatable for most large herbivores, particularly elephants (Conybeare 1991, Holdo 2006). Conversely, *Colophospermum mopane* is commonly browsed, but is highly resilient to elephant browsing (Ben-Shahar 1996). Vegetation communities of the park were classified as either “Baikiaea” or “Mopane” vegetation type if these species were present in > 80% of the plots used for ground-truthing of the vegetation map (Rogers 1993), or were classified as “Other”. “Baikiaea” and “Mopane” vegetation represented 22 and 28% of the park, respectively (Fig. 1). Vegetation and soil types were

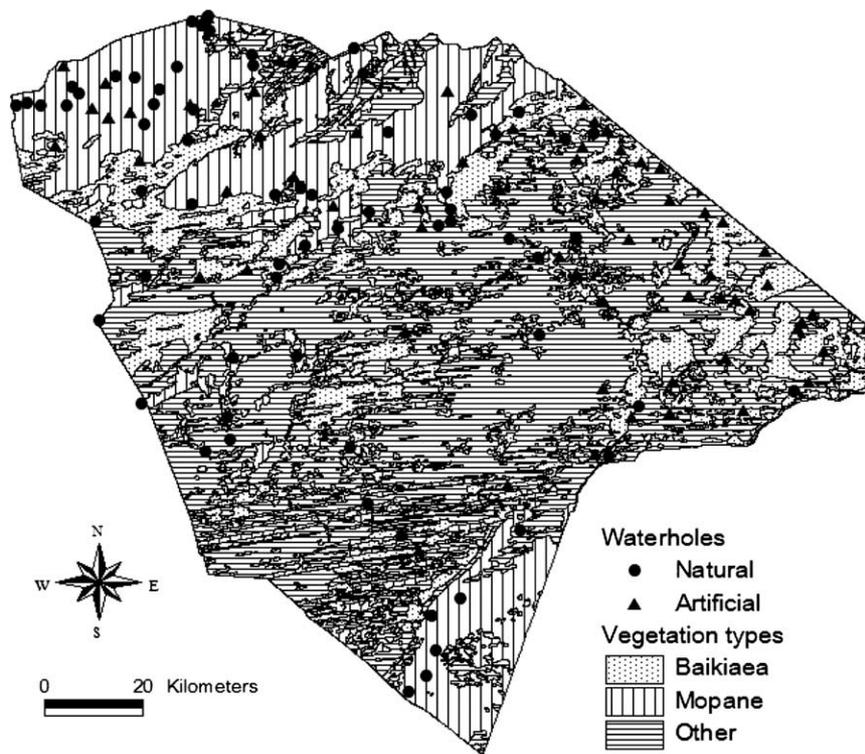


Figure 1. Map of Hwange National Park, Zimbabwe, showing the vegetation types used in this study as well as the distribution of waterholes that may retain water during the dry season.

strongly associated; 100 and 92% of the “Baikiea” and “Other” vegetation, respectively, were on poor Kalahari sands, whereas 80% of the “Mopane” vegetation was on richer basaltic soils in the northern and southern regions of the park. Soil type was therefore not included in the analyses to avoid collinearity. Rainfall mostly occurs between October and April, with an annual average of 606 mm in the northeastern section of the park, although a general east-west gradient of decreasing rainfall also exists (Chamaillé-Jammes et al. 2006). Natural surface water is scarce during the dry season, as only a few pools remains in the river network, and most natural pans dry up during low rainfall years (Chamaillé-Jammes et al. 2007b). Sixty-seven boreholes were established between the 1930s and early 1980s to provide year-round water supply by groundwater pumping. These artificial waterholes are distributed unevenly across the park, most being located in the northern and eastern regions (Fig. 1) and not all are active in any given dry season. HNP has one of the world’s largest elephant populations (Blanc et al. 2007), but in the early 1980s elephant densities were kept at ca 1 elephant km⁻² via culling operations (discontinued in 1986). Elephant densities increased subsequently to over 2 elephants km⁻² across the park (Chamaillé-Jammes et al. 2008), representing over 70% of the large herbivore biomass (Valeix et al. 2007).

Woody cover data

Woody cover percent estimates were obtained from the Vegetation Continuous Fields produced by the Univ. of Maryland (Hansen et al. 2003), downloaded from the Global Land Cover Facility <www.landcover.org>. The product was derived from data collected in 2000–2001 by the MODIS satellite sensor, and is available at a spatial resolution of 500 m; our whole study therefore comprises 56 845 pixels. Field validation has been conducted successfully in neighbouring areas of similar vegetation types (Hansen et al. 2002), and the range of values observed for HNP was consistent with independent visual estimates of woody cover (Ganzin et al. pers. comm.). For the analyses each pixel was also attributed a unique vegetation type (“Baikiea”, “Mopane”, or “Other”).

Herbivore data at waterholes

Twenty-four hours herbivore counts were conducted at waterholes from 1967 to 2005 (except in 1968–1971, 1976–1981 and 1983). Once a year during the hot dry season (late September–early October) at full moon, from midday, the number of animals coming to drink was recorded for all species. Although these data only cover a limited period of time, they represent a tentative index of herbivore abundance during the dry season when animals concentrate around waterholes, and when mix-feeders (particularly elephants) are predominantly browsers and thus most likely to affect woody cover (Makhabu 2005). Not all waterholes were surveyed every year, and the census became more general in 1982. We therefore averaged data from 1982 to 2001 for each waterhole that had ≥ 8 yr of data. It rained during the censuses in 1986 and 1997, and

animals were able to drink in the numerous ponds created. Consequently, the number of animals counted at waterholes was very low and not representative of dry season abundance, and these data were not used in analyses.

Statistical analyses

Various statistical approaches have been used in piosphere studies, but to the best of our knowledge none has investigated potential confounding effects of spatial autocorrelation in the studied vegetation parameters. Here we first compared the ability of several statistical models fitted over the whole range of distance-to-water to generate reliable estimates of piosphere effects, comparing parameter estimates of OLS models based on aggregated data, raw data, raw data resampled to remove spatial autocorrelation, and of SAR models explicitly accounting for autocorrelation. Secondly, using the most consistent of these models we re-estimated piosphere effects taking into account only the data lying within the observed piosphere extent, and investigated the relationships between herbivore attendance and piosphere effects. Mechanistic modelling and empirical studies have suggested various shapes for the gradients developing within piospheres (e.g. logistic; Thrash and Derry 1999). However, when trying to obtain accurate descriptions of piospheres, selecting best-fit models rather than a priori models of lower fit should be favoured, as they could otherwise cause inaccurate estimation of piosphere dimensions (Thrash and Derry 1999). Here we used third and lower-order polynomial functions of distance-to-water as flexible tools to achieve an accurate quantitative evaluation of the extent and importance of piospheres. In all analyses woody cover was normalized and variance stabilized using the arc-sin square-root transformation. Model selection was based on Akaike information criterion (AIC) and Δ AIC (Burnham and Anderson 2002). Models with Δ AIC < 2 were considered the most likely. Akaike weights (w_i ; i.e. the likelihood that a model was the best model among the whole set of candidate models) of the lowest-AIC models often equal 1 due to our large sample size, and are reported only when otherwise. Goodness-of-fit of models and their predictive power was assessed using the generalised coefficient of determination (Nagelkerke 1991). All analyses were conducted with the R software (R Development Core Team 2007) and the *spdep* package (Bivand 2005).

Model comparisons

We first fitted for each vegetation type OLS regressions on data aggregated (i.e. averaged) across 500 m distance-to-water classes. Conversely, the full variability of woody cover was taken into account using OLS regression models on raw data. From our field experience we assumed that woody cover exhibited large-scale changes over HNP following the north-east–south-west rainfall gradient, and we investigated this effect by fitting a third-order polynomial trend surface (using standardized coordinates: Legendre and Legendre 1998). We built an OLS regression model (hereafter referred to as the piosphere OLS model) as follows:

$$WC = TS + VEGTYPE \times (DW + DW^2 + DW^3) + \varepsilon \quad (1)$$

where WC is a vector of woody cover, TS a third-order polynomial trend surface, VEGTYPE a categorical vector identifying vegetation types, DW a vector of distance-to-water, and ε the spatially-independent errors.

OLS models are not appropriate in the presence of spatial autocorrelation in the residuals, a common case for vegetation models (Miller et al. 2007), as it violates the assumption of independently and identically distributed errors, resulting in deflated standard errors when autocorrelation is positive (Legendre and Legendre 1998). We assessed autocorrelation in woody cover and in the piosphere OLS model residuals using Moran's I, and as it proved important (Results), we used 2 alternative procedures.

1) We resampled the full dataset 500 times, selecting 300 pixels randomly, although constraining them to be ≥ 5 km away from each other (autocorrelation in the residuals of the OLS model conducted on all data was low at such distance: $I=0.14$; Fig. 3), and fitted eq. (1) by OLS regression.

2) We fitted SAR models that explicitly integrate autocorrelation terms in the model formulation. The choice of SAR model types may affect parameter estimates, and we fitted both SAR error (incorporating autocorrelation in the error term) and SAR mixed models (accounting for autocorrelation in both the response and the explanatory variables). Standard errors for parameter estimates could not be computed SAR mixed models due to the very large sample sizes (R. Bivand pers. comm. 2007/10). See Supplementary material Appendix S1, Anselin (1988), Haining (2003), and Kissling and Carl (2008) for model formulations.

Testing for herbivore effects

We used the herbivore census data to investigate the relationship between piospheres and elephants, smaller browsers (common duiker *Sylvicapra grimmia*, giraffe *Giraffa camelopardalis*, impala *Aepyceros melampus*, greater kudu *Tragelaphus strepsiceros* and steenbok *Raphicerus campestris*), grazers (African buffalo *Syncerus caffer*, roan antelope *Hippotragus equinus*, sable antelope *Hippotragus niger*, warthog *Phacochoerus africanus*, waterbuck *Kobus ellipsiprymnus*, blue wildebeest *Connochaetes taurinus*, and Burchell's zebra *Equus quagga*) or the ratio of browsers (including elephants) to grazers. To correct for allometric effects on consumption when studying guild effects, we converted browser and grazer abundance to metabolic biomass using data from Cumming and Cumming (2003). We studied the effects of the herbivore-related variables and of the nature of waterholes (artificial vs natural) by entering these variables in a multiplicative way into eq. (1), as it proved to be the most consistent model (Results and Discussion). Each pixel was attributed herbivore abundance data from the closest waterhole, or were excluded from the analysis if the closest waterhole had no data.

Results

Model comparisons

OLS models based on aggregated data provided statistical evidence for a relationship between woody cover and distance-to-water in HNP (Fig. 2a; Supplementary material Appendix S2). However, such analyses masked dramatic heterogeneity in woody cover (Fig. 2b) and ignored important aspects of landscape configuration. For instance, waterhole density was higher in the northeastern region of the park (Fig. 1), and thus areas beyond 10 km from water occurred primarily in the southwest and driest regions of the park where woody cover was lower. A model based on the raw data, integrating this gradient in woody cover (via a trend surface) and the effects of vegetation types and piospheres (eq. (1)) was more likely and provided a slightly better fit than the model of this gradient alone (Table 1). The estimated intercept value of tree cover for the Mopane vegetation type differed between the OLS models conducted on aggregated data and the OLS model on raw data (Table 2).

Woody cover exhibited strong spatial autocorrelation (Fig. 3), as did residuals of the OLS model on raw data (Fig. 3), indicating that the OLS assumption of independently and identically distributed errors was not fulfilled. Sub-sampling the dataset at locations ≥ 5 km apart effectively removed spatial autocorrelation (mean first lag Moran's $I = 0.06 \pm 0.04$ SD) and produced parameter estimates which did not differ from the OLS model on raw data (Table 2). This result also indicated that the relatively close spacing of waterholes (particularly in the northern area of the park) did not bias parameter estimation. Both SAR error and mixed models also successfully removed autocorrelation in the model residuals (Fig. 3), and had lower AIC and higher R^2 than the OLS model on raw data (Table 1). However, some parameter estimates differed between the OLS model on raw data and the SAR error model (and most confidence intervals of the differences were large; Table 2). Those estimated by the SAR mixed model differed markedly from those of all other models (Table 2), although the absence of standard errors for this model prevented further comparisons. Because the resampling exercise demonstrated that removing autocorrelation should not cause parameter shifts, the changes in parameters observed when fitting the SAR models cautioned against the use of these models to estimate piosphere extent (Discussion).

Herbivore effects on piospheres

Woody cover was strongly affected within the first 2 km of the piospheres, but reduction in woody cover still occurred up to 5 km of water in "Mopane" and "Other" vegetation types (Fig. 2a). We therefore used an OLS regression on raw data to re-estimate piosphere parameters using data within 5 km of water, considering areas ≥ 5 km of water as unimpacted. Woody cover in the immediate vicinity of water was 21.7, 15.4, and 38.7% lower than at 5 km from water in "Baikiea", "Mopane", and the "Other" vegetation types, respectively. The modelled piosphere effects had very large prediction intervals (Fig. 2c), indicating

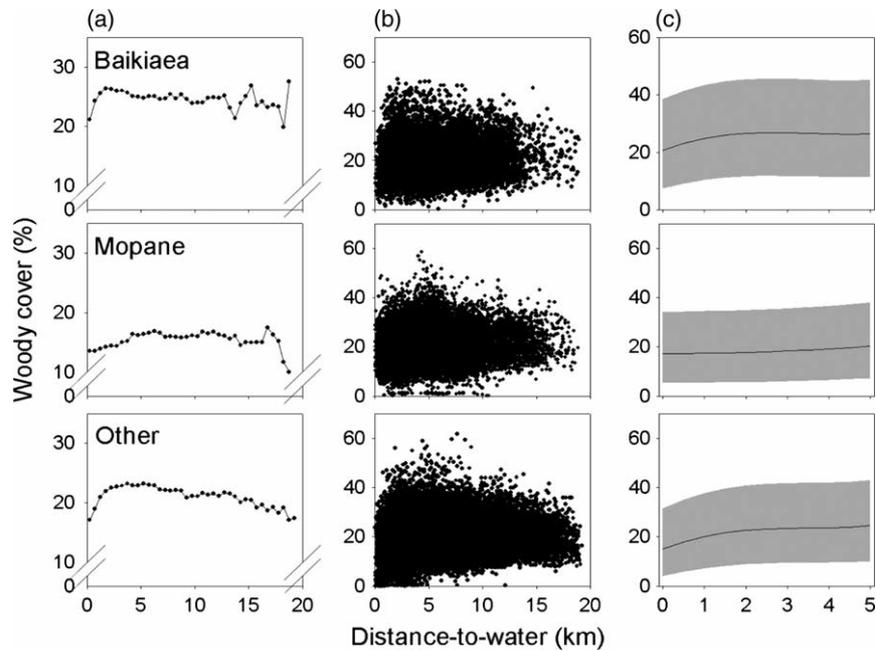


Figure 2. Relationships between woody cover and distance-to-water for “Baikiaea”, “Mopane” and “Other” vegetation types. (a) Typical visual output of piosphere studies based on data aggregated across distance to water classes; (b) the full set of pixel values (corrected for a large-scale gradient using a third-order polynomial trend surface – see text for details); note that the scaling of the ordinate axis differs between (a) and (b), reflecting the loss of information induced by data aggregation; (c) the modelled piosphere effects within 5 km of water, showing the very large 95% prediction band (light grey).

limitations to predicting woody cover on the sole basis of distance to water (distance-to-water contributed only for 1.3% of the variance in woody cover within piospheres; Table 3). Adding the identity of the closest waterhole as an explanatory variable only produced a 2% increase in explained variance (Table 3), indicating that the low predictive power of distance-to-water did not result from across-piosphere differences, but that most woody cover heterogeneity was unrelated to distance-to-water within piospheres.

On average, woody cover was lower in the immediate vicinity (<1 km) of artificial waterholes compared to natural waterholes, but became similar (“Baikiaea” and “Mopane” vegetation types) or slightly higher (“Other” vegetation type) further away (Fig. 4a, Table 3). Woody cover in “Baikiaea” and “Mopane” vegetation types was also lower on average in the vicinity of water where elephant

numbers were higher, whereas the opposite was observed in the “Other” vegetation type, and these effects decreased with increasing distance-to-water (Fig. 4b; Table 3). Opposite relationships were found with the metabolic biomass of smaller browsers (Fig. 4c; Table 3). Higher grazer metabolic biomass was not consistently associated with higher or lower woody cover in the “Baikiaea” and “Mopane” vegetation type, whereas it was associated with lower woody cover in the “Other” vegetation type (Fig. 4d; Table 3). The relationship between the browser/grazer ratio and woody cover also differed between vegetation types (Fig. 4e; Table 3).

Overall, taking into account the effect of the type of waterholes or of any herbivore variable provided only a negligible improvement of our ability to describe woody cover heterogeneity (note the low increase in goodness-of-fit of the models integrating either the nature of waterholes or

Table 1. Statistics for OLS and SAR models of woody cover in relation to a third-order trend surface (TS), three distinct vegetation types (VEG) and distance-to-water (DW) modelled via a third-order polynomial. Models with lower-order polynomials for distance-to-water were not selected on the basis of the Akaike information criterion (AIC). Sample size equals 56845 in all case. Log-likelihood, number of free parameters (Np), Akaike information criterion (AIC), Δ AIC and R^2 are shown. Models with Δ AIC < 2 are in bold.

Model	Model type	Log-likelihood	Np	AIC	Δ AIC	R^2
NULL	OLS	43754	1	-87504	39513	
TS	OLS	50699	10	-101377	25640	0.217
TS+VEG	OLS	52616	12	-105206	21811	0.268
TS+VEG \times DW (poly. order 3)	OLS	53020	21	-105996	21021	0.278
TS+VEG	SAR error	62882	13	-125735	1282	0.490
TS+VEG \times DW (poly. order 3)	SAR error	62974	22	-125902	1115	0.491
TS+VEG	SAR mixed	63441	24	-126832	185	0.500
TS+VEG \times DW (poly. order 3)	SAR mixed	63552	42	-127017	0	0.502

Table 2. Parameter estimates (\pm SE) for alternative models of woody cover in “Baikiea”, “Mopane”, and “Other” vegetation types in relation to distance-to-water (DW; modelled as a third-order polynomial). Models are an OLS model on raw data, OLS models on data aggregated by 500 m distance-to-water classes, OLS on subsampled data removing spatial autocorrelation, and SAR error and mixed models. SE for the SAR mixed model could not be obtained due to the large sample size. All models incorporate a third-order polynomial trend-surface to account for the underlying large-scale gradient in woody cover across the park. Differences between estimates of the OLS model on raw data and other models are shown, and differences for which the 95% confidence interval of the difference does not include 0 are in bold. Woody cover have been arcsin-square-root transformed. See text for further details on model specifications.

	OLS (raw data)			OLS (aggregated data)			OLS (sub-sampled data)			SAR error			SAR mixed		
	Estimate	\pm SE	95% CI	Estimate	\pm SE	95% CI	Estimate	\pm SE	95% CI	Estimate	\pm SE	95% CI	Estimate	\pm SE	95% CI
Baikiea															
Intercept	0.517	\pm 0.005	0.502	\pm 0.011	0.014	(-0.010-0.039)	0.513	\pm 0.004	0.004	(-0.008-0.016)	0.478	\pm0.006	0.038	(0.024-0.053)	0.166
DW	0.003	\pm 0.002	0.009	\pm 0.005	-0.006	(-0.017-0.006)	0.006	\pm 0.002	-0.003	(-0.009-0.003)	0.011	\pm0.003	-0.008	(-0.015--0.001)	0.035
DW ²	<0.001		-0.001	\pm 0.001	0.001	(0.000-0.003)	-0.001	\pm 0.000	0.001	(0.000-0.001)	-0.001	\pm 0.000	0.001	(0.000-0.002)	-0.004
DW ³	<0.001		<0.001		<0.001		<0.001		<0.001		<0.001		<0.001		<0.001
Mopane															
Intercept	0.412	\pm 0.004	0.367	\pm0.010	0.046	(0.024-0.067)	0.408	\pm 0.003	0.005	(-0.005-0.015)	0.441	\pm0.006	-0.028	(-0.042--0.014)	0.159
DW	0.011	\pm 0.002	0.007	\pm 0.004	0.004	(-0.006-0.014)	0.012	\pm 0.001	-0.002	(-0.007-0.004)	0.013	\pm 0.003	-0.002	(-0.009-0.005)	0.037
DW ²	-0.001	\pm 0.000	<0.001		-0.001	(-0.002-0.001)	-0.001	\pm 0.000	0.000	(-0.001-0.001)	-0.001	\pm 0.000	0.000	(-0.001-0.001)	-0.004
DW ³	<0.001		<0.001		<0.001		<0.001		<0.001		<0.001		<0.001		<0.001
Other															
Intercept	0.445	\pm 0.003	0.436	\pm 0.007	0.009	(-0.007-0.025)	0.443	\pm 0.002	0.002	(-0.005-0.008)	0.456	\pm 0.005	-0.011	(-0.022-0.000)	0.165
DW	0.019	\pm 0.001	0.018	\pm 0.003	0.000	(-0.007-0.007)	0.019	\pm 0.001	0.000	(-0.003-0.003)	0.015	\pm 0.002	0.004	(-0.001-0.009)	0.034
DW ²	-0.002	\pm 0.000	-0.002	\pm 0.000	0.000	(-0.001-0.001)	-0.002	\pm 0.000	<0.001		-0.001	\pm 0.000	-0.001	(-0.001-0.000)	-0.004
DW ³	<0.001		<0.001		<0.001		<0.001		<0.001		<0.001		<0.001		<0.001

herbivore-related variables compared to the general piosphere model: Table 3).

Discussion

Guidelines for the use of statistical models in piosphere studies

Analyses based on aggregated data revealed substantial differences between vegetation types in the relationship between woody cover and distance-to-water in HNP. However, although this method may be appealing for the “convincing” aspect of its results (smoothed data, likelihood of higher R^2), it masked the poor power of distance-to-water to predict woody cover at any location, despite taking vegetation types into account. This could be highly prejudicial in a management context as it will cause an over-estimation of the ability to manipulate woody cover using surface water management. This method also has limitations for the analysis of complex landscapes. In this study for instance, the interaction between the large-scale gradient and the uneven distribution of waterholes could not be accounted for. Conversely, OLS models on raw data allowed the integration of all explanatory variables (large-scale gradient, vegetation types, etc.) into a single analysis which assessed the contribution of distance-to-water to the general heterogeneity in woody cover. Spatial autocorrelation of woody cover was not accounted for by the explanatory variables and remained in the residuals of the OLS model. Nevertheless, parameter estimates did not differ between OLS regressions on the full dataset or on the dataset subsampled to remove autocorrelation, confirming the results of Hawkins et al. (2007) that autocorrelation does not lead to biased parameters in OLS models. Using models that explicitly integrate spatial autocorrelation is appealing, and SAR models have recently been used increasingly (Miller et al. 2007). In our study the SAR error and mixed models differed when estimating parameters: the SAR error model produced estimates that differed slightly from those estimated by the OLS model, while the SAR mixed model differed widely. Other studies have reported shifts in parameter estimates when using SAR mixed or error models compared to OLS models (Tognelli and Kelt 2004, Kühn 2007, Kissling and Carl 2008). This is problematic, as correcting for autocorrelation should not cause parameter shifts (Beale et al. 2007, Hawkins et al. 2007, this study). Interpretation of these parameter shifts in SAR models remains controversial but it has been suggested that SAR models operate a “scale-shift” which remains poorly understood (Diniz-Filho et al. 2003), and these methods are currently under much scrutiny (Beale et al. 2007, Diniz-Filho et al. 2007, Dormann et al. 2007, Hawkins et al. 2007). As explicit modelling of the autocorrelation structure will be beyond the goal of many piosphere studies, we recommend the use of OLS models on raw data for the study of piospheres, particularly as they will allow for unbiased estimation of effect size (i.e. piosphere influence and dimension). However, we encourage further investigations of spatially-explicit models that may ultimately lead to more precise parameter estimation.

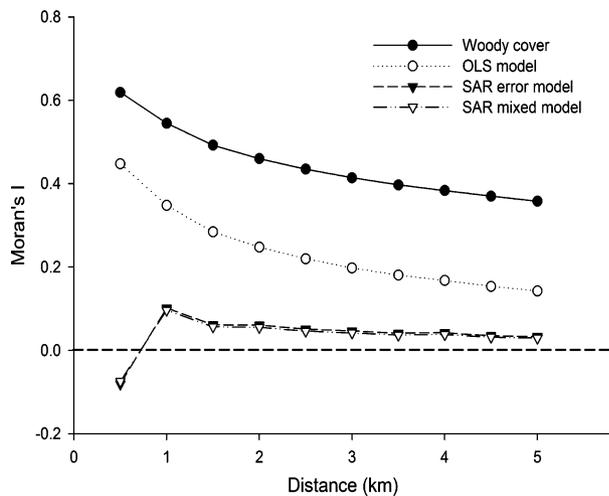


Figure 3. Moran's I correlograms of woody cover, of the residuals of the OLS regression on raw data, and of SAR error and SAR mixed models.

Piosphere contribution to landscape heterogeneity in woody cover

Woody cover is often strongly affected by the increase in grazing pressure occurring around waterholes in semi-arid pastoral and commercial rangelands (beyond a sacrifice area of bare ground caused by heavy trampling; Thrash and Derry 1999). Various types of responses have been documented (Landsberg et al. 2003, Todd 2006), but mechanistic models suggest that pure grazing should increase woody dominance (Weber et al. 1998). In our study, conducted in an ecosystem with a rich diversity of herbivores, piospheres were characterized by a decrease in woody cover closer to water. A decrease in tree and shrub density in the vicinity of water has also been observed in Kruger National Park (Brits et al. 2002). This suggests that herbivore community composition affects the development of piospheres and that browsing may have a fundamental role in counteracting the facilitating effects of grazing on woody plants, although snapshot studies cannot rule out

potential encroachment of unpalatable woody species. In our study piospheres were less marked in "Mopane" woodlands, where *Colophospermum mopane*, very resilient to elephant damage (Ben-Shahar 1996), develops in monospecific stands. Piospheres were larger in the "Baikiaea" vegetation type, although *Baikiaea plurijuga* is an unpalatable species that is virtually untouched by elephants (Conybeare 1991, Holdo 2006). *Baikiaea plurijuga* develops in mixed-stands and the decline in woody cover in this vegetation type might be mostly attributed to decline of other species (Conybeare 1991), and ground validation is needed. Piospheres were most marked in the "Other" vegetation type, dominated by elephant-palatable species, where mean relative woody cover reduction was up to 39% of the woody cover observed outside piospheres. Our results suggest that ecosystem function may be greatly modified within piospheres: for instance, woody cover affects water and nutrient dynamics (Ludwig et al. 2004), determines resource availability for both grazers and browsers, and may affect predator-prey relationships (Hopcraft et al. 2005). As most large herbivores concentrate within 5 km of water during the critical dry season in semi-arid regions (Redfern et al. 2003), piospheres are likely to affect the ecology of most herbivores, including elephants, within HNP.

Piospheres were most marked around artificial waterholes which experienced higher and more continuous herbivore pressure than natural ones, with lower woody cover within the first km from water. Unexpectedly, however, woody cover was higher where elephant abundance was greater in the vegetation type considered the most sensitive to elephant, whereas the opposite was observed in other, unpalatable or resilient vegetation types. Intriguingly, this pattern was reversed for the smaller browsers. Thus, there was no consistent relationships between piosphere effects on woody cover and herbivore attendance at waterholes, and assessing the contribution of herbivore guilds to reduced woody cover proved difficult. Lower grazer biomass at high woody cover in the "Other" vegetation type for instance suggested that our results may partly reflect habitat-selection processes rather than actual herbivore effects on vegetation. Longitudinal studies would

Table 3. Statistics of OLS models of woody cover within 5 km of water in relation to vegetation types (VEG), distance-to-water (DW; modelled as a third-order polynomial), and information about the closest waterhole: identity (WP ID), type (artificial/natural; PUMP), elephant abundance (ELE), metabolic biomass of smaller browsers (BRWSE), metabolic biomass of grazers (GRZE) or the ratio of the metabolic biomass of all browsers (including elephants) on the metabolic biomass of grazers (RATIO B/G). Sample size is reduced when studying relationships with herbivores as not all waterholes have been surveyed. All models incorporate a third-order polynomial trend-surface to account for the underlying large-scale gradient in woody cover across the Park. Log-likelihood, number of free parameters (Np), Akaike information criterion (AIC), Δ AIC and R^2 are shown. Models with Δ AIC < 2 are in bold.

	Log-likelihood	Np	AIC	Δ AIC	R^2
With all data (n = 26624)					
NULL	18702	1	-37400	10371	
VEG	23289	12	-46551	1220	0.291
VEG \times DW	23536	21	-47028	743	0.305
VEG \times DW \times WP ID	23933	22	-47771	0	0.325
VEG \times DW \times PUMP	23690	33	-47312	459	0.313
With herbivore surveyed (n = 11880)					
NULL	7929	1	-15854	5316	
VEG \times DW	10333	21	-20622	548	0.333
VEG \times DW \times ELE	10370	33	-20673	497	0.337
VEG \times DW \times BRWSE	10365	32	-20663	507	0.336
VEG \times DW \times GRZE	10619	33	-21170	0	0.364
VEG \times DW \times RATIO B/G	10486	33	-20905	265	0.350

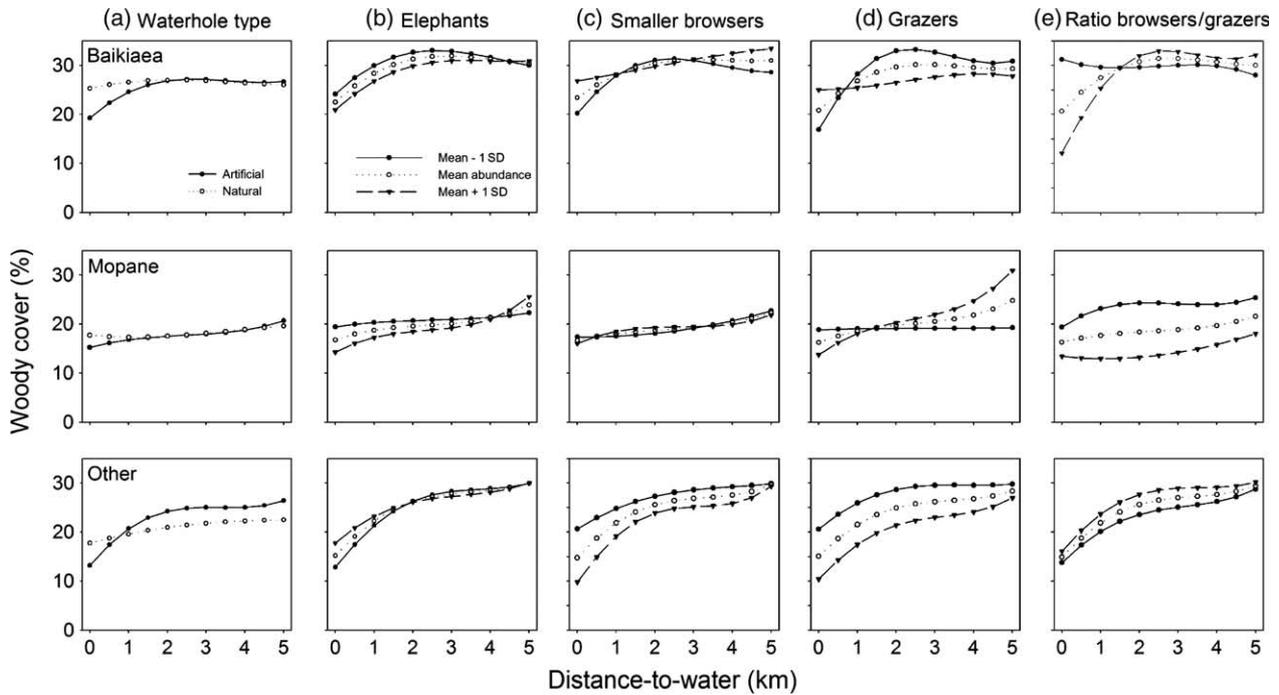


Figure 4. Modelled relationships between woody cover at waterholes in “Baikiaea”, “Mopane”, and “Other” vegetation types and the effects of distance-to-water (as a third-order polynomial) and (a) the type of waterhole (artificial vs natural), (b) elephant abundance, (c) metabolic biomass of smaller browsers, (d) metabolic biomass of grazers, (e) the ratio of browsers to grazers (both converted to metabolic biomass). For b, c, d, e, the herbivore-related effects are modelled using the mean and mean \pm 1 SD of the herbivore abundance observed at waterholes across the park. Lines are not parallel because the type of waterhole or herbivore-related variables interacted with distance-to-water to affect woody cover. Data points are not shown for clarity, but the predictive powers of these relationships were low (see text for details).

better allow disentangling between potential effects of elephants or other herbivores on woody cover.

The often assumed large contribution of elephants to habitat openness may, however, be moderated here, as woody cover was higher in the eastern region of the park where elephant densities have been historically higher due to artificial water provision (Chamaillé-Jammes et al. 2007c). This was likely due to an underlying gradient in rainfall, lower in the western regions of the park (Chamaillé-Jammes et al. 2006). Scholes et al. (2002) found a positive relationship between annual rainfall and both tree basal area and tree height in neighbouring regions on Kalahari sands, consistent with studies conducted at the continental scale, demonstrating that rainfall defines potential woody cover which may actually not be achieved due to disturbances (Sankaran et al. 2005). This suggests that under the current water provision scheme current climatic change and increased drought severity occurring in HNP (Chamaillé-Jammes et al. 2007a) may be of more concern than high elephant densities for woody cover and habitat openness.

The most striking result of this study was that despite important mean effects, distance-to-water and herbivore abundance were very poor predictors of woody cover at any location. Not only do piospheres extend barely beyond 5 km of water, leaving >60% of the park unaffected (Chamaillé-Jammes et al. 2007b), but heterogeneity remained high within piospheres (Fig. 2b). Under the restricted policy of artificial water supply implemented in

Hwange NP, and despite the presence of one of the world’s largest elephant populations, the creation of piospheres by herbivores does not threaten ecosystem heterogeneity in woody cover, although this should be investigated further for other ecological variable such as species composition or structural elephant damage.

A recent study (Jafari et al. 2008) also suggested that heterogeneity may be increased within piospheres under commercial sheep grazing. Recognising that heterogeneity can be maintained within piospheres at any distance-to-water is important as heterogeneity may buffer the effects of reduced woody cover within these vital areas of the landscape, providing refuges for both animals and plants and offering persistence opportunities (Berryman and Hawkins 2006, Owen-Smith 2008). However, the causes underlying this heterogeneity remain poorly understood. Heterogeneity in both the initial vegetation and the foraging patterns of herbivores may affect vegetation patterns (Adler et al. 2001, in a piosphere context see for instance Weber et al. 1998), and ultimately herbivory is only one of many factors affecting woody cover (Sankaran et al. 2008), making local predictions on woody cover difficult without a complete knowledge of those determinants. As such knowledge is unlikely to be accessible to managers, our study thus suggests that surface-water provision policies directed at influencing woody cover would be effective only when considered at large landscape scales, with an underlying understanding that small-scale unpredictable heterogeneity within piospheres will persist.

Such knowledge should be taken into account when managing water-remoteness to moderate herbivore impacts across landscapes (O'Connor et al. 2007, Fensham and Fairfax 2008). These results also have implications for the use of piospheres in ecological modelling (Thrash and Derry 1999), suggesting that modelling vegetation responses as a purely deterministic function of distance-to-water would be greatly misleading. Ecologists should go beyond recognising the importance of mean effects of piospheres in the functioning of arid and semi-arid ecosystems, and gain an understanding of the role of persisting heterogeneity within these key areas.

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