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**Insignificant human
footprint on Sahel
vegetation greenness**

J. W. Seaquist et al.

Disentangling the effects of climate and people on Sahel vegetation dynamics

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Abstract

The Sahel belt of Africa has been the focus of intensive scientific research since the 1960s, spurred on by the chronic vulnerability of its population to recurring drought and the threat of long-term land degradation. But satellite sensors have recently shown that much of the region has experienced significant increases in photosynthetic activity since the early 1980s, thus re-energizing long-standing debates about the role that people play in shaping land surface status, and thus climate at regional scales. In this paper, we test the hypothesis that people have had a measurable impact on vegetation dynamics in the Sahel for the period 1982–2002. We compare potential natural vegetation dynamics predicted by a process-based ecosystem model with satellite-derived greenness observations, and map the agreement between the two across a geographic grid at a spatial resolution of 0.5° . As aggregated data-model agreement is very good, any local differences between the two could be due to human impact. We then relate this agreement metric to state-of-the-art data sets on demographics, pasture, and cropping. Our findings suggest that demographic and agricultural pressures in the Sahel are unable to account for differences between simulated and observed vegetation dynamics, even for the most densely populated areas. But we do identify a weak, positive correlation between data-model agreement and pasture intensity at the Sahel-wide level. This indicates that herding or grazing does not appreciably affect vegetation dynamics in the region. Either people have not had a significant impact on vegetation dynamics in the Sahel or the identification of a human “footprint” is precluded by inconsistent or subtle vegetation response to complex socio-environmental interactions, and/or limitations in the data used for this study.

1 Introduction

The Sahel belt of Africa has been the focus of intensive scientific research in recent decades, spurred on by the chronic vulnerability of its population to recurring drought

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and the threat of long-term land degradation. Century-long records of annual rainfall totals show that a lengthy period of desiccation began in the mid-1960s, accompanied by a marked decrease in interannual rainfall variability (Hulme, 2001). Evidence is mounting that the rainfall climate of the Sahel is ultimately driven by changes in ocean circulation and sea surface temperatures and further amplified by internal non-linear biogeophysical feedback mechanisms that operate between the vegetation and the atmosphere (e.g. Zeng et al., 1999; Wang and Eltahir, 2000; Giannini et al., 2003). This feedback is thought to have led to an abrupt change to a persistently drier climate compared to the first half of the 20th century (Foley et al, 2003).

Recent research has re-invigorated long-standing debates about the direct impact people have on observed changes in the Sahel's land cover status (e.g. Hein and de Ridder, 2006; Prince et al., 2007). The paradigm of geographically extensive and irreversible land degradation has been challenged by satellite observations of vegetation greenness (NDVI – Normalized Difference Vegetation Index) that showed the return of vegetation in years that received favourable rainfall (Helldén, 1991; Tucker et al., 1991). Even more recent findings using data from the same satellite sensors show a widespread increase in photosynthetic activity since the early 1980s (Eklundh and Olsson, 2003; Olsson et al., 2005; Hermann et al., 2005; Seaquist et al., 2006; Heumann et al., 2007). Proposed explanations have included increasing rainfall, CO₂ enhancement effects, agricultural intensification, extensification, and land abandonment stemming from socio-economic change and conflict.

Using a process-based vegetation model, LPJ-DGVM (Lund Potsdam Jena-Dynamic Global Vegetation Model), Hickler et al. (2005) identified rainfall change as the primary regulator of vegetation dynamics in the Sahel between 1982 and 1998 (with CO₂ having a minor positive influence), albeit at the aggregated level. They closely reproduced the satellite-observed greening trend and its interannual variability by holding all driving variables in the model constant except rainfall. In another study, Hermann et al. (2005) used a data-driven approach to reach a similar conclusion by statistically relating gridded, satellite-derived rainfall data (at 2.5° and 1.0° spatial resolution) with satellite-

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based NDVI observations (at 8 km spatial resolution) for the period 1982–2003. But after removing the influence of rainfall from the NDVI data, spatially coherent, statistically significant residual trends remained, showing where the land surface has either been greening faster (possibly indicating land “rehabilitation”) or slower (possibly indicating land degradation) than can be accounted for by rainfall alone. These findings are echoed by Evans and Geerken (2004) and Wessels et al. (2007) who used similar NDVI-rainfall residual trend analyses (at NDVI resolution of 8 km and interpolated rainfall data) in order to isolate possible human-induced degradation signals in the drylands of Syria and the rangelands of South Africa respectively. Additionally, Li et al. (2004) applied NDVI-rainfall regression diagnostics to assess land cover performance in Senegal.

Though Hickler et al. (2005) present convincing evidence that rainfall governs vegetation dynamics in the Sahel at the aggregated level, the spatial details of data-model agreement were not resolved. It is possible that minor differences in aggregated simulated versus observed vegetation dynamics stem from substantial differences in sub-regions where human impact may be measurable. Since the LPJ-DGVM simulates potential natural vegetation while satellite-derived greenness represents actual vegetation, differences between the two could be due to anthropogenic pressures. The possibility therefore exists that the human “footprint” in dryland regions, including the Sahel, may be significant enough to alter broad-scale biogeophysical processes, carbon cycling, and climate through direct impact on vegetation dynamics. But the human impact hypothesis remains largely untested for the Sahel at broad spatial extents.

In this paper, we test the hypothesis that people have had a measurable impact on vegetation dynamics in the Sahel for the period 1982–2002. Like Hickler et al. (2005), we compare vegetation dynamics predicted by the LPJ-DGVM with satellite-based greenness observations, but we extend their approach by distributing model output across a geographic grid. We then relate a data-model agreement metric to state-of-the-art data sets on demographics, pasture, and cropping intensity on a cell-by-cell basis. If human impact has been significant, we should then expect to find an associa-

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tion between data-model differences and land use/population pressures.

2 Data and methods

2.1 Satellite-derived greenness data

We used the Global Inventory Modeling and Mapping Studies (GIMMS) 10-day maximum value composite NDVI dataset derived from the National Oceanic and Atmospheric Administration's (NOAA) series of Advanced Very High Resolution Radiometer (AVHRR) instruments with a spatial resolution of 8 km (Tucker et al., 2005). The NDVI is computed from the red and near infrared bands of the AVHRR sensor and is correlated with photosynthetic activity and leaf area index of green vegetation (Sellers, 1989). The NDVI also reduces unwanted variations in the data due to topography, sensor calibration, and viewing geometry, while maximum value compositing reduces the effects of cloud cover and the atmosphere (Holben, 1986). The GIMMS data set has been corrected for sensor differences, sensor drift, and the effects of volcanic eruptions. We extracted peak NDVI observations ($NDVI_{max}$) for each growing season from 1982–2002. We then projected them to a geographic grid while re-sampling to 0.5° (using bi-linear interpolation) in order to match the resolution of the climate input data used for driving LPJ-DGVM. Data were extracted for 12° N to 20° N and 19° W to 40° E (Fig. 1). A southern limit of 12° N was chosen to avoid saturation of the NDVI observations which would make vegetation changes difficult to discern.

2.2 Vegetation model

LPJ-DGVM is a coupled biogeography-biogeochemistry model, which incorporates process-based representations of terrestrial vegetation dynamics and biogeochemical cycling. A full description of the model can be found in Sitch et al. (2003). Processes governing water uptake by vegetation were updated by Gerten et al. (2004).

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The model is used by a broad community of global-change researchers¹ and has, for example, been shown to successfully reproduce the distribution of global biomes (Sitch et al., 2003; Hickler et al., 2006), variations in NPP across biomes (Hickler et al., 2006; Zaehle et al., 2005), satellite-derived high-latitude greening trends in the 1980s and 1990s (Lucht et al., 2002), and site-scale and global patterns in the water balance of terrestrial ecosystems (Gerten et al., 2004). We used the C++ implementation of LPJ-DGVM within the generalized modelling framework LPJ-GUESS (Smith et al., 2001).

2.3 Modelling protocol and climate data

LPJ-DGVM was driven with monthly data for air temperature, precipitation, number of rain days, and sunshine hours from the global CRU05 dataset for the region bounded by 12° N to 20° N and 19° W to 40° E at a 0.5° resolution (Mitchell and Jones, 2005). Monthly temperature and sunshine data were interpolated to provide quasi-daily time series. Daily precipitation fields were generated with a stochastic weather generator (Gerten et al., 2004). Annual global atmospheric CO₂ concentrations were obtained courtesy of the Carbon Cycle Model Linkage Project (McGuire et al., 2001) and TRENDS². Climate data for a 1000-year model spin-up were derived from the same data by repeating detrended values of the climate input for 1901–1930, using pre-industrial CO₂ content of the atmosphere. The model was run as to simulate the potential natural vegetation; information on land use was not included. Growing season maximum LAI (LAI_{max}) were then extracted for the period 1982–2002.

2.4 Data-model agreement and greenness trends

Spearman's rank-order correlation coefficient was used to gauge data-model agreement ($r_{s[\text{NDVI-LAI}]}$). Spearman's coefficient varies between -1 and +1, where large

¹<http://www.nateko.lu.se/embers/Research/LPJ-GUESS>; <http://www.pik-potsdam.de/lpj>

²<http://cdiac.esd.ornl.gov/trends/co2/contents.htm>

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positive values indicate strong agreement, large negative values indicate strong disagreement, and values near 0 indicate random agreement. The purpose of this coefficient is to measure the association between two variables (e.g. LAI_{max} and NDVI_{max}) whose scores are in rank order (McGrew Jr. and Monroe, 2000). The reason for choosing this coefficient was to remove any non-linearity that could undermine the detection of a monotonic relationship between LAI_{max} and NDVI_{max}.

For comparison, we also applied a temporal trend analysis the NDVI_{max} observations. Curves were fitted to every cell using ordinary least-squares regression. The slope coefficient of the regression was used for determining the sign and magnitude of the trends.

2.5 Population density and land use

Gridded data on population density (persons km⁻²) for the years 1980, 1990, and 2000 were downloaded from the Africa Population Distribution Database³, resampled to a 0.5° resolution and subset to the same spatial extent as all other layers (Fig. 2a). These grids were derived from census data, transportation networks (roads, railroad, and navigable rivers) and information on the location of urban centres. The underlying assumption for the generation of these data is that population density is strongly dependent on accessibility via transportation routes.

We used the Agricultural Lands in the Year 2000 (AL2000) data set described in Ramankutty et al. (2008)⁴. This is a state-of-the-art global data set depicting cropland use and pasture use intensity (values ranging between 0 and 1) at a spatial resolution of 5 min (approximately 10 km). The AL2000 was produced by merging agricultural inventory data for different countries with satellite-derived land cover data derived from Boston University's Moderate Resolution Imaging Spectrometer (MODIS) land cover product and Satellite Pour l'Observation de la Terre (SPOT) Vegetation's Global Land

³http://na.unep.net/globalpop/africa/Africa_index.html

⁴available at <http://geomatics.geog.mcgill.ca/~navin/pub/Data/Agland2000>

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Cover 2000 product. This is the first data set of its kind to attach statistical confidence intervals to land use estimates. We extracted data for the study area, while coarsening the resolution to 0.5° using bi-linear interpolation (see Fig. 2b and c).

2.6 Data-model agreement vs. population density and land use

- 5 Finally, we related level of data model agreement ($r_{s[\text{NDVI-LAI}]}$) to estimates of population density and its change from the Africa Population Distribution Database, as well as cropping and pasture from the AL2000 for all terrestrial surfaces ($n=1780$).

3 Results

3.1 Data-model comparison

10 On an aggregated level, LPJ-DGVM generally reproduced the overall trend and pattern of interannual variation in observed vegetation greenness between 1982 and 2002 (Fig. 3). The simulated mean LAI_{max} was 3.15 while the mean NDVI_{max} was 0.36, averaged over all cells for all years. Regressing the yearly spatial mean NDVI_{max} anomaly against the yearly spatial mean LAI_{max} anomaly yields a Pearson correlation coefficient
15 0.77 with a small bias ($\text{LAI}_{\text{max}}=0.77 \times \text{NDVI}_{\text{max}} - 0.004$).

Geographically, $r_{s[\text{NDVI-LAI}]}$ is fair-to-strong for a relatively contiguous band stretching from the coastal area of northern Senegal, southern Mauritania, central Mali, and western Niger (Fig. 4a). Agreement drops off in Chad before picking up again throughout central Sudan and into Eritrea. 542 cells (0.5°) show statistically significant positive correlations, corresponding to 30.4% of the total land area (mean $r_{s[\text{NDVI-LAI}]}=0.58$, $\alpha=0.05$, threshold $r_{s[\text{NDVI-LAI}]}$ for statistical significance = 0.44). A large patch of strong disagreement is found in northern Niger, with smaller patches in southwest Mali and Ethiopia. 61 cells show statistically significant negative correlations, corresponding to 3.4% of the total land area (mean $r_{s[\text{NDVI-LAI}]}=-0.56$, $\alpha=0.05$, threshold $r_{s[\text{NDVI-LAI}]}$ for
25 statistical significance = -0.44).

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For comparison, Fig. 4b shows the strength of the trends in $NDVI_{max}$ for 1982–2002 in percent ($\alpha=0.05$). Statistically significant increases in $NDVI_{max}$ occur in a relatively uninterrupted band stretching from the Atlantic coast to the Red Sea. Strongest trends occur in central Chad and western Sudan with increases in excess of 100% for the 1982 to 2002 period. The latter areas correspond to refugee and conflict zones whose populations have recently been receiving massive food aid through the World Food Programme. 683 cells or 38.3% of the area show trends that are statistically significant. Negative trends are confined to three cells in the southwest corner of Niger with decreases around 20%.

$r_{s[NDVI-LAI]}$ tends to be higher for areas with strong positive $NDVI_{max}$ trends (Fig. 5a). Poor data-model agreement is associated with negative trends in observed vegetation indicating poor model performance for these areas. However, negative trends in $NDVI_{max}$ are generally much smaller than positive trends when trends are expressed in percent (Fig. 5b).

3.2 Relationship between $r_{s[NDVI-LAI]}$ and population density and land use

There is no strong association between $r_{s[NDVI-LAI]}$ and either total population (Fig. 6a), relative changes in population density between 1980 and 2000 (Fig. 6b), or cropping intensity (Fig. 6c); Pearson correlation coefficients $r < 0.12$ (i.e. less than 2% of the variance explained). But for areas experiencing depopulation, data-model agreement is always positive (Fig. 6b). The mean population density was 17.5 persons km^{-2} with a maximum of 994.1 persons km^{-2} . Though not reproduced here, a scatter-plot of data-model agreement versus the absolute change in population density between 1980 and 2000 was very similar to Fig. 6a. Rates of population growth throughout the period ranged from -0.54 to 26.5 persons $km^{-2} yr^{-1}$ with a mean of 0.36 $km^{-2} yr^{-1}$. Relative change in population ranges from -39.3% to 492.4% , with a mean of 43.3% . However, $r_{s[NDVI-LAI]}$ increases with pasture intensity (Fig. 6d), indicating that the greater proportion of pasture in an area, the better the model simulates actual vegetation. For this relationship, $r=0.46$. Log-transforming population and agricultural parameters do not

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result in increased levels of association with data-model agreement, and there were no strong associations between population, cropping intensity, and grazing intensity.

Since most of the densely populated areas occur within or nearby urban centres, we also investigated the hypothesis that data-model agreement would be most affected by population and land use only in those areas undergoing the most rapid population growth. We therefore isolated areas with different thresholds in population growth between 1980 and 2000, and retained the threshold that gave an acceptable sample size (2.4 persons km⁻² yr⁻¹ $n=58$). We then repeated our analysis, relating data-model agreement to population/population change, cropping, and pasture. r for $r_{s[NDVI-LAI]}$ versus pasture was 0.58. r for all other relationships was below 0.07. The results did not vary appreciably for neighbouring population growth thresholds, either higher or lower.

4 Discussion

Demographic and agricultural pressures in the Sahel were largely unable to account for differences between simulated and observed vegetation dynamics for the period 1982–2002. However, we did identify a positive relationship between data-model agreement and pasture intensity at the Sahel-wide level (Fig. 6d). As the model predicts potential natural vegetation dynamics (without animal grazing and human influences), this suggests that livestock grazing is generally not an important driver of vegetation greenness in the Sahel, at least at the scale of our study. As mentioned in Sect. 3.2, data-model agreement is always positive for areas experiencing depopulation (Fig. 6b), but most of these cells already have very low population densities and occur within the broad area of greening that roughly corresponds with the pastoral zone. And since there was a moderate relationship between data-model agreement and pasture with high population growth rates (2.4 persons km⁻² yr⁻¹ $n=58$) from between 1980 and 2000 ($r=0.58$), the implication is that areas near urban centres did not undergo degradation, but on the contrary, became greener. It also re-enforces the hypothesis that animal density

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does not appreciably impact vegetation dynamics, at least at this scale. This finding is consistent with the non-equilibrium hypothesis of rangeland ecology (e.g. Behnke and Scoones, 1993).

It is important to keep in mind that human modification of vegetation over large areas occurs within a social context and can be the result of a myriad of decisions and behaviours that may either act to suppress or augment vegetation amount and its variability (Turner, 2003). If consistent vegetation response to human modification is dependent on the local context, then relationships between data-model agreement and human activity measures might be embedded within the scatter-plots shown in Fig. 6a–d. We provisionally tested this hypothesis by focusing on relationships for an area of large, positive data-model agreement extending from western Mali to western Niger ($n=190$), and an area of random-to-negative data-model agreement stretching from eastern Niger to eastern Chad ($n=196$). No appreciable differences in the strength of the relationships were observed comparing them with Fig. 6a–d, except for the Mali area, which showed no relationship between data-model agreement and pasture. This is not surprising as the bulk of the $r_{s[NDVI-LAI]}$ values was >0.50 . In contrast, the bulk of the $r_{s[NDVI-LAI]}$ values in the low agreement zone in Chad occupied a much wider range.

Our experimental design carries with it the assumption that random or negative data-model agreement would be attributed to the direct impact that people or animals have had on the landscape, but other factors may also be important in certain areas. For example, low data-model agreement could be caused by poor performance of the vegetation model and error in model input in terms of climate data and soil texture. The climate data might be a particular source of error in central and northern Niger and northern and central Chad where low or negative data-model agreement coincides with a relatively low number of precipitation stations (New et al., 2002). The situation is compounded by scattered mountain ranges where are larger number of climate stations would be necessary to derive reliable gridded data. However, the good agreement between modelled and observed trends at the aggregated level (Fig. 2) and across

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large areas of the study area (Fig. 3b), and various tests of the LPJ model in general (see model description) suggest that LPJ is capable of reproducing changes in vegetation greenness in the Sahel when driven with the CRU05 climate data. Nevertheless it is impossible to quantify this potential source of error. Regarding satellite data, NDVI observations from NOAA are affected by various sources of noise, but observations over the Sahel are less affected by cloud contamination than more humid areas (Chappell et al., 2001). Furthermore, the NDVI is fairly sensitive to vegetation changes since NDVI values are below the point of saturation for large parts of the growing season. Systematic shifts due to orbital drift and sensor differences during the observation period are concerns but a recent analysis showed that trends in a related AVHRR data product (NOAA/NASA Pathfinder AVHRR Land Data Set) were not affected by solar zenith angle variations (Lindström et al., 2006). Detecting trends over short time periods using generally noisy satellite sensor data with ordinary least-squares regression is problematic due to the low number of observations, but a spatio-temporal statistical model that more efficiently analyzes the trends has been tested over the Sahel and generates homogeneous areas of strong and statistically significant areas of change (Bolin et al., 2008⁵). Finally, locust swarms are a possible reason for reduced data-model agreement in some areas but the effect is likely marginal. Tratalos and Cheke (2006) emphasize that locusts are usually found for areas receiving above normal rainfall and are associated with good harvests. Moreover, such occurrences are likely to have only short-term impacts in individual years (Hermann et al., 2005).

We have conducted this study using highly generalized data sets with respect to information content and spatio-temporal resolution. Though the AL2000 is the most robust, comprehensive, widely available characterization of agricultural activity at a global extent, it summarizes agricultural status for roughly the year 2000, while our study considers vegetation dynamics for the period 1982 to 2002 (Ramankutty et al.,

⁵Bolin, D., Lindström, J., Eklundh, L., and Lindgren, F.: Fast estimation of spatially dependent temporal vegetation trends using Gaussian Markov Random Fields, *Computat. Statist. Data Analysis*, in review, 2008.

2008). Consequently, we could not consider changes in land use over time. We have also aggregated cell size to 0.5° in order to be able to compare observed and simulated vegetation dynamics which resulted in a loss of spatial fidelity. Additionally, the definition of pasture and cropping in the AL2000 product follows the definition from the Food and Agricultural Organization, but there has been confusion regarding the characterization of both croplands and pasture, especially in census data (Ramankutty et al., 2008). For example, areas designated as cropland may actually be fallow for long periods of time. Much of the agricultural land is also multifunctional, though it has not been possible to incorporate this type of information into these data products. Regarding population data, they have not been evaluated thoroughly for Africa, though evaluation of the Asia Population Distribution Database (derived using the same methods) shows good agreement for relatively homogeneous regions, but agreement drops where population distribution is scattered (Nelson, 2004).

LAI and NDVI are widely used variables for characterizing vegetation structure, which are also highly relevant for vegetation functioning (e.g. photosynthesis, NPP, transpiration and interception). But some aspects of vegetation dynamics might not be covered by these variables. Structurally very different vegetation types, such as grassland, shrubland or savanna, can have similar LAI and NDVI, and there can be substantial turnover of species without any effects on vegetation structure. For example, new plant species gaining a foothold through agricultural extensification or land abandonment could respond in a similar way to rainfall than the vegetation they are replacing, and subtle differences in vegetation response may not be able to be picked up using our methodology at this level of spatial aggregation. Along similar lines, an invasion of locally exotic plant species may also result in little or no change in peak growing-season biomass levels (Evans and Geerken, 2004). However, if humans were a major driver of vegetation dynamics in the Sahel, one would also expect some influence on vegetation greenness.

In summary, there exist a number of potential sources of error in our analyses, but the consistency and robustness of our results – no or positive relationships between

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data-model agreement and all potential human pressures included – suggest that the general conclusions of our study hold true.

5 Conclusions

We tested the hypothesis that people have had a measurable impact on vegetation dynamics across the Sahel for the period 1982–2002. To the best of our knowledge, this is the first study to tackle this question at the Sahel-wide extent. Our methodology rests on the assumption that low or negative agreement between simulated and observed vegetation dynamics is related to the impact that people have on vegetation. But our results indicate that there is generally no relationship between data-model agreement and the best available estimates of population density agricultural activity. However, a positive relationship was established between level of data-model agreement and pasture intensity, indicating that animal presence did not appreciably affect vegetation dynamics in the region over the period. Either people have not had a significant impact on vegetation dynamics across the Sahel, or the identification of a human “footprint” is precluded by inconsistent or subtle vegetation response to complex socio-environmental interactions, and/or data limitations.

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**Fig. 1.** Study area, restricted to 12° N to 20° N and 19° W to 40° E.[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[◀](#)[▶](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

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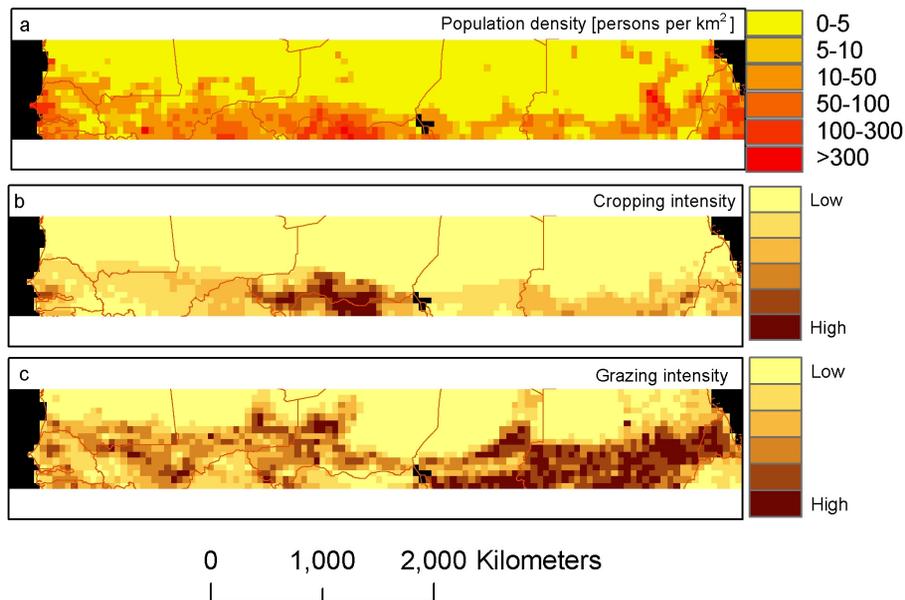


Fig. 2. (a) Population density for year 2000 (Nelson, 2004), (b) cropping intensity ca. year 2000 (Ramankutty et al., 2008), and (c) grazing intensity ca. year 2000 (Ramankutty et al., 2008).

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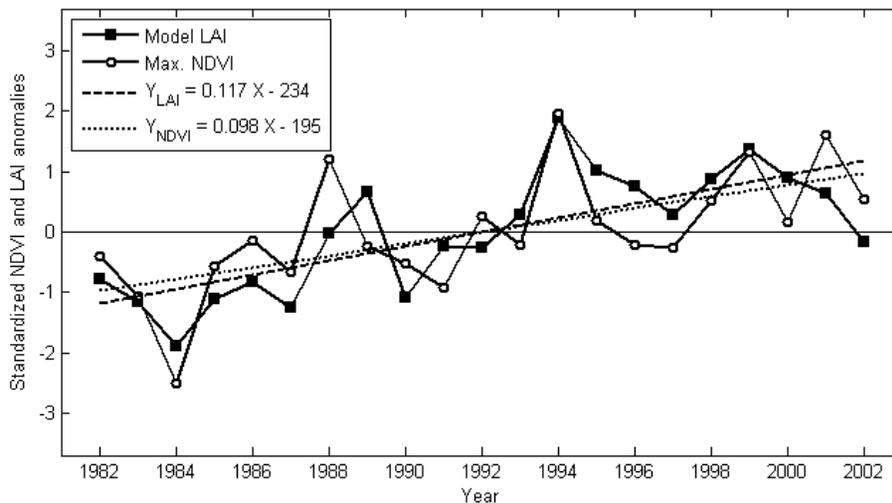


Fig. 3. Aggregated standardized anomalies of modelled LAI_{max} and observed NDVI_{max} 1982–2002, and linear regression lines for the data vs. time.

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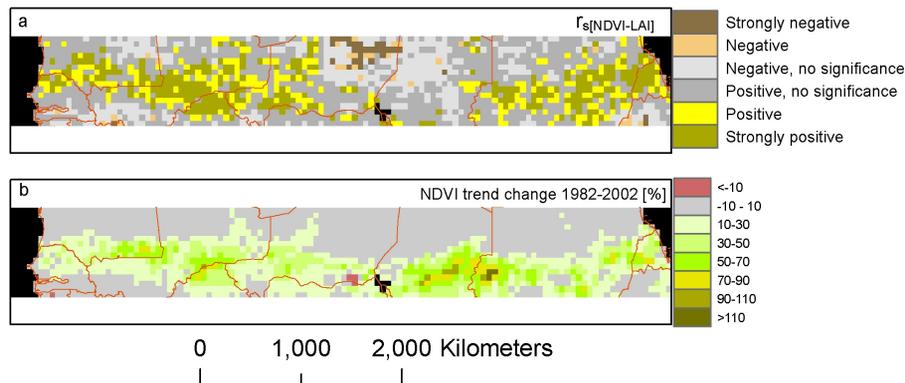


Fig. 4. Spearman rank correlation coefficient between **(a)** simulated LAI_{max} and observed NDVI_{max} between 1982–2002 (strongly positive/negative and positive/negative denote statistical significance thresholds of $\alpha=0.01$, $r_{s[\text{NDVI-LAI}]}=0.55$, and $\alpha=0.05$, $r_{s[\text{NDVI-LAI}]}=0.44$, respectively), and **(b)** NDVI_{max} trend change 1982–2002 expressed as a percentage.

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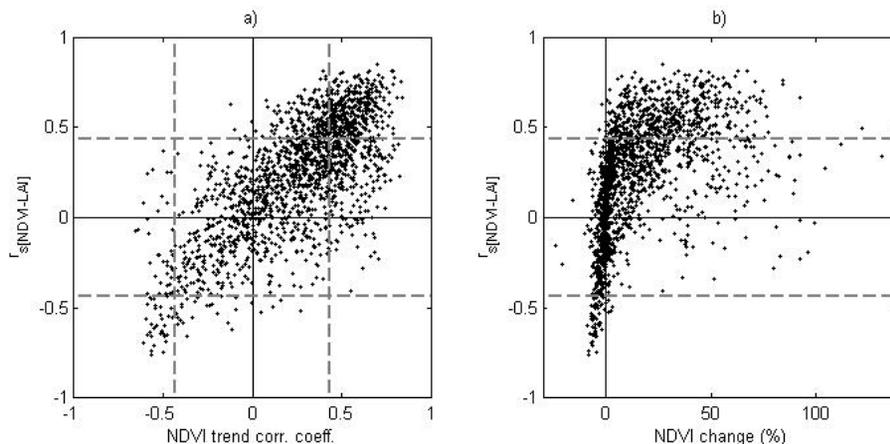


Fig. 5. Plots of Spearman rank correlation coefficient ($r_{s[NDVI-LAI]}$) against **(a)** $NDVI_{max}$ trend correlation coefficients, and **(b)** change in $NDVI_{max}$ over time. Dashed grey lines indicate thresholds of statistical significance ($\alpha=0.05$) for data-model comparison and temporal least-squares regression for $NDVI_{max}$.

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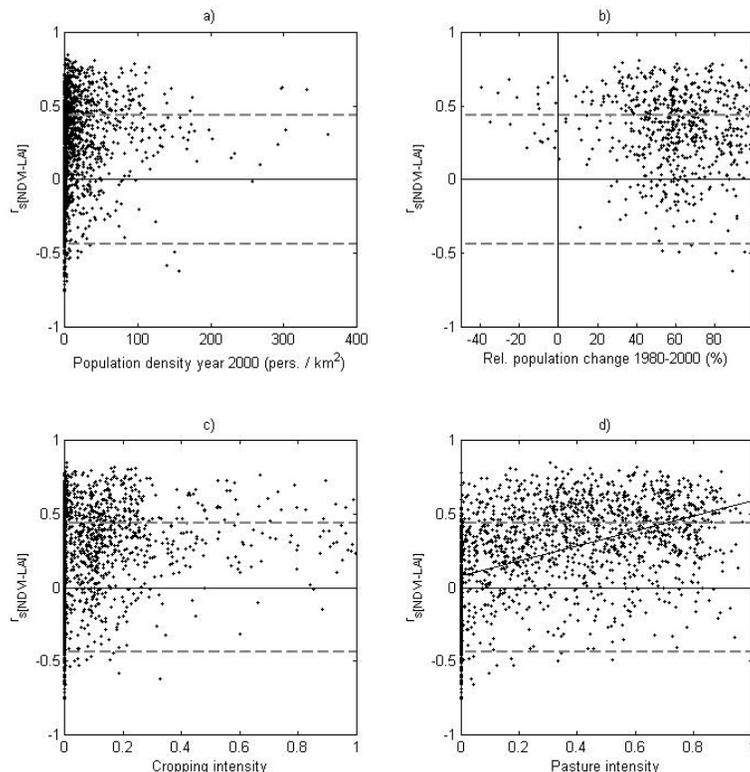


Fig. 6. Plots of Spearman rank correlation coefficient ($r_{s[\text{NDVI-LAI}]}$) against **(a)** population density in the year 2000, **(b)** relative population change from 1980 to 2000, **(c)** cropping intensity, and **(d)** pasture intensity. Dashed grey lines indicate thresholds of statistical significance for data-model comparison ($\alpha=0.05$). Solid line in (d) indicates regression for Spearman rank correlation coefficient vs. pasture intensity; $y=0.078+0.513 x$; $r=0.46$.

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