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ROLE OF NATIVE HERBIVORES IN THE INCREASING ABUNDANCE OF *SOLANUM MARGINATUM* L.F. (SOLANACEAE) IN THE NORTHERN BALE MOUNTAINS, ETHIOPIA

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ABSTRACT: *Solanum marginatum* L. f. (Solanaceae) is a weedy shrub native to Ethiopian highlands, including the Bale Mountains National Park (BMNP) where it is currently rapidly increasing in abundance. In this study, based on two independent datasets, we examined whether and how herbivory activities (e.g., grazing/browsing, and soil disturbance) by wild ungulates might have facilitated the performance of the shrub in the BMNP. In the first dataset, we set up a wire-fenced enclosure to examine the effects of herbivory activities on the survival of *S. marginatum* seedlings. We collected another independent data set from a total of 88 sample plots established at sites disturbed by Common Warthogs' [*Phacochoerus aethiopicus*, (Gmelin, 1788)] herbivory activities (i.e., ground digging) and at sites not disturbed, to examine the effect of these digging activities on seedling establishment of the shrub. Our results indicated that mean *S. marginatum* seedling abundance was significantly greater outside than inside the enclosure, and in the Warthog-dug sites than the non-dug sites. In contrast, herbaceous vegetation height and cover were significantly greater inside than outside the enclosure and in the non-dug sites than in the dug sites. Herbaceous vegetation cover and height were significantly (negatively) correlated with *S. marginatum* seedling abundance, while bareground is positively correlated. In conclusion, our findings indicate that herbivory activities of wildlife facilitates the performance of *S. marginatum* shrub by reducing herbaceous biomass, thus leading to increased resource available to *S. marginatum* seedlings to establish. Implications of results of the study and future actions needed to manage the shrub in the study area are discussed.

Key words/phrases: Afromontane woodlands, herbivory enclosure, overgrazing hypothesis, shrub encroachment, *Solanum marginatum*, Warthogs' ground digging

INTRODUCTION

Currently, rapid increase in woody cover and/or abundance, often referred to as "shrub encroachment", has been observed worldwide (Roques *et al*., 2001; Li *et al*., 2013). Encroacher species displace other co-occurring native species and have the ability to dominate an ecosystem, posing severe threats to biological diversity, ecosystem processes and/or socio-economic development (Chown, 2010). Despite this, the causes and mechanisms of shrub encroachment have been poorly understood (Chown, 2010; Naudiyal and Schmerck, 2018). Shrub encroachment has been variously attributed to, *inter alia*, climate change (Sturm *et al*., 2001), fire and rainfall regimes (Roques *et al*., 2001) and herbivory (Aucamp, 1976; Tessema Zewdu *et al*., 2011). However, these factors operate in a complex way and their effects vary across different ecosystems and regions; hence, there are no clear-cut simple generalities regarding causal mechanisms of shrub encroachment (Fuhlendorf *et al*., 2001; Joubert, 2014).

Overgrazing generally facilitates shrub encroachment by reducing above-and below-ground grass biomass (Holland and Detling, 1990; Davis *et al*., 2000). Similarly, browsing promotes encroachment, particularly unpalatable shrub species (i.e., those species that are provided with morphological and/or chemical herbivory defensive mechanisms; Augustine and Mcnaughton, 2004), by suppressing recruitment of young plants and growth rates of twigs and causing adult mortality of neighboring palatable shrub species (Aucamp, 1976; Brown *et al*., 1998; Augustine and Mcnaughton, 2004). Consequently, herbivory activities lead to increased resource availability (space, soil moisture, nutrient and light) and reduced competition from herbaceous

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vegetation and woody species, enabling the establishment and spread of encroaching shrub species. However, most of such evidences on the causes and mechanisms of plant encroachment are based on studies conducted in savanna land ecosystems and studies in montane woodland ecosystems, which, like savannas, usually exist as tree-grassland matrices, have generally received little attention (Naudiyal and Schmerck, 2018).

The Bale Mountains National Park (BMNP) is part of Conservation International's 'Eastern Afromontane Hotspot Biodiversity Area'; it contains exceptionally high diversity and endemism of fauna and flora species and provides vital ecosystem services (OBARD, 2007). However, the National Park has been under severe human-induced threats, including livestock overgrazing, settlement expansion and deforestation for cultivation (OBARD, 2007; Addisu Asefa *et al*., 2017). As a result, many changes have occurred in the park since its establishment in 1970, for example, in vegetation cover (Eyob Teshome *et al*., 2011), plant species diversity and composition (Addisu Asefa *et al*., 2015a), and distribution and abundance of key wildlife species (Yosef Mamo *et al*., 2015). Another notable indicator of ecosystem change in the park, particularly in the northern montane woodlands, is increasing abundance of *Solanum marginatum* L.f. (Solanaceae) has been observed in recent time (Williams, 2002; Addisu Asefa, 2005; Addisu Asefa *et al*., 2015a).

S. marginatum, known in its common name of as White-edged Nightshade, is a native shrub to highlands of Ethiopia and Eritrea, usually occurring in disturbed areas between altitudes of 2000 m and 3000 m a.s.l. (Fichtl and Admasu Adi, 1994). In Ethiopia, this species is found in Tigray (TU), Gondar (GD), Shewa (SU), Arsi (AR), Gamogofa (GG), Sidamo (SD), Bale (BA) and Hararge (HA) floristic regions (Friis, 2006). It occurs in other continents as an introduced weedy species (USDA, 2018). *S. marginatum* is thought to be inedible to herbivores (Williams, 2002), as it contains a poisonous alkaloid chemical compound known as solasodine (Dawit Abebe *et al*., 2003). Despite this, Addisu Asefa (2005) has reported from the present study area that Mountain Nyalas (*Tragelaphus buxtoni*) feed on fruits of the shrub. Reports from long-term residents of the area (A.A., pers. commu.) indicate that *S. marginatum* did rarely occur in the BMNP in the past, but it has substantially increased in abundance over the past three decades (Williams, 2002; Addisu Asefa, 2005). In agreement with the opinion of local communities, a recent vegetation study conducted by Addisu Asefa *et al*. (2015a) in the northern montane woodlands of the park show that *S. marginatum* occurs with a density of 308 adult plants per ha and is the first and the third most abundant shrub species and woody species, respectively.

Consequently, given the general presumption that such increase in abundance of a particular shrub species can pose adverse impacts on biodiversity (Chown, 2010), the increasing abundance of *S. marginatum* in the BMNP has become one of the major conservation management concerns of the National Park at present. A management intervention aimed to reduce its abundance was made in 2008, by manually removing (using axes) stems of the shrub; unfortunately, it was unsuccessful as the sites where the shrub was cleared were reinvaded by *S. marginatum* seedlings in the following growing/wet season (BMNP, Unpublished data). Thus, appropriate management of *S. marginatum* in the area requires not only understanding of the factors causing increase in its abundance, but also the mechanisms how they cause it.

The causes of increasing abundance of *S. marginatum* in the BMNP have not been clearly investigated yet. However, our long-term (since 2002 to present) *ad hoc* field observations show the occurrence of unusually high abundance of *S. marginatum* seedlings at sites disturbed by herbivory activities of native (wildlife) fauna and domestic animals and at sites where canopy trees are removed. Our most frequent observations have been at sites disturbed by Common Warthog's (*Phacochoerus aethiopicus*) herbivory activities, particularly of ground digging activity that result in vegetation removal and top-soil disturbance. Warthogs are mostly grazers, but their diet also consists of items such as roots and fruits (Abdulfatah Abdu and Demeke Datiko, 2017). In the BMNP, they do much digging of topsoil during dry season for sedge corms and roots (Hillman, 1986), where ~10-20% of area of the northern woodlands of the BMNP is estimated to be dug annually (Addisu Asefa, personal observation). From these observations (i.e., occurrence of extensive ground digging and massive seed germination at such dug sites), it is therefore possible to hypothesize that ecosystem disturbances caused by herbivory activities of wild ungulates might be one of the factors that have facilitated the dominance of the shrub in the BMNP.

In this study, based on two independent datasets, we examined whether herbivory activities of native (wildlife) ungulates might have influenced some demographic aspects (seedling germination/establishment and survival) of *S. marginatum* in the northern woodlands of the BMNP. First, in March 2007, during the beginning of the small rains in the Bale Mountains region (Hillman, 1986), ~250 m^2 of a 30-year old *Cupressus lusitanica* Mill. plantation was clear-cut in the Dinsho Hill woodland forest. After a couple of months, the cleared site (where understory vegetation was virtually absent prior to the clear-cut) was found to be covered by herbaceous vegetation (grasses and herbs) and some native woody species, with most of the cleared area being covered by *S. marginatum* seedlings (BMNP, 2007, unpublished report).

Following this observation, we experimentally manipulated wildlife herbivory disturbance, using a fenced enclosure, as one main component of the environment to address the main question: What is the effect of the treatment on fitness components of *S. marginatum* seedling (i.e. seedling survival and growth)? The experimental treatment was herbivory enclosure vs control. In this case, we hypothesized that after-treatment (at the end of the experiment) mean *S. marginatum* seedling abundance (number of survived individuals) and height would be significantly higher outside than inside the enclosure, and the converse is true of mean herbaceous vegetation height and cover. In the second dataset, we used Warthog ground digging activities (treatment levels: dug vs non-dug) and microhabitat type (two levels: openland vs under tree shade) as other two main components of the environment to address the questions: i) what are the individual and interactive effects of the treatments on the establishment (abundance) of *S. marginatum* seedlings? Here, we hypothesized that *S. marginatum* seedlings would be more abundant in the Warthog dug sites than in the non-dug sites and in open grassland micro-habitat than under tree canopy.

MATERIALS AND METHODS

Study Area

The BMNP is situated in the southeastern highlands of Ethiopia (6°30'-7°00' N, 39°30'-39°55' E), about 400 km away from the capital (Fig. 1). It encompasses an area of 2200 km^2 and contains a landscape ranging from 1500 to 4377 m a.s.l. The National Park contains five vegetation zones (Hillman, 1986): the northern montane grasslands, the northern montane woodlands, ericaceous forest, the Afroalpine moorland and grassland, and the southern Harenna forest. Seventy-eight mammal and 278 bird species have been recorded for the area; of these, 17 mammal and 6 bird species are endemic (Addisu Asefa *et al*., 2017). The area experiences two rainy seasons, heavy and small rains. The heavy rain lasts from July to October, while the small rain lasts from March to June. The highest temperature is 18.4°C in February and the lowest is 1.4°C in January (Hillman, 1986).

Montane woodlands in the Bale Mountains occur in northern slope of the Mountains between altitudes of 3000-3400m a.s.l. They exist in six isolated patches, covering a total area of ~72 km^2 (Addisu Asefa *et al*., 2017). Dominated by *Juniperus procera* and *Hagenia abyssinica* tree species, vegetation of these woodlands is classified as a dry evergreen Afromontane forest which is characterized by a single vegetation layer with a discontinuous canopy formation and with a good herbaceous cover in the open areas (Hillman, 1986). In these woodlands, Yosef Mamo *et al*. (2015) have reported an increase of 90% shrub cover since 1980s (20% in 1980s vs 38% at present), particularly due to increasing cover of *S. marginatum* (Addisu Asefa, *et al*., 2015a). In contrast, cover of open grassland habitat has declined from 15% in 1980s (Hillman, 1986) to~8% at present (Yosef Mamo *et al*., 2015). These woodland patches are critical habitats for the endangered antelope, Mountain Nyala (*Tragelaphus buxtoni*) and the endemic subspecies Menelik's Bushbuck (*Tragelaphus scriptus meneliki*), but also supports high populations of other ungulates, including Bohor Reedbuck (*Redunca redunca*) and Common Warthog (Addisu Asefa, 2005; OBARD, 2007). These ungulates use open grassland microhabitats of the woodlands for foraging and trees for cover and shade (Yosef Mamo *et al*., 2015).

The present study was undertaken in Dinsho hill woodland (Fig. 1; altitude 3150 m a.s.l.) which is a wire-fenced 120ha area where the headquarters of the BMNP are located. Dinsho hill woodland is relatively well protected than the other patches, as it supports disproportionately a larger number of populations of wild ungulates of the park (OBARD, 2007; Addisu Asefa *et al*., 2017).

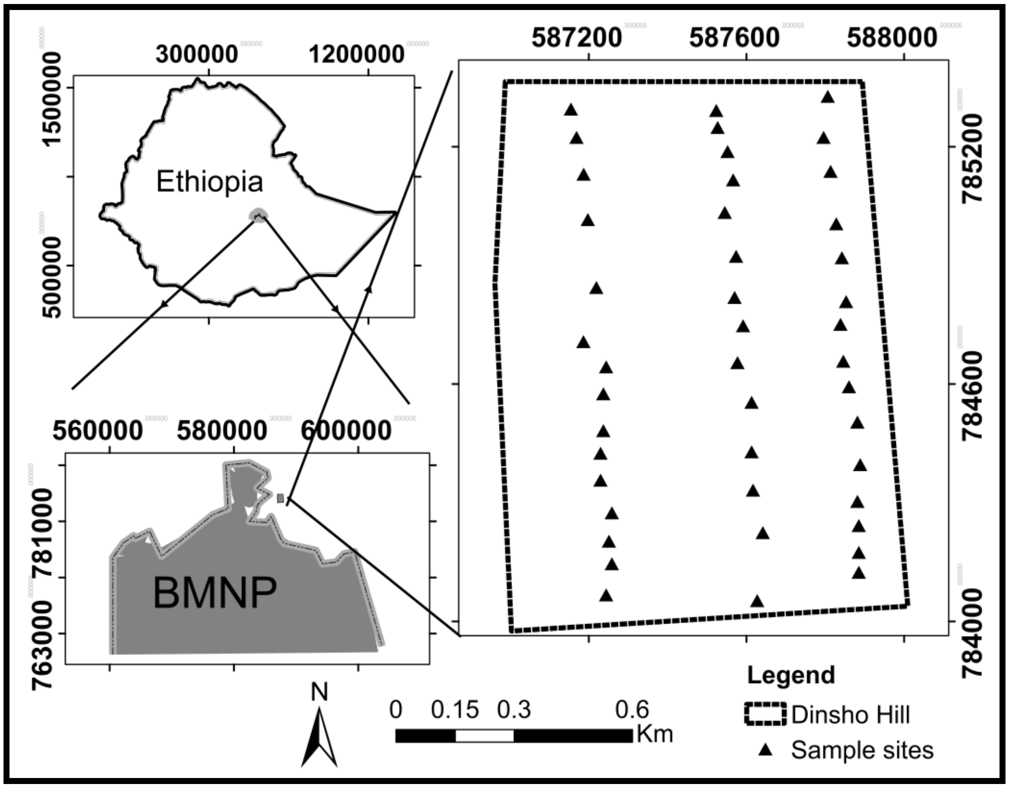


Figure 1. Map showing the location of Bale Mountains National Park (BMNP) in Ethiopia, Dinsho Hill (the study site) in the BMNP and sample sites in the Dinsho Hill.

Data Collection

In this study, we used two independent datasets collected under different spatiotemporal conditions: one collected between June-September 2007 and the other between September-October 2017. These months, which represent the time when livestock use of the woodland is absent or minimal, were chosen to reduce the confounding effects of livestock herbivory with the effects of wildlife herbivory on *S. marginatum* might be found. In the first dataset (hereafter called the "herbivory enclosure study"), in June 2007, we setup a wire-fenced enclosure of 3m×3m area and 1.5m height at the site where *Cupressus* plantation was cleared 3 months ago (location, UTM east: 587077, north: 784238; altitude = 3177 m a.s.l.). The entire site where the plantation was removed was homogenous in vegetation and topography, and there were no signs of Warthog digging activities from the preceding dry season as there was no or little herbaceous vegetation during then. Thus, the enclosure was established at the center of the cleared site. In the meantime, we also recorded vegetation variables at the time of fence construction (i.e., in June 2007; hereafter referred to as 'before-treatment enclosure data') within nine 1m×1m quadrats. Vegetation variables recorded in each quadrat were: abundance (number of individuals) and height of *S. marginatum* seedlings, cover and height of herbaceous vegetation (i.e., grasses and herbs), and proportion of bareground. Heights of seedlings and herbaceous vegetation were determined from averages of up to five, whenever available, randomly taken measurements using a 1.5m high labeled measuring stick, while herbaceous cover was visually estimated (Newton, 2007). In each quadrat, herbaceous cover was estimated by viewing, from directly above, at the proportion of ground within a quadrat covered by the above-ground parts (horizontal projections) of herbaceous vegetation and recording in 10% ranges (Newton, 2007). We also established other nine 1m×1m quadrats outside the enclosure and took the same data on the variables described above. These plots were systematically chosen by evenly distributing in the four cardinal directions relative to the enclosure and by limiting a minimum distance of 3m from edges of the enclosure and from each other and 5m from edges of uncleared sites (i.e., areas still covered by Cupressus or by natural vegetation). Position of each of these outside enclosure plots was permanently marked using tree stumps (where available) or using wooden-pegs and were sketch-mapped on square paper along with description of their relative position (direction and distance) from each other and from the fence. This had helped us locate the plots during re-sampling. Accordingly, after three months of the enclosure set up, we again recorded similar data (hereafter referred to as 'after-treatment enclosure data') on all variables described above in each plot both inside and outside the enclosure.

The second dataset (hereafter called the "Warthog ground digging effect study") was collected in September/October 2017 from 88 randomly selected sample plots, excluding plots that fell in the Cupressus plantation-cleared site (i.e., where the first dataset was collected), to examine the effect of Warthog ground digging on seed germination/seedling establishment of *S. marginatum* and how this may differ between micro-habitat types. Thus, we used a factorial design with two main factors: Warthog digging (two levels: dug vs non-dug sites) and micro-habitat type (two levels: tree-/shrub-less open grassland vs under tree canopy). To select sample plots, we first selected three 1.5 km parallel line transects (running from south to north) at 200m distance apart from each other and from habitat edges. Along each transect, all freshly Warthog-dug sites were searched for within 20m width on both sides. This was done in February 2017, as it represents end of dry season of the year before the dug sites are colonized by new vegetation growth. Those dug sites with minimum length and width (regardless of their shape) of greater than 1m each, and at least are 10m away from adult (fruiting) *S. marginatum* plants, were identified, numerically coded and locations marked with Garmin GPS unit. This yielded a total of 197 dug sites across the three transects and we used them as sample population from which to select sample units. Then, total of 44 dug sites (22 for each of microhabitat type), 14 sites along each of the two transects and 16 along the third transect, were randomly selected from the sample population and sampling was undertaken within 1m×1m quadrat. Random selection of sample units was made for each microhabitat type along each transect using the "RANDBETWEEN" function of Excel application (Microsoft Corporation, 2010), using as an input the numerical code assigned to each dug site described above. At each of these dug sites (quadrats), a 1m×1m quadrat was also randomly selected from non-dug sites at 3-5m distance from edges of the dug quadrats. This was achieved by perpendicularly dropping the vegetation measuring stick to the ground at the center of the dug quadrat and selecting suitable sample site in the direction the stick fell. In each of these dug and non-dug quadrats, we recorded data on the following four variables: abundance of *S. marginatum* seedlings, height and cover of herbaceous vegetation and proportion of bareground. Height and cover estimations were made as described above for the herbivory enclosure study. We did not record data on *S. marginatum* seedling height, because our preliminary field observations showed that, in most cases, its height was taller than height of herbaceous vegetation.

Data Analysis

Prior to analysis, all variables were tested for normality of mean and homogeneity of the variance by using the Kolmogorov–Smirnov and Levene's tests, respectively. If the data were found to deviate from these assumptions, these variables were transformed applying appropriate procedure (Quinn and Keough, 2002). All statistical analyses were carried out using SPSS version 20.0 (IBM, 2001) and results were reported, where applicable, after back-transforming to original scale.

Effect of herbivory exclusion on performance of S. marginatum seedlings

Prior to examining the effect of herbivory (or herbivory enclosure effect) on *S. marginatum* seedling performances, we tested, using one-way ANOVA, the lack of significant inherent difference between quadrats inside and outside the enclosure in their before-treatment mean: i) abundance of Soalnum seedlings, ii) height of solanum seedlings, iii) height of herbaceous vegetation, iv) cover of herbaceous vegetation, and v) proportion of bareground. To examine the effect of herbivory (enclosure) on Solanum seedlings performance, we compared after-treatment mean seedling abundance between inside and outside the enclosure in two ways: without and with accounting for inherent (before-treatment) differences in abundance between treatment levels. In the first approach (without accounting for inherent differences), we compared after-treatment mean seedling abundance between inside and outside the enclosure quadrats, using one-way ANOVA. In the second approach, to account for the effect of inherent differences in seedling abundance between treatment levels on their after-treatment abundances, we calculated proportion of *S. marginatum* seedling survival (i.e., change in seedling abundance at the end of the experiment compared to abundance at the beginning of the experiment) using the number (abundance) of living plants (not dried) counted during the after-treatment sampling period in a quadrat minus the original number (i.e., before-treatment abundance). This proportion survival per quadrat was used as a replicate to test the null hypotheses that: (i) there was no significant difference between inside and outside the enclosure in mean proportion survival of seedlings (i.e., there was no treatment effect on changes of seedling abundance from before- to after-treatment), using one-way ANOVA; and, (ii) mean change of seedling abundance was not significant (i.e., proportion survival not significantly different from zero) both inside the enclosure and outside the enclosure, using one-sample t-test. We also used one-way ANOVA to test the effect of enclosure on after-treatment mean herbaceous vegetation height and herbaceous vegetation height and proportion of bareground.

We assumed that the effect of herbaceous vegetation height on *S. marginatum* seedling abundance is mainly *via* competition for light, suggesting that, if this assumption holds true, the effect might be minimal when seedling height is taller than herbaceous vegetation height. Thus, we derived new data values, separately for before-treatment data and the after-treatment data, for the herbaceous vegetation height variable (referred to as 'relative herbaceous vegetation height') by subtracting seedling height from herbaceous vegetation height recorded in each quadrat. We then used these relative herbaceous vegetation height values to assess the effects of herbaceous vegetation height and other predictor variables (herbaceous vegetation cover and proportion of bareground) on *S. marginatum* seedling abundance. To do so, we first calculated 18 contrast values (i.e., nine values each for inside and outside the enclosure samples) for each variable, as well for seedling abundance and height, by subtracting their after-treatment values at each quadrat from the before-treatment values. Based on these contrast values, we examined the relationships (collinearity) between the predictor variables using Pearson's correlation test. As all the predictors were strongly correlated to each other (see Table 1a), we carried out simple linear regression analyses to test the effect of each predictor variable on *S. marginatum* seedling abundance (Quinn and Geough, 2002).

Effects of Warthog ground digging and micro-habitat on S. marginatum seedling abundance

We used generalized linear models (GLMS) to test the effects of treatments (Warthog digging and micro-habitat type effects) and their interactions on both probability of occurrence (modeled as binomial distribution and logit link function) and mean abundance of *S. marginatum* (modeled as negative binomial distribution with log-link function). GLMS were also used to test the effects of the treatments and their interaction on mean values of the three predictor variables (all modeled as normal distribution and identity link function), after applying arcsin-transformations to herbaceous vegetation cover and proportion of bareground and $\log_{10}(x+1)$ to herbaceous vegetation height (IBM, 2001; Quinn and Geough, 2002). Pearson's correlation tests were conducted to examine the relationships between the predictor variables. Results of these tests showed that there were strong collinearities between the predictor variables (see Table 2a), thus we used generalized linear model with negative binomial distribution and log-link function to examine the relationship of *S. marginatum* seedling abundance with each predictor variable, separately.

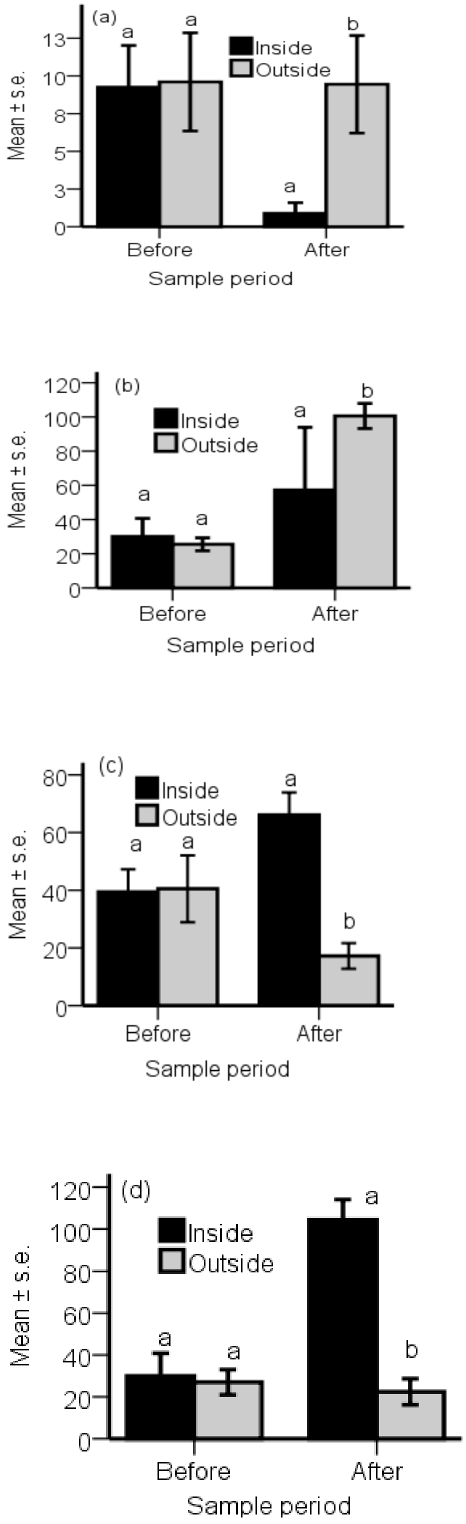
RESULTS

Effect of Herbivory Exclusion on Performance of S. marginatum Seedlings

Before the treatment, total of 89 (on average ~10 seedlings per quadrat) and 81 (9 seedlings per quadrat) individual *S. marginatum* seedlings were counted inside and outside the enclosure sample plots, respectively. However, data collected after 3 months (after-treatment enclosure data) showed total of 8 alive (survived seedlings) and 77 dead seedlings inside the enclosure and 73 alive and 5 dead seedlings outside the enclosure. These data indicate that four and three seedlings were missed, and the rate of seedling survival appeared to be ~9% and ~90% inside and outside the enclosure, respectively.

Results of the one-way ANOVA showed non-significant differences between inside and outside the enclosure in the before-treatment mean *S. marginatum* seedling abundance and seedling height, herbaceous variables (height and cover), and proportion of bareground (in all cases, $F_{1,16}$ = 0.281-3.556, $P > 0.05$; Fig. 2a-e). In contrast, after-treatment mean values of all these variables were significantly different between inside and outside the enclosure, except *S. marginatum* seedling height ($F_{1,16}$ = 2.538, P =0.131). After-treatment mean *S. marginatum* seedling abundance ($F_{1,16}$ = 26.779, $P < 0.001$) and proportion of bareground ($F_{1,16}$ = 12.591, $P < 0.05$) were significantly greater outside the enclosure than inside, while both herbaceous vegetation height ($F_{1,16}$ = 97.350, $P < 0.05$) and cover ($F_{1,16}$ = 17.942, $P < 0.05$) were significantly greater inside the enclosure (Fig. 2c-e). Mean change of seedling abundance (proportion survival) was significantly different between inside and outside the enclosure, with greater change detected inside the enclosure (mean change ± se: inside = -0.825 ± 0.060; outside = 0.028 ± 0.023; $F_{1,16}$ = 36.444, $P < 0.0001$). Results of one-sample *t*-test also showed that mean change of seedling abundance was significantly lower (average reduction of ~83%) than zero inside the enclosure (t = -6.075, df = 8, $P < 0.005$), but that of outside the enclosure was not significantly different from zero (t = 1.066, df = 8, P =0.318).

Simple linear regression analysis results showed that herbaceous vegetation cover (R^2 = 0.605; $F_{1,15}$ = 24.540, $P < 0.05$) and herbaceous vegetation height (R^2 = 0.343; $F_{1,15}$ = 8.354, $P < 0.05$) had significant negative relationships with *S. marginatum* seedling abundance, but proportion of bareground (R^2 = 0.828; $F_{1,15}$ = 77.158, $P < 0.05$) was positively related. However, herbaceous vegetation height was the only predicator variable that had significant relationship (negative) with seedling height (R^2 = 0.733; $F_{1,}$ = 54.477, P <0.05) (Table 1b).



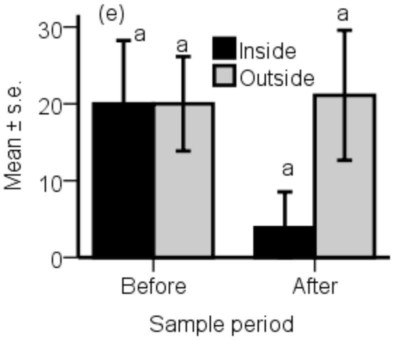


Figure 2. Before-treatment and after-treatment mean *S. marginatum* seedling abundance (a), seedling height (b), herbaceous height (c), herbaceous cover (d), and bareground (e). For each variable, significant mean difference between treatment levels (inside vs outside enclosure) in each sampling period are indicated by different letters.

Table 1. Pearson's correlation coefficients (a) between *S. marginatum* seedling abundance (S. abundance) and seedling height, cover and height of herbaceous vegetation, and proportion of bareground (in all cases, n = 18), and results of linear regression analyses (b) relating *S. marginatum* seedling abundance and seedling height with herbaceous vegetation variables and bareground (given values are: R^2, ANOVA'S *F*-values and coefficients of model parameter estimates; in all cases, df $_{1,2}$ = 1, 15).

Variables	Herbaceous cover	Herbaceous height	Bareground
(a) Correlations			
Herbaceous cover		0.702**	-0.873**
Herbaceous height			-0.800**
(b) Regression			
S. abundance			
R^2	0.605	0.343	0.828
F-value	24.540*	8.354*	77.158*
Par. coefficient	-1.299(0.262)	-0.004(0.001)	2.161(0.246)
S. height			
R^2	0.17	0.733	0.149
F-value	2.12	54.477*	3.969
Par. coefficient	-1.258(0.695)	-0.010(0.001)	1.936(0.972)

Note:- * = Significant relationship at *P* <0.05

Effects of Warthog Digging on S. marginatum Seedling Abundance

Overall, *S. marginatum* seedlings were encountered at 39 (44%) of the total 88 quadrats. Of the total 44 quadrats sampled in each treatment level seedlings were encountered at 35 (85%) and 4 (9%) quadrats in the dug and non-dug sites, and at 27 (61%) and 12 (27%) quadrats in the openland and under canopy microhabitat types, respectively. Number of individuals ranged between 1 to 21 seedlings per plot. Results of GLMS analyses showed that probability of occurrence of seedlings (proportion of quadrats where seedlings were present) across sample plots was significantly higher in the Warthog-dug sites than the non-dug sites (mean ± se, dug site = 0.73 ± 0.08; non-dug sites = 0.18 ± 0.06; Wald's chi-square = 21.341, df = 1, *P* <0.05) and in the open micro-habitat than under tree canopy (mean: open = 0.67 ± 0.09; under canopy = 0.23 ± 0.07; chi-square = 12.431, df = 1, *P* <0.05), but their interaction was not significant (chi-square = 0.801, df = 1, *P* =0.371). Similarly, mean *S. marginatum* seedling abundance was greater in Warthog-dug sites that non-dug sites (Wald chi-square = 26.878, df = 1, *P* <0.001; Fig. 3a) and greater in the open micro-habitat than under tree shade (chi-square = 21.678, df = 1, *P* <0.001; Fig. 4a). The effect of treatment interaction on seedling abundance was non-significant (chi-square = 4.003, df = 1, *P* <0.05). Significant effects of treatments were also found on mean herbaceous vegetation cover (arcsin-transformed), which was significantly higher in the Warthog non-dug sites compared with the dug sites (chi-square = 8.447, df

= 1, *P* <0.05; Fig. 3b-d), and proportion of bareground, which was significantly higher under tree canopy than in the open microhabitat (chi-square = 4.621, df = 1, *P* <0.05; Fig. 4b-d). Results of GLMS analyses showed that herbaceous vegetation cover was the only predicator variable that had significant (negative) relationship with *S. marginatum* seedling abundance (*P* <0.05; Table 2b).

Table 2. Pearson's correlation coefficients (a) between herbaceous vegetation cover, herbaceous vegetation height and bareground (in all cases, n = 88); and results of generalized regression model analysis (b) relating *S. marginatum* seedling abundance with each of herbaceous vegetation cover, herbaceous vegetation height and bareground (values given are: Wald's chi-square and model parameter estimates; in all cases, df = 1).

Variable	Herbaceous vegetation cover	Herbaceous vegetation height	Bareground
(a) Correlation			
Herbaceous vegetation cover		0.207	-0.224*
Herbaceous vegetation height			-0.681*
(b) GLM			
Wald χ^2	12.884*	1.721	1.357
Parameter	-1.118 ± 0.330*	-0.421± 0.321	0.761 ± 0.653

Note:- * = Significant relationship at *P* <0.05

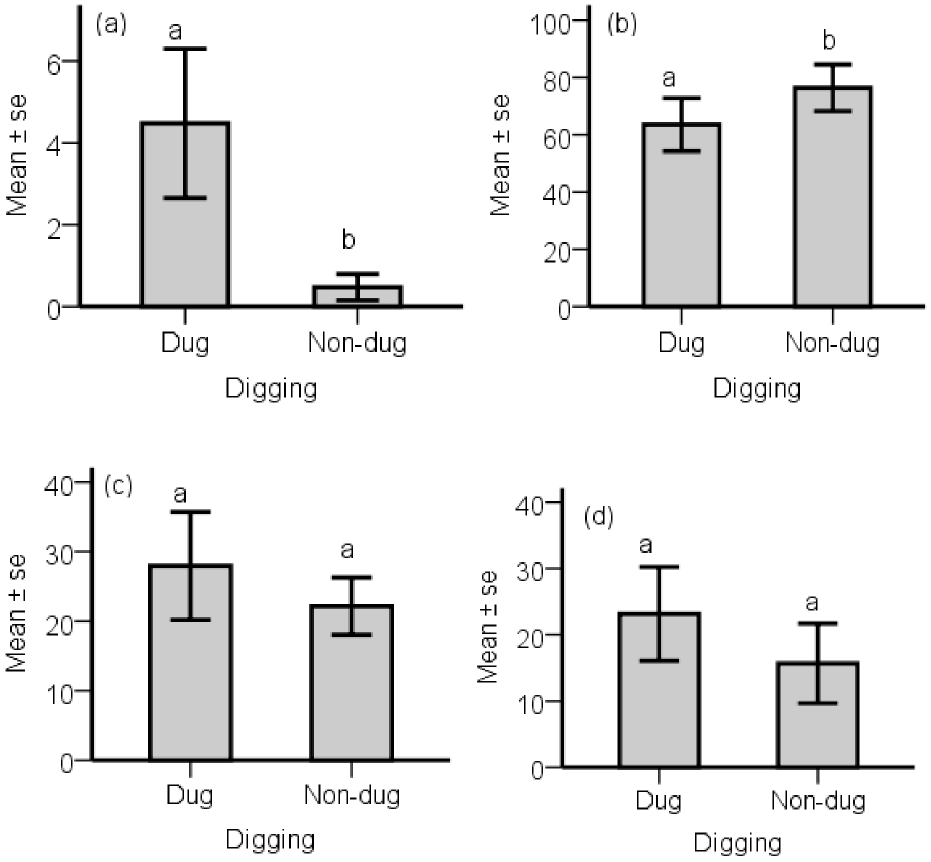


Figure 3. Effect of common Warthog ground digging on *S. marginatum* seedling abundance (a), herbaceous cover (b), herbaceous height [in cm; (c)] and bareground (d). For each variable, significant mean difference between treatment levels are indicated by different letters.

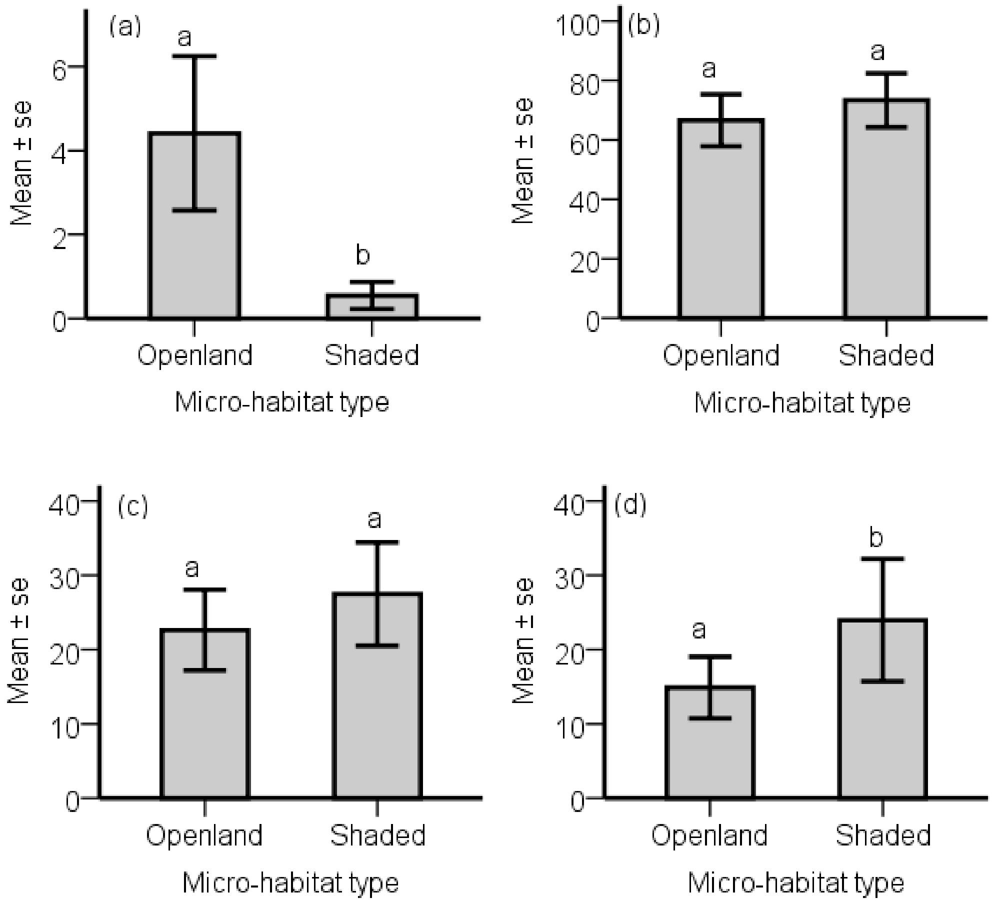


Figure 4. Effect of microhabitat type on *S. marginatum* seedling abundance (a), herbaceous vegetation cover (b), herbaceous vegetation height (c) and proportion of bareground (d). For each variable, significant mean difference between treatment levels are indicated by different letters.

DISCUSSION

Our results demonstrate that herbivory of native fauna is one of the factors that facilitate the increasing abundance of *S. marginatum* shrub in the northern montane woodlands of the Bale Mountains, Ethiopia. For example, fenced exclusion of herbivory activities (our first dataset) had led to significantly higher rate of seedling mortality (9% vs 90% rate of survival), resulting to 10 fold higher rate of survival of *S. marginatum* seedling outside the enclosure compared to inside the enclosure. Similarly, Warthog ground digging (the second dataset) had also resulted to increased abundance of *S. marginatum* seedling, particularly in open grassland micro-habitat. In contrast, herbivory activities have resulted to reduced cover and height of herbaceous vegetation. Several studies (e.g., Belsky *et al*., 1993; Ludwig *et al*., 2004; Adugna Angassa and Oba, 2010; Bradd *et al*., 2011; Temesgen Yadeta *et al*., 2018) have reported similar role of herbivory in facilitating the rapid spread and increase in abundance of encroaching [unpalatable] shrub species in natural ecosystems, which usually occurs in the expense of herbivory-sensitive (palatable) species.

Our results suggest that the processes involved in the increasing abundance of *S. marginatum* under herbivory disturbance conditions in the present study could be explained by the 'overgrazing hypothesis' (for detail on this hypothesis, see Holland and Detling, 1990; Davis *et al*., 2000; Shea and Chesson, 2002). For example, our results showed (i) at least in one of the two datasets, lower herbaceous vegetation cover and height, but greater proportion of bareground at sites disturbed by herbivory (outside the enclosure and/or at Warthog dug sites), (ii) that seedling abundance was negatively related to herbaceous vegetation cover and height, but positively to proportion of bareground, and (iii) that Solanum seedling height was negatively related with herbaceous height. These findings thus may clearly demonstrate, similar to the mechanism described in the 'overgrazing hypothesis', that biomass destruction (cover and height reduction) of herbaceous vegetation by wildlife (native) herbivory activities might have released *S. marginatum* seedlings from competition with herbaceous vegetation for limiting resources (e.g., space, light and soil mineral and moisture). This herbivory-induced release of the shrub from competition with herbaceous vegetation, and thus increased availabilities of resources, could have enabled *S. marginatum* seedlings to germinate and grow during these windows of opportunity (Brown *et al*., 1998; Davis *et al*., 2000; Li *et al*., 2013), perhaps facilitating the dominance of the shrub in the study area. Furthermore, Warthog digging also leads to increased soil aeration and water retention capacity (Davis *et al*., 2000). The increasing abundance of *S. marginatum* in response to Warthog digging could also be due to such increased soil water availability in the dug soils, which is one important requirement for the germination and establishment of Solanum seeds.

Despite the overall (regardless of micro-habitat type) positive effect of Warthog ground digging activity on the performance of *S. marginatum* seedlings in the study area, this facilitation role was found to be significant only in the openland microhabitat type but not under tree canopy. The finding (i.e., dependence on microhabitat of Warthog ground digging effect on Solanum seedling) is unsurprising, because shrub encroachment usually occurs in open habitats (grassland ecosystems and openland micro-habitats embedded within woodland ecosystems) (Roques *et al*., 2001; Joubert, 2014). Similar studies (Ehrlén *et al*., 2005; Gurvich *et al*., 2005; Temesgen Yadeta *et al*., 2018) have also reported that microhabitat type is among the factors that determine the effect of herbivory on the performance of understory plant species, depending on the plant species-specific traits related to their light requirement (e.g., shade-tolerant vs light-demanding). Our findings of lower seedling abundance, and thus the weak evidence we found on the importance of herbivory activities in promoting the performance of the shrub under tree canopies, could therefore be attributed to the primary effects that tree canopies have, by limiting the amount of light available to understory, on the performance of light-demanding species like *S. marginatum* shrub (Scholes and Archer, 1997; Ludwig *et al*., 2001; Scheffer *et al*., 2001; Ludwig *et al*., 2004). However, regardless of presence/absence of herbivory disturbance and/or amount of light available to understory vegetation, it is possible that trees root-competition for resources (e.g., soil nutrient and moisture) could also have limited the germination, growth and survival of *S. marginatum* under canopies (Scholes and Archer, 1997; Ludwig *et al*., 2001, 2004).

Overall, our study has provided an insight into the effects of native herbivores in shaping woody plant dynamics in the northern BMNP which may provoke further actions towards appropriate management of *S. marginatum* in the study area. In the Dinsho hill woodland patch, livestock use was absent during our study period and thus our findings are mainly attributable to wildlife herbivory activities.

However, one important question associated to our study and its findings is that, given both *S. marginatum* and the wild ungulates are native to Bale region: why herbivory activities of the ungulates did not facilitate expansion of the shrub in the study area in the past (before three decades)? Addressing this question may not be so simple and straight forward, but it could be associated to the unprecedented rate of anthropogenic-induced ecosystem degradation that have been noted in the Bale Mountains region in recent times (Eyob Teshome *et al*., 2011; Addisu Asefa *et al*., 2015b), which might have triggered the effect of wildlife herbivory on the *S. marginatum* (see also Roques *et al*., 2001; Scheffer *et al*., 2001). Thus, our results may corroborate the notion that the rapid shrub encroachment caused by herbivory activities of native herbivores in some other areas, combined with some form of anthropogenic factors, should be treated as one major threat to biodiversity conservation, rather than treating as a natural ecological succession (Fuhlendorf *et al*., 2001; Roques *et al*., 2001; Li *et al*., 2003; GIZ-BFP, 2016).

Although the impacts of *S. marginatum* expansion on biodiversity and ecosystem processes of the BMNP have not been clearly known, following the general presumption that shrub encroachments have negative consequences (Chown, 2010; Li *et al.*, 2013), there are a number of reasons why the expansion of *S. marginatum* in the BMNP may remain a major conservation management concern. Reports of previous studies indicate that high seed production and dispersal (e.g., Gurvich *et al.*, 2005; Joubert, 2014) and presence of viable soil seedbank (Tessema Zewdu *et al.*, 2012) are critical factors for shrub encroachment. *S. marginatum* appears to possess such traits of successful encroacher plants, because (i) it exhibits high seed production (Fichtl and Admassu Adi, 1994), (ii) its fruits are browsed by Mountain Nyalas which subsequently disseminate the seeds in dug (Addisu Asefa, 2005), and (iii) as can be judged from the mass seed germination observed after tree clear-cut and in Warthog dug sites of our study area, it has viable soil seedbank. Therefore, these traits and of its less susceptibility to herbivory damages (inedibility) may not only enable *S. marginatum* to increase in abundance under continued heavy herbivory disturbance regimes, but may also make difficult to control its spread (Roquest *et al.*, 2001; Gurvich *et al.*, 2005; Newton, 2007). The overall implication of our findings is that factors, including anthropogenic disturbances, that lead to reduction of tree cover and herbaceous vegetation height and cover will likely accelerate expansion rate of the shrub in the study area. However, there is still a gap in knowledge of the germination requirements, allelopatic properties, tolerance to herbivory pressure, disturbance requirements, seed longevity, establishment requirements and stress tolerance of *S. marginatum* in other ecosystems and regions. All these factors are known to contribute to the establishment and encroachment of plant species, but with varying degrees of effects in different ecosystems and regions (Gurvich *et al.*, 2005).

Furthermore, scientific evidences (e.g., Sturm *et al.*, 2001; Chown, 2010; Joubert, 2014) showing the impact of climate change (positive or negative) on the abundance and distribution of plant species have been growing. Future research works are needed to elucidate whether climate change has contributed to the current expansion of *S. marginatum* in the study area.

CONCLUSIONS

Our findings indicate that wildlife herbivory activities play facilitation role in increasing the performance (seed germination and seedling survival) of *S. marginatum* shrub, particularly in open grassland micro-habitat. This facilitation role appears to be achieved by decreasing herbaceous vegetation cover and height, and thus reducing competition from herbaceous for space, light and other essential resources. Coupled with the fact that *S. marginatum* is a light-demanding shrub species (Fichtl and Admassu Adi, 1994)—thus germinate and grow better in open areas where herbaceous cover is sparse and height is low—, the results may suggest that disturbances that cause tree canopy openings (e.g., tree removal) and that reduce herbaceous vegetation cover and height (e.g., heavy herbivory activities of wildlife and/or livestock) may further accelerate expansion of the shrub in the Bale Mountains Region. As such, human-induced disturbances (tree cutting and livestock use) should be avoided in the study area to mitigate the current expansion rate of the shrub. However, the effect of Warthog ground digging on *S. marginatum* performance reported herein should be treated cautiously, because currently we do not know the resultant ecosystem consequences of this digging activity. While keeping in mind the reduced herbaceous cover in Warthog dug sites, these digging activities, for example, may induce the germination of more diverse and nutritious herb and grass species that may be preferred by wild ungulates. Thus, studies examining the effects of Warthog digging on herbaceous species composition and biomass, as well as on soil properties, are required before devising and taking management measures to control/mitigate expansion of the shrub in the study area. Ecological monitoring programme should also be setup to track changes in the spatiotemporal distribution and abundance/cover of *S. marginatum* in the BMNP.

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