

# Quantifying the effects of diverse private protected area management systems on ecosystem properties in a savannah biome, South Africa

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**Abstract** The effects of management on ecosystem diversity, structure and function must be understood for the sustainable integration of conservation and development. A potential source of experimentation and learning in ecosystem management is the array of private protected areas worldwide. Autonomous management systems can be seen as natural experiments, presenting an opportunity to explore the consequences of manipulating ecosystem properties. By quantifying management diversity and developing an index of management intensity we assessed the ecological correlates of private protected area management within the savannah biome in South Africa. Management intensity is positively correlated with herbivore density, predator density and ecotourism lodge density and negatively with herbivore community heterogeneity, reintroduction success and primary productivity at the local protected area scale. However, these trade-offs are tantamount to functional diversity as different management systems play unique roles in the regional socio-ecological and socio-economic systems, which range from animal production centres high in commercial value to low density areas that may sustain landscape processes. Furthermore, fenced private protected areas are necessary to safeguard rare species that cannot sustain viable populations in altered ecosystems. Thus, when considered at the regional scale, a private protected area network that constitutes a patchwork of management systems will create a coincident conservation and production landscape. We suggest that maintaining management heterogeneity will provide net benefits to biodiversity and potentially galvanize locally sustainable, wildlife-based economies.

**Keywords** Conservancy, functional diversity, herbivore community, management, natural experiment, private protected areas, social-ecological system

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## Introduction

Protected areas remain the cornerstones of conservation efforts worldwide. Although the total area under protection has increased significantly, protected areas suffer from isolation, external human population growth, poor funding, and inflexible management systems (Hansen & Defries, 2007; Wittemyer et al., 2008; Venter et al., 2008). Additionally, many protected areas are created by evicting local inhabitants, which may lead to the displacement of negative human impacts to other areas and diminish participatory approaches to conservation (Brockington & Igoe, 2006). Consequently, much research has focused on integrating conservation and development goals and promoting collaborative management systems that can deal with uncertainty, change and social equity (Leader-Williams, 2002).

Private protected areas are an increasingly important component of conservation planning. Private lands can form buffer zones, staging areas for migratory species, gap-fills for key habitats, and are often wildlife ranches that fulfil dual economic and conservation objectives (Du Toit & Cumming, 1999; Langholz & Lassoie, 2001; Bond et al., 2004; Langholz & Kerley, 2006). The management objectives of private protected areas range from intensive farming of a single species to mixed agriculture-wildlife ranches and conservancies (Bond et al., 2004). Through the wide range of land-tenure rights and fast-paced transactions characteristic of their owners, private protected areas may exhibit greater adaptive capacity compared to legislatively encumbered statutory parks (Carter et al., 2008), although such innovation is likely to vary according to national land legislation (Pasquini et al., 2011). However, there has been little research that addresses the effectiveness of private protected area management in conserving biodiversity at local or regional scales or in achieving economic and social development (Bond et al., 2004).

Conservancies are thought to have the greatest potential benefits for biodiversity and are expanding rapidly in southern Africa (Lindsey et al., 2009). They are formed when landowners eliminate internal fences and enter multi-tenure systems where land management is promulgated

through a constitution that binds landowners together in a shared vision of the landscape (Kreuter et al., 2010). This cooperative ethos presents opportunities for innovative partnerships between government agencies, conservation NGOs and private landowners in managing ecosystems (Leader-Williams, 2002; Carter et al., 2008; Lindsey et al., 2009). As such, conservancies can be viewed as natural experiments in management methodology that can be empirically tested for conservation effectiveness. The potential to learn from diverse management systems is enhanced by the difference between 'open' conservancies, which are those with all boundary fences removed between other conservancies and national parks, and 'closed' conservancies, which remain fenced from surrounding reserves and other land uses.

To increase operational efficiency, many conservancies implicitly manage within a balance of nature paradigm in which herbivore stocking rates are carefully controlled and practices such as supplementary feeding, predator contraception and artificial water-point construction are employed (Peel et al., 1999; Cronje et al., 2005; Kettles & Slotow, 2009). Intensive management is usually more common in smaller, closed conservancies (Peel et al., 1999). Intensifying management by overstocking herbivores and increasing artificial water-point density, however, may inadvertently undermine the resilience of the ecosystem by degrading local vegetation communities and homogenizing the landscape, which may lead to mammal population crashes and local extinctions (Walker et al., 1987; Owen-Smith, 1996; Harrington et al., 1999; Parker & Witkowski, 1999; Thrash, 2000).

However, the impact of overstocking and increased water provision is likely to be scale-dependent and contingent on the relative management objectives of small, isolated vs large, interconnected conservancies (Peel et al., 1999), which necessitates assessing the implications of conservancy management for biodiversity in regional contexts. Although numerous studies have documented the financial incentives for using wildlife as a resource (Langholz et al., 2000; ABSA Report, 2003; Langholz & Kerley, 2006), few studies have explored the subsequent trade-offs between economic optimization, ecosystem functioning and the diversity of plant and animal communities. Here we quantify the diversity of conservancy management systems within the eastern lowveld, South Africa. Our primary aim is to explore the consequences of conservancy management systems on key ecological variables and to assess whether differing levels of management intensity could produce regional benefits to biodiversity.

### Study area

We analysed a sample of 13 private conservancies located within the lowveld savannah biome to the east of the Drakensberg escarpment between 30°35' E and 30°40' E, and

24°00' S and 25°00' S (Peel et al., 2004, 2007). Unlike many conservancies in southern Africa that do not explicitly stock wildlife or that mix wildlife and livestock (Bond et al., 2004), the conservancies in the lowveld focus exclusively on wildlife management. Kruger National Park, because it is contiguous with or adjacent to all the study sites, was used as a reference national park management system. Some conservancies have dropped boundary fences to form part of the greater Kruger National Park ecosystem (albeit with autonomous management systems) whereas others have remained fenced (Fig. 1; note that labelling of conservancies has been anonymized for data privacy).

### Methods

Mammal count data for the private conservancies were obtained from the Agricultural Research Council's Animal Production Institute (ARC-API) in Nelspruit, South Africa. The data comprised annual (from 1992 in some conservancies) aerial surveys (total area counts from fixed-wing aircraft; 300–500 m strips) in late winter (August–September) when reduced vegetation growth facilitated highest visibility of animals. These surveys are solicited by conservancy managers as independent ecological audits and are thus performed by the same ARC-API team using the same methodology each year and are amongst the most reliable, long-term ecological datasets in Africa (Peel et al., 1999). Mammal count data for Kruger National Park, where total area counts for 1977–1997 and strip transect sampling for 1998–2008 were undertaken using a fixed-wing aircraft (Kruger et al., 2008), were obtained from South African National Parks (SANParks), Scientific Services, Skukuza. To make the transect data of the Park comparable with the total area counts of the conservancies, the effective strip widths were obtained from Kruger National Park Scientific Services and density was calculated by converting the transects to area (strip length × strip width). Densities of white rhinoceros, elephant and buffalo were calculated from a separate helicopter census (focusing on drainage networks; for 1985–2007) and were subsampled from the transects described above. Only the common time period shared amongst all conservancies was used (1999–2007). The common and Latin names of all species used in the analyses are listed in Appendix 1.

To calculate stocking rates the unit mass (the mean body mass of an age-structured population) of the species was used. However, the combined adult male and female body mass of each species was used when calculating offtake and translocation biomass values, as it is mostly adult animals that are hunted, culled or sold (Damm, 2005). Unless otherwise stated only the central section of Kruger National Park, which bounds the upper and lower limits of latitude of the private conservancy sample, was

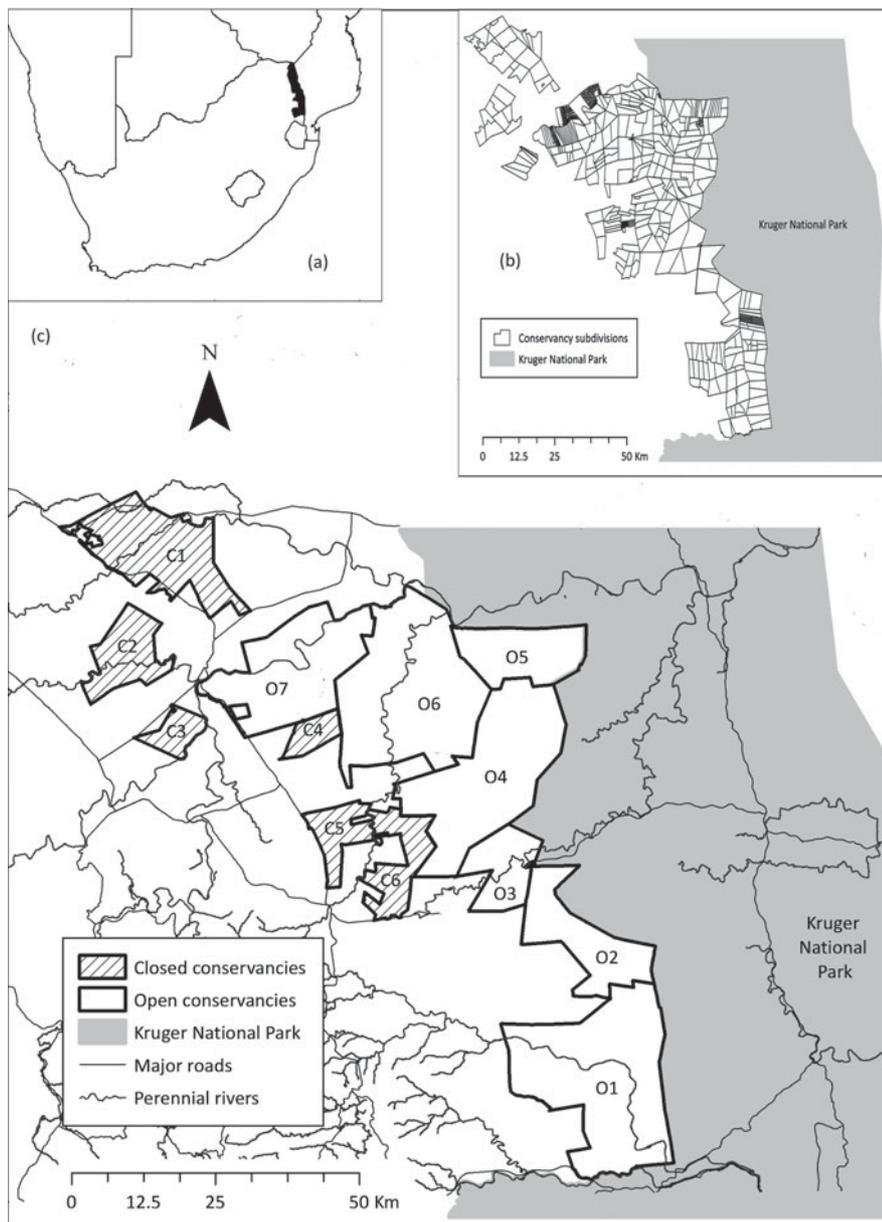


FIG. 1 (a) The study area borders Kruger National Park (shaded black) and is situated within the eastern lowveld savannah biome of South Africa. (b) The conservancies were heavily subdivided through cattle farming, peaking between the 1920s and 1960s. (c) Following the conversion from livestock farming to wildlife ranching (from 1948), internal fences were dropped and some conservancies became open to Kruger National Park (O1–O7), whereas others have remained fenced (C1–6).

used in the analyses (Fig. 1). Grass standing crop was measured annually as a function of primary productivity at multiple sites within each conservancy (longest time series: 1979–2009; time period shared across conservancies: 1992–2009). The surveys focus on the perennial grass component and are a good indicator of habitat condition (Peel et al., 1999). Grass communities were measured on transect lines using a disc pasture meter and converted to biomass using the calibration equation from Trollope & Potgieter (1986). Landscape vegetation structure has been classified at broad scales by using satellite imagery that has been corroborated by local empirical data (Peel et al., 2007). We summarized these data by calculating the proportion of closed woodland, open woodland, riverine woodland and grassland from each plant community within each conservancy.

Quantitative and qualitative variables relating to management were determined through 21 semi-structured interviews (lasting 50–70 minutes) with conservancy managers, from March to June 2010. Most were interviewed in person on the conservancy ( $n = 15$ ), but some were interviewed by telephone ( $n = 6$ ). Managers from all conservancies from which ARC-API data were available were interviewed, as well as representatives from other private protected areas within the area (all interviewees were informed beforehand of strict confidentiality). The interviews were primarily aimed at securing permission to access the ARC-API mammal count and grass biomass data, as well as quantitative records relating to culling, hunting, reintroductions and translocations. In the absence of quantitative records of other management variables (for example, burning and bush-clearing records), managers

were asked standardized questions with binary answers relating to the degree of management of other variables (Appendix 2). These answers were transcribed by hand and coded as ordinal variables for use in the management index.

Spatial analyses were carried out in *ArcGIS v. 9.3* (ESRI, Redlands, USA) and other statistics in *SPSS v. 17.0* (SPSS Inc., Chicago, USA). Although the total conservancy sample size was 14 (including Kruger National Park), most analyses were performed with 10–12 conservancies because data were unavailable for particular variables in some conservancies. All variables were checked for normality and homoscedasticity, using a Kolmogorov–Smirnov test and Levene’s test, respectively. If the variables did not conform to parametric assumptions a non-parametric test was used to corroborate or refute the results and Monte Carlo simulations were used to assess the significance of the test statistic. The large scales of the study necessitated the inclusion of many variables, which could have led to confounding effects. Before every analysis involving large variable sets a multiple regression was used to detect redundant variables, thereby reducing conflation between predictor variables. Ordinary least squares (OLS) regression or logistic regression models were used for univariate analyses of continuous and ordinal variables, respectively. Analyses of variance (ANOVAs) were corrected post hoc through the Bonferroni test for multiple comparisons, to minimize Type I error. Partial regressions were used when two or more explanatory variables correlated significantly with the response variable, to ascertain the independent effect of each explanatory variable. An analysis of covariance (ANCOVA) was employed to control for the effects of rainfall on primary productivity and the residual variation was correlated with management intensity. The success or failure of reintroductions (species new to or not currently found in the conservancy) and translocations (species already present within the conservancy) was also explored through binary logistic regressions. Reintroduction success was defined as the presence of the species for each year subsequent to the reintroduction. Environmental variables (rainfall, altitude, landscape structural diversity and plant community richness) were used as control explanatory variables in all analyses.

Because of data insufficiency and the limitations of traditional multivariate analyses (Appendix 3), a novel approach to quantifying management patterns was used. We hypothesized that the effects of management interventions might be hierarchically nested and exert different scales of influence on ecosystem properties. To create a hierarchical management intensity index (MII) we used eight management predictor variables (road density, building density, artificial water-point density, burning practice, bush-control practice, mammal biomass removal, mammal biomass addition and the number of species manipulated). We then allocated each variable to one of three levels. Level 1

variables (artificial water-point density, building density, road density) were classified as ‘fixed’, and exert a sustained spatio-temporal influence on ecological variables. These variables may also be indirect indicators of unseen management intensity mechanisms such as infrastructural disturbance and fine-scale habitat alteration (for example, bush thickening on road verges; Smit & Asner, 2012). Level 2 variables (burning, bush-control) were classified as ‘periodic’, and exert broad-scale but intermittent influences. Level 3 variables (hunting, culling, translocation) were classified as ‘continuous’, and equate to small-scale community or species-specific practices (Appendix 4).

All data were standardized (Appendix 4) and relativized (giving each variable the same overall weight within the hierarchical level) to correct for measurement inequalities. This was achieved by dividing each value of each variable by the sum total for that variable, then multiplying by the conservancy sample size ( $N$ ; Equation 1). The multiplication step created an intuitive index whereby each conservancy occupied on average one unit of the total ‘management space’ for that variable. The relativized values from each hierarchical level were then summed. Each sum was multiplied through by a correction factor so that the number of variables in each hierarchical level did not bias the index. Thus, the weight of each variable was equalized throughout the sample and the variance structure was conserved. The final step was to weight the hierarchical levels differentially. Level 1 landscape features were assumed to have the most explanatory power, thus were weighted 3. Level 2 periodic disturbances were weighted 2, and Level 3 community disturbances weighted 1. These three values were then summed to produce the final MII (Equation 1).

$$\text{MII}_c = \left[ \text{SF}_1 \times \text{CF}_1 \times \left( \sum_{i=1}^3 \frac{N \times V_{ci}}{\sum v_i} \right) \right] + \left[ \text{SF}_2 \times \text{CF}_2 \times \left( \sum_{j=1}^2 \frac{N \times V_{cj}}{\sum v_j} \right) \right] + \left[ \text{SF}_3 \times \text{CF}_3 \times \left( \sum_{k=1}^3 \frac{N \times V_{ck}}{\sum v_k} \right) \right] \quad (1)$$

where  $\text{MII}_c$  = the management intensity index for conservancy  $c$ ,  $N$  = number of conservancies,  $i$  = variables in level 1,  $j$  = variables in level 2,  $k$  = variables in level 3,  $V_{ci}$  = value of variable  $i$  in conservancy  $c$ ,  $\text{SF}$  = hierarchical scaling factor, and  $\text{CF}$  = correction factor. Equation 1 can be expanded to include more hierarchical levels or different weighting as appropriate for each context. We tested the efficacy and explanatory power of hierarchically organizing the MII by repeating all analyses with a non-weighted index. Similarly, the summed variables from each hierarchical level were used as separate predictors to test whether one hierarchical level of management could parsimoniously explain ecological variance.

## Results

Management systems were significantly different between conservancies (Kruskal–Wallis:  $H_{13, 14} = 25.3$ ,  $P = 0.02$ ,  $n = 14$ ). The combination of management practices employed, as well as the degree of commercial diversification and specialization, varied considerably across conservancies (Table 1). Management infrastructure was denser in the private conservancies than in Kruger National Park (Student's  $t$ -test:  $t_{13, 14} = 31.4$ ,  $P < 0.05$ ,  $n = 14$ ; Fig. 2). At the conservancy scale fixed management variables generally did not correlate with each other (Pearson correlation: average  $r = 0.35 \pm \text{SD } 0.36$ , average  $P = 0.22 \pm \text{SD } 0.20$ ,  $n = 132$  correlations). However, road network, artificial water-point density and lodge density were positively related and appeared to form a management syndrome (Pearson correlation:  $0.57 < r < 0.83$ , all  $P < 0.05$ ,  $n = 19$  correlations). The average biomass input and output per year was significantly higher in closed conservancies (Student's  $t$ -test:  $t_{11, 12} = 1.9$ ,  $P = 0.02$ ,  $n = 12$ ; and  $t_{11, 12} = 1.8$ ,  $P = 0.04$ ,  $n = 12$ , respectively; Fig. 3). Conservancy O7 was the only open conservancy to import biomass on a level comparable to its exports ( $1.1 \pm \text{SD } 0.7$  compared with  $1.6 \pm \text{SD } 0.7 \text{ kg ha}^{-1} \text{ year}^{-1}$ ).

Management variables were combined hierarchically into an MII, which is a significantly better indicator of ecological properties than non-weighted or single-hierarchy indices (Appendix 4). MII and lodge density showed the strongest positive correlation (OLS regression:  $r = 0.83$ ,  $F_{13, 14} = 22.1$ ,  $P < 0.01$ ,  $n = 14$ ). Lodge density as an explanatory variable also had high correlative significance, although the average coefficient of determination value across response variables was half that of MII ( $R^2 = 0.62 \pm \text{SD } 0.09$  and  $0.33 \pm \text{SD } 0.16$ , respectively; Student's  $t$  test:  $t_{6,9} = 2.31$ ,  $P = 0.01$ ,  $n = 6$ ). Overall, univariate regressions revealed insignificant trends and the MII possessed by far the strongest correlative values (Appendix 3).

Most climatic and environmental variables were similarly distributed amongst conservancies (Kruskal–Wallis:  $H_{13, 14} = 10.3$ ,  $P = 0.75$ ,  $n = 14$ ). Landscapes were dominated by closed woodland and, to a lesser degree, open woodland (Table 2; Peel et al., 2007). There was little grassland cover (0.5–1.2%). Thus, landscape structural diversity was comparable amongst the conservancies at a broad scale. Rainfall distribution, however, was significantly different between the conservancies (ANOVA:  $F_{10, 14} = 3.2$ ,  $P < 0.05$ ,  $n = 14$ , range 224–1,164 mm in a season). Rainfall is the strongest driver of primary productivity in the lowveld savannah systems (Peel et al., 2004, 2007) and, as expected, there was a strong linear relationship between average annual grass biomass and rainfall (OLS regression:  $r = 0.87$ ,  $F_{9, 10} = 24.7$ ,  $P < 0.01$ ,  $n = 10$ ). Average grass productivity was significantly different between conservancies when factoring out the covariance of rainfall (ANCOVA:  $F_{9, 10} = 26.1$ ,  $P < 0.01$ ,

$n = 10$ ) and the residual variation was significantly negatively correlated with MII (OLS regression:  $r = -0.70$ ,  $F_{11, 12} = 7.4$ ,  $P = 0.02$ ,  $n = 10$ ; Fig. 4a).

Herbivore density (both numbers  $\text{ha}^{-1}$  and biomass  $\text{ha}^{-1}$ ) was significantly positively correlated with MII (OLS regression:  $r = 0.73$  and  $0.84$ , respectively,  $F_{11, 12} = 11.1$  and  $24.4$ , respectively, both  $P < 0.01$ , both  $n = 12$ ; Fig. 4b) but not with individual management variables (partial correlations:  $0.10 < r_p < 0.69$ , all  $P > 0.13$ ,  $n = 18$  correlations). Although total herbivore biomass was not significantly higher in closed compared to open conservancies ( $31.1 \pm \text{SD } 13.8$  and  $43.4 \pm \text{SD } 13.4 \text{ kg ha}^{-1}$ , respectively; Student's  $t$ -test:  $F_{12, 14} = 0.1$ ,  $n = 14$ ,  $P = 0.76$ ), herbivore density was almost double that of open conservancies ( $0.30 \pm \text{SD } 0.11$  and  $0.16 \pm \text{SD } 0.8 \text{ herbivores ha}^{-1}$ , respectively; Student's  $t$ -test:  $F_{12, 14} = 5.9$ ,  $n = 14$ ,  $P < 0.01$ ). Density estimates were not an artefact of temporal sample size (OLS regression: adjusted  $R^2 = 0.22$ ,  $F_{11, 12} = 4.2$ ,  $P = 0.11$ ,  $n = 14$ ), and were confounded by neither rainfall (OLS regression: adjusted  $R^2 = 0.17$ ,  $F_{11, 12} = 1.8$ ,  $P = 0.20$ ,  $n = 12$ ) nor biomass (OLS regression: adjusted  $R^2 = 0.10$ ,  $F_{12, 14} = 0.5$ ,  $P = 0.51$ ,  $n = 14$ ). The MII was also significantly positively correlated with predator density (OLS regression:  $r = 0.78$ ,  $F_{12, 13} = 10.1$ ,  $P < 0.01$ ,  $n = 11$ ; Fig. 4c).

There were significant differences in herbivore community composition between conservancies (MANOVA:  $F_{11, 12} = 75.2$ ,  $P < 0.01$ ,  $n = 12$ ), and the pairwise species differences were significantly correlated with MII (OLS regression:  $r = 0.80$ ,  $F_{13, 14} = 17.8$ ,  $P < 0.01$ ,  $n = 12$ ; Fig. 4d). Herbivore community evenness was significantly higher in closed compared to open conservancies ( $0.73 \pm \text{SD } 0.09$  and  $0.57 \pm \text{SD } 0.07$  respectively, Student's  $t$  test:  $t_{11, 13} = 3.2$ ,  $P < 0.05$ ,  $n = 14$ ). A series of linear regression models was used to estimate population trends for each species in each conservancy. Although species showed varied population trends within different conservancies, there were clear subsets of species that were prospering and those that were declining or kept at low densities: larger herbivores such as elephant, buffalo, kudu and white rhinoceros, and mixed feeders such as impala, showed strong increases in most conservancies, whereas specialist grazers such as sable, roan, tsessebe and eland were declining or locally extinct in the majority of conservancies (Table 3); many of these species were the subjects of reintroduction attempts. Out of 43 recorded reintroduction and translocation attempts, 40% led to local extinctions of the reintroduced/translocated species, 22% exhibited declining populations, and 38% exhibited stable or increasing populations. Of reintroduction attempts alone ( $n = 28$  records, comprising primarily obligate or specialist grazer species) 72% resulted in local extinction of the reintroduced species. Reintroduction success was significantly negatively correlated with MII and significantly positively correlated with primary productivity (binary logistic regression:  $\chi^2_{4, 41} = 12.8$ ,  $P = 0.01$ ,

TABLE 1 A summary of the differences between the 13 conservancies and Kruger National Park in quantitative and qualitative management variables. All density variables are units per 1,000 ha.

Conservancy	Artificial water-point density	Building density	Road density	Commercial lodge density	Mean lodge price per night $\pm$ SD (USD)	Reintroductions/translocations	Hunting/culling	Live animal sales	Rare species breeding camp	Supplementary feeding	Burning <sup>1</sup>	Bush clearing <sup>2</sup>
C1	0.6	3.3	12.2	0		Y	Y	Y	Y	Y	Block	Extensive
C2	1.2	6.0	16.9	0.15	440 $\pm$ 80	Y	Y	Y	Y	Y	None	Fine scale
C3	0.7	10.0	19.5	0		Y	N	Y	Y	Y	None	Fine scale
C4	3.6	9.0	14.1	0.21	80	Y	N	Y	Y	Y	None	Fine scale
C5	4.3	6.6	27.6	0.46	420 $\pm$ 70	Y	N	Y	N	N	Block	Extensive
C6	3.0	5.5	22.2	0.95	490 $\pm$ 160	Y	Y	N	N	N	Block	Extensive
O1	6.2	9.5	17.5	0.52	200 $\pm$ 110	Y	Y	Y	N	Y	None	Fine scale
O2	1.9	2.3	15.6	0.07	300 $\pm$ 30	Y	Y	Y	N	Y	ARC	Fine scale
O3	2.9	5.1	23.5	0.05	480	N	Y	N	N	N	ARC	Extensive
O4	3.5	2.7	15.8	0.13	450 $\pm$ 180	N	Y	N	N	N	ARC	Fine scale
O5	1.3	1.3	13.8	0		N	N	N	N	N	PM	None
O6	1.6	1.4	13.2	0.13	360 $\pm$ 140	N	N	N	N	N	Block	None
O7	4.7	5.3	31.0	0.47	770 $\pm$ 370	Y	N	Y	N	Y	Block	Extensive
Kruger National Park (central district) <sup>3</sup>	0.1	0.4	4.7	0		N	N	N	N	N	PM	None

<sup>1</sup>None, no burning was implemented because of poor fuel load; PM, patch mosaic burning practice; ARC, burning prescribed by Agricultural Research Council; block, regular burning of reserve on rotation

<sup>2</sup>Fine-scale, practices such as bush-cutting and individual shrub thinning, tends to occur in small patches largely dependent on the individual landowner; extensive, an institutionalized policy involving the removal of swathes of bush, often with the use of a bulldozer, across large areas to create artificial savannahs

<sup>3</sup>Managers in Kruger National Park engage in small-scale bush-clearing along road verges, game capture for translocations and sales, and lease limited numbers of private concessions within the Park. However, these practices are not on the same scale as in the private conservancies and were assumed to be negligible in the context of this study. Reintroductions (e.g. rhino, Lichtenstein hartebeest) occurred in the Park formerly but not in recent years. Two rare antelope breeding camps occur in the northern district of the Park. No large-scale culling has taken place in the Park since 1994.

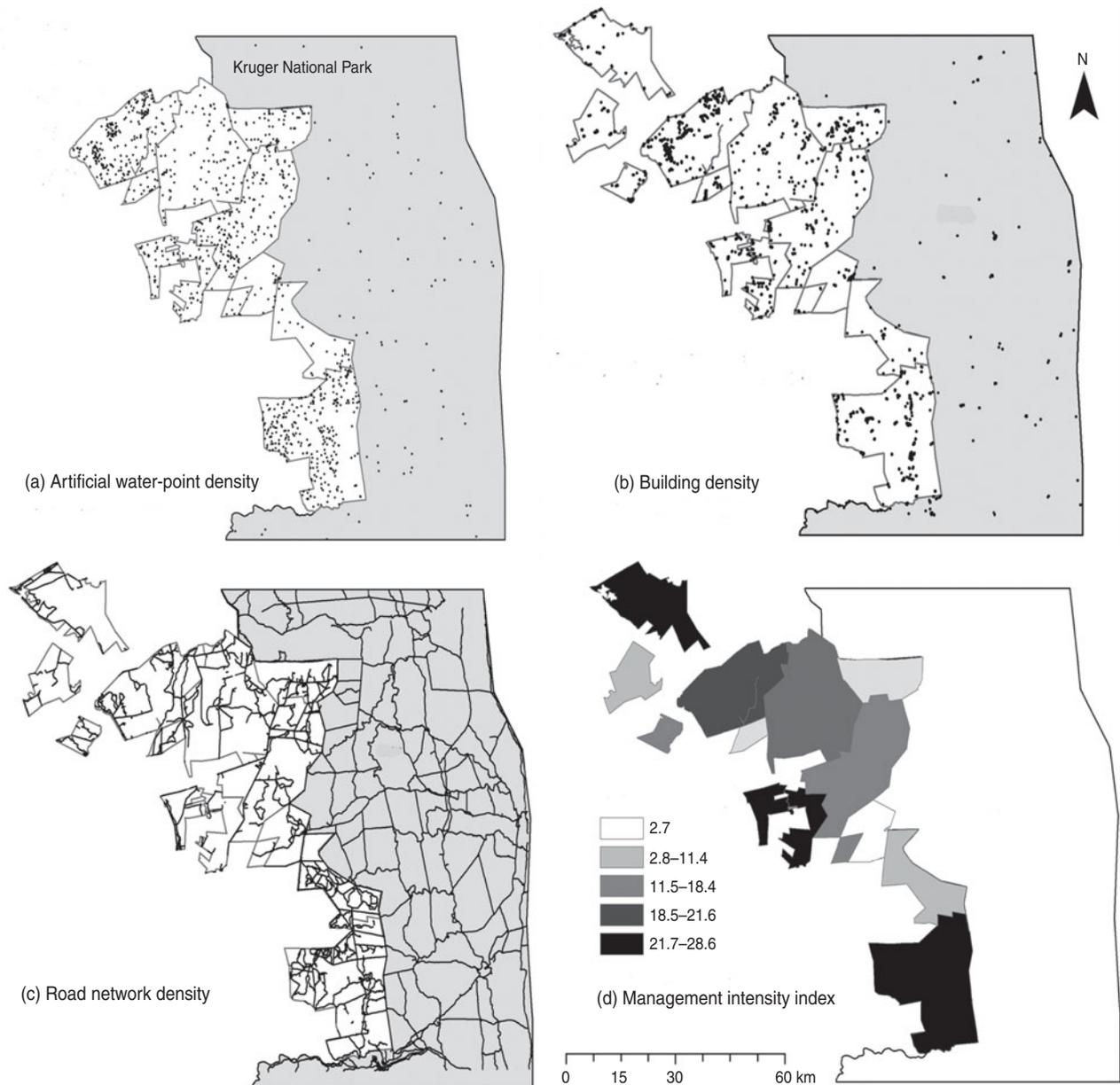


FIG. 2 Management infrastructure is significantly denser in the private conservancies than in Kruger National Park for (a) artificial water-point density (only georeferenced data shown), (b) building density, and (c) road network density (only tarred roads). Overall, there are also significant differences in (d) management intensity between conservancies as measured by the management intensity index (MII, see text for details).

$n = 41$  reintroduction attempts, Wald statistic = 3.9 and 7.2 for MII and primary productivity respectively, both  $P < 0.05$ ).

## Discussion

Conservancy management systems are significantly heterogeneous within the lowveld region of South Africa. Management heterogeneity has emerged in this region in response to the numerous economic and cultural values of wildlife (Kreuter et al., 2010), and these diverse management paradigms have distinct impacts on ecosystem properties.

Management intensity correlates positively with herbivore density and stocking rate, predator density, commercial lodge density and herbivore community heterogeneity but negatively with primary productivity and reintroduction success. Thus, there are local trade-offs involved with both low and high intensity management, but which may generate net benefits to both conservation and the rural economy at the regional scale.

Intensively managed conservancies may provide greater revenue through ecotourism, hunting and live animal sales but are more likely to diminish habitat condition and species richness. These conservancies have both higher

TABLE 2 A summary of the environmental and broad-scale landscape properties across conservancies.

Reserve	Mean annual rainfall $\pm$ SD	Mean annual temperature ( $^{\circ}$ C)	Mean altitude $\pm$ SD (m)	Structural landscapes (n) <sup>1</sup>	Closed woodland (%)	Open woodland (%)	Structural diversity <sup>2</sup>	River length (km ha <sup>-1</sup> )
C1	480 $\pm$ 139	21	517 $\pm$ 39	2	76	21	0.34	0.9
C2	450 $\pm$ 154	21	482 $\pm$ 25	3	72	15	0.28	1.3
C3	473 $\pm$ 180	21	471 $\pm$ 34	2	76	21	0.34	1.8
C4	452 $\pm$ 124	21	465 $\pm$ 23	1	76	21	0.34	0.0
C5	560 $\pm$ 135	20	539 $\pm$ 30	5	67	19	0.35	0.9
C6	579 $\pm$ 203	20	526 $\pm$ 29	5	69	18	0.33	1.0
O1	423 $\pm$ 140	21	414 $\pm$ 39	4	82	23	0.34	1.1
O2	463 $\pm$ 178	21	405 $\pm$ 45	4	76	21	0.34	0.9
O3	447 $\pm$ 184	22	345 $\pm$ 20	2	77	21	0.34	0.0
O4	582 $\pm$ 199	21	443 $\pm$ 49	5	76	22	0.35	0.4
O5	563 $\pm$ 221	21	474 $\pm$ 23	4	76	25	0.37	1.3
O6	590 $\pm$ 280	21	419 $\pm$ 29	5	72	25	0.38	0.0
O7	685 $\pm$ 221	21	366 $\pm$ 41	5	71	24	0.38	0.8
Kruger National Park (central district)	523 $\pm$ 213	22	310 $\pm$ 65	5	42	13	0.36	0.9

<sup>1</sup>The number of broad-scale landscape habitats within the conservancy region, including both grassland and woodland communities (sensu Peel et al., 2007)

<sup>2</sup>Structural diversity, as estimated through Simpson's evenness index, was calculated using all classified landscape types within the conservancy

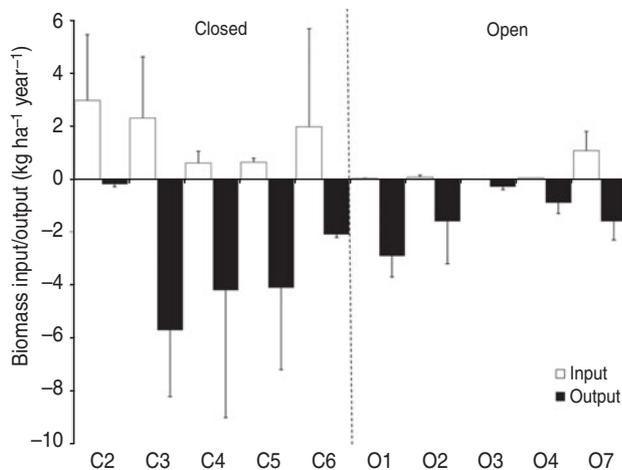


FIG. 3 Annual mammalian biomass input (translocation, reintroductions) and output (culling and hunting) across conservancies (Fig. 1c). Mammalian biomass is intensively managed on most conservancies, especially closed conservancies. Nearly all conservancies take more biomass out of the system than they add.

animal density and biomass than Kruger National Park whereas less intensively managed conservancies have herbivore densities comparable to those of the Park. The bulk of this difference comprises megaherbivores (elephant, buffalo and white rhino), some of which are prime trophy-hunting species, and generalist antelopes, such as impala, which are an alternative source of protein to cattle. Thus, intensively managed conservancies could function as

animal production centres, providing low-cost, low-carbon and resource-efficient protein for rural communities and catalyse sustainable development in these areas (Du Toit & Cumming, 1999; Leader-Williams, 2002; ABSA Report, 2003), as well as potentially increasing revenue from trophy hunting. High-intensity management also requires many subsidiary services, such as game capture teams, veterinarians, hunting equipment suppliers, accommodation and supplementary feed farms (as primary productivity declines more forage must be imported during lean periods), which stimulates the local economy (ABSA Report, 2003; Langholz & Kerley, 2006). Several conservancies have even founded Wildlife Colleges that provide ecological education and diplomas in game ranging and management (M.F. Child, unpubl. data). An economy based on wildlife, therefore, might become more self-sustaining and reduce resource leakage associated with exclusionary ecotourism (Leader-Williams, 2002; Ewers & Rodrigues, 2008). Conversely, low-intensity management may not be as economically lucrative but is more likely to support specialist and rare herbivore species, provide refugia for vegetation sensitive to high levels of herbivory, and act as reserve forage areas in periods of intense droughts (in open systems). Thus it is likely that low-intensity conservancies perform key ecological roles within the broader landscape.

Differing levels of management intensity correlates with herbivore mammal community heterogeneity. In open conservancies managers use artificial water-points to prevent game from moving into adjacent conservation areas

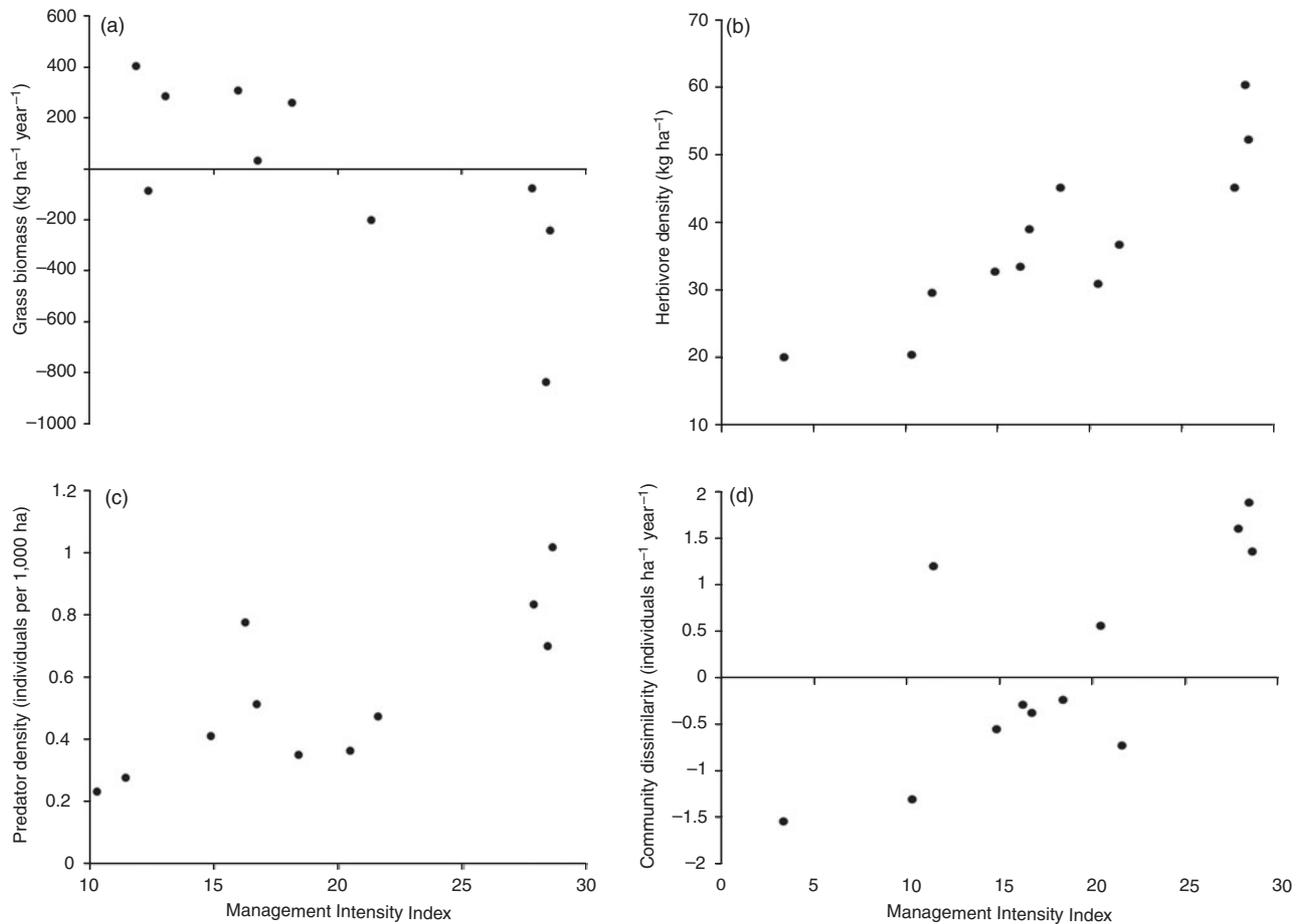


Fig. 4 The management intensity index (MII, see text for details) is a strong predictor of several important ecological variables at the conservancy scale: it is (a) negatively correlated with the residual variation in primary productivity, where negative residuals indicate that the conservancy exhibits lower grass biomass than expected by rainfall, (b) positively correlated with herbivore stocking rate, (c) positively correlated with predator density, measured as the numbers of lion, leopard, cheetah, hyena and wild dog per 1,000 ha, and (d) positively correlated with the pairwise species density differences in the composition of the herbivore community, in which more intensive management is associated with the largest positive differences (i.e. higher densities) between species.

(Cronje et al., 2005). However, water provision is irregular across conservancies. For example, the managers at conservancy O6 do not pump water into artificial dams, effectively transforming them into seasonal sources of water (Cronje et al., 2005). O6 is the only conservancy to show decreases in highly water-dependent species, such as impala and waterbuck, and to have recorded natural (i.e. not reintroduced) populations of sable in its most recent census, which perhaps indicates a gradual ecological specialization in areas with low management intensity. Such differentiation could accommodate a range of tourist viewing preferences, in which conservancies with high management intensity provide so-called big-five tourism and those with low management intensity facilitate sightings of rare antelopes (Lindsey et al., 2007). In Kruger National Park different recreational zones incorporate diverse societal values and tourist experiences (Freitag-Ronaldson et al., 2003). The zones delineate areas intended for high impact recreation (high-density development, extensive road

networks, artificial water provision and motorized game drives) and areas that preserve a feeling of remoteness or wilderness. Conservancies could be zoned according to similar criteria, thus creating a mosaic landscape of conservation and economic benefits.

Both open and closed conservancies are necessary to achieve development and conservation goals. The biomass output from closed systems is significantly higher than in open conservancies and thus closed systems are crucial in the broader socio-ecological system as sites for live animal auctions that can provide species for other conservancies. Closed conservancies (especially intensively managed conservancies) also retain specialist grazers such as sable that are struggling to persist in open systems within the regional landscape and therefore contribute to biodiversity conservation. As our data show, four of the six closed conservancies contained rare species' breeding camps or disease-free buffalo breeding projects, compared to none of the open conservancies (but see Table 1).

TABLE 3 Estimates of species trends (1999–2007) as determined by linear regressions for each species in each conservancy and in Kruger National Park (KNP). Species (rows) display divergent success rates (+ and – indicate positive and negative trends, respectively, over the time period) in different conservancies. Some species have become locally extinct (le). Missing data for a particular species in a conservancy is indicated by ‘md’ and neutral population trajectories are ‘nt’. Species with asterisks are extralimital. These trends are summarised by species and conservancy in the last four columns and rows, respectively. The Latin names of all species are given in Appendix 1.

Species	Conservancy												KNP (central district)	Increasing	Stable	Decreasing	Locally extinct
	C2	C3	C4	C5	C6	O1	O2	O3	O4	O5	O6	O7					
Black rhino	md	md	md	md	nt	md	nt	md	md	md	nt	md	nt	0	4	0	0
Blue wildebeest	+	+	–	–	–	–	–	–	–	+	–	+	+	5	0	8	0
Buffalo	md	md	+	nt	+	+	+	+	+	+	+	+	–	9	1	1	0
Bushbuck	+	nt	nt	nt	nt	nt	+	nt	nt	nt	+	–	md	3	8	0	0
Duiker	+	nt	nt	–	+	–	+	nt	nt	–	–	–	md	3	4	5	0
Eland	+	+	nt	–	le	le	md	md	md	md	md	md	nt	2	2	1	2
Elephant	+	md	nt	+	+	+	+	+	+	+	+	+	+	11	1	0	0
Gemsbok*	le	le	le	+	md	le	md	1	0	0	4						
Giraffe	+	nt	–	nt	nt	nt	–	–	–	–	–	–	+	2	4	7	0
Grysbok	le	nt	md	md	md	nt	nt	nt	md	md	md	md	md	0	4	0	1
Hartebeest*	le	md	le	md	le	md	md	md	le	md	md	md	md	0	0	0	4
Hippopotamus	nt	nt	md	+	+	+	+	nt	+	nt	nt	+	md	6	5	0	0
Impala	+	+	+	–	+	+	+	+	+	+	–	–	+	10	0	3	0
Klipspringer	md	nt	md	md	md	nt	nt	nt	md	md	md	+	md	1	4	0	0
Kudu	+	+	–	–	+	+	+	+	+	+	–	+	+	10		3	0
Mountain reedbuck	md	le	le	le	md	0	0	0	3								
Nyala	+	+	le	+	+	nt	nt	nt	nt	md	nt	+	md	5	5	0	1
Reedbuck	le	md	le	le	le	md	md	md	md	md	nt	nt	nt	0	3	0	4
White rhino	nt	nt	+	nt	+	+	+	nt	+	+	–	+	+	8	4	1	0
Roan	md	md	md	md	le	le	md	le	le	le	md	le	le	0	0	0	6
Sable	le	md	le	md	md	le	le	md	md	md	+	le	nt	1	1	0	5
Sharpe’s grysbok	md	md	md	md	md	le	le	md	md	md	md	md	md	0	0	0	2
Steenbok	+	nt	nt	nt	nt	–	+	+	+	+	+	nt	md	6	5	1	0
Tsessebe	md	le	le	le	md	nt	0	1	0	3							
Warthog	+	+	–	–	+	–	–	nt	–	+	–	–	+	5	1	7	0
Waterbuck	+	+	–	–	+	–	–	nt	+	+	–	+	+	7	1	5	0
Zebra	+	+	+	–	+	–	–	–	–	+	–	–	+	6	7	0	0
Increasing	13	8	4	4	11	5	9	5	8	10	4	9	9				
Stable	2	8	5	4	4	5	4	9	3	2	4	2	5				
Decreasing	0	0	5	8	1	6	5	3	4	1	9	6	1				
Locally extinct	5	3	7	2	4	6	2	1	2	1	1	2	1				

Thus, although high-intensity management generates economic and conservation value, the negative consequences of high-intensity management on reintroduction success and primary productivity highlight the necessity for a comprehensive regional management plan. The functional effects of each conservancy should be maintained and its economic, social and ecological outputs integrated into local development, with each conservancy aware of its role within the system and how its experiences can be fed back into regional management objectives. For example, although there are many positive aspects to conservancy expansion and de-fencing conservation areas (Lindsey et al., 2009), the functional value of closed conservancies may be negated by coalescing into larger, interconnected conservancies, which could erode biodiversity both locally and regionally (Child, 2010). Rather, a medley of management regimes and fenced vs unfenced conservancies may be needed to sustain stable populations of rare species and provide support services to larger conservancies (Langholz & Kerley, 2006; Child, 2010). The elucidation of the positive role of private conservancy management heterogeneity can help garner public support for wildlife entrepreneurship and encourage government agencies to provide appropriate services to landowners (sensu Pasquini et al., 2010).

This study has demonstrated that private conservancies in South Africa's lowveld possess a high degree of diversity in management practice, with concomitant differences in ecosystem properties. We suggest that management heterogeneity corresponds to socio-economic and socio-ecological functional diversity. Intensively managed conservancies produce high mammal densities, which generate revenue from both ecotourism and hunting, and create demand for subsidiary services within a wildlife-based economy. Less intensively managed conservancies tend to preserve a greater wilderness aesthetic, reflected ecologically by greater primary productivity, lower overall mammal densities, and the greater likelihood of the persistence of specialist grazers. Furthermore, both open and closed conservancies play vital functional roles: closed conservancies not only produce higher biomass output but often develop fenced-off species' breeding camps within the conservancy. Conservancies open to Kruger National Park tend to have diversified commercially into areas of big-five ecotourism and form important components of trans-frontier endeavours (Venter et al., 2008). Thus, there is empirical evidence that, within this regional array of conservancies, both economic and conservation objectives can be mutually satisfied (sensu Polasky et al., 2005). Governmental conservation bodies and conservation NGOs should promote and support the management heterogeneity that exists within private protected areas. This, we believe, will be an effective method of integrating conservation and development.

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## Appendices 1–4

The appendices for this article are available online at <http://journals.cambridge.org>

## Biographical sketches

MATTHEW CHILD is interested in the relationship between biodiversity and society, particularly the ways in which effective conservation could promote a culture of ecological mindfulness. MICHAEL PEEL initiated the Savanna Ecosystem Dynamics Project in the eastern lowveld in 1989. He researches the potential of the natural resources of savannahs to contribute to the economic development of southern Africa in harmony with social and environmental needs. IZAK SMIT conducts research on the use of geographical information systems and remote sensing for detecting spatio-temporal ecological patterns that may be of relevance to the effective management of conservation areas. WILLIAM SUTHERLAND has wide interests in conservation biology and is committed to making global conservation practice more rigorous. His work involves using evidence-based conservation to collate experience of the effectiveness of interventions (see <http://www.conservationevidence.com>) and then using this evidence to advise practice.