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# Elephant seasonal vegetation preferences across dry and wet savannas

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ABSTRACT

As African savanna elephants (*Loxodonta africana*) become increasingly confined to smaller fragmented landscapes, concern over their potential detrimental impacts on vegetation and biodiversity has increased. Understanding elephant vegetation preferences across relevant spatial and temporal scales is a critical step towards managing protected areas for the persistence of both elephants and biodiversity. To better understand elephant vegetation selection, we fitted 68 elephants with GPS collars across a strong rainfall gradient spanning seven southern African countries over a period of 6 years. We compared elephant locations with remotely-sensed environmental data that measure bi-monthly vegetation greenness across the study area. Elephants consistently seek out greener than expected vegetation throughout the year. Interestingly, they do so by utilizing vegetation with different phenologies and by selecting landscapes when they are greener than their surroundings. We found no differences between dry and wet savannas. These patterns persist even when elephants are constrained by seasonally available water. In the wet season, elephants select seasonally variable landscapes such as open woodlands, shrublands, and grasslands. These landscapes have a lower average annual greenness but become very green for a few months in the wet season. In the dry season, elephants prefer less variable landscapes that are more consistently green year-round such as well-wooded areas and closed woodlands. Because elephants prefer different vegetation types at different times of the year, small homogeneous protected areas may be unsuitable for elephants. Since elephants prefer woody vegetation during the dry season when they are constrained by water, human actions that increase dry season water availability may contribute to detrimental elephant impacts on vegetation and biodiversity.

## 1. Introduction

Across their range, human persecution that has eliminated the African savanna elephant (*Loxodonta africana*, hereafter "elephants") from wide areas or else left them at very low numbers (Brugiere et al., 2006; Douglas-Hamilton, 1987; Dublin et al., 1995). In some areas, however, effective protection has allowed them to increase rapidly (Dunham, 1988; Skarpe et al., 2004). A major consequence of these changes is that elephants are an increasingly perennial presence on relatively small protected areas as opposed to a dispersed and often seasonal presence across much larger areas (Van Aarde and Jackson, 2007). As a result, there has been increasing concerns over the detrimental effects of localized elephant impacts on vegetation and biodiversity (Cumming et al., 1997; Kerley et al., 2008). To effectively manage elephant populations within protected areas and to better understand the possible impacts of elephants on biodiversity, understanding how elephants interact with vegetation over relevant spatial and temporal scales is critical.

Most elephant vegetation selection evidence comes from localized studies from single sites (Guldemond and Van Aarde, 2008). If elephant vegetation preferences vary across precipitation gradients, we would expect different localized studies to yield different results. Likewise, other factors that trade-off with herbivore foraging choices such as predator avoidance (Kie, 1999) and water availability (Redfern et al., 2003) vary geographically. Separating the influence of these factors from the influence of greenness requires a large study area with diverse combinations of landscapes. We characterize elephant vegetation preferences for 68 elephants across a broad precipitation gradient spanning seven countries. We evaluate vegetation preferences by comparing where elephants are to where they are not. To control for the influence other landscape factors that may complicate this comparison, we use two different approaches for defining "counterfactual" locations from which elephants are absent.

We characterize vegetation using remotely sensed estimates of greenness. Greenness can be measured across large spatial scales

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and often correlates with vegetation nutritional quality (Macandza et al., 2004; McNaughton, 1985). In many seasonal savanna ecosystems, the phenology of vegetation is critical towards predicting use by herbivores (Fryxell et al., 2004). Accordingly, we gather remote sensing images every 16 days to ensure that we are measuring greenness of each location when it was visited by elephants. Greenness changes dynamically from month to month, but vegetation types are relatively static across the landscape. To understand the roll of greenness in the context of these different vegetation types, we generate long term greenness statistics and vegetation classifications.

To structure the analysis, we define three objectives in the form of the following questions: (1) do elephants select vegetation that is greener than the surrounding vegetation? (2) What types of vegetation, as characterized by mean annual greenness and variability, do elephants select? (3) Does characterizing vegetation based on greenness and variability provide insight into the vegetation's structure selected by elephants? The interpretation of these results provides insight into the seasonal role vegetation plays in sustaining elephant populations in protected areas. We end by placing these results in a broader discussion of elephant impacts on biodiversity by considering how human modifications to natural landscapes might interact with elephant vegetation choices.

## 2. Methods

### 2.1. Elephant telemetry data

We compiled 67,029 locations from 68 collared adult elephants in 12 sites across seven countries. We collared an average of 5.5 elephants at each site with a high of 10 and a low of two. Sixteen of the elephants were bulls. All elephant handling operations were conducted under permit from the relevant conservation organization and the animal ethics committee of the University of Pretoria (permit number AUCC-040611-013), and elephants were tranquilized by qualified wildlife veterinarians.

The elephant collars were all GPS units except for nine Argos units in the Maputuland site. All locations from the Argos collars with errors greater than 350 m were excluded. The standard deviation of the locations from the GPS collars was 50 m. This error is small in comparison to the average distance between adjacent points and the 250 m grid cell size of the remotely sensed imagery. Each elephant was tracked for an average of 691 days (ranging from 264 to 1215 days) and had an average of 1016 locations (ranging from 294 to 2169 locations). To ensure robust and balanced wet season dry season comparisons, we ensured that each elephant had at least 100 locations per season. The majority of the locations were separated by 8 h followed by separations of 24 h. The mean separation was 15 h with a few larger intervals up to 685 h.

Several analyses – the spatial comparisons described below – required locations separated by a standardized time interval. Here, we used the subset of elephants that had at least 100 locations after keeping only those separated by 24 ± 2 h. This required removing several elephants with predominantly irregular location intervals including the nine Maputuland elephants with Argos collars. The remaining 58 elephants had a mean of 460 standardized locations. For analyses specific to the wet or dry season, 55 elephants met these criteria in the dry season with a mean of 271 locations per elephant and 50 elephants met these criteria in the wet season with a mean of 225 locations per elephant. As described above, there is a trade off between large sample sizes of elephants and large sample sizes of locations per elephant. Throughout, we mention the number of elephants used in each analysis. The sample sizes vary but are always greater than 100 locations per elephant for the spatial comparisons and 294 locations per elephant for the remaining analyses. We include in Supplementary material more information on the elephant telemetry data and the geographic sites.

### 2.2. Vegetation data

Moderate Resolution Imaging Spectrometer (MODIS) provides 16 day summaries of an Enhanced Vegetation Index, EVI, a measure of the greenness of the landscape (Pettorelli et al., 2005). EVI discriminates high biomass habitats (such as the woodland of our study areas) better than the related Normalized Difference Vegetation Index (NDVI) (Huete et al., 2002). The spatial resolution of these images is 250 m. We compiled 158 of these images from February 2000 to January 2007 (downloaded from modis.gsfc.nasa.gov). For each year, there are 23 composite images. Each image has an associated map of data quality that, *inter alia*, indicates when cloud cover degrades the EVI quality. When a grid cell has the maximum data quality — the great majority of the grid cells in each image on any given date — we use its EVI. When the data quality falls below this, we substitute the average EVI of the grid cell from the same ordinal day across all 6 years.

We use the EVI time-series to address objective one because it allows us to determine the EVI of each grid cell at roughly the same time it was visited by an elephant. In this time-series, $EVI_{i,j,t}$, is the EVI of the *j*th grid cell at time *t* which was visited by elephant *i* at time *t*. Here and throughout, *t* refers to the date and time of the elephant locations the associated 16 day EVI image that the times fall within. To address objective two, we computed two long-term statistics from this time-series that characterize the landscape. They were "greenness", the mean annual EVI computed from the set *T* of all $n = 158$ images such that $G_{i,j} = \frac{1}{n}\sum_{t\in T} EVI_{i,j,t}$, and "variability", the coefficient of variation of the 158 images such that $V_{i,j} = G_{i,j}^{-1} \times \frac{1}{n-1}\sum_{t\in T}(EVI_{i,j,t}) - G_{i,j})^2$. We emphasize that unlike the EVI time-series, these long-term statistics do not change with time.

To address objective three, we connect these long-term statistics with vegetation types using existing landscape maps for nine of our 12 sites. Details of the methods used to derive these maps are described elsewhere (Harris et al., 2008; Ott, 2007). In brief, they are supervised classifications of Landsat ETM + images trained and evaluated with geo-located vegetation measurements made from the ground. They were evaluated using a kappa statistic ranging from 0% to 100% that accounts for errors of omission and commission in each vegetation class (Wilkie and Finn, 1996). The kappa values for these maps had a mean of 72% and ranged from 51% to 82%. We grouped the 23 vegetation types originally used to produce these maps into seven categories: shrubland, open woodland, grassland and dambo, miombo woodland, closed woodland, well-wooded areas, and other. Dambo represents flooded grasslands, and miombo woodland represents a distinctive assemblage of partially evergreen species dominated by trees of subfamily Caesalpinioideae particularly *Brachystegia*. Well-wooded areas are forest-like and include broadleaf vegetation in places where water is prevalent such as riparian areas and ravines. In general, the dominance of dense woody vegetation types such as miombo and closed woodland increases with increasing precipitation. Herbivory and fire are necessary to maintain grasslands when precipitation reaches about 65 cm annually (Sankaran et al., 2005). For simplicity, we follow these authors and call this collection of ecosystems "savannas," except when we need to distinguish particular habitats. We note that savannas range from well-wooded areas with a closed canopy and few trees losing their leaves seasonally, through seasonal woodlands (with open canopies), to areas that bushes dominate, to open habitats with few trees at all.

We divided the year into wet and dry season using rainfall data from the Tropical Rainfall Monitoring Mission (TRMM) 3B42 product. This product includes TRMM data merged with calibrated Infrared and other satellite measurements to estimate tropical rainfall every 3 h on a scale of 0.25°spatial resolution, (~28 km, for the areas we consider) (Kummerow et al., 1998). We sum these data to provide daily rainfall totals. The daily rainfall totals were summed to produce annual and monthly precipitation totals. We used the daily rainfall totals to define the limits of the wet season in each site as the period in which 95% of precipitation for the water year (August – July) fell. The total annual precipitation for a particular elephant was determined by averaging the total annual precipitation for all grid cells visited by the elephant during the study.

### 2.3. Statistical analysis

To address objective one – whether elephants select vegetation that is greener than the surrounding vegetation – we use the EVI time-series. Animal resource selection theory assumes that an animal's visits to resources are related to animal's preferences (Manly et al., 1992). Accordingly, an animal's preferences can be quantified by comparing where an animal is to where it is not. A challenge with resource selection theory is defining appropriate counterfactual locations where the animal is not. To be comparable, these locations must be equally available (Cooper and Millspaugh, 1999). We use two complementary approaches for defining counterfactual locations: (1) we compare the location the same elephant selects at a certain time with the locations selected at

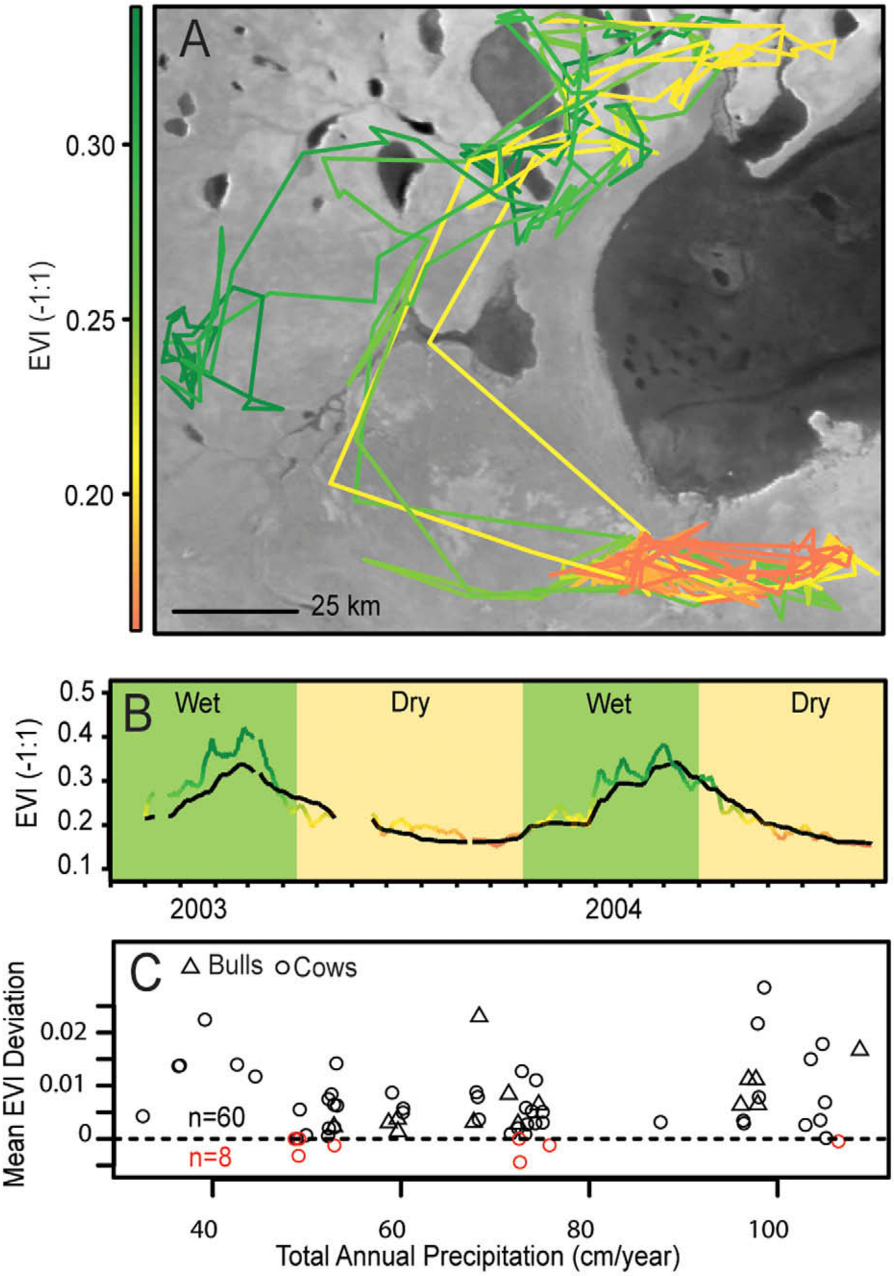

**Fig. 1.** (A) A single elephant path from Etosha National Park. The colour of the path indicates the mean EVI of the landscape when the movement occurred. (B) For the same path, the black line is the mean EVI of the background landscape changing over time ($C_{i,t}$, see text). The coloured line is the EVI the elephant selected ($EVI_{i,j,t}$, see text). (C) The mean deviation from the background for all elephants plotted against total annual precipitation (cm). The binomial probability of 60 of 68 elephants (black points) selecting higher EVI values than the average is very small (sign test, $p = 5.7 \times 10^{-11}$, $n = 68$ elephants). Triangles indicate bull elephants.

some other time during the study (hereafter "temporal comparison"). (2) We compare the location an elephant selects with a nearby location not selected at that time (hereafter "spatial comparison"). The temporal comparison provides insight into why elephants move and the spatial comparison provides insight into why they avoid certain areas. Importantly, in the spatial comparison the counterfactual is constrained to be near the elephant. This controls for seasonal constraints on elephant distributions such as water availability that could complicate comparisons.

For the temporal comparison we compare the EVI of the elephant's location with the average EVI of the rest of the path it travels during the study (Fig. 1). Let $EVI_{i,j,t}$ be the EVI of the $j$th 250 m grid cell occupied by elephant $i$ at time $t$. If $K$ is the set of all $n$ grid cells visited by the elephant during the study other than $j$, then $C_{i,t} = \frac{1}{n}\sum_{k \in K} EVI_{i,k,t}$ is the average counterfactual EVI of where each elephant $i$ is not at each time $t$. For a given time interval $T$, we calculate the average temporal comparison deviation, $D_i^T$, of the selected EVI from the counterfactual EVI where $D_i^T = \frac{1}{t}\sum_{t \in T}(EVI_{i,j,t} - C_{i,t})$. Lastly, we group $D_i^T$ by their sign and calculate the binomial probability of the frequency of each group against the null hypothesis that the probability is 0.5.

For the spatial comparison, we compare the EVI of the elephant's location with the EVI of a nearby unoccupied "ghost" location (Fig. 2). At time $t$ elephant $i$ moves from location $x_{i,t-1}$ to $x_{i,t}$. Let $y_{i,t}$ be the location the same distance away from $x_{i,t-1}$ as $x_{i,t}$, but in the opposite direction. Because distances do not scale linearly with time, to ensure that $x_{i,t}$ and $y_{i,t}$ were equally available, we used the subset of elephant telemetry data in which each location was separated by $24 \pm 2$ h. This ensured that both $x_{i,t}$ and $y_{i,t}$ were within 1 days travel of $x_{i,t-1}$.

To determine $EVI_{i,l,t}$, the EVI of the $l$th 250 m grid cell occupied by $y_{i,t}$ We imagine that there is a counterfactual "ghost" elephant near (within 1 day of travel from) the actual elephant but never at the same location at the same time. In some instances, ghost elephants landed on obvious features such as water bodies or mountains, which real elephants very rarely occupied. We excluded such locations. As with the temporal comparison, for each elephant we calculate the average spatial comparison deviation, $D_i^S$, of the EVI in the occupied and unoccupied locations such that $D_i^S = \frac{1}{t}\sum_{t \in T}(EVI_{i,j,t} - EVI_{i,l,t})$. Again, we group $D_i^S$ by their sign and calculate the binomial probability of the frequency of each group against the null hypothesis.

To address objective two – what types of vegetation elephants select as characterized by greenness and variability – we use the long-term EVI statistics. To compare locations occupied by season, we modified the temporal comparison described above for the long-term EVI statistics (Fig. 3). First, we grouped grid cells occupied by each elephant $i$ into two sets: members of set $W$ were occupied during the wet season and members of set $D$ were occupied during the dry season. Next, we calculated the mean greenness of each set such that $G_i^W = \frac{1}{n}\sum_{w \in W} G_{i,w}$ and $G_i^D = \frac{1}{n}\sum_{d \in D} G_{i,d}$ where $n$ is the length of the set. We calculated the deviation $G_i^W - G_i^D$ and, grouped by their sign, calculated the binomial probability of the frequency of each group against the null hypothesis. We repeated this step to calculate mean variability $V_i^W$ and $V_i^D$.

To compare locations occupied with locations not occupied, we modified the spatial comparison described above (Figs. 4 and 5). Again using the subset of locations separated by 24 h, let $J$ be the set of all grid cells occupied by elephant $i$. As described above, we computed the set of ghost grid cells $L$ such that each element

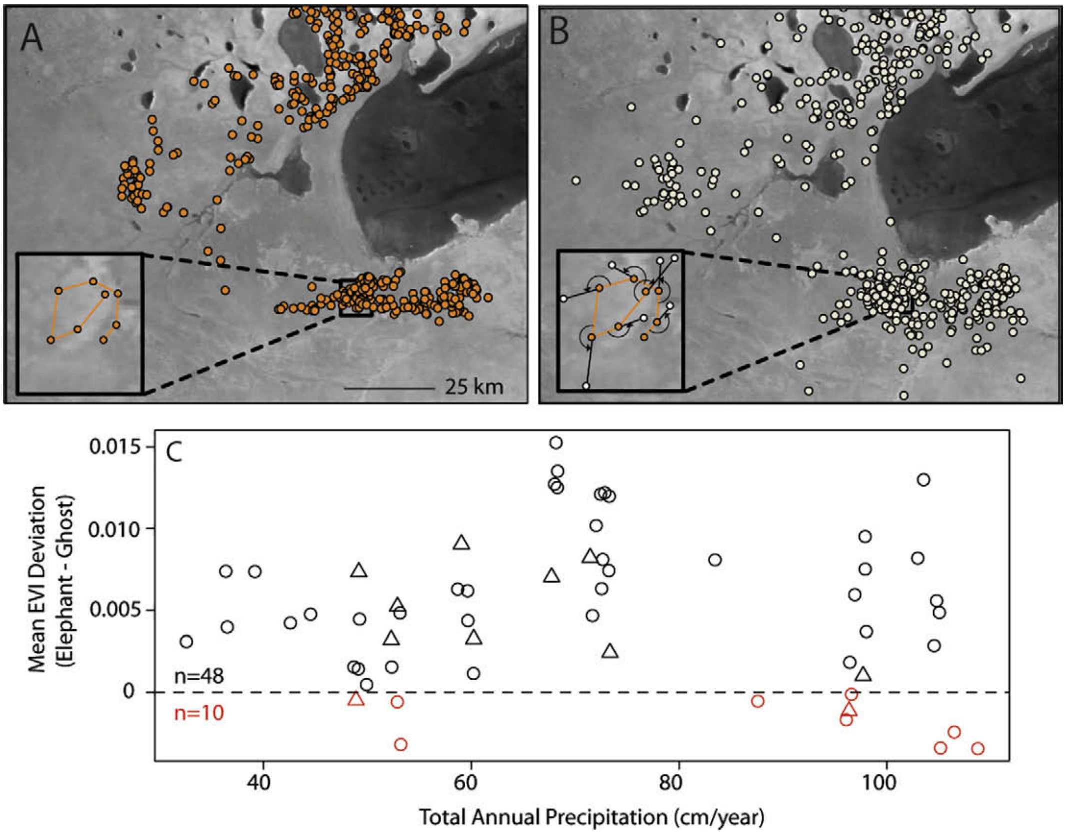

**Fig. 2.** (A) Dry season locations separated by 24 h intervals for a single elephant in Etosha National Park. The inset shows eight locations connected in time. (B) Analogous "ghost" locations calculated by reflecting each location at time $t + 1$ about the location at time $t$. The inset shows this algorithm on eight locations. (C) The deviation of the EVI under the elephant observations ($EVI_{i,j,t}$, see text) minus the EVI under the ghost observations ($EVI_{i,l,t}$, see text) averaged for each elephant and plotted versus total annual precipitation (cm). The number of positive deviations is significant (sign test, $p = 4.5 \times 10^{-7}$, $n = 58$ elephants).

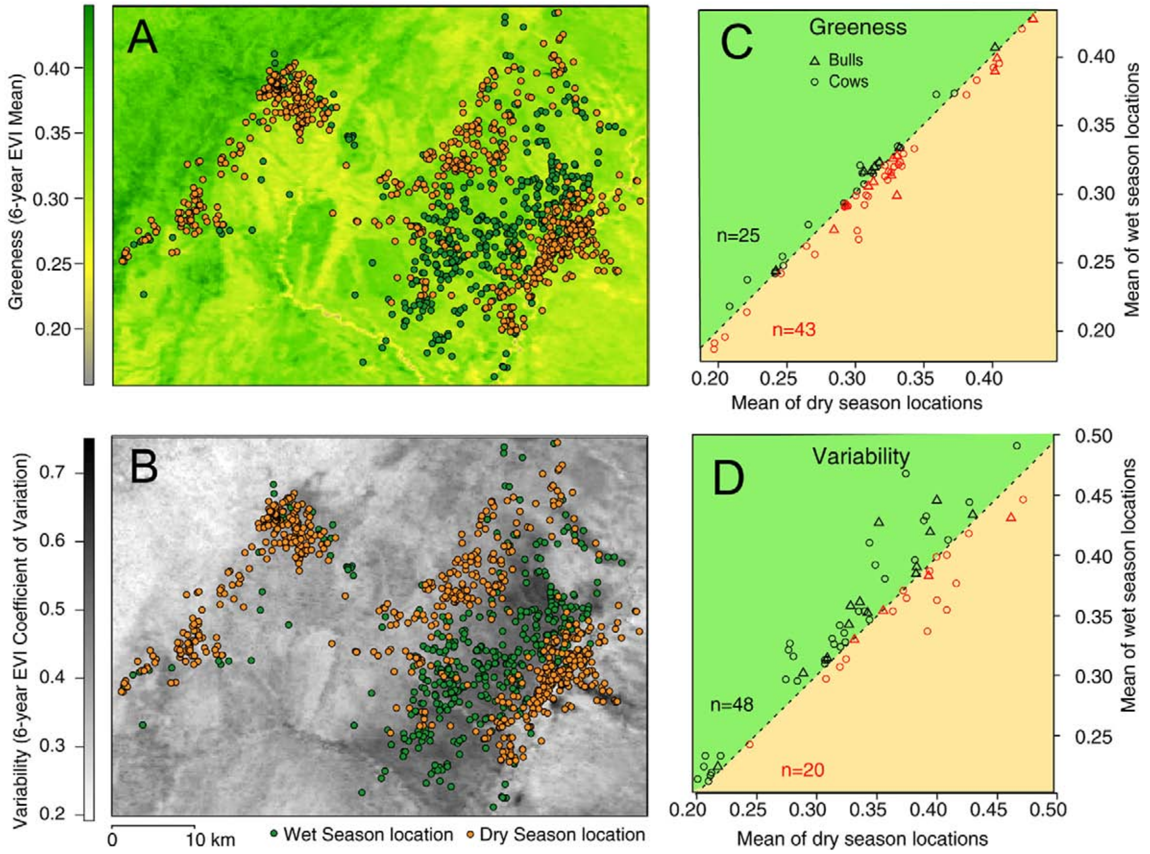

**Fig. 3.** (A) Locations from three elephant from North Luangwa grouped by wet (green) and dry (orange) season. The background is EVI averaged across 6 years (greenness). (B) The same points are displayed on a background of the coefficient of variation across EVI for 6 years (variability). These elephants are on greener vegetation in the dry season and more variable vegetation in the wet season. (C) The greenness of wet season and dry season points averaged for each elephant across all sites. The greenness is higher during the dry season for a significantly large number of elephants (sign test, $p = 4.8 \times 10^{-2}$, $n = 68$; elephants). (D) The variability of wet season and dry season points averaged for each elephant. The variability is higher during the wet season for a significantly large number of elephants (sign test, $p = 9.1 \times 10^{-4}$, $n = 68$ elephants). Triangles indicate bull elephants.(For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

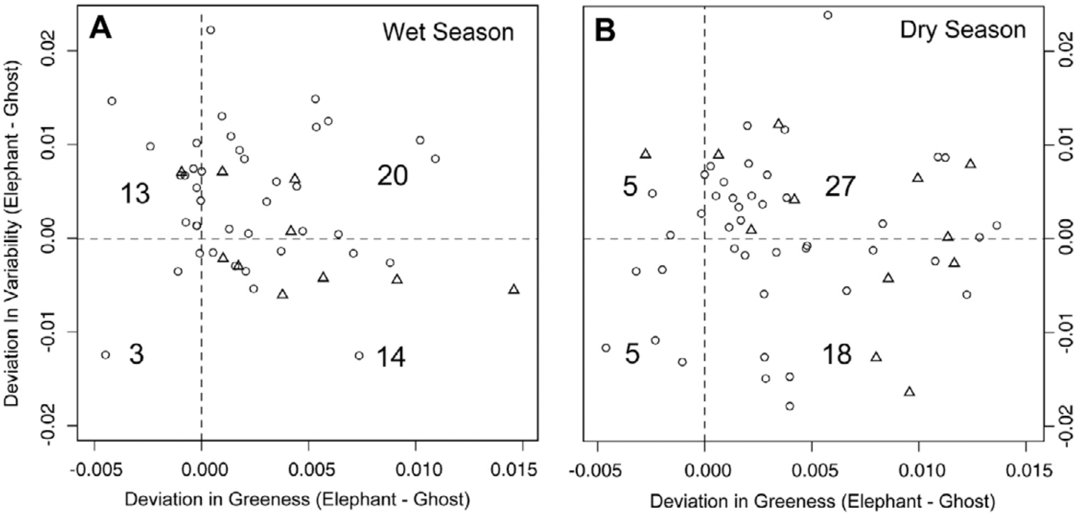

**Fig. 4.** (A and B) Average Greenness and Variability of deviations in elephant locations minus ghost locations for (A) wet season and (B) dry season. In each quadrant, numbers indicate the number of elephants in each quadrant. Significant numbers of elephants are on vegetation greener (sign test, $p = 0.015$, $n = 50$ elephants) and more variable vegetation (sign test, $p = 0.032$, $n = 50$ elephants) than do their ghosts in the wet season. Significant numbers of elephants are on greener vegetation (sign test, $p = 2.1 \times 10^{-6}$, $n = 55$ elephants) than are their ghosts in the dry season but not more variable vegetation (sign test, $p = 0.28$, $n = 55$ elephants). Triangles indicate bull elephants.

$j$ of set $J$ is paired with an element $l$ of set $L$. As before, we calculated the average deviation $\frac{1}{n}\sum_{j\in J}(G_{i,j} - G_{i,l})$ and performed the binomial test on the deviations grouped by their sign. We repeated the analysis with variability.

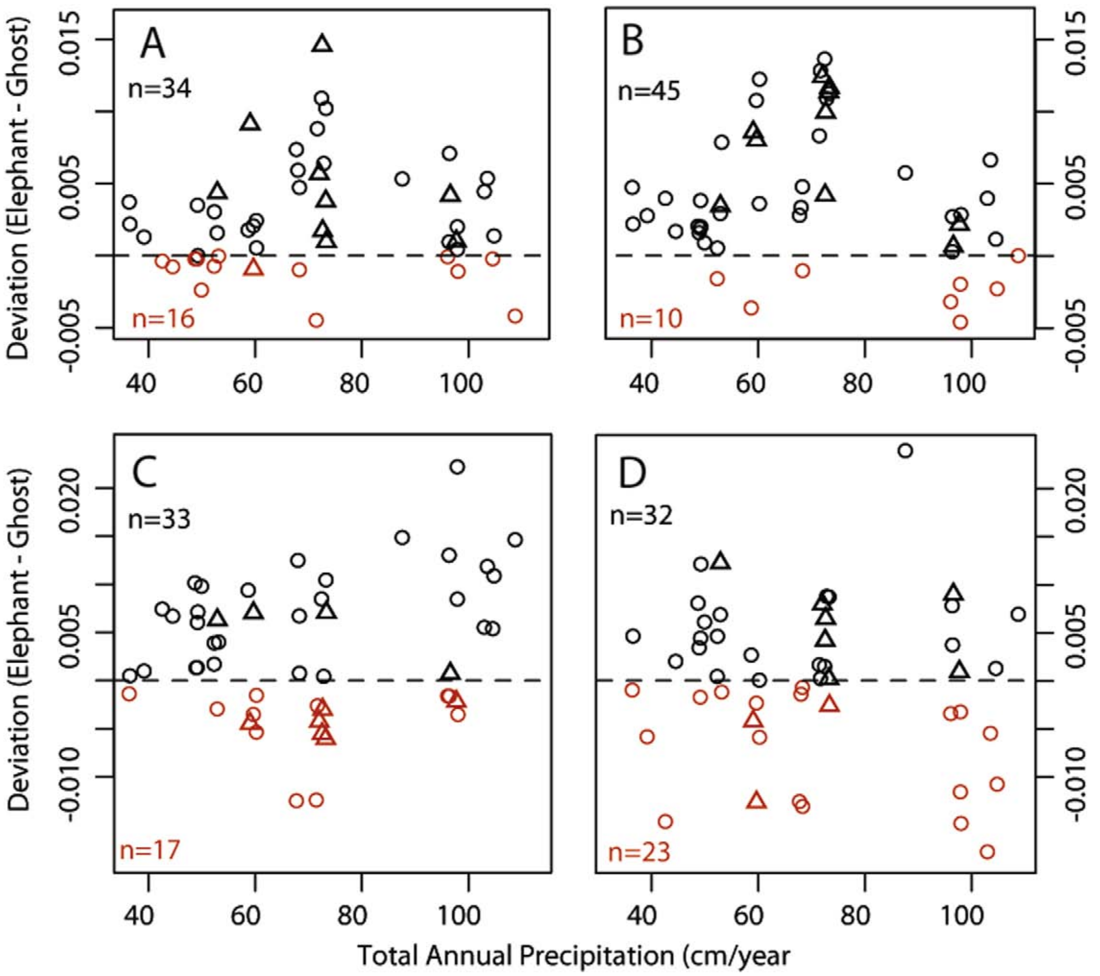

**Fig. 5.** Average deviation of elephant locations minus ghost locations for greenness (A and C) and variability (B and D) grouped by wet (A and B) and dry (C and D) seasons plotted against total annual precipitation (cm). Triangles represent bull elephants.

Throughout, we repeated all analyses excluding the small number of bulls. In Figs. 1–5, we represent bulls as triangles. As suggested by the inspection of these figures, none of the results were significantly different if the bulls were removed. We caution that the small number of bulls prevents a robust comparison of bulls and cows across all sites — only that including bulls does not alter our results.

To address objective three – whether characterizing vegetation based on greenness and variability provide insight into the vegetation's structure – we plotted the greenness and variability of 9000 ground verified samples in eight of the 12 sites and grouped them by the six vegetation categories (Fig. 6). We excluded the "other" vegetation category.

## 3. Results

### 3.1. Objective one – temporal comparison

Our first objective asks to what extent does the greenness of the landscape influence elephant movements. The temporal comparison tests whether elephants visit locations when they are relatively greener. Fig. 1A shows the path of a female elephant in Etosha National Park. The colour of the line indicates the 16 day average EVI of the landscape used by the elephant over that interval. For this *i*th elephant, the coloured line of Fig. 1B is $EVI_{i,j}$, the same line plotted over time, not space. The black solid line of Fig. 1B is $C_i$, the average EVI of all the locations that the particular elephant visited during the study. This line changes in time be-

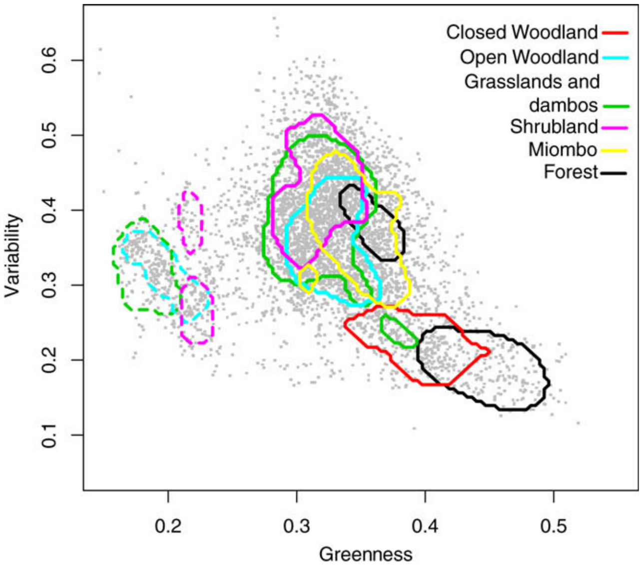

**Fig. 6.** Greenness and variability of vegetation types. Points represent 9000 samples from 8 of 12 sites. Lines encompass 50% of all points from each vegetation type. Solid lines group all sites except Etosha National Park (dotted lines).

cause of the phenology of the landscape, not because the elephant is moving.

The coloured line is nearly always above the black line causing the deviation $D_i^T = \frac{1}{t}\sum_{t\in T}(EVI_{i,j,t} - C_{i,t})$ to be positive. This conjures up a "Lake Wobegon" effect. (In this fictional area of the USA, all the children are, famously, above average.) In the elephant case, this can only occur if at one time area $X$ is greener than area $Y$, at another time $Y$ is greener than $X$, and the elephants chose $X$ and $Y$ accordingly.

These results are consistent across elephants. The deviations are positive for 60 out of 68 elephants (Fig. 1C). The binomial probability of this occurring by chance is small (sign test, $p = 5.7 \times 10^{-11}$, $n = 68$ elephants). This result does not vary seasonally. Grouping by seasons, a significant number of elephants have positive deviations for both the wet ($p = 2.3 \times 10^{-3}$, $n = 68$ elephants) and dry seasons ($p = 1.1 \times 10^{-15}$, $n = 68$ elephants). Likewise, there is no strong correlation between the deviations and precipitation ($cor = 0.02$).

### 3.2. Objective one – spatial comparison

The spatial comparison tests whether the locations elephants visit are greener than locations they did not visit. Fig. 2A shows dry season locations from six elephants in Etosha National Park. Fig. 2B shows the paired ghost locations. They necessarily remain near the actual elephant throughout the year but are in unoccupied locations. Fig. 2C shows the average deviation of the EVI where the elephants occurred from the EVI where the ghost elephants occurred over time. On average, a significant number — 48 out of 58 — of elephants occupy greener grid cells than do their ghosts (sign test, $p = 4.5 \times 10^{-7}$, $n = 58$ elephants). Again, this result does not vary seasonally and there is no correlation between the average deviations and precipitation ($cor = 0.04$).

### 3.3. Objective two – temporal comparison

The above results confirm that elephants select vegetation when it is green, but what are the long term characteristics of this vegetation? Do the characteristics of the selected vegetation vary seasonally or geographically? Fig. 3 overlaps locations of three elephants from North Luangwa on maps of average greenness (Fig. 3A) and variability (Fig. 3B). The points are coloured by wet (green points) and dry (orange points) seasons. The wet season locations are on grid cells with higher average greenness and lower variability in greenness, opposite to what was observed in the dry season locations.

Fig. 3(C and D) plot wet season and dry season averages for greenness and variability for all 68 elephants. If the deviations of wet season minus dry season averages were all zero, the points would lie on the 1 to 1 line. In fact, the deviations are significantly negative for greenness and significantly positive for variability ($P = 4.8 \times 10^{-2}$ and $P = 9.1 \times 10^{-4}$, respectively, using sign tests, for each $n = 68$ elephants). These results indicate that elephants consistently select greener, less variable vegetation in the dry season than in the wet season. There was no strong correlation between these deviations and precipitation for greenness and variability respectively ($cor = -0.01$, $cor = 0.02$).

### 3.4. Objective two – spatial comparison

Fig. 4 plot the deviation in elephant locations minus ghost locations for vegetation greenness and variability grouped by season. Elephants select locally greener vegetation during both the wet (sign test, $p = 0.015$, $n = 50$ elephants) and dry seasons (sign test, $p = 2.1 \times 10^{-6}$, $n = 55$ elephants) than do their ghosts. Elephants select more seasonally variable vegetation (sign test, $p = 0.032$, $n = 50$ elephants) than do their ghosts in the wet season but not during the dry season (sign test, $p = 0.28$, $n = 55$ elephants). Fig. 5 plots these deviations against precipitation. There is no indication that these deviations vary with precipitation ($cor < 0.25$).

### 3.5. Objective three

Our last objective asks whether characterizing vegetation based on greenness and variability provide insight into the vegetation's structure as measured on the ground. Fig. 6 plots the greenness and variability of 9000 ground verified samples of six vegetation types for eight of the 12 sites. They are Etosha, Kafue, Zambezi, South and North Luangwa, Kasungu, Vwaza, Nyika, and Maputu. Etosha (dotted lines) stands out as being the most arid site and having very low greenness values. Across the other eight sites, there is much overlap, but nonetheless a clear trend from forest and closed woodland, with high average greenness and low variability across and within years, to vegetation that is less green and shows greater variability — shrublands, dambos and grasslands.

## 4. Discussion and conclusions

In this paper, we characterized elephant vegetation preferences seasonally and across a large geographic gradient using remotely sensed landscape greenness. Throughout the year, elephants use places with a higher EVI than the average of all the places they visit. They do this by tracking different types of vegetation at different times of year (Fig. 1) and by avoiding less green areas (Fig. 2). These patterns do not change from season to season or across the rainfall gradient. In both seasons and across the rainfall gradient, elephants consistently prefer landscapes with a higher average greenness than local alternatives (Figs. 4 and 5). That elephants select greener vegetation than their nearby "ghost" locations reveals that they track green vegetation despite being constrained by seasonal water availability.

An advantage of our study is that rather than summarizing these dynamic landscapes over coarse time periods, we match EVI data with the elephant locations in both time and space. Many landscapes such as well-wooded areas and closed woodlands have the highest mean greenness but are not exclusively utilized by herbivores (McNaughton and Georgiadis, 1986). Our approach reveals that while these landscapes are greenest on average, there are times of the year when other landscapes such as grasslands are greener. We caution that the link between greenness and vegetation quality is complex, but there are several reasons to suspect that green vegetation would be nutritionally superior. Green landscapes likely have more standing biomass and nitrogen (Thoma et al., 2002). Wittemyer et al. (2007) linked the greenness of available vegetation to elephant conception probabilities.

Another advantage is that we use two counterfactuals to control for other landscape features that influence elephant movements – many of which may be unobservable. In the temporal comparison we compare places elephants are known to have visited. This controls for many factors that may lead areas to be unsuitable for elephants for reasons other than greenness such as unseen fences or human activity (Grant et al., 2007). In the spatial comparison, we compare places where elephants were not observed but were within 1 day of travel. This controls for seasonal constraints on elephant distributions such as seasonal water availability (Smit et al., 2007).

The analysis of long-term EVI statistics and vegetation classifications reveal that elephants track green vegetation by using different vegetation types at different times of year. In the wet season, elephants seek out landscapes such as shrublands, grasslands and dambos (Fig. 6) that are more variable from season-to-season or year-to-year (Figs. 4 and 5) despite being less green on average (Fig. 3). In the dry season, these variable landscapes have very little palatable vegetation interspersed with bare ground (Thouless, 1995), but in the wet season they are covered with lush grass. Elephants select these variable, grassy landscapes in the wet season when they are primarily grazers (Cerling et al., 2006; O'Connor et al., 2007).

Importantly, our results show that in order to access different types of vegetation in different seasons elephants require heterogeneous landscapes. This result is consistent with other remote sensing studies showing that elephants select heterogeneous foraging areas – but we show that the role of this heterogeneity plays out over seasonal cycles (Murwira et al., 2006). Our results are consistent with other studies that show the importance of variable vegetation in the wet season (Young et al., 2009). These results have important conservation implications. Because protected areas must be large enough to have both variable wet season habitat and stable, green dry season habitat, small homogeneous protected areas may be unsuitable for elephants.

There has been much recent discussion of elephant impacts on vegetation and biodiversity (Cumming et al., 1997; de Beer et al., 2006; Dublin et al., 1990; Laws, 1970). In some cases elephants have been shown to promote biodiversity by creating habitat through their use of vegetation (Pringle, 2008). In others, elephants have been shown to reduce biodiversity by eliminating well-wooded areas (Kerley et al., 2008). Whether these detrimental impacts are natural consequences of the recovery of elephant populations or detrimental consequences of an unbalanced system is controversial (Guldemond and Van Aarde, 2008; Owen-Smith et al., 2006; Skarpe et al., 2004).

Our results add the following insight. When pointing to the damage done by elephants, a few examples are quoted repeatedly. Declining mature riparian forests, such as those along the Chobe River in Chobe National Park, suggest there is something historically exceptional in the present day (Barnes, 2001; Herremans, 1995). In the dry season, browse is an important part of elephant's diet (Cerling et al., 2006), and our data show they select the greenest vegetation on the landscape — well-wooded areas and closed woodlands. But because their movements are constrained to be near permanent water, many well-wooded landscapes may be out of reach. Areas within reach contain riparian forests. Some may be unable to withstand the pressure. In fact, large trees may have never been common along rivers in dry savannas, and may rather be the result of episodic low elephant numbers caused by hunting and rinderpest during the first half of the last century (Skarpe et al., 2004). If so, the difficulties of finding browse in the dry season near rivers may have been an important factor in limiting elephant numbers. These long treks to find food at the end of the dry seasons likely kill many young elephants (Dudley et al., 2001; Loveridge et al., 2006; Van Aarde et al., 2008).

Elephant vegetation interactions are complicated by human modifications to the landscape. Networks of water holes now expand the areas where elephants will affect well-wooded areas in the dry season (Chamaille-Jammes et al., 2007; Grainger et al., 2005; Smit et al., 2007; Van Aarde et al., 2008). These waterholes may enable elephants to reach browsing habitats that were out of reach in the dry season. Moreover, away from water, these habitats would be passed over in favour of grasslands and shrublands in the wet season. Fences may interfere with elephant vegetation preferences to concentrate elephant feeding, which likely increases their impact on the vegetation (Grant et al., 2007). Potentially more importantly, they may act as barriers to these seasonal movements and their associated vegetation shifts, forcing elephants to utilize the same landscape year-round. This could be especially important in relatively small protected areas and ones designed to represent a few special habitat types.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.08.021.

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