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The impact of invasive species on social-ecological systems: Relating supply and use of selected provisioning ecosystem services

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ABSTRACT

Understanding the sustainability of social-ecological systems requires quantifying the relationships between ecosystem service supply and use. However, these relationships, and the influence of environmental change on supply and use, are poorly known. Here we apply a nested sampling design to analyse supply-use relationships in ten administrative units in each of two Eastern African regions undergoing invasion by an alien tree, *Prosopis juliflora*. Ecological data on supply of two key provisioning services, woody and herbaceous biomass, were collected in field plots and the use, defined here as income and livestock numbers, was assessed using household surveys. Supply and use were then up-scaled to the level of the smallest administrative unit. High Prosopis cover affected the supply of both services, with increased woody biomass but reduced herbaceous biomass. We found that supply of woody biomass was positively associated with income from wood sales. Prosopis invasion reduced income from livestock and slightly decreased cattle numbers over the past ten years. We propose that biophysical and socio-economic data collected at the same scale can help to determine supply-use relationships for ecosystem services and we discuss how integration of supply-use data can inform sustainable management of social-ecological systems in the context of environmental change.

1. Introduction

Rural people in low-income countries are often directly reliant on provisioning services from nature, such as food, fuel, fibre and water, and have limited capacity to compensate for reductions in service supply (Kumar, 2010). The ecosystem services concept, defined as the benefits that people obtain from ecosystems (Díaz et al., 2015), has been used to demonstrate the links between natural and socio-economic systems (Binder et al., 2013). Changes in the supply of a provisioning ecosystem service may be the result of alterations to ecosystem functioning, which in itself is affected by a range of anthropogenic environmental changes, such as overexploitation or invasion by alien species (Pejchar and Mooney, 2009). Such changes in ecosystem service supply can lead to cascading effects (Haines-Young and Potschin, 2010) that may be visible as changes in ecosystem service benefits and ultimately in human well-being (Potschin and Haines-Young, 2016).

Although a good understanding of the relationship between supply, use and demand of ecosystem services is fundamental for determining the pressure on social-ecological systems and for finding management options, this relationship is often not well understood (Fig. 1; Fisher et al., 2008; Wei et al., 2017). Many studies on ecosystem services have used detailed proxies of ecosystem service supply at local scales but these studies have not considered whether there is demand for the services, or to what extent they are used (e.g. Allan et al. 2015). On the other hand, many studies have measured use and demand but generally only at larger spatial scales and using coarse proxies (e.g. Burkhard

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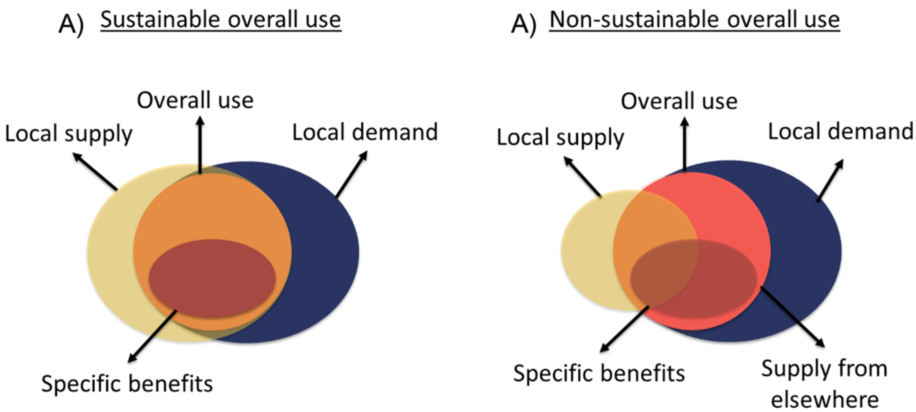

Fig. 1. Conceptual relationship between provisioning ecosystem-service supply (light brown), demand (blue), overall use (red) and specific benefits from the use of ecosystem services (e.g. income from livestock; dark brown). A) illustrates a potentially sustainable scenario where overall use is lower than the local supply, while B) illustrates an unsustainable scenario where overall use cannot be met by local supply and thus requires on supply from elsewhere. Adapted from Yahdjian et al. (2015).

et al. 2012). One of the major objectives of ecosystem service research is to understand the flow of ecosystem services from the environment to society (Geijzendorffer et al., 2015). It is therefore crucial to directly link ecosystem service supply, i.e. ecological data, to ecosystem service use and demand, i.e. socio-economic data (Schröter et al., 2012). In the literature there is considerable confusion over what constitutes use and demand of ecosystem services and multiple studies (e.g. Martín-López et al., 2014; Wei et al., 2017) equate use with demand. We follow Yahdjian et al. (2015) in separating use from demand, i.e. the actual consumption and social values of ecosystem services from what people want or need from an ecosystem (Fig. 1). Here we focus on ecosystem service use, i.e. the level of ecosystem services that are actually used, as opposed to demand, which is an indication of the level of ecosystem service supply that is desired (Fig. 1). Directly comparing supply with use can give an insight into the sustainability of the system and highlight mismatches in use and supply.

Comparisons of ecosystem service supply and use have typically been made at regional and national scales (Wei et al., 2017). These studies have generally used secondary data, such as land cover and national or regional statistics, to quantify supply (Larondelle and Lauf, 2016; Martínez-Harms and Balvanera, 2012). At smaller spatial scales, it is possible to collect high quality primary data on ecosystem service supply (Martínez-Harms and Balvanera, 2012), for instance by using precise indicators, such as measures of pollinator visitation rates to represent pollination or herbaceous biomass as a proxy for forage production. It is especially crucial to work at small scales when trying to assess the effects of environmental change drivers, as their impacts are often site-specific and context-dependent (Liao et al., 2016). Indicators of income, expenditure or capital might be good measures of use, as they quantify specific benefits derived from the use of ecosystem services and have a direct link to human well-being and demand (Haines-Young and Potschin, 2010). For example, income from livestock sales represents a benefit from the local supply of forage production. In this study we therefore focus on the relationship between ecosystem service supply and specific benefits derived from the local use of these ecosystem services.

In principle, the ecosystem service supply-use relationship at a defined spatial scale can take different forms and the particular form has important consequences for sustainability. If overall use of services is consistently lower than local supply, then exploitation is likely to be sustainable (Fig. 1A). However, if service use equals or consistently exceeds the amount supplied locally, then use is-likely to be unsustainable as it requires the local supply of ecosystem services to be supplemented by supply from elsewhere. For instance, if land degradation leads to a reduction in supply of forage and livestock numbers are too high for the forage supplied locally, then communities may have to search for forage elsewhere, leading to resource use conflicts, or they may depend on forage provided by governmental or aid organizations (Fig. 1B). Moreover, the ecosystem service supply-use relationship may also be non-linear, which may lead to unsustainable use at certain levels of supply: a threshold relationship, for instance, could indicate that low levels of ecosystem service supply are insufficient to meet societal needs or that below a threshold there is no value for the potentially available resource (Manning et al., 2018). Alternatively, use might be limited in cases where the extra cost or effort involved exceeds the additional benefits (Farber et al., 2002), leading to a saturating relationship where use does not increase beyond a certain level of supply. The shape of the relationship depends on more factors than only service supply and might be strongly influenced by drivers of change that affect either supply or use, such as climate change or invasive species. Understanding or describing the relationship therefore requires empirical data on supply and use; however, these data are rarely simultaneously available, in particular not at the same spatial and temporal scale.

In rural areas of the developing world, most individuals depend on locally produced ecosystem services for their livelihoods, contrary to developed countries where provisioning services are sourced worldwide. In developing countries small-scale quantification of ecosystem services is therefore essential. In addition, many services that rural people depend on are incompletely captured in national statistics. To improve our understanding of the relationship between ecosystem service supply, use and demand, ecological and socio-economic datasets should be collected at the same spatial units (Scholes et al., 2013). Data on ecosystem service use are often based on coarse datasets like regional statistics (Wei et al., 2017) and can therefore not be deployed to test for differences at small spatial scales. Testing for supply-use relationships at these small scales therefore requires ecological data on service supply, which can be linked to quantitative socio-economic data on use derived from these ecosystem services. Primary data collection has the additional advantage that pairs of indicators can be chosen more freely based on their likely relevance for the service. Despite the importance of understanding the effects of environmental change on social-ecological systems (Ohl et al., 2010), we are not aware of published studies that have used such detailed primary measurements of both ecosystem service supply and use.

Eastern African pastoralist and agro-pastoralist communities are among those human societies that are particularly reliant on ecosystem services (Witt, 2010), since livestock are of direct importance for their culture and wealth (Ouma et al., 2005). Over the last decades, land degradation due to overgrazing, land tenure insecurity, extreme weather events and biological invasions has put these social-ecological systems under increasing pressure (Dregne, 2002). As a way to halt land degradation and improve livelihoods, various woody plants, such as *Prosopis juliflora* (Sw.) DC. and other congeneric taxa (Fabaceae; Prosopis henceforth) were introduced to Eastern Africa during the 19th and 20th centuries (Binggeli, 1996). Prosopis was introduced to provide important ecosystem services such as wood-based products, e.g. firewood and charcoal, and to increase available fodder for livestock, as the pods can be eaten by cattle and goats, to increase sustainability of livelihoods (Pasiecznik, 2001). However, Prosopis invasion also leads to a serious reduction in existing ecosystem services, including groundwater supplies (Dzikiti et al., 2013) and grassland forage availability (Ndhlovu et al., 2011). The reduced grazing capacity might increase vulnerability of livelihoods that depend on livestock and lower resilience (Rettberg, 2010). Additionally Prosopis has led to an increase in ecosystem disservices by increasing vectors of human diseases (Lyytimäki, 2015; Muller et al., 2017). Hence, Prosopis has positive and negative impacts on rural livelihoods and its negative impacts might lead to higher livelihood vulnerability (Shackleton et al., 2019). These trade-offs between ecosystem services and disservices highlight the need for an approach that integrates multiple ecosystem services to assess how ecosystems and livelihoods are affected.

We used Prosopis invasions in Eastern Africa as a model system to explore the relationships between supply and use of two provisioning ecosystem services in ecosystems undergoing substantial environmental change. We explored these relationships in two agro-pastoralist systems: Afar, Ethiopia, and Baringo, Kenya. We implemented a nested sampling design that allowed us to collect paired environmental and socio-economic data at the same spatial scales (lowest administrative units). We hypothesized that 1) Prosopis significantly increases the supply of woody biomass but decreases the supply of herbaceous biomass. 2) Prosopis changes use of ecosystem services by increasing income from wood, and decreasing income from livestock and livestock numbers. 3) Ecosystem service supply is positively related to ecosystem service use, but the shape of the relationship between ecosystem service supply and use differs between different pairs of indicator variables.

2. Methods

2.1. Study areas

Data were collected in Baringo County, Kenya, and Afar Region, Ethiopia, both located in the Great Rift Valley (Fig. 2). In Baringo, data were collected around Lake Baringo and Lake Bogoria (between 0°15′ and 0°36′North and between longitude 35°58′ and 36°08‘East). The region is characterized by a semi-arid climate; the average annual temperature is 24.6 °C and mean annual rainfall is 635 mm, which traditionally fell in two distinct rainy seasons, March-May and November (Kassilly, 2002). With climate change traditional weather patterns are changing with increased incidences of extreme weather events (Ministry of Agriculture, Livestock & Fisheries, 2017). Historically, Baringo was dominated by grasslands. The region has a long history of high human disturbance and is currently sparsely vegetated and dominated by shrubs and small trees (Andersson 2005). Currently livestock, charcoal making and agriculture are the main sources of income. Afar (between 8°49′ and 14°30′North and between 39°34′ and 40°28′East) has a similar, semi-arid climate as Baringo County, with an average annual temperature of 27.6 °C and a mean annual rainfall of 564 mm. The main rain season is in the period July-September (Werer Agrometeorology Station, 2000). Traditionally, pastoralism was the main livelihood and most inhabitants were semi-nomadic. In recent decades, land conversion to agriculture and increased population densities have led to widespread land degradation (Haregeweyn et al., 2013). The original vegetation consisted mostly of wooded savannah and scrublands (Ministry of Agriculture, 1997) and these are still present, although perennial grasses and herbs have disappeared over large areas.

Prosopis was introduced in Afar and Baringo in the early 1980 s (Swallow and Mwangi, 2008; Kebede and Coppock, 2015). In Baringo County, multiple Prosopis species and their hybrids were introduced but in both regions most of the invasive Prosopis trees belong to *P. juliflora* (M. Castillo, unpublished results). Soon after its introduction, *P. juliflora* became invasive and now covers 1.3 million hectares in Afar alone (Shiferaw et al., 2019) and 19,000 hectares in Baringo (Mbaabu et al., 2019). While use of Prosopis charcoal and pods was actively promoted in Kenya (Choge et al., 2007), there are no incentives to promote Prosopis utilization in Ethiopia (Bekele et al., 2018).

2.2. Data collection

In each region, ten communities were selected that represent as wide a range of Prosopis cover as possible. A community was defined as the smallest administrative unit in a given region, i.e. a Kebele in Ethiopia and a Sub-location in Kenya. Prosopis cover ranged from 7-68% cover in the communities in Kenya and from 4-59% cover in the communities selected in Ethiopia (Table 1).

2.2.1. Ecological data

In each community, we established five to eight 15x15 m plots that covered the whole Prosopis cover gradient in the community (including uninvaded plots; Table 1). Within communities, plots were chosen to be as similar as possible in terms of land use and history, except that they differed in Prosopis cover. All plots were located on (former) grazing land, however, the degree of previous disturbance by overgrazing and the habitat type (floodplain, rain-fed grazing land or shrubland) differed between communities. Prosopis cover was estimated visually by two persons independently. Plots were divided into nine 5x5 m subplots. Sampling was performed in the central and in the corner subplots. We used woody and herbaceous biomass as indicators for the supply of provisioning ecosystem services, because they represent the key ecosystem service trade-off caused by Prosopis. The main reason for the introduction of Prosopis was to increase the supply of wood but this may come at the cost of herbaceous biomass, which is the key provisioning service for agro-pastoralists, given their dependence on livestock. Additionally, wood and livestock are the two main income sources of rural people in the study regions.

We measured the basal diameter (30 cm above ground) of all individual stems of Prosopis within three randomly selected subplots. Native tree species were not sampled as they were almost entirely absent in our plots. Basal diameter was converted to aboveground dry woody biomass using an allometric equation based on the data from Muturi et al. (2012; Appendix A):

$$\ln\left(Dry\ woody\ biomass\ (kg/stem)\right) = -10.67 + 8.71 * Stem\ basal\ diameter^{0.2}$$

Herbaceous biomass was sampled on a 25x50 cm area in the centre of four randomly selected subplots. All herbaceous biomass was cut at ground level and stored in paper bags. Samples were dried at 70 °C for 24 hours and weighed, and total biomass (dry weight / 225 m^2) was calculated for each plot. Due to logistical limitations we did not separate herbaceous biomass of palatable and unpalatable species. Grass abundance was however affected the same way by Prosopis as abundance of all herbaceous plants. Therefore, it seems unlikely that there was no shift from palatable to unpalatable species or vice versa along the Prosopis cover gradient

2.2.2. Socio-economic data

Household interviews were conducted to quantify use of ecosystem services. In 2016, 250 households were interviewed in Kenya and 253 in Ethiopia. The number of interviewed households per community was based on its population size (Table 1). Within each community households were selected randomly by a draw. Structured questionnaires were used to collect data on the total income per household, together with income sources, livestock numbers, livestock movements and demographic and socio-economic characteristics (see Appendix B). Income from livestock and wood as well as livestock numbers were taken as specific benefits to analyse ecosystem service use. We analysed cattle separately from goat and sheep as cattle are of high cultural importance (Schneider, 1957). Goat and sheep were assessed together, even though

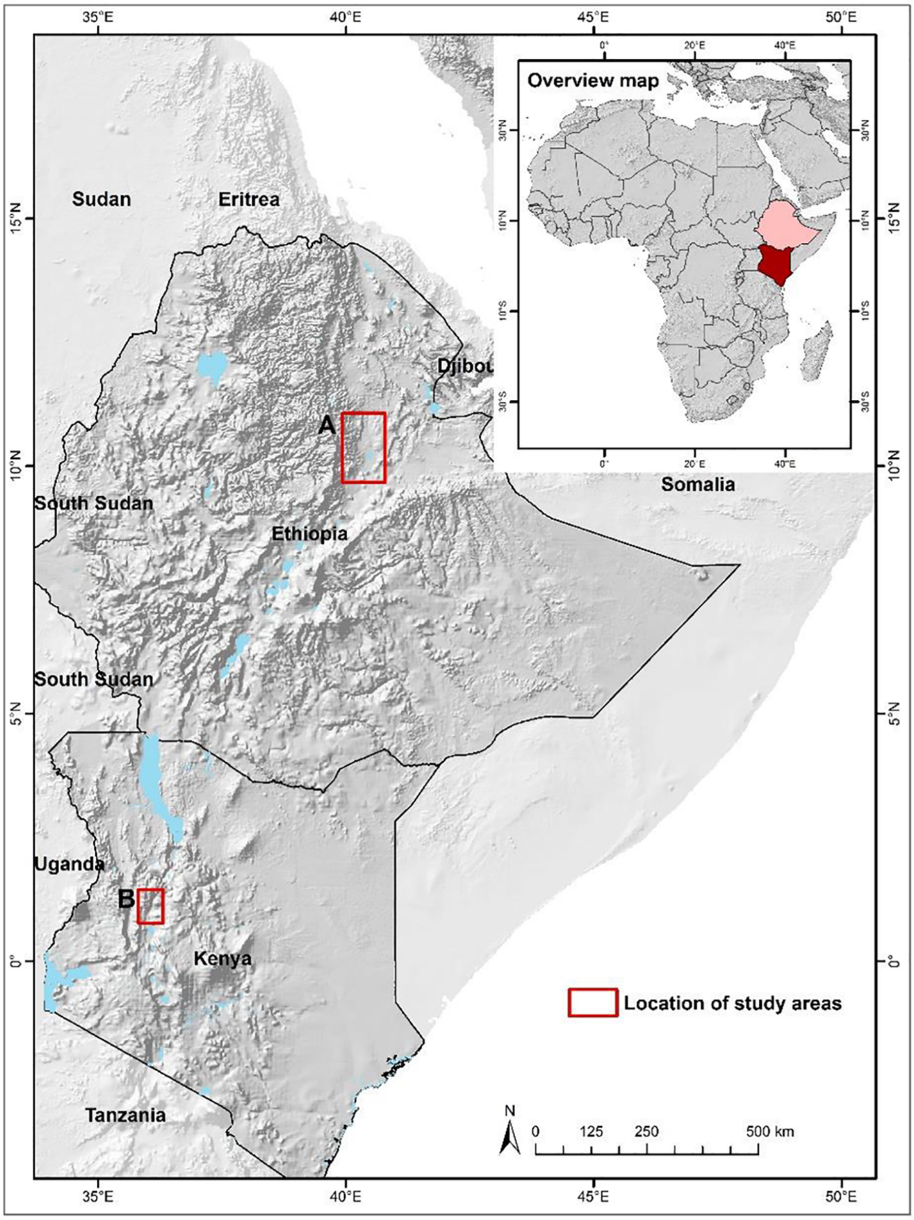

Fig. 2. Location of study areas Afar (A) and Baringo (B) in Eastern Africa.

they have different feeding behaviour, because they are of similar importance to pastoralists. Interviews were conducted by trained enumerators, who had experience with conducting similar surveys and were fluent in the respective local languages. To control data quality, three supervisors were recruited per study area. Monetary values were converted from local currencies to USD, using mid-2016 exchange rates. Income diversity was calculated using Shannon-Wiener method with the *vegan* (Oksanen et al., 2018) package in R (R Core Team 2018).

2.3. Prosopis fractional cover map

In order to scale up plot-level data to the smallest administrative units, we created fractional cover maps for Prosopis for both study areas. The fractional cover maps had a 15 × 15 meter resolution and show where Prosopis is present and at what density, i.e. each pixel has a continuous range of Prosopis cover. Georeferenced presence-absence data were collected throughout the study regions. A total of 2722 and 885 sample plots of 20x20 meter were sampled in 2016 and 2017 in Ethiopia and Kenya respectively. Prosopis was absent in about 70% and present in about 30% of the plots. These proportions correspond to the amount of invaded and uninvaded lands in the regions, in order to avoid bias towards either presence or absence of Prosopis (Jiménez-Valverde and Lobo, 2007). A plot was considered a presence plot when at least one Prosopis plant was present. The cover of Prosopis was estimated visually to the nearest ten percent. About 80% of the sampling plots were randomly selected for model calibration and the remaining 20% were used for model verification (Meynard and Quinn, 2007). In addition to the presence/absence plots, 17–19 spatial variables were used to explain Prosopis distribution (Appendix C). All spatial datasets were projected to UTM projection and resampled to 15 m spatial pixel resolution so that the size of sampling plots for ecological variables matched the spatial variables (Guisan and Thuiller, 2005). A Random Forest (RF) regression algorithm (Breiman, 2001) was then used to model the fractional cover map based on the field reference plots and the spatial variables. The kappa accuracy of the fractional cover maps was 0.80 in Ethiopia and 0.82 in Kenya.

Mean Prosopis cover was calculated for each community by averaging the Prosopis cover across all pixels of the fractional cover map.

Table 1
Overview of the sampled communities, including sample sizes for both ecological and socio-economic data collection.

Study site	Community name	Community size (ha)	Population	Prosopis cover (%)	Sample size	
					# of plots	# of households
Ethiopia	Aledeghi	13,104	812	15	7	29
	Angelele	14,586	3042	13	6	26
	Doho	13,092	4452	29	8	30
	Dudub	7769	1287	4	7	24
	Kabena	3961	2265	59	8	30
	Kalatburi	7049	2327	13	8	12
	Melka Sadi	20,889	12,299	12	8	30
	Orafito	10,690	3877	19	8	25
	Sarkamo	24,169	8162	26	8	31
	Yigile	2271	2619	41	8	16
Kenya	Meisori	6531	2810	15	7	29
	Logumgum	5449	1279	11	6	18
	Ngambo	3739	3345	46	6	25
	Eldume	2589	2590	50	5	24
	Kaptombes	2601	499	9	7	24
	Sandai	1965	1199	17	8	25
	Salabani	1468	1915	49	7	34
	Sintaan	1401	1979	68	7	17
	Kailer	1542	709	28	6	23
	Shelaba	2538	1059	7	7	31

Mean cover was used instead of total cover as communities varied widely in size. Mean cover was used as the explanatory variable in the analyses of Prosopis effects on ecosystem service supply and use.

2.4. Combining ecological and socio-economic data

In order to calculate ecosystem service supply and use, we upscaled values from local plots or households. To upscale ecosystem service supply, we used the relationship between Prosopis cover and the supply indicators. We first analysed the change in herbaceous and woody biomass as a function of Prosopis cover using mixed effect models with the *nlme* package (Pinheiro et al., 2018). Prosopis cover in each plot was fitted as a fixed effect and the community as a random effect to correct for differences between communities. Separate models were calculated for Ethiopia and Kenya. Conditional R-squared for the woody biomass models was 0.76 ($P < 0.0001$) for Ethiopia and 0.82 ($P < 0.0001$) for Kenya. R-squared for the herbaceous biomass models was 0.44 ($P = 0.002$) for Ethiopia and 0.36 ($P = 0.02$) for Kenya. The relationship between Prosopis cover and service supply was used to assign values to each 15 × 15 m pixel in the fractional cover map, thereby creating maps of ecosystem service supply. Individual pixel values for woody and herbaceous biomass were summed per community and divided by the total population to produce per capita values of ecosystem service supply. We did not use per hectare values as smaller communities were on average more highly invaded and Prosopis cover was unrelated to population density. We used per capita rather than per household values as we did not have data on the number of households for all communities.

Socio-economic data were upscaled to the community level by dividing the household responses by household size to calculate per capita use of each specific benefit for each household. These per capita values were then averaged for each community. Thus, both ecosystem service supply and use were calculated as per capita values.

2.5. Statistical analysis

We used regression analysis to determine how ecosystem service supply and use were affected by Prosopis cover and how ecosystem service supply was related to use. Differences between Ethiopia and Kenya were assessed using t-tests and, as there were large differences in mean values between the regions for all response variables, we corrected for these differences by using residuals as response variables in the analyses. The residuals were taken from linear models with each measure of ecosystem service supply or use as the dependent variable and region as the explanatory variable. Using residuals allowed us to examine trends across regions, given that the regions differ in overall service values. In one case an outlier was removed from the dataset because it differed by more than two standard errors from the mean. One community from Kenya was removed because livestock income and numbers were greatly exaggerated in the household interviews. The livestock numbers reported in surveys were normally 2–3 times higher than official statistics, but cattle numbers in this community were reported to be 10 times higher than the official statistics. This outlier significantly influenced the relations, e.g. between Prosopis cover and income from livestock (outlier included: $P = 0.96$ $R^2 = 0.0001$, outlier excluded $P = 0.01$ $R^2 = 0.28$). Relationships between cover and livestock income were the same when using official statistics and when using reported data without the outlier.

We first tested the effect of Prosopis cover on the indicators of ecosystem service supply and use and whether its effects differed between regions. We then tested the effect of current Prosopis cover on the change in livestock numbers over the past ten years (in Kenya only) as a measure of adaptation to Prosopis invasion. Then we tested whether Prosopis cover influenced whether livestock were grazed outside the community, both in terms of distance travelled and frequency of trips, to explain potential supply-use mismatches. The ratio between cattle and sheep and goats and the change in this ratio was analysed to determine if there has been a shift to smaller livestock species with increasing invasion. Finally, we tested the relationship between ecosystem service supply and ecosystem service use. An overview of the tested combinations is summarized in Table 2. For all combinations we tested for linear relationships using linear regression and the *nls* function for exponential relationships. The best models were selected as those with lowest AIC. When comparing supply with use indicators, a Model II regression was used to account for the error in both independent and dependent variable.

3. Results

3.1. Effects of Prosopis on ecosystem service supply

Potentially available woody biomass per capita was on average

Table 2
Overview of the tested relationships of Prosopis on ecosystem service supply and use, Prosopis on capital and relationships between ecosystem service supply and specific benefits derived from ES.

Independent variable	Dependent variable
Prosopis cover (%)	Woody biomass kg/capita (residuals) Herbaceous biomass kg/capita (residuals) Total income USD/capita (residuals) Income diversity (residuals) Income from wood USD/capita (residuals) Income from livestock USD/capita (residuals) Livestock change Tropical Livestock Unit/capita Frequency that livestock leaves community per year (residuals) Distance livestock moves outside community km (residuals) Cow / sheep + goat ratio currently Cow / sheep + goat ratio change in past 10 years
Woody biomass (residuals)	Income from wood USD/capita (residuals)
Herbaceous biomass (residuals)	Income from livestock USD/capita (residuals) Livestock number DSE/capita (residuals)

more than twice as high in Kenya as compared to Ethiopia (7,563 ± 3,109 vs 3,109 ± 2,010 kg; $P < 0.01$) at the community level. Woody biomass increased linearly with Prosopis cover (Fig. 3A; $P < 0.01$), a pattern that was similar in both regions (Prosopis * Region interaction: $P = 0.92$). Available woody biomass increased from 672 kg to 4,149 kg in Afar and from 3,541 kg to 12,606 kg in Kenya. Average herbaceous biomass was more than ten times higher in Ethiopia than in Kenya (4,787 ± 3,043 and 403 ± 418 kg; $P < 0.01$). Herbaceous biomass declined exponentially with increasing Prosopis cover (Fig. 3B; $P < 0.01$) and the decline was steeper in Ethiopia than in Kenya (interaction: $P = 0.04$). Herbaceous biomass decreased from 11,071 kg to 1,051 kg in Ethiopia and from 1,268 kg to 48 kg in Kenya with increasing Prosopis cover.

3.2. Effects of Prosopis on income

Total annual income was lower in Ethiopia than in Kenya (USD 400.3 ± 83.8 and USD 778.0 ± 211.1; $P < 0.01$) and was not affected by Prosopis cover (Fig. 4A; $P = 0.25$). This pattern did not differ between the two regions (interaction: $P = 0.3$). There was also no effect of Prosopis cover on income diversity, measured as Shannon's Diversity ($P = 0.47$) or as number of income sources ($P = 0.64$). This pattern was not different between the regions (interaction: $P = 0.59$ and $P = 0.70$ respectively).

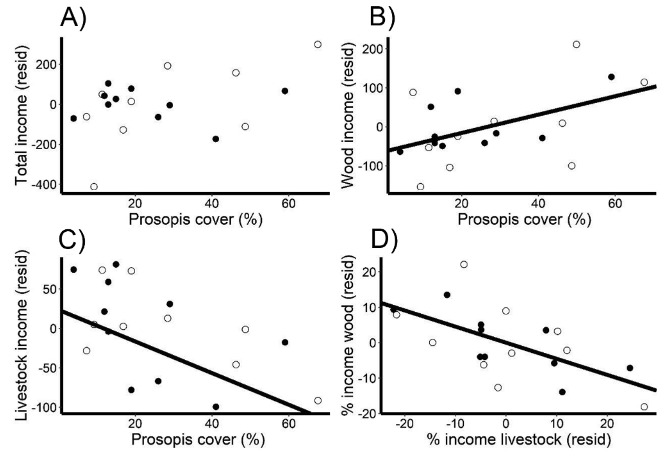

Fig. 4. Relationship between Prosopis cover and (A) Total income, (B) Income derived from wood and (C) Income derived from livestock. (D) The relationship between the percentage of income derived from livestock and the percentage of wood derived income at the community level. Closed dots and solid lines indicate Ethiopian kebeles and open dots and dashed lines Kenyan sublocations.

Average annual income from wood sales in Ethiopia was half that in Kenya (USD82.0 ± 65.8 and USD164.5 ± 112.4; $P = 0.03$). Income from wood increased significantly with increasing Prosopis cover (Fig. 4B; $P = 0.03$) in the two regions in a similar way (interaction: $P = 0.79$). Income from wood increased from USD 5.7 to USD 197.3 in Ethiopia and from USD 16.3 to USD 381.2 in Kenya.

Annual income from livestock was significantly higher in Ethiopia than in Kenya (USD 162.7 ± 64.8 and USD 96.6 ± 52.7; $P = 0.02$; Fig. 4C). Income from livestock decreased significantly with increasing Prosopis cover ($P = 0.009$) in both regions (interaction: $P = 0.16$). Average income from livestock decreased from USD 243.3 to USD 62.8 in Ethiopia and from USD 169.3 to 3.9 in Kenya. While total income was not significantly affected by Prosopis cover, there was a significant shift in income source, as indicated by a negative relationship between the percentage income derived from livestock sales and the percentage income derived from wood sales (Fig. 4D; $P = 0.005$). The highest percentage income from livestock was 66% in Ethiopia and 49% in Kenya; with increasing income from wood, income from livestock decreased to 19% and 1% in Ethiopia and Kenya, respectively. With increasing Prosopis cover, the percentage income from wood changed from 4% to 31% in Ethiopia and from 5% to 45% in Kenya.

3.3. Effects of Prosopis on livestock numbers

Cattle numbers were comparable between Ethiopia and Kenya

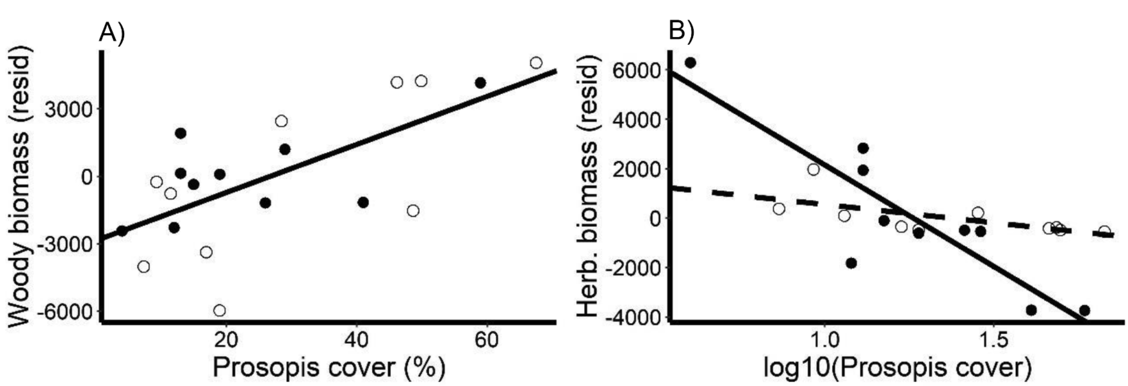

Fig. 3. (A) The relationship between Prosopis cover and woody biomass (kg/ capita) per community. The line indicates a significant relationship for both regions combined. (B) The relationship between Prosopis cover and herbaceous biomass (kg/ capita) at the community level. Closed dots and solid lines indicate Ethiopian kebeles and open dots and dashed lines Kenyan sublocations.

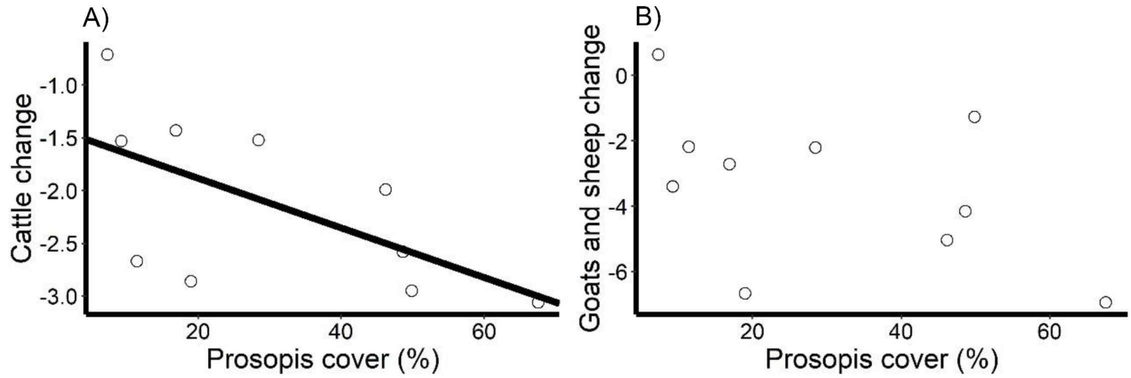

Fig. 5. The relationship between Prosopis cover and the change in (A) Cattle (B) Sheep and goat numbers per capita over the past ten years in at the community level. Closed dots and solid lines indicate Ethiopian kebeles and open dots and dashed lines Kenyan sublocations.

(2.9 ± 2.0 cows and 2.3 ± 1.1 cows per capita, respectively; $P = 0.58$). The same was true for sheep and goat numbers (6.4 ± 2.5 sheep & goat and 5.6 ± 2.6 sheep & goat in Ethiopia and Kenya, respectively; $P = 0.84$). No significant relationship was found between Prosopis cover and livestock numbers, neither for cattle ($P = 0.33$) nor for sheep and goats combined ($P = 0.45$). This pattern was not significantly affected by region, neither for cattle (interaction: $P = 0.52$) nor for sheep and goats combined (interaction: $P = 0.41$). In Kenya we found a marginally significant, negative linear relationship between Prosopis cover and the change in cattle numbers over the past ten years (Fig. 5A; $P = 0.06$), however, no significant relationship was found for sheep and goats combined (Fig. 5B; $P = 0.15$). The number of cattle declined by only 0.7 of a cow per capita in the community with the lowest Prosopis cover but by 3.1 cows per capita in the community with the highest cover. However, we did not find more goat and sheep relative to cattle in more highly invaded communities ($P = 0.57$) and this pattern was not significantly affected by region (Interaction = 0.71). The cow to sheep and goat ratio did not change in the past ten years in Kenya ($P = 0.94$) relative to Prosopis cover.

On average, people led livestock outside the community in search of grazing lands more often in Kenya than in Ethiopia (4.8 ± 1.2 vs 2.8 ± 0.9 times per year; $P < 0.01$). The distance travelled outside the communities was, however, larger in Ethiopia compared to Kenya (82.9 ± 62.6 km versus 4.8 ± 2.1 km; $P < 0.01$). Neither the frequency with which people led livestock outside the community ($P = 0.32$) nor the distance travelled ($P = 0.38$) was related to Prosopis cover. This pattern was not significantly different for both frequency (interaction: $P = 0.44$) and distance travelled (interaction: $P = 0.44$) between regions.

3.4. Relationship between ecosystem service supply and ecosystem service use

Woody biomass was positively and linearly related to annual income from wood (Fig. 6A; $P = 0.03$). Herbaceous biomass was positively related to income from livestock (Fig. 6B; $P = 0.05$). Current livestock numbers remained stable: neither the number of cattle ($P = 0.99$) nor the number of goats and sheep combined ($P = 0.60$) changed with herbaceous biomass. All these relationships did not significantly differ between Ethiopia and Kenya (interaction: $P > 0.45$).

4. Discussion

Analysing and managing ecosystem services requires a thorough understanding of how these services are supplied and how they are used in interconnected social–ecological systems (Reyers et al., 2013). To our knowledge, our study is the first to use a replicated, nested sampling design to identify alterations in both ecosystem service supply and use in response to environmental change at the same spatial and temporal scale. We found that invasion by the alien tree Prosopis affected the supply of two key provisioning services, i.e. woody and herbaceous biomass, and that these changes in ecosystem supply triggered cascading effects on the ecosystem service use by rural people and ultimately on their livelihoods.

4.1. A framework to integrate supply and use

The number of papers on ecosystem services has increased substantially over the past 20 years (Costanza et al., 2017), but relating ecosystem service supply and use at a meaningful spatial scale has remained a challenge (Geijzendorffer et al., 2015), even though this is essential to understand social-ecological systems (Ohl et al., 2010). Nested sampling designs, such as used here, allow integration of ecosystem service supply and use variables and analysis of their relationship at scales relevant for management (Scholes et al., 2013), but several challenges remain with regards to indicator selection, choosing the appropriate scales for data collection and retaining sufficient statistical power after upscaling.

In order to relate supply and use it is important to choose relevant indicators. Use indicators should be specific to the service: we found that general indicators, such as overall income, did not show any relationship with supply of wood and herbaceous biomass. Supply and use of a given service may not always be related, as ecosystem service use can become disconnected from supply when people maintain high levels of use despite declining local supply, which could explain why we found no relation between livestock numbers and supply of herbaceous biomass. This suggests that additional forage from outside the local area was needed to support high livestock numbers. It is also likely that local forage use is unsustainable because more biomass is removed by grazing than can be replaced, leading to long term declines in plant productivity. Such unsustainable use would also lead to a decoupling between supply and use because use would be high even at relatively low supply rates. Ilukor et al. (2016) found that there was a shift from grazers to browsers following Prosopis invasion, which indicates high attachment to livestock despite adverse conditions. Given the different cultural importance of different livestock species, total livestock numbers might not be the most appropriate indicator in our study system and livestock should be separated by species or feeding guild. In our study areas sheep and goats are kept in mixed flocks and are of similar cultural importance. And we therefore assessed them together, even though goats are browsers and sheep are grazers. These issues illustrate the challenge of choosing indicators that are relevant from a socio-economic and ecological perspective and selection of indicators should thus be done by interdisciplinary teams.

The second challenge is selection of the appropriate spatial scale for upscaling of ecological and socio-economic data. We chose the smallest

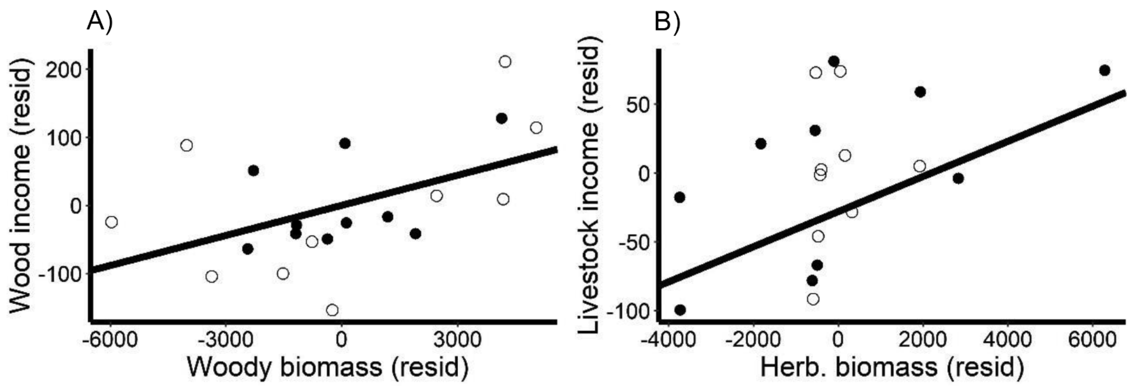

Fig. 6. The relationship between (A) Woody biomass per capita and the income from wood per capita and (B) Herbaceous biomass per capita and income from livestock per capita for both regions at the community level. Closed dots and solid lines indicate Ethiopian kebeles and open dots and dashed lines Kenyan sublocations.

administrative unit for this, as people in a community share access to resources, such as grazing land and wood, and we expected that supply and use would be related at this level. Had we chosen a larger spatial scale, then the relationship may not have been detectable. A comparison of ecological and economic variables to assess supply and use relationships at a smaller spatial scale, is not appropriate for the provisioning services that our study focussed on, because of the largely communal land tenure system in these agro-pastoralist communities. Hence, we expected that many people in each community are affected by Prosopis and we expected it to be the most important driver of change in supply of our chosen ecosystem services. We therefore used Prosopis cover alone for the upscaling and calculated the Prosopis-ecosystem service supply relationship based on all plots across communities. We acknowledge that other factors may also affect ecosystem service supply. For example, herbaceous biomass is also dependent, e.g. on grazing pressure (Tessema et al., 2011), other disturbances or soil conditions. In these communities, however, Prosopis is a driving factor of ecosystem change (Linders et al., 2019).

A main challenge in a nested sampling design, where both ecological and socio-economic are upscaled for comparison (Gardner et al., 2013), can be the relatively low statistical power. A balance has to be found between statistical power (for instance more communities) and sufficient representation of each community. Our combined analysis with 503 household interviews and 141 ecological plots in two regions only had a sample size of 20 communities to test for the supply-use relationship. Nevertheless, this allowed us to test different shapes of the relationship and we found significant correlations between supply and use. A potential challenge of nested designs is that the small number of communities can lead to disproportional effects of outliers. For example, we found a negative relationship between livestock income and herbaceous biomass, which seemed to be driven by a single community with high livestock numbers and this result should thus be regarded with caution. Yet, our study shows that it is possible to integrate ecosystem service supply and use with integrated research programmes involving interdisciplinary collaboration.

4.2. Assessing sustainability in Prosopis-invaded areas

Integrating supply with use, i.e. ecological with socio-economic data, is essential to be able to assess whether current resource use is sustainable (Wei et al., 2017). Our findings that Prosopis increases woody biomass and decreases herbaceous biomass fit a pattern found throughout its introduced range (Kaur et al., 2012; Ndhlovu et al., 2011; van Klinken, 2012), but supply data alone cannot reveal the effect of Prosopis on the sustainability of resource use. Combining our data on estimated fodder availability at the local scale and capital, in the form of livestock numbers in Ethiopia and Kenya, suggests that there is a strong overconsumption, implying that demand for herbaceous biomass outstrips supply and that the current livestock numbers in the studied regions in Ethiopia and Kenya are unsustainable. Although the average supply and use of the services differed between the countries, the relationships between supply and use and effects of Prosopis on both were the same in most cases. The only difference was that herbaceous biomass declined more steeply with increasing Prosopis cover in Ethiopia compared to Kenya, which is because herbaceous biomass was far higher in Ethiopia than in Kenya. The lower average value of herbaceous biomass in Kenya has an impact on the sustainability of the supply-use relationship. Supply of herbaceous biomass decreased over 90% with increasing Prosopis cover in both regions and supplementing biomass with Prosopis pods is unfeasible in both countries, because pods are only a healthy substitute for up to 20% of the diet of cattle, goats or sheep (Mahgoub et al., 2004; Shukla et al., 1981). This means that in the most heavily invaded communities in Kenya the local availability of herbaceous biomass was 6.84 kg per tropical livestock unit (TLU; Jahnke 1982). With a consumption of 1 kg per day for a sheep or goat (0.1 TLU; Krausmann et al. 2008) and 6.8 kg for a cow (0.7 TLU) all available biomass would thus be consumed within 1–2 days in heavily invaded communities, which is likely to be too high a rate of consumption to allow the vegetation to regrow. In the least invaded communities in Kenya there would only be enough herbaceous biomass for one month based on the biomass produced during the long rains (assuming no regrowth during the rainy season). Rain normally falls in two distinctive rainy seasons in both regions and herbaceous plants are only able to grow during these periods. We sampled during the long rainy season, in which 30% percent of the annual rainfall occurs, when herbaceous biomass levels are particularly high (Ekaya et al., 2001). Vegetation regrowth after the second rainy season and a limited supply of Prosopis pods may yield sufficient fodder to support the current livestock numbers, but only in the least invaded areas in Ethiopia, where there was 1,583 kg of dry herbaceous biomass per TLU. Moreover, we sampled during a good rain season, but when rains fail there is no resilience against drought, as no herbaceous biomass would be available. In heavily invaded communities in Ethiopia there was insufficient herbaceous biomass, indicating that the use depends on supply from elsewhere, e.g. by migrating to other grazing areas over extended periods or by receiving fodder from governmental or aid organizations (Fig. 1B); both are practiced in the study areas.

An important reason for simultaneously quantifying supply and use is that their relationship is not necessarily linear (e.g. Schulp et al. 2014). The shape of the relationship has important consequences for management that aims to optimise the supply of multiple services (Manning et al. 2018). Even though we did not find any non-linear relationships for the two provisioning services which we examined, there is a possibility that we did not adequately capture the supply-use relationship. One possible explanation is that our measures of supply are measures of total potential supply rather than the actual supply. For example, accessibility of grassland might be limited by natural barriers like waterways, dense Prosopis thickets or cultural barriers like tribal conflict. This would have resulted in an over-estimation of supply of fodder and the real relationship is likely to flatten off, indicating that the available resources are utilized more heavily than in our estimates. Both the accurate mapping of accessibility of resources would increase reliability of fodder supply measures. Additionally, the maximum mean Prosopis cover in our communities was 60% and it could be that wood consumption does not increase further with increased supply at higher Prosopis cover levels.

Livestock are moved outside the community borders to find complementary fodder in all studied communities, but the frequency and distance travelled were not related to current Prosopis cover. This can at least partly be explained by the fact that in these regions livestock have always been moved between dry and wet season grazing grounds (Kloos, 1982). Livestock has been increasingly moved outside community borders over the past 10 years though (K. Bekele pers. obs.). This could highlight the mismatch between supply and use within communities and that these mismatches have increased in recent years following Prosopis invasion. Access to grazing lands and overgrazing are already important causes of tribal conflicts and Prosopis appears to increase the frequency and intensity of these conflicts by further reducing the accessibility of grasslands and amount of herbaceous biomass in Ethiopia (Berhanu and Tesfaye, 2006) and Kenya (Anderson and Bollig, 2016). Hence, our results show that Prosopis invasions aggravate an already severe shortage of fodder in the two study areas (Birhane et al., 2017), indicating that the current use for a key ecosystem service in these semi-arid regions, herbaceous biomass, is unsustainable. This is further illustrated by the importation of fodder from outside the region (Nangole et al., 2013). The Prosopis invasion in Ethiopia and Kenya will further expand if left uncontrolled and it is likely that the fodder shortage will become worse, with significant negative consequences for the people depending on these services.

As expected, Prosopis did increase income from wood, and wood sales are now an important income source in highly invaded areas. Estimates of per capita income from wood were over twice as high in Kenya compared to Ethiopia. This is likely because Prosopis is regularly cut for firewood and charcoal in Kenya, where this is forbidden in Ethiopia, and because there is more woody biomass available in Kenya. Woody biomass per capita was also twice as high in Kenya, 75,000 kg as compared to 31,000 kg in Ethiopia.. According to the household interviews the community with the highest Prosopis cover in Kenya had a supply of 12,606 kg of woody biomass and 284.3 USD of income from wood sales per capita. With an average price of 4 USD for a bag of charcoal of 25 kg and a wood to charcoal conversion rate of 25% (Pandey et al., 2012), this income represents 7,108 kg of wood, or ca. 71 bags of charcoal per capita. Forty-eight percent of the population is below 15 years of age (Kenya National Bureau of Statistics 2010), and is not involved in charcoal making, thus each person produces an average of 5.4 bags of charcoal per week, as women are normally not involved in harvesting charcoal. Our calculation suggests that ca. 56% of the estimated total woody biomass is harvested annually, which appears to be an overestimate. Prosopis does coppice profusely when the main stem is cut and the growing point in the root crown is most often not removed, so using Prosopis for wood will likely not have reduced invasion rates. After coppicing there are a larger number of thinner Prosopis stems, which are less suited for charcoal making, although it is still promoted (Goel and Behl, 2000). Coppicing happens fast and Prosopis cover can be high within six months after cutting (Shiferaw et al., 2004). As a consequence, the relationship between Prosopis cover and woody biomass is quite noisy at high cover levels and it is impossible to determine woody biomass in an area with a high degree of accuracy based on fractional cover alone. Additional information about vegetation height, for example based on Lidar images from the area, or detailed spatial and temporal information about charcoal making activities could be used to improve the estimates. The combination of the inaccurate estimate of available biomass and the apparent overestimate of income from charcoal suggests that the linear relationship between these variables may not be exact. Moreover, the supply of Prosopis wood, and thus the shape of this relationship, may vary over time as a result of the variable quality of the coppices following charcoal making. Better management of the cut trees to improve wood quality or replacement of Prosopis following charcoal making with native trees that produce higher quality wood should be considered to increase the sustainability of this important income source.

Prosopis was originally introduced to diversify livelihoods and increase income to increase sustainability of livelihoods (Pasiecznik et al., 2001). However, in our study income diversity was unrelated to Prosopis cover and overall income did not change with Prosopis, suggesting that its introduction has not had the intended effect. The only income increase was from wood, which was accompanied by a decrease in income from livestock. Although the introduction of Prosopis was intended, among other things, to increase the availability of fodder (Pasiecznik et al., 2001), the opposite has occurred and available fodder has decreased due to Prosopis invasion (Ndhlovu et al., 2011) as Prosopis pods can only replace a small fraction of herbaceous biomass. Prosopis has thus likely reduced resilience against drought. Moreover, it is questionable whether income from Prosopis wood can replace income from livestock, as livestock, apart from being an income source, are of high cultural importance. Livestock numbers can however, be expected to drop further and therefore future income from livestock will probably also decline. Our results are thus similar as a cost-benefit study in South Africa, which found that on the longer term the cost of Prosopis invasion is larger than the benefit (Wise et al., 2012). Our assessment only included provisioning services and including a measure of cultural importance of livestock, could more clearly quantify the negative impact of Prosopis on the social-ecological system. In general, the inclusion of Prosopis effects on regulating and cultural services will likely add to understanding supply-use relationships and the effect of an alien invader on them.

Our case study in Eastern Africa suggests that Prosopis transforms the social-ecological system to a wood-dominated system. Despite the decline of grassland availability, livestock remain important for the inhabitants, suggesting that income from charcoal cannot replace the cultural value of livestock and might currently increase vulnerability of livelihoods to droughts. A strategy to manage the Prosopis invasion, while keeping the benefits Prosopis has provided (Bekele et al., 2018), and the simultaneous restoration of grasslands is therefore urgently needed to increase resilience of livelihoods. Management strategies should ensure that ecosystem service supply is restored to, and maintained at the levels required to sustain the livelihoods of the agro-pastoralist communities in Ethiopia and Kenya.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

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Appendix A. Relationship between woody biomass and basal diameter

Fig. A1.

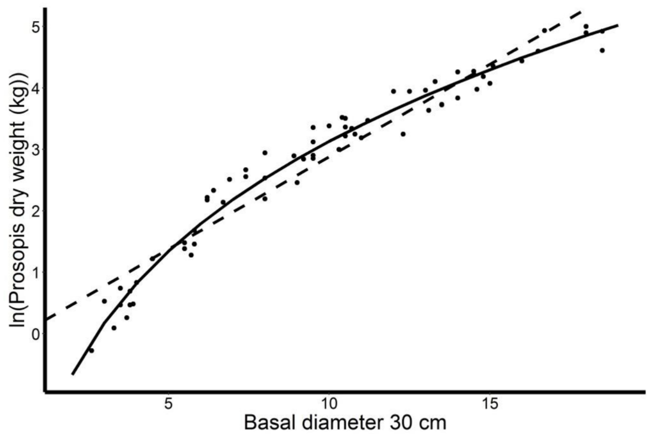

Fig. A1. Relationship between basal diameter and ln (Prosopis dry weight). The dashed line indicates the original equation in Muturi et al. (2012) and the solid line indicates the equation based on the power model.

The equation in Muturi et al. (2012), based on measurements of basal diameter (30 cm above the ground) and dry weight of 66 *Prosopis juliflora* stems in Kenya, describes a linear relationship between basal diameter and ln (Prosopis dry weight). This relationship is highly significant ($p < 0.0001$, $r^2 = 0.92$, AIC = 64.4), but visual examination of the data suggest that a power model fits the data better. Based on AIC the following model performed best: ln (Prosopis dry weight = -10.672 + 8.71*Basal diameter$^{0.2}$ ($p < 0.0001$, $r^2 = 0.97$, AIC = -0.49).

Appendix B. Socio-economic interviews

1. Household current livestock population and annual income from livestock and their products in **the last production year.**

Live Animals	№ owned	№ Sold	Unit Price	Annual Costs			
				Feeding	Veterinary	Labour	Other
Camel							
Calves							
Bulls/Oxen							
Cows/Heifer							
Sheep							
Goats							
Donkeys							
Horses/Mules							
Livestock Products	Unit						
Meat							
Beef meat							
Goat meat							
Milk							
Cow milk							
Goat milk							
Other milk products							
Egg							
Other (specify)							

2. Household livestock population and annual income from livestock and their products in **ten years ago** production year.

Live Animals	No̲ owned	No̲ Sold	Unit Price	Annual Costs			
				Feeding	Veterinary	Labour	Other
Camel							
Calves							
Bulls/Oxen							
Cows/Heifer							
Sheep							
Goats							
Donkeys							
Horses/Mules							

Livestock Products	Unit
Meat	
Beef meat	
Goat meat	
Milk	
Cow milk	
Goat milk	
Other milk products	
Egg	
Other (specify)	

3. How far in Kilometres you have/had to travel with your livestock to find dry season grazing sources from your home?

	Currently	10 Years ago	Before *P.juliflora* invasion
Community or geographical description of area			
Distance from home			

4. How often you have/had to leave the boundaries of your community with your livestock to find dry season grazing sources?

	Currently	10 Years ago	Before *P.juliflora* invasion
Never			
Everyday			
Once a week			
Once a month			
Once every 3 months			
Once every 6 months			
Once a year			

5. Annual income from land/agriculture in the **last production year**.

Crop	Total area (Hectare)	% of area invaded	Total Production	Yield per area (not invaded)	Yield per area (invaded)	Unit Price	Unit own consumption (kg, bags etc)	Unit Sold (kg, bags etc)	Total Income
1. Onion									
2. Sugar cane									
3. Vegetable									
4. Fruit									
5. Spices									
6. Rent									
7.									
8.									

6. Do your household have other sources of income? 1. Yes 2. No
7. If answer to question № 33 is 1, what is the estimated average net income in *Birr/KSH* last year from the following activities?

1. *P.juliflora* pods selling	1. Yes________	0. No
2. Wage labour	1. Yes _________	0. No
3. Petty trade	1. Yes _________	0. No
4. Remittance	1. Yes _________	0. No
5. Salary	1. Yes _________	0. No
6. Pension	1. Yes _________	0. No
7. Charcoal production	1. Yes _________	0. No
8. Fuel wood selling	1. Yes —————	0. No
9. Honey production	1. Yes —————	0. No
10. Medicinal values	1. Yes —————	0. No
11. Other (specify)	1. Yes _________	0. No

8. Name of the interviewee _________________if not the household head, your relationship to household head ______________
9. Main occupation (income source) of the household (Code 1) ________
10. How long have you been in this occupation? ____ years.
11. Family members including the household head.

I.D. code	Age (yrs)	Sex (Code 2)	Marital status (Code 3)	Education Level (Code 4)	Occupation (Code 5)
01*					
02					
03					
04					
05					

06
07
08
09
10
11
12

* Fill about the **household head** in I.D. 01. Note that family members refer to persons currently living in the roof

12. What is your household monthly expenditure? Birr——————— per month.
13. For how long have you been living here? 1. Born here 2. ——— years.

Appendix C

Table A1.

Table A1
Variables used to create Prosopis fractional cover maps in Ethiopia and Kenya.

Description	Source
Mean annual rainfall	Ethiopian National Meteorological Agency
Mean monthly temperature	
Monthly land surface temperature during daytime and nighttime; for the modelling 5-year averages were calculated.	MODIS, NASA
Monthly land surface temperature during night time; for the modelling 5-year averages were calculated.	MODIS, NASA
Panchromatic (PAN) reflectance	Landsat 8 OLI, USGS
Red reflectance	Landsat 8 OLI, USGS
Near-infrared (NIR) reflectance	Landsat 8 OLI, USGS
Shortwave infrared band 6 reflectance	Landsat 8 OLI, USGS
Normalized difference vegetation index (NDVI)	
SRTM (30 m spatial resolution) digital elevation model (DEM); elevation is directly linked with climatic variables (temperature, rainfall).	USGS
Derived from Elevation; strongly influences land use and land cover classes.	
Derived from Elevation; may affect soil moisture holding capacity	
Distances derived from road network data; movements of goods, services, and animals increase spread of *Prosopis* seeds and pods	Ethiopian Road Authority
Distances derived from settlement data; human and animal movements in settlement areas increase spread of *Prosopis* seeds and pods	EthioGIS and Central Statistical Agency
Distances derived from data on watercourses; rivers, streams, canals, and floods transport *Prosopis* seeds and pods to downstream areas	EthioGIS
Livestock movement routes and livestock markets (Kenya only)	Pastoralist workshops

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