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Variations in soil properties and native woody plant species abundance under *Prosopis juliflora* invasion in Afar grazing lands, Ethiopia

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Abstract

Introduction: Pastoralism and agro-pastoralism are the major modes of life in arid and semi-arid rangelands. However, rangeland quality and quantity are rapidly deteriorating due to a number of natural and human-induced factors, one of which is bush encroachment. Little is known on how bush encroachment affects the ecosystem functions and services expressed in terms of the native vegetation composition and structure, status of the soil seed bank, soil chemical and physical properties, and the abundance of mycorrhiza spores.

Methods: We assessed woody species in 64 plots distributed across four levels of *Prosopis juliflora* invasion (high, medium, low, and none) at two sites, Amibara and Gewane, in the Afar Region, Ethiopia. We collected composite soil samples to investigate the soil seed bank, mycorrhizal associations, and spore abundance.

Results: Plant biodiversity was generally low, with eight and four woody species in Gewane and Amibara, respectively. *Prosopis juliflora* was dominant in highly, moderately, and lowly invaded areas while *Acacia senegal* dominated the non-invaded areas. The average number of *P. juliflora* individuals ranged from 3/ha at non-invaded areas in Gewane to 4200/ha at highly invaded areas in Amibara while the total individual number of native woody species ranged from 0 to 88/ha at highly and lowly invaded areas, respectively. The population structure of trees/shrubs in all invasion areas showed an inverted J-shaped distribution, characterized by a high abundance of small individuals. *Prosopis juliflora* invasion was associated with high soil OC, Na, Ca, P, bulk density, and moisture content. Herbaceous seed numbers and species richness were highest in the moderately and highly invaded areas. All sampled tree species were associated with mycorrhiza but the percentage of root length colonization by different arbuscular mycorrhizal fungus structures varied significantly ($p < 0.05$) across invasion categories and sites.

Conclusions: Our results revealed that although *P. juliflora* invasion negatively impacted the availability of native woody livestock forage species, it had a positive effect on most soil physical and chemical properties. Such variable effects call out for sustainable management practices when invaded areas are restored.

Keywords: Encroachment, Structural and species diversity, Shrubs, Arbuscular mycorrhiza, Rangelands

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Introduction

Drylands are areas where the potential amount of water that is transferred from land to atmosphere is at least 1.5 times greater than the mean precipitation (Davies et al. 2012). According to the Millennium Ecosystem Assessment (MEA (Millennium Ecosystem Assessment) 2005), drylands are defined as areas with an aridity index value of less than 0.65, which means that annual precipitation is less than about two thirds of potential evapotranspiration. Such drylands cover more than 40% of the world's land area (UNCCD 2000), including shrubland, grassland, and forest (White and Nackoney 2003). Drylands are often regarded as being unproductive and barren, but they host over one third of the global human population, 90% of whom live in developing countries (MEA (Millennium Ecosystem Assessment) 2005).

Despite their aridity, drylands mainly support livestock while rain-fed agriculture is only practiced in small pockets (Ffolliott et al. 2002; Georgis 2005). Drylands contain a great variety of biodiversity (Redford et al. 1990), which is essential to the survival of species as well as to the livelihoods of people. This biodiversity plays a pivotal role in the global fight against poverty, climate change, and desertification (Smith et al. 2010). The majority of rural people living in drylands are pastoralists, semi-pastoralists, transhumant, and sedentary smallholders (Ffolliott et al. 2002). Pastoralism relies on a diversity of grasses and shrubs as key productive inputs (Blench 2001). However, pastoralism is challenged by a rapid decline in rangeland productivity caused by habitat conversion, climate change, over-harvesting, over-grazing, bush encroachment, and inappropriate soil management of rangelands (MEA (Millennium Ecosystem Assessment) 2005).

Bush encroachment is expressed as an excessive increase in the number of undesirable or unpalatable woody species that limit the growth of grasses and herbs palatable to livestock (Walker and Noy-Meir 1992; Ward 2005). The increase in bush tickle at the expense of perennial grasses is a commonly observed problem in dryland areas of the world (Archer 2008; Eldridge et al. 2011) as it leads to degradation (Saco et al. 2007) due to low fire frequencies and invasive species proliferation (Pasiiecznic et al. 2004). An increase in the abundance of encroachers suppresses the diversity, production, and productivity of forage plants and other multipurpose tree/shrub species with high food security importance in rangelands (Oba et al. 2000). Such species shifts are accompanied with fundamental alterations of habitat for animals (microbes, invertebrates, and vertebrates) and often result in a change of an ecosystem's trophic structure (Havstad et al. 2006). The rapid shift in species composition and abundance triggered by bush encroachment often enhances primary production, nutrient

cycling, and accumulation of soil organic matter but can also have a negative effect on streamflow, groundwater recharge, livestock production, and biological diversity (Archer et al. 2001; Knapp et al. 2008). The increases in woody plant cover have become a major threat to pastoral livelihoods and ecosystems within the arid and semiarid areas (Eldridge and Soliveres 2015).

Rhizosphere microbial communities have been found to affect directly soil fertility by carrying out essential processes that contribute to nutrient cycling, soil structural maintenance, and ecosystem productivity (Smith and Read 2008). Among the most influential members of soil microbiota, mycorrhizal associations are the integral functioning parts of terrestrial ecosystems (Barea et al. 2011) and are widely recognized as providing a direct physical link between soil and plant roots (Smith and Read 2008). Arbuscular mycorrhiza fungi (AMF) is the predominant and ancestral type of mycorrhiza in land plants (Wang and Qui 2006). The interactions between plant-AMF link biodiversity and ecosystem functioning (van der Heijden and Sanders 2002). The AMF has a contribution on plant species composition and diversity, plant productivity, ecosystem functioning, and stability to environmental stresses and variables.

The Afar Region of Ethiopia has strongly been affected by bush encroachment due to the introduction of *Prosopis juliflora* in the late 1970s (EARO (Ethiopian Agricultural Research Organization) and HADRA (Henry Doubleday Research Association) 2005) and was first introduced for the purpose of rehabilitating degraded lands and for the provision of forest products like fuelwood and fodder for the pastoral community (Pasiiecznic et al. 2001). However, *P. juliflora* has invaded large areas of grasslands, rangelands, water points, and croplands (Mekuyie et al. 2015) owing to its wide ecological adaptability (Pasiiecznic et al. 2004), fast growth habit (Manchester and Bullock 2000), and high competition ability for available soil and water (Oba et al. 2000). The spread of *P. juliflora* in the Afar Region has an impact on ecology (Birhane et al. 2017; Ilukor et al. 2016), socio-economics (Mehari 2015), and culture (Rogers et al. 2017) of the local people. However, little is known about the various levels of invasion by *P. juliflora* and its impact on the diversity and abundance of functional groups and different ecosystem services within invaded rangelands. Barbosa da Silva et al. (2016) and Pittarello et al. (2016) showed the negative effect of bush encroachment on the diversity and abundance of grasses and livestock forage provision. In contrast, Maestre et al. (2016) argued that bush encroachment could also have positive effects on certain biota and their associated functions and services in rangelands. While Soliveres et al. (2014) and Eldridge and

Soliveres (2015) indicated that plant diversity and multiple ecosystem functions are maximized under moderate levels of bush encroachment, it is not yet clear how the different levels of *P. juliflora* invasion density affect plant diversity and ecosystem functions in Ethiopia. Assessing the effect of *P. juliflora* on plant diversity and other ecosystem functions is crucial to plan control methods that can minimize this species' impact and provide crucial inputs for policy and strategy formulations in Ethiopia. In this context, the main objectives of this study were to determine the native woody plant species diversity, structure and density, soil seed bank of native plants, soil nutrient availability, and soil mycorrhizal associations and spore abundance across the various levels of *P. juliflora* invasion in the Afar Region, Ethiopia. The main research questions were (i) how do the abundance, structure, and diversity of native woody species vary across the habitats that differ in the levels of *P. juliflora* invasion? and (ii) how do soil seed banks of native plants, soil nutrient availability, and soil mycorrhizal associations and spore abundance vary across the various levels of *P. juliflora* invasion? We hypothesized that the abundance and species richness of native woody species would be higher in the low invasion level while the diversity of native plant species in the soil seed bank, the availability of soil nutrients, mycorrhizal associations, and spore abundance would be higher at a high invasion level.

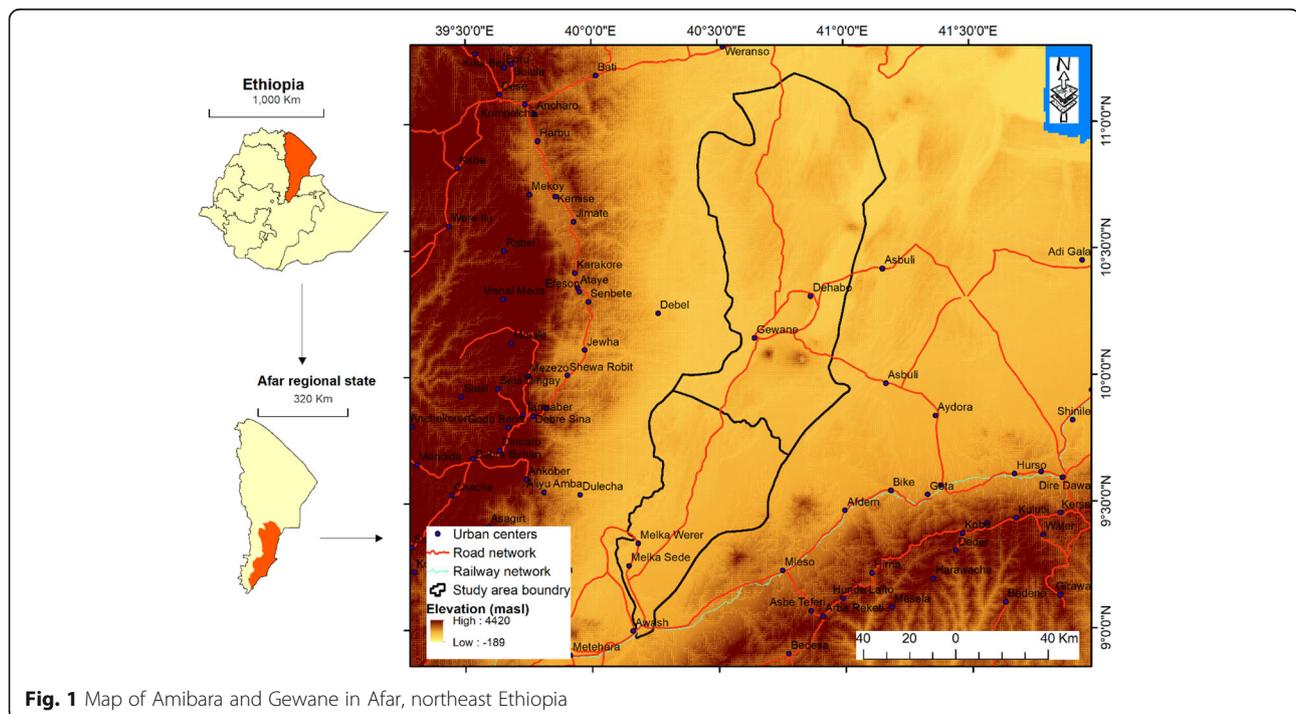
Materials and methods

Study area

The study was conducted in the Afar Region, eastern Ethiopia (Fig. 1). Afar is located in dryland areas of the country that cover more than 70% of the total landmass (Tamire 1997). These drylands have only a marginal potential for rain-fed agriculture but are highly suited for livestock husbandry (Hawando 1997), with 90% of the local population being pastoralists and agro-pastoralists (Dalle et al. 2005). *Acacia-Commiphora* woodland is the dominant vegetation in the Afar Region (Eshete et al. 2005). This vegetation provides a multitude of benefits to pastoralists and agro-pastoralists like forage/feed, food, herbal medicine, timber, or firewood (Ilukor et al. 2016; Worku et al. 2011). The *Acacia-Commiphora* woodland in the Afar Region is strongly affected by *P. juliflora* (Birhane et al. 2017). Among the five zones of the Afar Regional State, we investigated the impact of the different level of invasion in two districts, namely Amibara and Gewane, located in Zone 3. The site characteristics, climate, and vegetation of the study districts are described by Birhane et al. (2017). Most of the land had been used for pastoralism while only little of the area is covered by agriculture (Kotu 2009).

Study design and layout

Both study sites were categorized into four levels of invasion based on the *P. juliflora* cover percentages which were estimated visually (Birhane et al. 2017): no *P. juliflora* present ("none"; *P. juliflora* cover < 3%), low cover



("low"; *P. juliflora* cover 3–40%), intermediate cover ("med"; *P. juliflora* cover 40–60%), and high cover ("high"; *P. juliflora* cover > 60%, Fig. 2). The invasion rate of *P. juliflora* decreased with distance away from the road. In each of the studied districts, eight transects of 1000 m length were laid out perpendicular to the road at a distance of 1500 m apart from each other using a systematic random sampling technique. All transects crossed the four invasion rates (Fig. 2). A total of 64 plots (16 plots in each of the 4 invasion levels) were laid out along each transect at every 200 m. A plot size of 20 × 20 m (400 m²) was employed for the three levels of invasion: none, low, and medium, while a plot size of 5 × 5 m (25 m²) was employed for the high invasion level due to logistical reasons.

Vegetation inventory

In each plot, all tree and shrub species ≥ 1.5 m height were identified and measured for their root collar diameter (RCD) (cm) and their stem height (in m: to the top of the crown) using a height measuring graduated pole. All trees/shrubs ≥ 0.5 m and ≤ 1.5 m height were also systematically identified and counted. Local names of trees/shrubs were recorded and identified to the species level according to different volumes of the flora of Ethiopia (Hedberg 1996), with the help of locals and through comparisons with

voucher specimens from the National Herbarium at Addis Ababa University.

Soil seed bank sampling

Soil samples were collected from five small sub-plots of 40 × 40 cm (1600 cm²) and 30 cm deep at plots used to measure the diameter and height of woody plants, one at the center and the other four at the four corners. From each sub-plot, three successive soil layers (0–10 cm, 10–20 cm, 20–30 cm) were collected using a sharp knife. Soils from similar layers were mixed to form soil composites in order to reduce variability within the plot and divided into five equal parts, one of which was selected randomly as a representative soil sample (Mengistu 2001). The soil samples were transported to Mekelle University for soil seed bank analyses. A total of 192 pots filled with 1 kg soil sample were placed at random in the greenhouse and were hand-watered regularly until saturation. Pots were then examined to record data on the emergence of plants every 3 days for the first 2 months and thereafter weekly until the end of the experiment, i.e., for 6 months. Seedlings that started to emerge and were readily identifiable were counted, recorded, and discarded. Those difficult to identify at the seedling stage were first counted but maintained in the pots until they were identified. After 6 months, the number of emerging seedlings, particularly grasses and forbs,

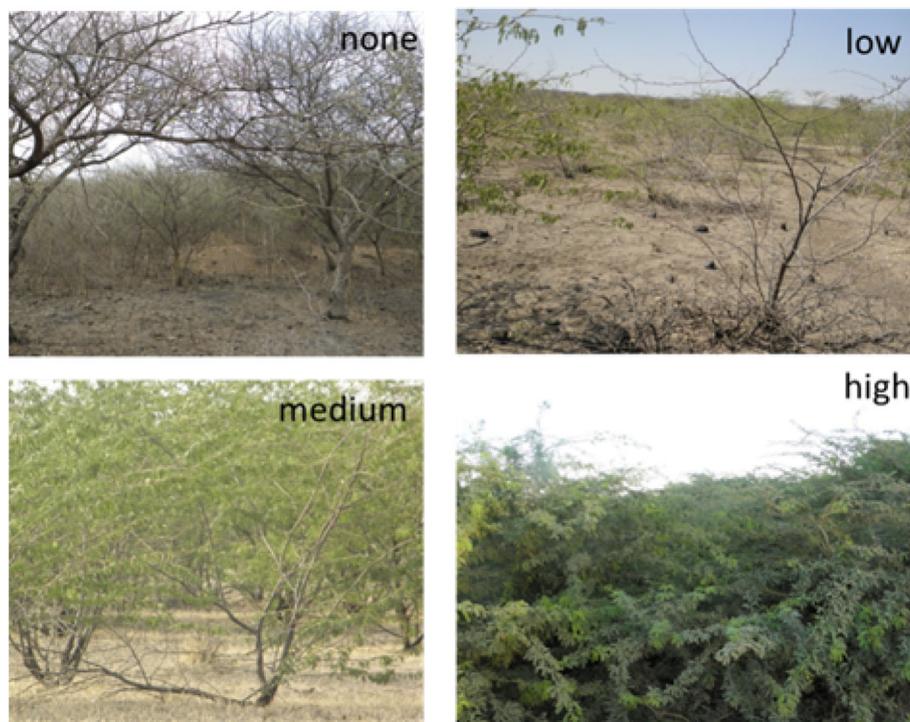


Fig. 2 The different invasion categories of *P. juliflora* in the two study sites. No *P. juliflora* individuals ("none"; *P. juliflora* cover ≤ 3%), low cover ("low"; *P. juliflora* cover 3–40%), intermediate cover ("med"; *P. juliflora* cover 40–60%), and high cover ("high"; *P. juliflora* cover > 60%)

declined considerably. Plant nomenclature followed the flora of Ethiopia (Hedberg 1996).

Collection of rhizosphere soil and root samples

Samples for spore analyses were collected from the already established plots for vegetation study. Rhizosphere soil and roots were collected in the dry season (December). The surface soil of about 1–2 cm was removed, and soil cores of 0–30 cm collected including fine roots and rhizosphere soils of the host plants using a cylindrical soil corer of 10 cm internal diameter. From each sample plot, three individuals of each dominant plant species with similar crown width (about 1.5 m) were randomly selected and samples were taken 50 cm away from the tree trunk in four compass directions. The four samples were mixed thoroughly to form a composite soil sample per each tree. Generally, two composite soil samples per species were taken from each plot. A total of 120 composite soil samples were collected. A sub-sample of approximately 100 g was taken for the extraction of arbuscular mycorrhizal fungus (AMF) spores. The soil samples were air-dried and passed through a 2-mm sieve, and then samples were stored at 4 °C before analysis. Alive fine roots were also collected from each plant for AMF colonization assessment. Roots were excised in the amount of about 1–5 g for each species and placed in a sealed plastic bag to protect from desiccation.

Physical and chemical analyses of soil samples

Selected physical and chemical properties were analyzed, such as available phosphorus (P), total nitrogen (N), organic carbon (OC), exchangeable sodium (Na), exchangeable potassium (K), exchangeable calcium (Ca), exchangeable magnesium (Mg), cation exchange capacity (CEC), bulk density (BD), moisture content (MC), and soil texture following standard soil analysis methods. OC was determined by the wet combustion procedure of Walkley-Black (Van Ranst et al. 1999) while N was determined by the wet-oxidation procedure of the Kjeldahl method (Bremner and Mulvaney 1982). Available P content was determined by the P-Olsen method (Olsen and Sommers 1982) while Na, K, Ca, Mg, and CEC were determined by the 1 M ammonium acetate (pH 7) method according to the percolation tube procedure (Van Reeuwijk 1993). The effective CEC was calculated as the sum of exchangeable cations extracted by the ammonium acetate buffered at pH 7 plus 1 M KCl extractable Al. Bulk density was determined by the core method (Blake and Hartge 1986). Soil texture was determined using the hydrometer method (Gee and Bauder 1982).

AMF fungal spore extraction

Spores were extracted from 100 g of air-dried sub-samples after wet sieving and decanting followed by flotation centrifugation in 50% sucrose (Brundrett et al. 1994). The soil samples were suspended in water for 30 s and decanted over a series of sieves with 750, 250, 100, and 38 µm mesh size. Soil material was recovered from each sieve, suspended in water, and centrifuged at 2000 revolutions per minute (RPM) for 5 min (Brundrett et al. 1994). After decanting the supernatant, each soil-spore mixture of the pellets was re-suspended in sucrose solution (50%) and centrifuged for 1 min at 2000 rpm. The supernatant containing spores was filtered under vacuum on filter paper and then transferred into a round petri dish with gridlines of 1 cm² and finally counted using a stereoscope microscope. For observation and identification of spore characters, spores were mounted on glass slides in polyvinyl alcohol-lactoglycerol (PVLG) and PVLG + Melzer's reagent and identified to the genus level using current taxonomic criteria (Brundrett et al. 1994) and information by INVAM (<http://www.invam.caf.wvu.edu>).

Assessment of AM fungi colonization

Collected sub-sample roots were chopped down into 1-cm-long segments. The chopped samples were treated with 10% KOH and autoclaved at 121 °C for 15 min. Dark pigmented roots were bleached with 10% H₂O₂ for 10 min and acidified with 3% HCl (v/v) for 30 min at room temperature. Cleared roots were transferred into a staining solution of trypan blue (0.05% w/v) in lactoglycerol (1:1:1, lactic acid to glycerol to distilled water) and autoclaved at 121 °C for 15 min (Brundrett et al. 1994). Afterwards, stained roots were left in a de-staining solution (50% glycerol) to remove colorations from empty root cells. Finally, six randomly selected stained roots of all plant species from each replicate were prepared and examined at × 100–400 magnification under a microscope for the presence of AM fungal structures (arbuscules, vesicles, and internal hyphae in the root cortex). The proportional root colonization by AMF was estimated using the magnified intersection method (Brundrett et al. 1994) with hairline reticule inserted into an eyepiece at × 400 magnification power under a compound microscope. The percentage of root length colonization was calculated from 100 or more intersections for each root sample. At each intersection, there were six possible mutually exclusive outcomes (Brundrett et al. 1994).

Data analysis

The densities of *P. juliflora* and the other woody species were calculated based on the total number of individuals recorded across all plots. To determine the population

structure of trees/shrub species as a whole, first, all individuals encountered in the plots were grouped into 5 root collar diameter classes: 1 \leq 5 cm, 2 = 5–10 cm, 3 = 10–15 cm, 4 = 15–20 cm, and 5 \geq 20 cm. The Mann-Whitney *U* test was applied to reveal the differences in the density of native woody species between two invasion rates while the differences between the four invasion rates were tested using Kruskal-Wallis analysis of variance (ANOVA) method, with a transgression probability of $p = 5\%$. Soil properties, AMF spore density, and soil seed bank difference between sites (Amibara and Gewane) and invasion rates were analyzed using two-way analysis of variance. Data on AMF and soil properties were log-transformed to conform to normal distribution. Pearson correlation test was used to analyze the AMF associations with soil properties along with invasion rates. All statistical analyses were conducted using SAS 9.0, and the level of significance was set at $\alpha = 0.05$. Tukey HSD test was performed to separate means of soil properties, AMF spore density, and soil seed bank.

Results

Species composition and stand structure

A total of eight and four tree and shrub species were recorded in Gewane and Amibara sites, respectively. The high, medium, and low invaded areas at the two study sites were almost fully occupied by *P. juliflora* while the non-invaded areas were dominated by *Acacia senegal* (Table 1). Few individuals of *Acacia mellifera* and *Dobera glabra* were found to coexist with *P. juliflora* in medium and low invaded sites at Amibara while no native tree/shrub species coexisted in medium and highly invaded sites at Gewane. Few individuals of *Balanites aegyptiaca*, *A. mellifera*, *Acacia tortilis*, and *D. glabra* were found in the low invasion sites and at no invasion

sites at Gewane (Table 1). The density (number of individuals/ha) of native woody species differed significantly between the four invasion rates at Gewane ($\chi^2 = 25.124$, $p = < 0.001$, $df = 3$) and Amibara ($\chi^2 = 15.042$, $p = 0.002$, $df = 3$). A Mann-Whitney test indicated that the density of native woody species at high invasion categories was significantly higher than at the other three invasion levels at both sites. There was no significant difference between the medium, low, and none invasion levels in the density of native woody species at both sites.

The RCD of *P. juliflora* ranged from 0.5 to 17 cm at Amibara and from 1 to 26 cm at Gewane. More than 86% and 90% of *P. juliflora* individuals had a RCD of < 5 cm at Amibara and Gewane, respectively. The number of all individuals/ha at the two sites was 1190, 175, 13, 0.8, and 0.4 at the 1st, 2nd, 3rd, 4th, and 5th diameter classes, respectively. The overall population structure of trees/shrubs in all invasion areas showed an inverted J-shaped distribution, characterized by higher proportions of smaller individuals (RCD ≤ 5 cm) and a gradually decreasing number of individuals with increasing diameter classes thereafter.

Soil properties along with invasion rates and sites

Soil physical and chemical properties differed significantly across *P. juliflora* invasion rates ($F = 7.79$, $p = 0.0019$, Table 2). Organic C, Na, Ca, P, BD, MC, and textural classes showed significant differences among the invasion categories and across Amibara and Gewane sites. The interaction of sites and *P. juliflora* invasion rates showed significant differences for OC, Na, P, BD, MC, silt, and sand ($F = 7.65$, $p = 0.002$, Table 2).

Soil seed bank along with invasion rates

The present study revealed the absence of seeds of woody species in the soil seed bank, and all seeds found were herbaceous. The invasion rate significantly affected soil seed bank abundance and the number of plant species. The highest soil seed bank density was recorded in the “medium” invasion area while the lowest was recorded in the “none” invasion area. The highest species richness was also recorded in the medium and high invasion areas followed by the low and none invasion areas (Table 3).

AMF root colonization and spore abundance by invasion rate and site

All sampled tree species were colonized by hyphal (HC), mycorrhizal (MHC), arbuscular (AC), and vesicle (VC) AMF structures in their roots. The percentage of root length colonization by different AMF structures (hyphal, arbuscule, and vesicle) was significantly ($p < 0.05$) different across invasion rates and sites (Table 4). The highest

Table 1 Density of observed woody species at different levels of *P. juliflora* invasion rates

Woody species	Amibara				Gewane			
	High	Med	Low	None	High	Med	Low	None
<i>Acacia mellifera</i>	0	9	25	0	0	0	0	3
<i>Acacia senegal</i>	0	0	0	928	0	0	0	216
<i>Acacia seyal</i>	0	0	0	0	0	0	25	0
<i>Acacia species</i>	0	0	0	0	0	0	50	0
<i>Acacia tortilis</i>	0	0	0	0	0	0	0	3
<i>Balanites aegyptiaca</i>	0	0	0	0	0	0	13	0
<i>Dobera glabra</i>	50	22	3	0	0	0	0	3
<i>Prosopis juliflora</i>	4200	503	325	44	3850	444	378	3

(“none”; *P. juliflora* cover $\leq 3\%$), low cover (“low”; *P. juliflora* cover 3–40%), intermediate cover (“med”; *P. juliflora* cover 40–60%), and high cover (“high”; *P. juliflora* cover $> 60\%$)

Table 2 The effect of *P. juliflora* species invasion rate on soil physical and chemical properties

Parameters	Site	Invasion rate			
		High	Medium	Low	None
OC (%)	Amibara	1.14 ± 0.04	1.14 ± 0.13	1.02 ± 0.1	1.89 ± 0.25
	Gewane	1.64 ± 0.09	1.75 ± 0.14	0.52 ± 0.07	0.75 ± 0.02
	Mean	1.39 ± 0.12 ^a	1.37 ± 0.27 ^a	0.77 ± 0.06 ^b	1.32 ± 0.01 ^a
Ex. Na (cmol (+)/kg)	Amibara	1.02 ± 0.44	2.68 ± 0.43	2.96 ± 0.29	1.07 ± 0.13
	Gewane	1.43 ± 0.07	3.21 ± 0.61	0.59 ± 0.08	0.81 ± 0.26
	Mean	1.22 ± 0.22 ^b	2.94 ± 0.35 ^a	1.77 ± 0.54 ^b	0.93 ± 0.14 ^b
Ex. K (cmol (+)/kg)	Amibara	0.89 ± 0.05	0.69 ± 0.06	0.87 ± 0.27	0.89 ± 0.12
	Gewane	1.0 ± 0.03	1.01 ± 0.04	0.83 ± 0.18	0.99 ± 0.18
	Mean	0.94 ± 0.03 ^a	0.85 ± 0.07 ^a	0.85 ± 0.14 ^a	0.93 ± 0.09 ^a
Ex. Ca (cmol (+)/kg)	Amibara	11.73 ± 0.72	11.23 ± 1.02	8.23 ± 0.77	7.1 ± 0.46
	Gewane	7.8 ± 1.39	9.83 ± 0.54	4.17 ± 0.12	5.73 ± 0.12
	Mean	9.76 ± 1.12 ^a	10.5 ± 0.60 ^a	6.2 ± 0.97 ^b	6.41 ± 0.37 ^b
Ex. Mg (cmol (+)/kg)	Amibara	2.4 ± 0.5	2.27 ± 0.42	2.77 ± 0.43	2.9 ± 0.15
	Gewane	3.03 ± 0.12	2.8 ± 0.25	2.6 ± 0.04	2.87 ± 0.24
	Mean	2.71 ± 0.27 ^a	2.53 ± 0.25 ^a	2.68 ± 0.19 ^a	2.88 ± 0.12 ^a
Av. P (mg/kg)	Amibara	3.57 ± 0.18	2.56 ± 0.59	4.25 ± 2.16	4.19 ± 0.38
	Gewane	24.04 ± 1.34	16.52 ± 6.63	2.31 ± 0.75	3.93 ± 0.44
	Mean	13.8 ± 4.61 ^a	9.53 ± 4.31 ^{ab}	3.28 ± 1.11 ^b	1.32 ± 0.26 ^b
TN (%)	Amibara	0.11 ± 0.01	0.12 ± 0.02	0.08 ± 0.01	0.074 ± 0.01
	Gewane	0.12 ± 0.05	0.14 ± 0.01	0.13 ± 0.02	0.11 ± 0.01
	Mean	0.11 ± 0.02 ^a	0.13 ± 0.01 ^a	0.10 ± 0.01 ^a	0.09 ± 0.01 ^a
CEC (meq/100 g)	Amibara	42.3 ± 0.86	43.3 ± 0.87	46.3 ± 0.37	43.3 ± 2.89
	Gewane	44.3 ± 5.6	49.6 ± 3.49	41.7 ± 9.0	44.1 ± 7.21
	Mean	43.3 ± 2.57 ^a	46.5 ± 2.14 ^a	44.0 ± 4.16 ^a	43.8 ± 3.47 ^a
BD (g/cm³)	Amibara	1.12 ± 0.04	1.23 ± 0.03	1.28 ± 0.05	1.21 ± 0.19
	Gewane	0.96 ± 0.03	1.12 ± 0.01	1.38 ± 0.01	1.39 ± 0.02
	Mean	1.07 ± 0.05 ^b	1.17 ± 0.02 ^{ab}	1.32 ± 0.03 ^a	1.30 ± 0.09 ^a
MC (%)	Amibara	13.22 ± 0.66	8.94 ± 0.33	8.19 ± 0.47	5.47 ± 0.74
	Gewane	15.45 ± 1.62	10.46 ± 0.38	6.04 ± 0.26	4.41 ± 0.24
	Mean	14.33 ± 0.92 ^a	9.69 ± 0.40 ^b	7.11 ± 0.53 ^c	4.94 ± 0.42 ^d
Clay (%)	Amibara	41.7 ± 2.9	33.7 ± 10.7	45.1 ± 1.3	27.1 ± 2.7
	Gewane	42.4 ± 9.2	46.4 ± 4.2	35.1 ± 1.8	22.4 ± 1.2
	Mean	42.0 ± 4.3 ^a	40.0 ± 5.8 ^{ab}	40.0 ± 2.4 ^{ab}	24.7 ± 1.6 ^b
Silt (%)	Amibara	43.3 ± 2.4	40.7 ± 5.2	30.0 ± 2.3	39.3 ± 1.3
	Gewane	49.3 ± 7.1	39.3 ± 7.4	7.3 ± 1.8	39.3 ± 3.3
	Mean	46.3 ± 3.59 ^a	40.0 ± 4.06 ^a	18.66 ± 5.23 ^b	39.3 ± 1.60 ^a
Sand (%)	Amibara	14.9 ± 0.7	25.6 ± 6.4	24.9 ± 1.3	33.6 ± 2.3
	Gewane	8.3 ± 2.4	14.3 ± 4.1	57.6 ± 1.2	38.3 ± 2.4
	Mean	11.6 ± 1.8 ^b	19.9 ± 4.24 ^b	41.26 ± 7.34 ^a	35.9 ± 1.8 ^a

Different superscript letters indicate significant differences ($p < 0.05$) among invasion rates according to Tukey's HSD test ("none"; *P. juliflora* cover $\leq 3\%$), low cover ("low"; *P. juliflora* cover 3–40%), intermediate cover ("med"; *P. juliflora* cover 40–60%), and high cover ("high"; *P. juliflora* cover $> 60\%$)

Values are mean \pm SEM (standard errors of the mean)

OC organic carbon, Ex. Na exchangeable sodium, Ex. K exchangeable potassium, Ex. Ca exchangeable calcium, Ex. Mg exchangeable magnesium, Av. P available phosphorus, TN total nitrogen, CEC cation exchange capacity, BD bulk density, MC moisture content

Table 3 Number and abundance of species in soil seed bank by invasion rate

Parameters	Site	Invasion rate			
		High	Medium	Low	None
Density	Amibara	65.2 ± 1.2	45.0 ± 0.89	25.0 ± 0.54	15.0 ± 0.78
	Gewane	56.0 ± 1.56	86.0 ± 1.78	8.0 ± 1.08	17.0 ± 1.42
	Mean	60.5 ± 0.76^b	65.5 ± 3.46^a	16.5 ± 1.43^c	16.0 ± 0.16^d
Species richness	Amibara	13.0 ± 0.52	12.6 ± 0.72	8.4 ± 0.25	6.5 ± 0.34
	Gewane	15.0 ± 0.45	16.2 ± 0.56	9.4 ± 0.24	8.0 ± 0.21
	Mean	14.0 ± 0.43^a	14.4 ± 0.63^a	8.9 ± 0.23^b	7.3 ± 0.27^c

("none"; *P. juliflora* cover ≤ 3%), low cover ("low"; *P. juliflora* cover 3–40%), intermediate cover ("med"; *P. juliflora* cover 40–60%), and high cover ("high"; *P. juliflora* cover > 60%). Different superscript letters indicate significant differences ($p < 0.05$) among invasion rates according to Tukey's HSD test

AMF colonization percentage of HC and MHC was observed at high invasion levels, followed by medium and low invasion rates across both sites (Table 4). The AC and VC structures did not show any consistency in their trend with increasing invasion rate. The percentage of root length colonization by spore abundance (number of spores per 25 g of dry soil) was significantly ($F = 139.14$, $p < 0.05$) different across invasion rates of *P. juliflora* (Table

4). The highest spore abundance was observed at high invasion rates, followed by medium and low invasion rates in both sites (Table 4).

Correlation between soil properties, AMF associations, and invasion rate

AMF spore abundance as well as HC was highly negatively correlated with increasing invasion rate ($r = -$

Table 4 The effect of *P. juliflora* invasion rates and site on AMF root colonization community structures

Parameters	Invasion rate	Sites		
		Amibara	Gewane	Mean
HC (%)	High	81.4 ± 1.3	74.9 ± 1.3	78.2 ± 1.1 ^a
	Medium	72.7 ± 1.3	70.3 ± 1.0	71.6 ± 0.9 ^b
	Low	69.3 ± 1.3	67.7 ± 1.1	68.5 ± 0.8 ^b
	None	70.8 ± 1.0	72.5 ± 1.2	71.7 ± 0.8 ^b
MHC (%)	High	70.6 ± 1.5	66.1 ± 1.4	68.4 ± 1.1 ^a
	Medium	66.9 ± 1.5	64.1 ± 1.5	65.5 ± 0.8 ^{ab}
	Low	63.8 ± 1.5	61.3 ± 1.5	62.6 ± 1.1 ^b
	None	63.5 ± 1.5	63.2 ± 1.7	63.4 ± 1.1 ^b
AC (%)	High	22.3 ± 1.0	19.1 ± 0.8	20.7 ± 0.7 ^a
	Medium	19.0 ± 0.9	14.3 ± 1.0	16.6 ± 0.8 ^b
	Low	15.9 ± 1.0	18.2 ± 0.7	17.1 ± 0.6 ^b
	None	15.8 ± 1.0	16.5 ± 1.1	16.2 ± 0.7 ^b
VC (%)	High	26.6 ± 0.8	26.7 ± 0.7	26.7 ± 0.5 ^a
	Medium	28.7 ± 0.8	26.7 ± 0.7	27.7 ± 0.6 ^a
	Low	20.7 ± 1.0	21.3 ± 0.8	21.1 ± 0.6 ^c
	None	23.5 ± 1.0	23.6 ± 0.8	23.6 ± 0.6 ^b
Number of spores	High	497 ± 14.7	459.2 ± 7.6	478 ± 8.8 ^b
	Medium	382.4 ± 10.3	337.5 ± 19.3	359.9 ± 11.4 ^c
	Low	271.5 ± 8.2	236.2 ± 9.6	253.8 ± 6.9 ^d
	None	517.4 ± 24.1	544.4 ± 16.5	530.9 ± 14.6 ^a

("none"; *P. juliflora* cover ≤ 3%), low cover ("low"; *P. juliflora* cover 3–40%), intermediate cover ("med"; *P. juliflora* cover 40–60%), and high cover ("high"; *P. juliflora* cover > 60%)

Different superscript letters indicate significant differences ($p < 0.05$) among invasion rates according to Tukey's HSD test
 HC hyphal colonization, MHC mycorrhizal colonization, AC arbuscular colonization, VC vesicular colonization

0.86, $p < 0.001$; $r = -0.57$, $p < 0.01$, respectively; Additional file 1). Soil properties such as soil OC, Ca, P, BD, MC, and the proportion of silt were significantly negatively correlated with increasing invasion rate (Additional file 1). Spore abundance was significantly and positively correlated with HC, OC, P, MC, and the proportion of silt. HC was significantly and positively correlated with TN, MC, and silt but significantly and negatively correlated with BD and clay (Additional file 1).

Discussion

Plant species composition and stand structure

Our findings indicated that *P. juliflora* invasion strongly suppressed native plant species in the study area. Most woody species individuals had a stem diameter of less than 5 cm across most invasion rates, indicating a high natural recruitment, predominately by *P. juliflora*. This trend is likely related to *P. juliflora*'s inherent characteristics to outcompete the native flora for scarce natural resources like water, space, soil nutrient, and light (Shiferaw et al. 2004). Our results agree with Getachew et al. (2012) and Nascimento et al. (2014), who reported that leaf, bark, and root aqueous extract of *P. juliflora* at higher concentrations can inhibit the seed germination and seedling growth of native woody and herbaceous plants, likely due to its allelopathic character, which resulted in lower native plant diversity. Invasive species also provide a shady condition in the systems that keep native forage species from getting quality light, essential resources for germination, survival, and growth (Vetaas 1992; Pons 2000). The shady condition in combination with other plant stresses (competition for water and soil nutrients) contributes to the difficulty of growing native forage species under dense thickets of invasive species (Flores and Jurado 2003). In contrast, a positive impact of *P. juliflora* on plant density and diversity was actually reported from Australia (Van Klinken et al. 2006) and India (Kumar and Mathur 2014). The future species composition of the plant community under invasion is dependent on whether the sites provide sufficient resources (Kimmins 1997).

Given the long time since its invasion in the Afar Region in the 1970s, and given this species' fast growth, we expected large-sized trees to dominate *P. juliflora* populations. The higher number of small-sized trees, however, is probably due to continuous commercial and non-commercial harvest of large-sized trees for fuelwood and charcoal production (Ilukor et al. 2016). The Regional Government had enacted a regional proclamation that aimed at controlling *P. juliflora* through utilization and allowed locally established cooperatives to harvest

the species for commercial purposes (Gebru 2008). Cooperatives have been selectively harvesting the larger trees since then, which yielded small-sized sprouts from the cut stump (Gebru 2008). Our findings are similar with those observed in South Africa and Kenya, where *P. juliflora* was composed of a young population and sustained recruitment, even in the absence of anthropogenic effects (Muturi et al. 2013; Shackleton et al. 2015).

Soil seed bank affected by *P. juliflora* invasion

In our study, we did not find any woody species seeds in the soil seed bank and all seeds found were herbaceous. This lack of woody vegetation seeds might be related to the absence of seed production as the system is dominated by one species (Tybirk et al. 1992), or seed predation and mortality due to aging and loss of viability or pathogens (Harper 1977; Thompson 1987). There might also be an induced different dormancy period to stabilize population dynamics against local extinction of the population under unpredictable environmental conditions (Thompson 1987). Woody plants generally have low seed numbers (Teketay and Granström 1995) and are short-lived in the soil (Teketay 1997). The reason why no *P. juliflora* seeds was found in the soil seed bank across the different invasion rates could be that the soil seed bank was collected at the end of the dry season, when all seeds had germinated. Generally, we found only few woody species growing in the study area, similar to other studies in northern Ethiopia (Tekle and Bekele 2000; Mengistu 2001), but in contrast to the Afromontane and rift valley areas (Senbeta 1998; Argaw et al. 1999).

The high seed number of herbaceous and grass seeds we found both in the high invasion rate and the open ("none") may be linked to a prolonged dry season, which helps with the accumulation of dormant seeds where no *P. juliflora* grew. In contrast, the high seed numbers under high encroachment might show that *P. juliflora* stands can protect seeds from being washed or blown away by water and wind erosion as other woody species do. The seed densities found in this study are comparable with investigations in other dry tropical ecosystems that have revealed 48–1890 seeds/m² (Garwood 1989) and 8–67 species. In our study, the soil seed bank types in the different invasion rates were similar while the ground cover of standing herbs differed substantially. The high levels of similarity in the soil seed bank indicate that the invaded area, if cleared, can regrow near-natural vegetation. The high number of herbaceous and grass species in invaded sites shows the role of *P. juliflora* in providing vegetative protection cover that could help in reducing degradation through erosion. For successful woody vegetation reestablishment, however, the seed banks may require supplementary planting of seedlings (Tekle and Bekele 2000).

Soil properties along with invasion rates and sites

Our results showed that *P. juliflora* invasion harbored increased soil nutrients, which was also found for *P. juliflora* by other studies (Tiedemann and Klemmedson 1977; Aggarwal 1980) and for other tree and shrub species at high density in dryland environments (Mazzarino et al. 1991; Rostagno et al. 1991). The enrichment of edaphic variables under the higher canopy can be explained by the redistribution of nutrients absorbed by the root system to the area (Treydte et al. 2007), the biological fixation of nitrogen by symbiotic rhizobium (Geesing et al. 2000), and through a higher organic matter input into the soil (Ilukor et al. 2016). Recently, some pastoralists have altered their way of life from livestock production to crop production in response to bush encroachment in rangelands (Mehari 2015; Ilukor et al. 2016). Therefore, the improvements of soil properties due to the invasion of *P. juliflora* are an important aspect for potential crop production, or reseeded of rangelands, particularly in the otherwise arid and nutrient-poor rangelands of Afar.

AMF root colonization and spore abundance

Our result showed the highest AMF colonization percentage of HC and MHC at high invasion categories. AMF structures (hyphal, arbuscule, and vesicle) were found in all sampled trees, indicating that dryland plant species with poorly developed roots commonly require mycorrhiza for their growth, reproduction, and survival in a stressful environment (Hailemariam et al. 2018). Tropical dryland species positively respond to inoculation with different AM fungal species by increased biomass, plant height, stem girth, number of leaves, and root length (Reena and Bayagaraj 1990; Caravaca et al. 2003). The outgrowth of mycorrhizal hyphae into the soil far beyond the root or root hair zone considerably increases the efficiency in attracting poorly mobile nutrients and translocating them to the root (Haselwandter and Bowen 1996; Joner et al. 2000). The larger soil volume explored and exploited increases the nutrient uptake by shortening the distance that nutrients have to diffuse from the soil to the roots (Kungu 2006), thereby increasing plant tissue P, K, N, Zn, Mg, Cu, and Ca mass fractions under drought conditions (Reena and Bayagaraj 1990; Huat et al. 2002).

In addition, mycorrhizal hyphae can penetrate soil pores that otherwise would be inaccessible to roots and may compete more effectively with saprotrophic microorganisms for recently mineralized nutrients than the plants themselves (Smith and Read 2008). AMF spore abundance can be promoted by appropriate management (Silva et al. 2005), e.g., by enclosures that increase herbaceous cover and decrease surface erosion. Therefore, the invaded *P. juliflora* sites confirm that this

vegetation stand, particularly at high density, can show higher propagule densities than degraded bushland and cultivated areas (Michelsen and Rosendahl 1989; Carpenter et al. 2001). Hence, after managing and harvesting *P. juliflora* stands, immediate seeding and/or supporting of native vegetation will foster a healthy rangeland restoration in the long run.

Conclusions

Our study suggests that *Prosopis juliflora* might have a positive effect on improving the soil properties and mycorrhizal activities. In addition, *P. juliflora* might not have such a negative effect on soil seed bank abundance and number of species as we had expected. Hence, although *P. juliflora* is considered as ecological challenge, this study highlights the potential benefits of *P. juliflora* in improving some ecological indicators. The positive effect of *P. juliflora* invasion on most soil physical and chemical properties calls out for sustainable management practices. Further research on the sustainable way of management of *P. juliflora* should be conducted to balance the negative and positive effects of *P. juliflora* on economic, social, and environmental aspects of the study area.

Supplementary information

Supplementary information accompanies this paper at <https://doi.org/10.1186/s13717-020-00240-x>.

Additional file 1. Pearson correlation coefficient of AMF associations with soil properties along invasion rate.

Abbreviations

AC: Arbuscular colonization; AM: Arbuscular mycorrhiza; AMF: Arbuscular mycorrhiza fungi; BD: Bulk density; CEC: Cation exchange capacity; EARO: Ethiopian Agricultural Research Organization; HADRA: Henry Doubleday Research Association; HC: Hyphal colonization; INVAM: International Culture Collection of (Vesicular) Arbuscular Mycorrhizal Fungi; MAE: Millennium Ecosystem Assessment; MC: Moisture content; MHC: Mycorrhizal hyphal colonization; OC: Organic carbon; PVLG: Polyvinyl alcohol-lactoglycerol; RCD: Root collar diameter; SEM: Standard errors of the mean; UNCCD: United Nations Convention to Combat Desertification; VC: Vesicular colonization

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Authors' contributions

AE analyzed and interpreted the inventory data regarding the species composition and prepared the first draft manuscript. EB analyzed and interpreted the soil seed bank, soil nutrient, and mycorrhizal-related data. AT has generally guided the manuscript. All authors read and approved the final manuscript.

Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Competing interests

The authors declare that they have no competing interests.

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