FUELWOOD EXTRACTION INTENSITY DRIVES COMPENSATORY REGROWTH IN AFRICAN SAVANNA COMMUNAL LANDS

Short title: FUELWOOD HARVESTING INTENSITY DRIVES REGROWTH IN SAVANNAS

Penelope J. Mograbi [1*], Ed T. F. Witkowski [1], Barend F. N. Erasmus [2], Gregory P. Asner [3], Jolene T. Fisher [1], Renaud Mathieu [4,5] & Konrad J. Wessels [4,6]

[1]School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, WITS 2050, Johannesburg, South Africa

[2]Global Change Institute, University of the Witwatersrand, Private Bag 3, WITS 2050, Johannesburg, South Africa

[3]Department of Global Ecology, Carnegie Institution for Science, 260 Panama Street, Stanford, CA 94305, USA

[4]Department of Geography, Geomatics, and Meteorology, University of Pretoria, Private Bag X20, Hatfield 0028, South Africa

[5]Ecosystems Earth Observation, Natural Resources and the Environment, Council for Scientific and Industrial Research, PO Box 395, Pretoria 0001, South Africa

[6]Remote Sensing Research Unit, Meraka Institute, Council for Scientific and Industrial Research, PO Box 395, Pretoria, 0001, South Africa

[*]corresponding author email: ORCID ID: 0000_0001_8437_7021; Penny.Mograbi@gmail.com; tel: +27 46 603 7011 6404, fax: +27 46 622 9319; Current affiliation: Department of Environmental Science, Rhodes University, Somerset Street, Grahamstown 6139, South Africa

Abstract

Woody biomass remains the primary energy source for domestic use in the developing world, raising concerns about woodland sustainability. Yet woodland regenerative capacity and the adaptive response of harvesters to localised fuelwood shortages are often underestimated or unaccounted for in fuelwood supply-demand models. Here we explore the rates and patterns of height-specific woody vegetation structural dynamics in three communal lands in a semi-arid savanna in South Africa. Using repeat, airborne light detection and ranging (LiDAR), we measured height-specific change in woody vegetation structure, and the relative influence of geology, fire, and ease of access to fuelwood. Monitoring 634 284 trees canopies over four years revealed high compensatory growth, particularly in the high wood extraction communal land: 34.1% of trees increased in height >1 m. Vegetation structural patterns were associated with ease of access to the communal land, but were mediated by wood extraction intensity. In these communal lands, vegetation structural dynamics show rapid woody thickening as a response to repeat harvesting. However, loss of height in vegetation structure did not follow a gradient of wood extraction intensity. We propose a conceptual framework to better understand change in vegetation structural metrics and the paradoxical phenomenon of high growth in high wood extraction scenarios. We also show co-adaptive responses of humans and woody vegetation to fuelwood harvesting in human-environment systems through patterns of regrowth response relative to ease of access to fuelwood resources.

Introduction

Woody biomass remains the primary energy source in the developing world, accounting for 60% of energy demand in sub-Saharan Africa (International Energy Agency 2014). Although fuelwood reliance is predicted to drop below 50% by 2040, 650 million people in sub-Saharan Africa will still be using solid biomass fuels for domestic use. The subsequent, often unsustainable, extraction of wood from ecosystems places humans in the role of agents of structural and compositional change (Shackleton *et al.* 1994; Galvin & Reid 2011). Wood extraction in developing countries has been implicated as a driver of forest and woodland degradation (Soussan 1988; Arnold *et al.* 2003). Fuelwood supply-demand models have predicted imminent "fuelwood crises" (e.g. de Montalembert & Clement 1983; Banks *et al.* 1996; Wessels *et al.* 2013), which have not yet occurred, in large

part because these models underestimated the adaptive capacity of natural-resource dependent communities (Dewees 1989; Mortimore & Adams 2001), and underestimated the regenerative capacity of woodlands (Foley 1987; Twine & Holdo 2016).

Rural energy problems often do not manifest in a direct lack of fuelwood resources, but rather a change in the quantity and quality of fuelwood available, i.e. available biomass (Luoga *et al.* 2002; Matsika *et al.* 2012), driving localised shortages. People can adapt to these shortages (Soussan 1988) through an increase in the average wood collection time; change of fuelwood species preference (Madubansi & Shackleton 2007); the development of fuelwood markets (Matsika *et al.* 2013); more efficient collection and transportation systems (Twine *et al.* 2003b); and change in energy use profiles (Hiemstra-van der Horst & Hovorka 2008). Woodlands also have adaptive responses to harvesting, including the rapid regenerative regrowth typical of many savanna tree species (Bond & Midgley 2001). Coppice shoots that form on woody plants after disturbance (e.g. fire, herbivory, harvesting) have accelerated growth relative to saplings of the same size as coppice accesses reserves stored in mature tree rootstocks (Holdo 2006; Tredennick *et al.* 2015). The regrowth response of savanna trees to harvesting mitigates fuelwood shortages substantially (Neke *et al.* 2006; Twine & Holdo 2016). These coupled responses, from both humans and ecosystems, form part of a complex non-linear relationship that is highly contextual (Mercer & Soussan 1992; Giannecchini *et al.* 2007) and difficult to predict.

While woodland 'collapse' may not have been realised due to adaptive response by both people and the resource base, high intensity wood extraction alters ecosystem structure and composition (Shackleton *et al.* 1994; Luoga *et al.* 2002). Wood harvesting changes the relative contribution of woody plant species and structural classes to total biomass (Mograbi *et al.* 2015), thereby affecting ecosystem functioning by reducing structural heterogeneity (Tews *et al.* 2004; Manning *et al.* 2006). As changes in woody vegetation structure and composition reflect ecosystem processes occurring at multiple spatio-temporal scales (Watt 1947; Levick & Rogers 2011), monitoring vegetation dynamics can aid understanding of these processes. Woody vegetation dynamics are increasingly being used to assess vegetation patterns relative to climatic and topoedaphic gradients (e.g. de Castilho *et al.* 2006; Colgan *et al.* 2012; Dahlin *et al.* 2012) and in response to disturbances (e.g. Dayton 1978; Chambers *et al.* 2004; Frolking *et al.* 2009; Shackleton & Scholes 2011). In the context of rural systems where fuelwood extraction is prevalent, measuring vegetation structural change is an underexploited method of inferring both past woodland use and future sustainability.

Here we used airborne light detection and ranging (LiDAR) technology to quantify three-dimensional (3D) woody vegetation dynamics across a wood extraction gradient. 3D data enable tracking of height-specific changes in vegetation, providing rich contextualisation of the drivers of change and ecosystem response. The surveyed communal lands form part of Bushbuckridge Municipality, South Africa, where widespread fuelwood harvesting has changed ecosystem structure and composition (Shackleton & Scholes 2011; Wessels *et al.* 2011), despite extensive electricity provision to rural households (Madubansi & Shackleton 2007). We explored the effect of fuelwood extraction on woody vegetation structural dynamics through the following questions: what are the height-specific changes and patterns of woody cover, and how do they differ between communal lands? What factors (geology, relative elevation, fire frequency, ease of access to communal lands) are associated with the spatio-temporal dynamics of woody vegetation structure and biomass? Monitoring canopy cover, vegetation structure and biomass dynamics within social-ecological systems can assist in understanding of local ecosystem drivers of change, and coupled human-environment vulnerability (Turner *et al.* 2003; Lambin *et al.* 2006). These data can also inform, and improve, predicted changes in natural-resource use ecosystems.

Methods

Study Site

The study site locations were in Bushbuckridge Municipality in the north-eastern portion of South Africa (Figure 1). The geology is dominated by Granite Lowveld vegetation (Rutherford *et al.* 2006) and the climate has hot, wet summers (500-900 mm annual rainfall; October-March: average minimum - average maximum: 20-31 °C) and warm, dry winters (April-September: 8-26 °C). Catenal sequences were characterised by *Terminalia sericea*, *Combretum zeyheri* and *C. apiculatum* on sandy, shallow, uplands and *Acacia nigrescens*, *Dichrostachys cinerea* and *Grewia bicolor* on clayey, deep, eutrophic lowlands (Rutherford *et al.* 2006).

Bushbuckridge Municipality was formed from joining portions of two former Apartheid 'homelands' (territory set aside for black South Africans) – Mhala from Gazankulu and Mpulaneng from Lebowa (Thornton 2002). Although Bushbuckridge is now state-owned land, there is customary tenure to the tribal chiefs who determine residential, arable and communal rangeland zoning. Communal lands are used for natural resource harvesting and livestock grazing. Settlements range from small, rural, isolated settlements to large, sprawling, urban areas along main transport routes. Bushbuckridge has the inherent social-economic challenges of former homelands: high unemployment, low education levels, and high population densities largely dependent on migrant worker

remittances and social grants (Thornton 2002). Thus, local populations are reliant on natural resources as a substantial contribution to their livelihoods (Twine *et al.* 2003a; Shackleton *et al.* 2007).

Within Bushbuckridge, we surveyed three communal lands from west (more mesic) to east (more arid); Site$_A$ (adjacent to Xanthia and Agincourt); Site$_B$ (adjacent to Justicia); and Site$_C$ (adjacent to the settlements of Croquetlawn, Ireagh and Kildare) (Figure 1). In previous studies of the area, fuelwood use was inelastic despite widespread access to electricity (Madubansi & Shackleton 2007). Matsika et al. (2013) found that different villages with similar socio-economic demographics used the same amount of fuelwood, regardless of the state of the communal land or the extra effort they would need to collect these resources. Thus, with similar household usage across the villages, fuelwood extraction intensity was mediated by the number of households per communal land area (Matsika et al. 2013). Using 2008 demographic data (from long-term MRC/WITS Rural Public Health and Health Transitions Research Unit demographic surveillance surveys (HDSS) – see Kahn *et al.* (2007) for HDSS project details), we used population and household density of the surrounding villages relative to communal land area as a proxy for wood extraction intensity: Site$_A$ – low extraction intensity (4425 communal land ha: 0.21 people ha^{-1}, 0.04 households ha^{-1}; Site$_B$ – intermediate extraction intensity (1815 communal land ha: 1.8 people ha^{-1}, 0.35 households ha^{-1}); and Site$_C$ - high extraction intensity (2155 communal land ha: 9.2 people ha^{-1}, 1.56 households ha^{-1}). Population demographics remained stable between the three sites over the study period (Table S1).

Although communal lands are zoned for use by their adjacent settlements, both residents and non-residents are known to harvest wood, occasionally for commercial purposes (Twine *et al.* 2003a). The location of Site$_B$, adjacent to Justicia and bordered by conservation land fences on the north and east (Figure 1), ensures almost exclusive access by this settlement (Tuinder 2009; Wessels *et al.* 2013). In contrast, Site$_A$ is surrounded by numerous settlements (Figure 1) and is utilised from all directions.

Light Detection and Ranging (LiDAR) data collection
Repeat airborne Light Detection and Ranging (LiDAR) surveys were conducted in April 2008 and 2012 using the Carnegie Airborne Observatory (CAO, https://cao.carnegiescience.edu) systems. Small-footprint, discrete-return LiDAR provides accurate three-dimensional (3-D) information on vegetation structure over large areas (see LiDAR coverage in Figure 1) (Methods S1a). A digital surface model (DSM) was interpolated from all LiDAR top-of-canopy returns and a digital terrain model (DTM) from the ground returns. The difference between the DSM and the DTM produced a canopy height model (CHM) at 1 m spatial resolution (Methods

S1a). We identified individual tree canopy objects, hereafter 'trees', using an object-based image analysis approach with a local maximum search algorithm (Kaartinen *et al.* 2012) using the 'imagery segmentation' package in SAGA GIS v2.0.6 (Conrad *et al.* 2015). The CHM was smoothed (circular Gaussian kernel smoothing), to optimise whole-canopy detection, and transformed, to maximise individual object identification in clumped canopies (Asner *et al.* 2015; Vaughn *et al.* 2015). The centre point of each tree was geotagged and the maximum canopy height for each tree was recorded for 2008 and 2012. Increase or decrease of each tree maximum height ≥1 m was classified as change, either 'growth' or 'loss'. Change of <1 m was considered 'persistence'. Reduction in height ≥75% was termed 'treefall' (Mograbi *et al.* 2017).

Aboveground woody biomass was estimated using LiDAR data, validated with field data collected concurrently with the 2012 LiDAR surveys. Field-based biomass was estimated using 25 m x 25 m plots (n = 56). All woody vegetation ≥1.5 m in height and ≥5 cm basal diameter was inventoried. These data were then used in the form of Colgan *et al.*'s (2013) plot-level allometric equations, derived from an extensive biomass harvesting effort in the South African Lowveld savanna. The woody species community composition and structural growth forms in our area, also in the Lowveld savanna, largely matched those in Colgan *et al.*'s (2013) research, although Bushbuckridge contained substantially more coppiced vegetation. We used the field-derived plot-level biomass to calibrate LiDAR-derived biomass models. A H x CC LiDAR metric was used, where H is mean top-of-canopy height and CC is the proportion of canopy cover for each plot. Both metrics were derived from the CHM. These models accounted for 68% (RMSE: 19.1 Mg ha^{-1}), 60% (RMSE: 4.8 Mg ha^{-1}), and 78% (RMSE: 18.6 Mg ha^{-1}), of the biomass variance for Site$_A$, Site$_B$, and Site$_C$, respectively (Mograbi *et al.* 2015). The LiDAR biomass models were then applied to LiDAR H x CC maps for 2008 and 2012 to create site-specific biomass estimates. Results from 2008 LiDAR biomass estimations were mean ± SD aboveground biomass of 9.42 ± 4.13 Mg ha^{-1} on predominantly gabbro and 21.18 ± 12.04 Mg ha^{-1} on granite communal lands (Mograbi *et al.* 2015). Riparian areas adjacent to rivers were removed from the biomass maps as they would require separate biomass models. Similarly, settlement and crop-farming areas were also removed. Details on the allometric equations used and the implications for accuracy and bias can be found in Colgan *et al.* (2013) and Mograbi *et al.* (2015).

Vegetation subcanopy information was derived from LiDAR voxels (volumetric pixels). The x-y-z laser point cloud enables quantification of the vertical vegetation structure through rendering of pseudo-waveform profiles in which vertical returns are aggregated into 1 m bins (Weishampel *et al.* 2000), known as voxels (3-D grid

cells: 25 m x 25 m x 1 m height). These data were normalised relative to the total number of LiDAR returns in the column, including the ground returns, as a percentage (%). Thus, each voxel represents the % LiDAR hits intercepted by the vegetation canopy in each 3-D grid cell, hereafter referred to as "subcanopy structure returns". For example, if a voxel in the 9-10m height class had a subcanopy structure of 60% (60% LiDAR hits were intercepted by vegetation at this height) in 2008, and in 2012 the same voxel value was 80%, the subcanopy vegetation structure in that voxel was 20% more dense in 2012. The 'total canopy structure' refers to the sum of the stacked 1 m voxels above 1 m in height (i.e. excluding ground returns), representing the total vegetation column structure.

Height-specific gains, loss and persistence of vegetation

The number of trees that had gained height (increase ≥1 m), lost height (decrease ≥1 m) or stayed unchanged (height change <1 m) were summed per hectare. Each hectare grid cell was then classified according to majority type: gains (the number of individuals that gained height exceeded the number that lost height or the number that stayed unchanged); loss (the number of individuals that lost height exceeded the number that gained height or the number that stayed unchanged); or persistence (the number of individuals that stayed unchanged exceeded or was equal to the number that gained or lost height). Patterns of vegetation structural dynamics were then examined through gains, loss, and persistence (GLP) maps between 2008 and 2012. These data, together with various environmental and anthropogenic variables (geology, relative elevation, burn frequency, distance from the nearest river, distance from the nearest settlement, and distance from the nearest road) were extracted using a 'spatial join' in ArcGIS v10.2 (ESRI 2012) for each hectare grid cell. The vertical vegetation profiles for GLP maps (as well as for the voxel and individual tree data) were divided into height classes: 1-3 m; 3-5 m; 5-10 m; and >10 m (Methods S1b).

Data Analysis

Known environmental and anthropogenic variables were chosen to explore environmental and anthropogenic associations to vegetation structure dynamics that have either been shown to affect savanna vegetation structure and composition (e.g. relative elevation, fire, geology) or were related to perceived ease of access to communal lands (distance to the nearest settlement/road) (Methods S1c). Bushbuckridge settlement features were manually digitised using aerial images from 2009 and 2012 (50 cm resolution; www.ngi.gov.za).

We used a constrained ordination technique, canonical correspondence analysis (CCA), to explore height-specific vegetation dynamics in relation to a suite of known environmental and anthropogenic drivers (Methods

S1d). Each ordination axis is a combination of different variables to explain 'species' abundance (here, each 'species' is a height-specific vegetation class of gains, losses and persistence) using a multivariate direct gradient analysis (Ter Braak 1986). To account for the non-linear relationships between variables, data were square-root transformed for ordination analysis. The analysis was conducted on a randomly selected distance-constrained subsample of hectare grid cell data and led to a varying number of samples for each site (n = 213, 378, 182 for Site$_A$, Site$_B$, and Site$_C$, respectively) including height-specific gains, losses and persistence. Spatial autocorrelation occurred within 40 m, calculated from a semivariogram in SAGA GIS v2.0.6. (Conrad *et al.* 2015), but we applied a distance constraint ≥160 m apart to avoid sampling adjacent grid cells. Total variation explained in each CCA was calculated using an R^2 analog of explained variance (all canonical eigenvalues) as a percentage of total variance (all eigenvalues).

Results

Landscape vegetation structural dynamics

We mapped over 630 000 individual trees ≥1 m in height in 2008 across three communal lands. Height change ≥1 m between 2008 and 2012 occurred in 32.6% of trees, of which 8.7% became shorter and 23.8% became taller (Table 1). Site$_C$ had the greatest height change (≥1 m) frequency of 42%, most of which were increases in height (Table 1). Although Site$_B$ had the greatest proportion of height losses (height reduction ≥1 m) and treefall (height reduction ≥75% of maximum height) of all sites, height gains still exceeded height losses (Table 1). Site$_A$ had the lowest height change frequency, the lowest treefall occurrences, and the highest tree density (Table 1).

Height-specific patterns of vegetation dynamics

Although Site$_C$ had a relatively high tree density (45.06 trees ha^{-1}; Table 1), most of these trees were taller than 5 m. Patterns show the 1-3 m height class experienced increases in all sites (Figure 2). Height gains occurred around the river in Site$_B$, and around a granite ridge running east-west across the centre of Site$_A$ (Figures 2-3). Fewer patches of vegetation height gains were noticeable in height classes >3 m, but loss patches were evident in the 3-5 m and 5-10 m height classes (Figure 2). In Site$_A$ and Site$_C$, these patches were adjacent to the settlements, whilst in Site$_B$ the patches of loss also occurred along the river and near the eastern fence line border with conservation land (Figure 2). Extensive patches of tall tree (>10 m) loss occurred in Site$_B$ (Figure 2), corroborated by the lowest persistence of trees in the >10 m height class relative to the other sites (Table 2).

The tall tree class (>10 m) was the most persistent height class (> 82%) across all sites). Persistence in vegetation taller than 5 m was greatest in $Site_A$ (Table 2). Conversely, $Site_C$ had the greatest persistence of 1-3 m vegetation (58%), and together with the relatively high transition from the 3-5 m to the 1-3 m class (11%) (Table 2), this indicates the site was shrub dominated. Gains in all sites were predominantly a transition from the 1-3 m height class to the 3-5 m height class (32%, 36%, 26% for $Site_A$, $Site_B$ and $Site_C$, respectively (Table 2).

Drivers of vegetation structural dynamics

The above results indicate that vegetation structure was most dynamic in the <5 m height classes and the changes were predominantly height gains. To explore this theme, we modelled the association between height-specific vegetation structure change and environmental and anthropogenic variables. However, the models had fairly low predictive power between sites (variation explained: all sites combined, 20.3%; $Site_A$, 6.8%; $Site_B$, 21.0%; $Site_C$, 15.3%). The major component of canonical axis 1 in the combined sites model was site, with $Site_A$ and $Site_C$ strongly negatively associated, despite having the same predominant geology (Figure 3a). In contrast, $Site_B$ was not associated with the other two sites as the ordination arrow is approximately perpendicular to the plane of the $Site_A$-$Site_C$ relationship (Figure 3a). The major contributing variable in the combined sites model to canonical axis 2 were the anthropogenic variables (distance from the nearest road, distance from the nearest settlement) and distance to river (Figure 3a). Indeed, distance from the nearest settlement was the most important factor influencing vegetation structural dynamics across all communal lands in the site-specific models too (Figure 3b,c,d). $Site_B$'s model had the highest predictive power and distance to the nearest road was related to dynamics in all height classes, but was strongest with the >10m height dynamics (Figure 3c). Despite the ordination models showing a relationship between vegetation structure change and anthropogenic variables (distance from the nearest road/settlement), investigating the effects of these variables separately on vegetation dynamics directly did not show significant patterns. Yet, a relationship emerged when looking at the *interactive effects* of distance from roads and settlements with vegetation dynamics (Figure 4).

We explored the relationship between estimated biomass (modelled in Mograbi *et al.* 2015), subcanopy structure and distance from road and settlements to demonstrate the spatial relationships in the low height classes (Figure 4). The association between biomass increase and the spatial intersection of distance from the nearest road and distance from the nearest settlement in $Site_B$ showed a 'hotspot' within 1 km of both surrounding settlements and roads (Figure 4A). The biomass hotspot in $Site_B$ matched the subcanopy returns hotspot for 1-3 m (Figure 4B), but less so for the 3-5 m and 5-10 m height categories (Figure 4). There was a

prominent spread of biomass increases in the high intensity communal land within 400 m of the surrounding

settlements and at all distances from roads (Figure 4C). In both $Site_B$ and $Site_C$, the biomass 'hotspot' were

large, cohesive areas of about 0.4 km^2 within 1 km from the settlement and the nearest roads (Figure 4A,C).

$Site_C$'s biomass hotspot most closely matched the spatial location of the 3-5 m subcanopy return increases

(Figure 4D). Both the biomass and subcanopy structural changes across all height classes were spatially variable

for $Site_A$, forming a mosaic of different values without coalescence between patches (Figure 4E). The pattern of

increasing biomass and subcanopy structural patch size in relation to distance from anthropogenic variables

(Figure 4) follows the same gradient of overall vegetation height change metrics (Table 2). That is, $Site_A$ had

29.7% height changes ha^{-1} (Table 1) and small, dispersed hotspots in relation to anthropogenic variables (Figure

4), while $Site_C$ had 41.9% height changes ha^{-1} (Table 1) and large, cohesive hotspots in relation to anthropogenic

variables (Figure 4).

Discussion

Compensatory regrowth was associated with increasing wood extraction intensity, with the greatest vegetation

height increases (Table 1, Figure 4) occurring in the communal land with the highest population density relative

to communal land area. Yet, while vegetation height gains increased with communal land population density

(Table 1), the same pattern was not present in vegetation height loss metrics. The intermediate population

communal land ($Site_B$) had the most spatially extensive changes to all height classes (Figure 2) and the highest

treefall and height losses, despite having the lowest tree density (Table 1). However, this site also had greater

numbers of trees in the >4m range relative to $Site_C$ (Figure S1), indicating a more heterogeneous height structure

to harvest from relative to $Site_C$ which was dominated by shrubs <3m tall.

Wood harvesting in high extraction intensity communal lands resulted in a homogeneous coalescence of

regrowth response close to communal land access points, whereas low extraction intensity communal lands

show more heterogeneous patterns of vegetation structure dynamics close to roads and settlements (Figure 4).

These patterns represent the complex trade-offs that people make in their natural resource collection (Arnold *et

al.* 2003; Giannecchini *et al.* 2007). The adaptive capacity of people to deal with fuelwood shortages has been

consistently underestimated (Mortimore & Adams 2001; Thomas and Twyman 2005), but these non-linear

responses are difficult to incorporate into fuelwood supply-demand models. As population and extractive

pressures increase in communal lands, people will co-adapt and innovate to mitigate these shortages (Marquette

1997; Raudsepp-Hearne *et al.* 2010) through behavioural change (e.g. 'fuel switching' (Hiemstra-van der Horst & Hovorka 2008), and increasing travel time (Madubansi & Shackleton 2007)). The expanding use of vehicles and wheel barrows for fuelwood collection (Dovie *et al.* 2002; Twine 2005) means harvesters will increasingly look to communal lands bordering roads to optimise wood collection gain for effort expended. These results show how highly utilised communal lands' functional response becomes spatially homogenised in response to an evenly distributed disturbance (Figure 4). In the case of less (or more recently) disturbed communal lands, the patterns of compensatory regrowth 'hotspots' could be temporally dynamic, shifting with changing extraction patterns (e.g. introduction of a new road) or as patches recover from previous disturbances. Research on Tanzanian miombo woodlands have demonstrated that woodlands used for wood extraction over a long period (1964-1996) were converted to shrubland, whilst those woodlands under more recent anthropogenic pressure with the construction of the Dar-es-Salaam-Morogoro highway showed different structural characteristics (Luoga *et al.* 2005). There is considerable insight to be gained by tracking these patterns over time to better understand shifting structural patterns of utilisation and ecosystem functional response to disturbance.

As fuelwood harvesting appears to drive tree resprouting, there is the potential for offsetting losses in extracted biomass and, potentially, maintaining the sustainability of the coupled human-environment system (Twine & Holdo 2016; Brandt *et al.* 2017). Tredennick and Hanan (2015) show that fuelwood harvesting was sustainable except under the most extreme extraction scenarios, mostly as a result of strong regrowth responses of savanna tree species. However, changes to the functional profile of a savanna woodland under high harvesting intensity to a highly productive, but structurally homogeneous shrub layer in the 'fuelwood trap', will have implications for ecosystem functioning and ecosystem services to the community. For example, grass biomass could decline in bush thickened areas, affecting livestock carrying capacity (e.g. Oba *et al.* 2000), and fewer tall trees have implications for critical ecosystem processes (Manning *et al.* 2006), with ramifications for ecosystem resilience through depauperate seedbanks and the proliferation of harvest-tolerant woody species. Homogeneous shrub-level vegetation structure may also affect the regrowth rates as a West African study found that initial tree height was a significant predictor of subsequent coppice growth rates, affecting the susceptibility of postharvest regrowth to fire (Tredennick *et al.* 2015). Our results suggest that the woody structural dynamics have shifted from a system that may have previously suppressed bush encroachment (Brandt *et al.* 2017), to a system undergoing rapid woody thickening. Although this study detailed changes in woody canopy dynamics, the information about shrub-level increases was not species specific. Shrub-level increases could be dominated by

species that are not appropriate for fuelwood use (e.g. *Lantana camara*, an alien invasive species) (Shackleton 1993). Similarly, the coppice stem diameters might not be of the preferred size class for fuelwood (Neke *et al.* 2006). It is likely that the addition of species-specific information would provide far more nuance to our findings and would have substantially improved the explanatory power of the ordination models.

Based on the results of this study, we suggest a relationship between intensity of natural resource use, vegetation dynamics, and structural heterogeneity (Figure 5). At low levels of natural resource use, both height-specific gains and losses of vegetation structural metrics are low and structural heterogeneity of the vegetation is maintained (Figure S1). As natural resource use intensity increases, so do losses in vegetation structural metrics as vegetation is being extracted. However, there may also be height-specific gains in some vegetation metrics as compensatory growth occurs with increasing harvesting. Indeed, intermediate use scenarios may contain increased biodiversity (Shackleton 2000; Smart *et al.* 2005) and higher structural diversity (Adler *et al.* 2001). But a counterintuitive relationship manifests at high usage, resulting in a situation of high compensatory growth metrics, predominantly in the shrub layers, whilst loss metrics decrease as fewer tall trees remain to be removed (Figure 5), as is the case for Site$_C$. For example, structural complexity reduction occurred in east African miombo savannas, where 50% of the woodlands were lost with an accompanying increase in shrublands (Luoga *et al.* 2005). Under extreme use scenarios, structural heterogeneity collapse could occur. This conceptual relationship demonstrates the importance of height-specific data collection for vegetation monitoring in social-ecological systems. There are important exceptions to the posited conceptual relationship between vegetation gains, losses and structural heterogeneity (Figure 5), dependent on the social-ecological systems context and land management. For example, remote, low use intensity communal lands and conservation land experience hard-wood poaching, such as *Pterocarpus angolensis* (*pers. obs.*) in Bushbuckridge, which would affect structural metrics. Conversely, in high intensity communal lands, culturally important trees, e.g. *Sclerocarya birrea*, are conserved for non-timber uses (Shackleton *et al.* 2003), which would result in a bi-modal structural profile of a homogeneous shrub layer, and conserved large trees.

Unsustainable fuelwood harvesting is often cited as the reason for deforestation in communal lands (de Montalembert & Clement 1983; Wessels *et al.* 2013); however, there is a growing consensus that agricultural and settlement expansion are the dominant drivers of degradation (Arnold *et al.* 2003; Defries *et al.* 2004). In our study, height loss in trees taller than 5 m was indicative of settlement and crop-land expansion, reducing the available land for natural resource provision – a twofold setback to ecosystem service provision with an

increasing population but decreasing natural land. Although biomass regrowth does occur, large tree loss can result in homogeneous shrubland. As yet, there is limited understanding of ecosystem function change in systems with high compensatory primary productivity or systems that are structurally deficient. But these height-class specific data on vegetation dynamics provide more refinement to natural resource use sustainability and the 'fuelwood crisis' narrative that centers on energy-deforestation links. Here we provide evidence of co-adaptive responses in human-environment systems to contribute to a more nuanced view of sustainability.

Supporting Information

Figure S1. Change in woody vegetation height class density distribution in 2008 and 2012 across three savanna communal lands.

Table S1. Household and population demographics for three villages in 2008 and 2012.

Supporting Methods S1. Supplementary methodological information on data collection and analyses.

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Table 1. Vegetation structural dynamics in three savanna communal lands. 'H' refers to canopy height and 'n' to number of samples of individually detected trees. The percentage frequency of H changes ≥1 m refers to both increases (i.e. growth) and decreases (i.e. loss) in canopy height. A portion of the decrease in canopy height can be expressed as the loss of individually tracked trees (≥ 75% reduction in height has been termed 'treefall'). Height frequency changes were tracked per tree between 2008 and 2012, and summed per hectare.

Site	Site area (ha)	n (trees)	Tree density (trees ha^{-1})	Frequency of H changes ≥ 1 m	Frequency of H increases ≥1 m / Frequency of H decreases ≥1 m	Frequency of treefall
All sites combined	10 534	634 284	60.21	32.6%	23.8% / 8.7%	2.2%
Site$_A$	5 020	428 110	85.28	29.7%	21.1% / 8.6%	1.6%
Site$_B$	3 359	109 070	32.47	35.5%	25.3% / 10.25%	4.5%
Site$_C$	2 155	97 104	45.06	41.9%	34.1% / 7.9%	2.6%

Table 2. Mean proportional transitions between vegetation height classes over four years in three communal lands: a) Site$_A$; b) Site$_B$; and c) Site$_C$. Total proportions do not add up to 1 because of loss to <1 m height class (which was excluded from the analysis), as well as the omission of growth and loss transitions <1 m (i.e. below the 'change' threshold). Shaded cells indicate persistence, cells to the right of shaded cells are gains, and to the left of shaded cells are losses.

a) Site$_A$

2008		2012				
		1-3 m	3-5 m	5-10 m	>10 m	Total
	1-3 m	0.41	0.32	0.01	0.00	0.74
	3-5 m	0.07	0.68	0.10	0.00	0.85
	5-10 m	0.02	0.06	0.87	0.01	0.95
	>10 m	0.01	0.02	0.05	0.90	0.97

b) Site$_B$

2008		2012				
		1-3 m	3-5 m	5-10 m	>10 m	Total
	1-3 m	0.42	0.36	0.01	0.00	0.79
	3-5 m	0.06	0.66	0.10	0.00	0.82
	5-10 m	0.04	0.04	0.83	0.01	0.91
	>10 m	0.04	0.04	0.04	0.82	0.94

c) Site$_C$

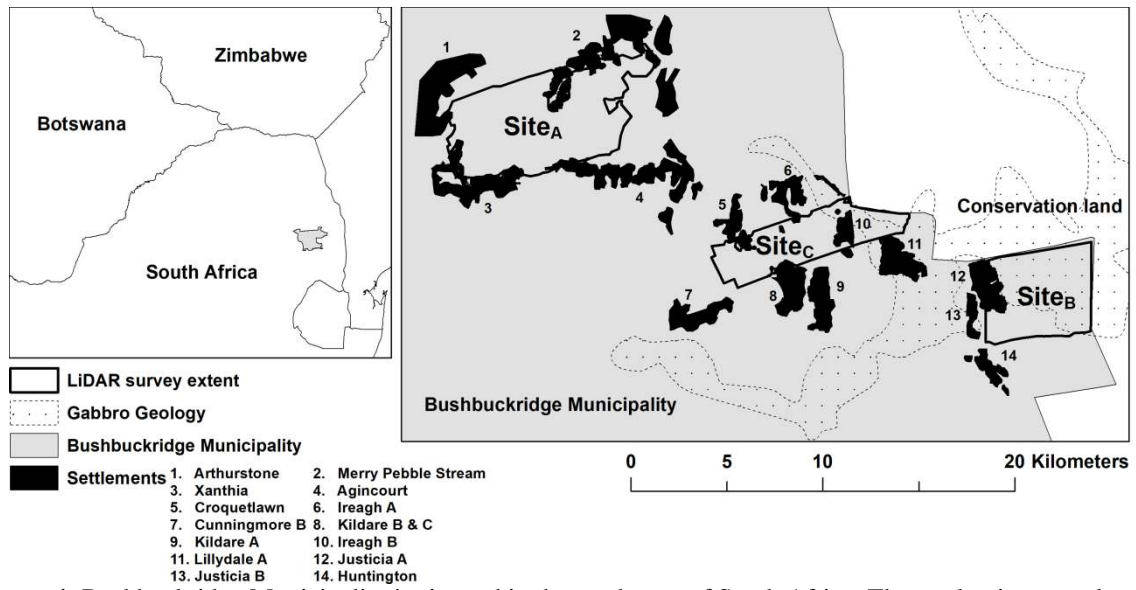| 2008		2012				
		1-3 m	3-5 m	5-10 m	>10 m	Total
	1-3 m	0.58	0.26	0.01	0.00	0.86
	3-5 m	0.11	0.58	0.11	0.00	0.80
	5-10 m	0.04	0.05	0.82	0.02	0.92
	>10 m	0.03	0.02	0.05	0.87	0.96

Figure 1. Bushbuckridge Municipality is situated in the north-east of South Africa. The predominant geology is granite with gabbro outcrops. Numbered settlements are described in the legend. Communal lands are utilised by adjacent settlements.
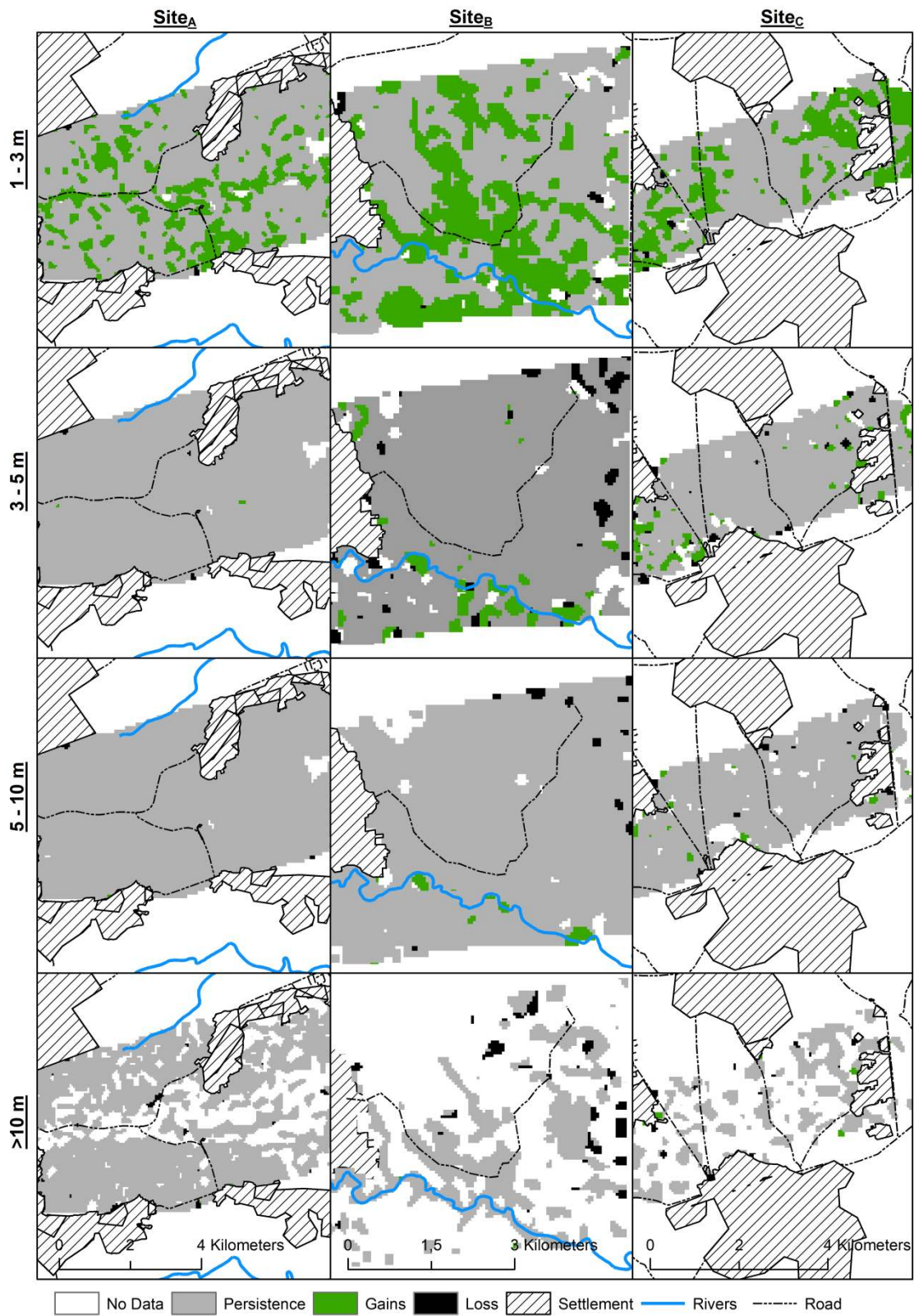
Figure 2. Maps of height-specific gains, losses and persistence per hectare in three South African savanna communal lands.
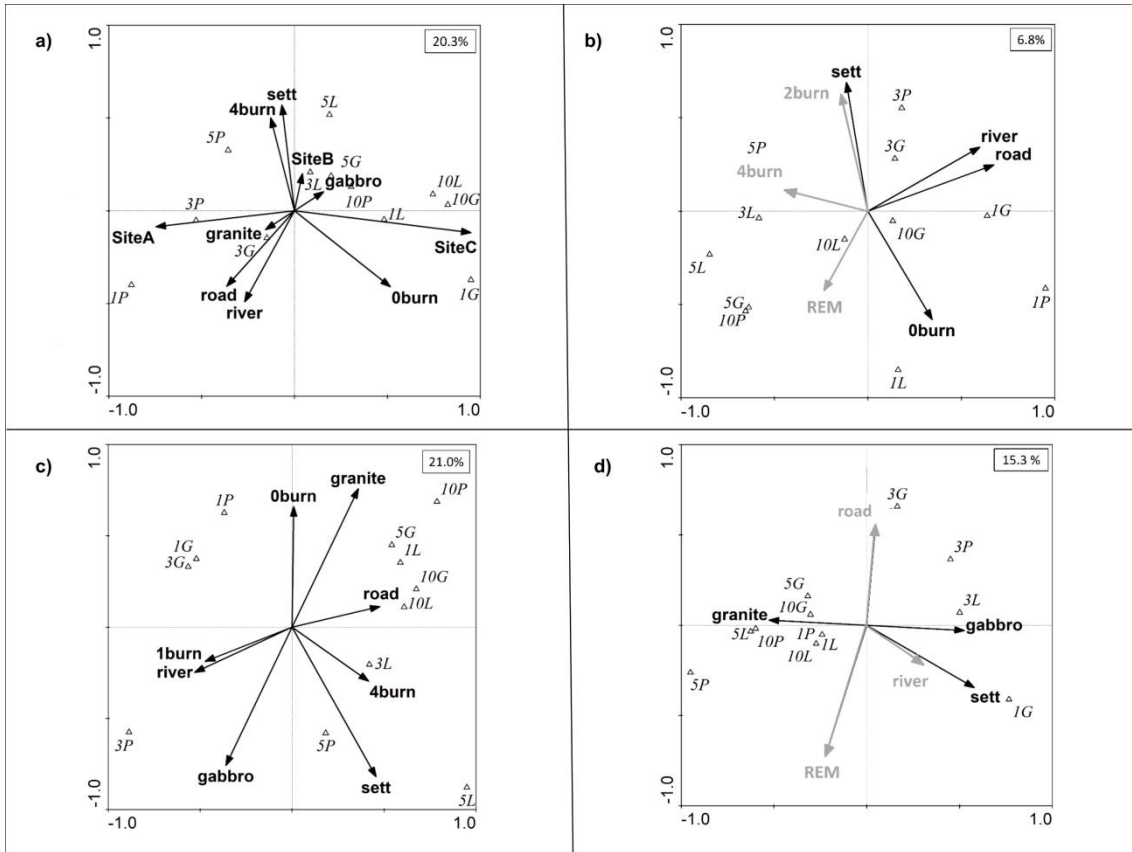
Figure 3. Canonical correspondence analysis (CCA) of height-class specific gains, loss and persistence (per hectare) of vegetation in relation to anthropogenic and environmental explanatory variables in a) all sites combined, b) Site$_A$, c) Site$_B$, and d) Site$_C$. 'Sett', 'road' and 'river' refer to distances from the nearest settlement, road, and river, respectively. '0burn' and '4burn' refer to fire frequency. 'REM' is relative elevation. Height class codes are: 1 (1-3 m), 3 (3-5 m), 5 (5-10 m) and 10 (>10m). Letters following height class codes refer to: G (gains), L (loss), and P (persistence). Non-significant variables are displayed in grey (see (Methods S1d for details).
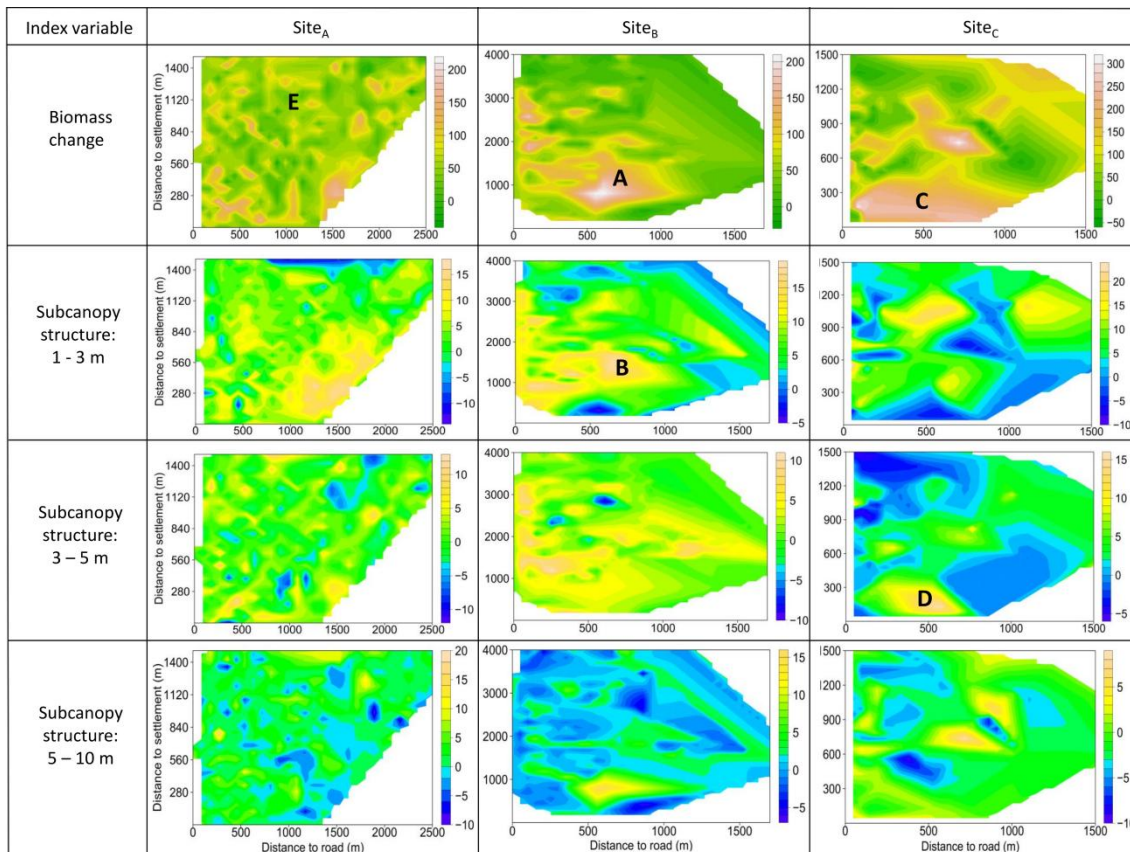
Figure 4. Changes in biomass (%) and height-specific subcanopy structure returns (%) in Site$_A$, Site$_B$, and Site$_C$. Biomass and height-specific subcanopy structure return change are presented relative to the spatial intersection between distance to the nearest roads and settlements for each communal land between 2008 and 2012. The index bar on the right of each graph provides a gradient of change for biomass change (%) or subcanopy structure return change (%). 'Hotspots' of high increases in biomass and subcanopy returns are indicated by warm colours. Letters A-E mark regions of interest that are referred to in-text.
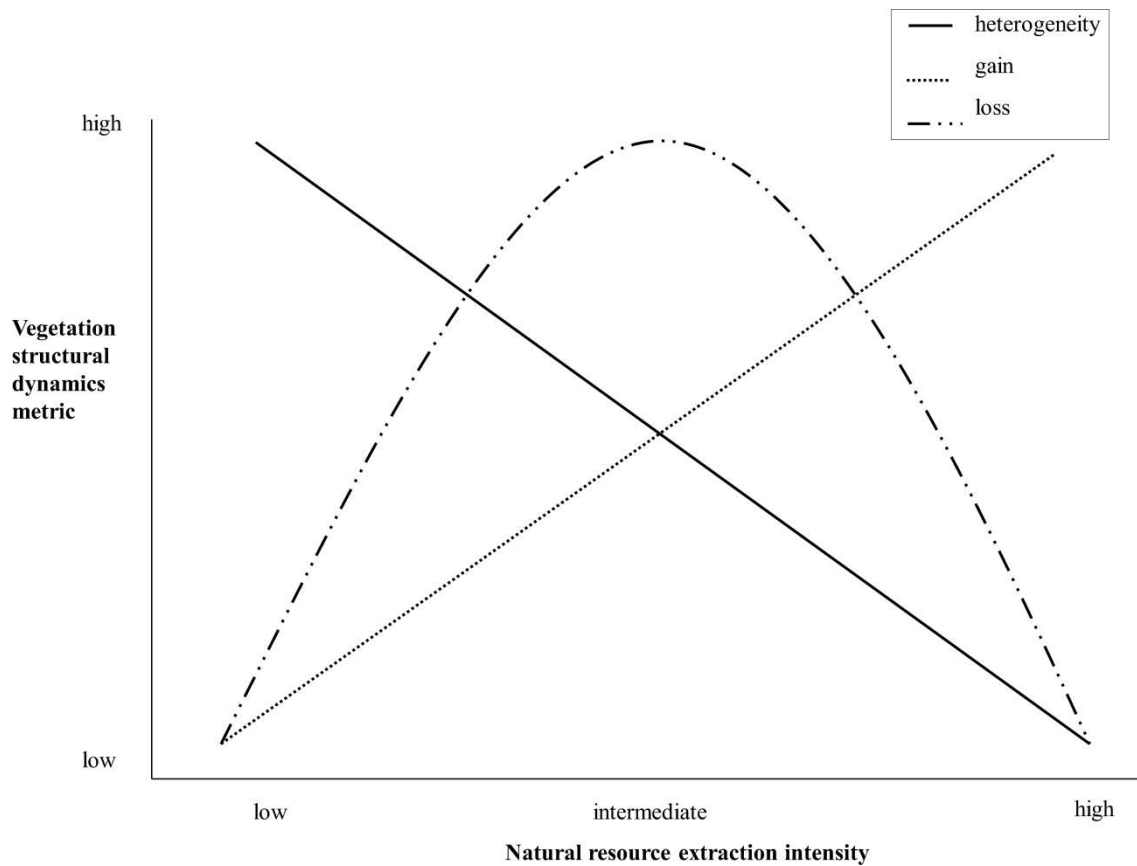
Figure 5. Conceptual changes in vegetation structural metrics in relation to a woody vegetation extraction gradient. Increasing natural resource use decreases structural heterogeneity, but vegetation structural dynamics show varying height-class specific responses. Corresponding conceptual links to resilience and ecosystem service (ES) provision are shown in relation to usage intensity.