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Unpacking the push-pull system: Assessing the contribution of companion crops along a gradient of landscape complexity

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ABSTRACT

The push-pull system, a stimulo-deterrent cropping strategy consisting of intercropping cereals with herbaceous legumes and surrounded by fodder grasses, is presented as a promising crop diversification strategy for smallholder farmers in Africa as it may contribute to maize stemborer *Busseola fusca* (Fuller) suppression, while improving soil fertility and providing feed for livestock. The push-pull system has often been assessed at plot level and as a package (e.g., Maize + *Desmodium* + Napier grass). However, it is unclear how the system performs in different landscape settings or when companion crops are changed to better meet household needs. Here we evaluate the potential of the push-pull system to suppress maize stemborer infestations in three landscapes in the Rift Valley region of Ethiopia along a gradient of landscape complexity. Within each landscape, experimental plots were established on four representative smallholder farms. At each farm we used a split-plot factorial design with main plots surrounded or not by Napier grass, and subplots consisting of sole maize, maize-bean or maize-*Desmodium*. We assessed stemborer infestation level and maize grain and stover yields during two years, as well as natural enemies abundance and egg predation at two maize development stages in the second year. In the simple landscape, which was dominated by maize, all treatments had high stemborer infestation levels, irrespective of within-field crop diversity; the presence of Napier grass was associated with higher predator abundance, while egg predation rates were the highest in the maize-bean intercrop. In the intermediate complexity landscape, subplots with sole maize had higher stemborer infestation levels compared to maize-bean or maize-*Desmodium*. In the complex landscape, infestation levels were low in all treatments. However, none of these effects led to significant differences in maize grain and stover yields among treatments in any of the landscapes. The benefits of the push-pull system accrued from the companion crops (bean, *Desmodium* and Napier), rather than from stemborer suppression *per se*. Our findings highlight the importance of the surrounding landscape in mediating the performance of the push-pull system, provide new insights on the contribution of the different components of push-pull system and can guide the design of ecologically intensive agroecosystems.

1. Introduction

There is increasing interest in multipurpose cropping systems able to deliver a range of products and services to meet the multiple needs of rural smallholder families and that capitalize on ecological processes rather than external inputs. In large parts of Africa, maize (*Zea mays* L.) is an important staple crop providing food, feed and fuel (Shiferaw et al., 2011). However, maize production can be severely compromised by pests, diseases and parasitic weeds in many parts of the region (Reynolds et al., 2015). Maize stemborers *Busseola fusca* and *Chilo partellus* are considered to be the most damaging insect pests, causing variable but sometimes devastating yield losses. Stemborer infestation is severe in Southern Ethiopia, where maize production is further limited by declining soil fertility (Corral-Nuñez et al., 2014) and unpredictable rainfall (Muluneh et al., 2015). These factors, in combination with decreasing farm size, threaten food security, as well as household incomes (Mellisse et al., 2018). There is a need for affordable strategies that can reduce pest incidence below economic thresholds, while improving soil fertility and fodder production.

Crop diversification strategies may offer scope for enhancing natural suppression of stemborers (Chabi-Olaye et al., 2008). While the use of chemical pesticides is a common control method across the world, it is not effective for stemborer control because of the cryptic behavior of the larvae in the stems. Moreover, chemical insecticides are often too

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expensive for smallholder farmers and often have adverse effects on non-target biota (including natural enemies), the environment and human health (Rusch et al., 2010). Crop diversification strategies may contribute to reducing crop losses by pests by limiting the pests' ability to locate host plants (Poveda et al., 2008), by repelling pests via plant-mediated semiochemicals (Bakthavatsalam, 2016), or by stimulating the abundance and diversity of natural enemies that may provide top-down control of pests (Mailafiya et al., 2011; Pickett et al., 2014). However, the effectiveness of pest suppression potential depends critically on the composition – in terms of species and cultivars – of the cropping system (Zhang et al., 2013), while the crop assemblage should meet the requirements of the household in terms of food, feed and/or cash.

The push-pull system is a crop diversification strategy based on intercropping maize with a legume species such as *Desmodium* spp., whose semiochemicals repel stemborers (´push´ effect), bordered by a trap crop (e.g., *Pennisetum purpureum* or *Brachiaria* spp.), which attracts stemborers (´pull´ effect) (Cook et al., 2007; Khan et al., 2010; Zhang et al., 2013). This system is also associated with enhanced suppression of the parasitic weed *Striga*, enhanced soil fertility through N-fixation by the legume *Desmodium* spp., and increased food and feed production (Cook et al., 2007; Belay and Foster, 2010). Perennial fodder crops alter the attractiveness of the crop habitat for potential natural enemies of stem borers in maize fields. For instance, Khan et al (2001) demonstrated that the parasitism of stemborers in push-pull systems is enhanced through attraction of parasitoids to molasses grass. Similarly, Mammo (2012) found that Napier and Sudan grass attractd predators of stemborers, such as ants, earwigs and spiders. The adoption of the push-pull system may be further stimulated by replacing the *Desmodium* spp., which can only be used for feed, by a multipurpose grain legume such as common bean, which is an important source of protein in local diets (Fischler, 2010). Beyond their ability to fix nitrogen, legume crops produce secondary metabolites as defense compounds against herbivores (Wink, 2013). Indeed, traditional maize/bean or maize/cowpea intercropping systems are less prone to stemborer infestations (Chabi-Olaye et al., 2002; Belay and Foster, 2010), and tend to provide higher maize yield than sole maize (Songa et al., 2007; Seran and Brintha, 2010). However, the push-pull system has often been assessed as a package and the contribution of each component is not clear. In addition, the performance of the push-pull system based on *Desmodium* spp. and other legume crops in different landscape contexts is not well known.

Despite the considerable research effort on push-pull systems, most studies have focused on assessing the effectiveness of this system at the field scale, often in research stations, without considering the effect of the surrounding landscape (Midega et al., 2014; Eigenbrode et al., 2016). Landscape context can influence the pest and natural enemy interactions by providing resources and shelter (Eigenbrode et al., 2016). For instance, while maize fields function as reproduction habitats for stemborers, perennial crops may support natural enemies in maize-based cropping systems (Kebede et al., 2018). Landscape factors that drive stemborer and natural enemy population dynamics at relatively large spatial scales may interact with within-field crop diversity factors that moderate stemborer repelling and attracting effects at smaller spatial scales. It is yet unclear how such interactions unfold in African smallholder landscape settings. Moreover, the push-pull system based on Napier-*Desmodium* may not fulfil the needs of smallholder farmers without livestock. In these cases, replacing the feed crop *Desmodium* by common bean may be beneficial, and Napier, which is also used for feed, may be less desired by farmers. There is a need to assess the performance of the different crop combinations and system components in the push-pull cropping system to meet the needs of different production situations of smallholders while considering the landscape context (Eigenbrode et al., 2016).

This paper has two objectives. The first objective is to assess the agronomic and pest suppression potential of push-pull systems in landscapes of increasing complexity, from landscapes dominated by maize to landscapes dominated by perennial crops and semi-natural vegetation. For this, we assessed the stemborer infestation levels in maize, the abundance of generalist predators, the associated predation rates, and maize grain and stover yields. Based on previous studies (Cook et al., 2007; Khan et al., 2008b; Pickett et al., 2014), we hypothesized that the push-pull system would suppress stemborers and result in higher maize yield, irrespective of the landscape setting. The second objective is to assess the performance of the alternative push-pull systems by varying or omitting one of the companion crops. We compared the performance of the traditional push-pull system based on Napier-maize-*Desmodium* (*Desmodium uncinatum* jacq) to the performance of Napier-maize-common bean (*Phaseolus vulgaris L.*) and Napier-maize, and also assessed the performance of these three cropping systems without Napier. We expected that replacing *Desmodium* with common bean and omitting the Napier trap crop would result in higher stemborer infestation levels and lower maize yields.

2. Materials and methods

2.1. Study area

The study area is located in the Hawassa region in the Ethiopian Rift Valley between 7°03′11″ to 7°08′4″ N latitude and 38°15′17″ to 38°38′47″E longitude (Fig. 1). The area is characterized by moist to sub-humid warm subtropical climate. Annual precipitation ranges from 750 to 1200 mm in a bimodal distribution pattern, expected in March to April and June to August (Dessie and Kleman, 2007). *Busseola fusca* is the major maize stemborer species found in the area. The average land holding per household is below one hectare of arable land (Dessie and Kleman, 2007; Dessie and Kinlund, 2016). We selected representative landscapes in three districts: Hawassa Zuria, Tula and Wondo Genet along a gradient of decreasing annual/perennial crops ratio. We refer to these three landscapes as simple, intermediate and complex landscapes, respectively. Hawassa Zuria is dominated by maize, while Wondo Genet contains a substantial proportion of woody semi-natural habitat and the perennial crops khat (*Catha edulis*) and enset (*Ensete ventricosum*). Tula has an intermediate proportion of maize and semi-natural habitat. Data on landscape composition and configuration were obtained by combining Landsat satellite images and focus group discussions with farmers (Kebede et al., 2018).

2.2. Experimental design and plot management

Prior to the installation of the experimental plots we evaluated the performance of five Napier grass genotypes (4 genotypes of *Pennisetum purpureum*: 16 803, 16 786, 16 837 and 14 984, and one of *Pennisetum riparium*: Sodo 88) obtained from the International Livestock Research Institute (ILRI) in Ethiopia. In the simple landscape we planted three rows of each genotype and replicated the experiment in three sites (Kebede, unpublished data). Based on the performance in terms of stemborer larvae density, leaf eating by stemborer and biomass productivity we selected the genotype 16 803 for the push-pull experiment (Appendix A). In each landscape, experimental fields were established on four farms, for a total of twelve fields. Each field was divided in two blocks separated by 5 m and surrounded by Napier grass or not (Fig. 2). Napier was planted a month prior to maize planting in 2014 at inter and intra-row spacing of 75 cm and 50 cm, respectively, using stem cuttings of *Pennisetum purpureum* (Genotype 16 803). Each block was divided in three plots (10 by 7.5 m) with an inter plot distance of two meters, the maximum distance possible given the small size of farmer's fields in the area. Three cropping systems were randomly assigned to each plot: sole maize, maize-silverleaf *Desmodium uncinatum* and maize-common bean (Fig. 2). The commonly used maize variety in the study area BH540 was planted at inter and intra-row spacing of 75 cm and 30 cm, respectively. We applied 100 kg ha^{-1} diammonium phosphate (DAP) at planting and

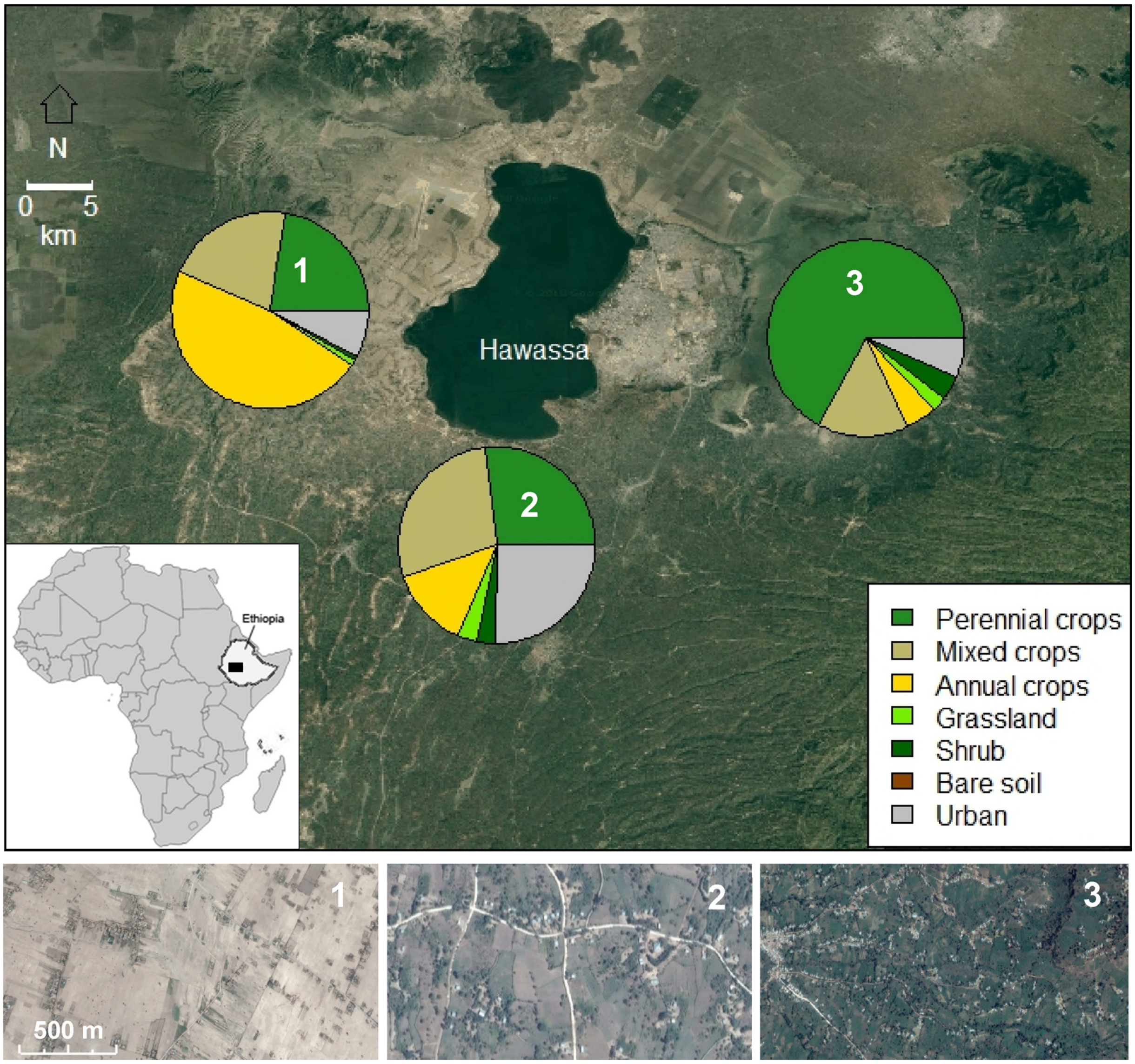

Fig. 1. Location of the study landscapes around Lake Hawassa in the Rift Valley region of Ethiopia: Simple (1), intermediate (2) and complex (3) landscapes. The simple landscape (1) is dominated by maize, the diverse landscape (3) by perennial crops and late successional non-crop vegetation, and (2) the intermediate landscape has a mixed composition of maize, perennial crops and non-crop vegetation.

top-dressed the crop with 100 kg ha^{-1} of urea, following national recommendation rates. In each landscape, the time of planting, weeding and harvest were as per farmers' practice.

2.3. Stemborer infestation and yield assessment

Maize infestation was assessed by randomly selecting twenty plants per plot at grain filling and maturity stages in 2014 and 2015. From each plant we recorded the number of holes in the stem, the stemborer tunnel length in the stem, the number of live and dead larvae, the number of pupae, and the proportion surface damage of the cob(s). Maize grain moisture (%) content was assessed using Dickey John portable grain moisture tester (http://www.dickey-john.com/product/m3g/). Maize grain yield in tonnes of dry matter per hectare (t DM ha-1) was calculated at plot level by multiplying the fresh weight by the DM content and converted into tonnes per hectare. Maize stems and leaves were weighted *in situ*, and a sub-sample was oven dried during 48 h at 70 °C and maize stover yield (t DM ha-1) calculated. The yield of common bean was assessed by destructive harvesting of five sections of one meter of bean plants along the row and assessing the fresh and dry weight of grain and crop residues.

2.4. Generalist predator abundance and egg predation

The abundance of natural enemies of maize stemborers and egg predation were assessed in each of the 72 plots during grain filling and maturity in 2015. The arthropod community was sampled by placing yellow pans and pitfall traps at two locations within each sub-plot (Fig. 2) for three days as described in Kebede et al. (2018). Arthropod samples were sorted and generalist predators were identified at the order, or family level following the identification key of Polaszek et al. (1998) and Bonhof et al. (1997). Specimens belonging to the order Araneida, the families Forficulidae, Staphylinidae and Formicidae, and the genus Cheilomenes were considered as main predators of maize stemborers (Kfir, 1997). Parasitoid abundance was low and was not analyzed. To assess egg predation, we prepared cards with *Ephestia kuehniella* eggs by sprinkling the eggs uniformly on a standardized sticky area of 28.27 mm^2 using a hole punch and removed excess eggs that did not touch the sticky surface. Five egg cards were placed in each subplot in a Z-shape pattern in the plot interior, at least two meters

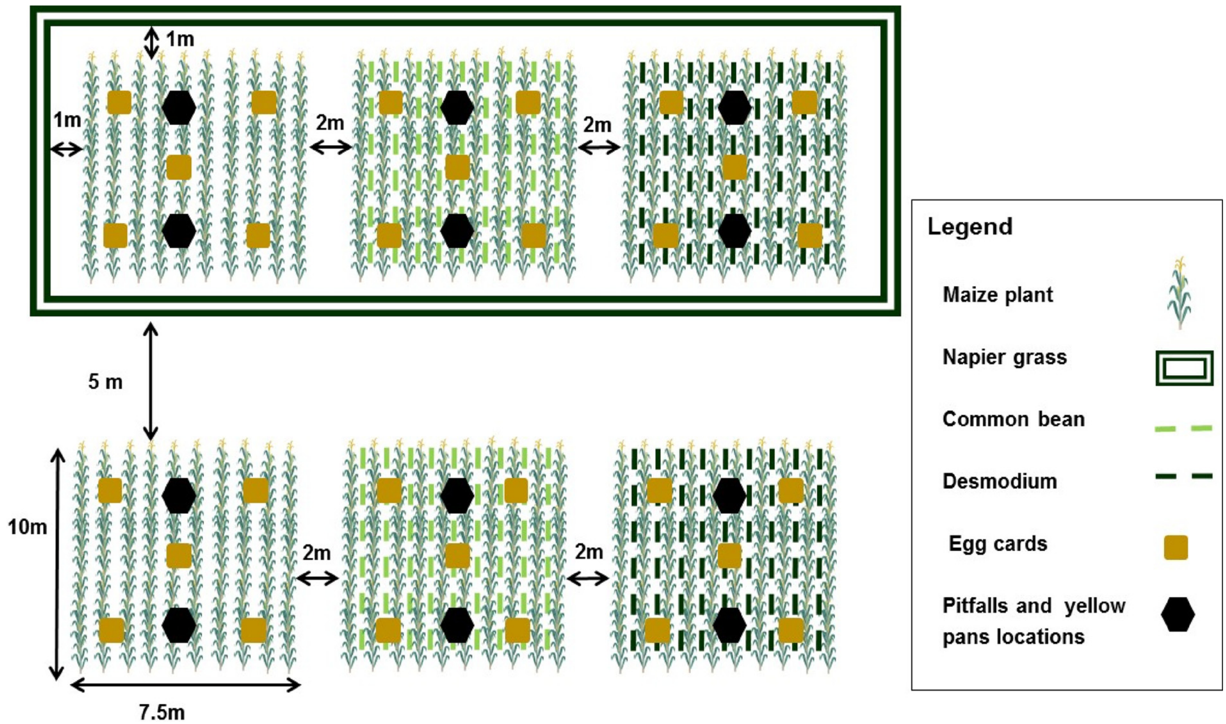

Fig. 2. Experimental design of the study. Four farms were selected in each of the three landscapes. In each farm a randomized block design was established, with two blocks (absence or presence of Napier grass) and three cropping systems randomly assigned within blocks (sole-maize, maize-common bean and maize-Desmodium).

from the plot border (Fig. 2). The egg cards were stapled at the top of maize plants in the leaf sheaths, which is the natural place where female stemborer deposit egg batches, and were left in the field for three days. The fraction of eggs removed by predators was assessed by comparing pictures before and after field exposure using ImageJ software (https://imagej.net/Welcome).

2.5. Data analysis

The number of holes, number of larvae, proportion of cob damage and length of tunnelling were pooled for the twenty plants in each plot. To reduce the number of response variables associated with stemborer infestation we assessed the Pearson correlation between the number of holes, proportion of cob damage, length of tunnelling, and number of larvae. Since the four proxies were significantly correlated ($P < 0.001$; $R = 0.74$ or higher; Appendix B), we selected length of tunnelling for further analysis because this proxy captures information about stemborer infestation and crop damage throughout the growing season. The length of tunnelling was log(x + 1)-transformed and the relationships between this transformed variable and landscape and crop diversity variables were analyzed using a linear mixed model (Eq. (1)):

$$\boldsymbol{Y_{ijk}} = \alpha + \boldsymbol{\beta LN_i} + \boldsymbol{\gamma NP_j} + \boldsymbol{\lambda CR_k} + \tau(\boldsymbol{LN_i} * \boldsymbol{NP_j}) + \delta(\boldsymbol{LN_i} * \boldsymbol{CR_k}) + \mu(\boldsymbol{NP_j} * \boldsymbol{CR_k}) + \rho(\boldsymbol{LN_i} * \boldsymbol{NP_j} * \boldsymbol{CR_k}) \tag{1}$$

where, $\boldsymbol{Y_{ijk}}$ represents the log(x + 1)-transformed length of tunnelling, $\boldsymbol{LN_i}$ is the landscape (simple, intermediate and complex), $\boldsymbol{NP_j}$ is Napier grass (presence or absence), $\boldsymbol{CR_k}$ is the cropping system (sole maize, maize-bean, maize-*Desmodium*) and where α, β, γ, λ, τ, δ, μ, and ρ represent regression coefficients for the main and interaction effects. “Farm” was nested in “landscape” and both “farm” and “year” were considered random effects. The same model structure and analysis was applied for the response variables maize grain and stover yields.

The response variables “generalist predator abundance” and “egg predation” (fraction of the *Ephestia* eggs removed) were count and binomially distributed data respectively, and were analyzed using generalized linear mixed models. For “generalist predator abundance” we tested a Poisson and negative binomial error distribution with “farm” as random factor and selected the negative binomial error distribution because this model had the lowest Akaike Information Criterion (AICc) value. For “egg predation”, we used a logit link function. We used a similar model structure as presented in Eq. 1, but since these data were collected over a single year (2015) at two maize development stages (grain filling and physiological maturity of the maize), we adjusted Eq. 1 by removing “year” and adding “maize development stage” as a fixed factor. All analyses were conducted in R (R Core Team, 2012) and we used the chart.Correlation function from PerformanceAnalytics package for constructing correlation plots (Peterson and Carl, 2018), the lmerTest package for linear mixed models (Kuznetsova et al., 2017), and the GLMER function in the lme4-package for generalized linear mixed models (Bates et al., 2014)

3. Results

3.1. Stemborer infestation

The length of stemborer tunnelling in maize stems was significantly influenced by the landscape context ($P < 0.01$; Table 1; Fig. 3) with the highest length of tunnelling in the simple landscape. However, there were also significant landscape by cropping system interactions in the intermediate landscape where the length of tunnelling was higher in sole maize ($P < 0.05$) compared to maize-bean or maize-*Desmodium* cropping systems. These interactions indicate that the stemborer suppression potential of push-pull systems may differ in different landscape settings.

3.2. Generalist predator abundance and egg predation

The interaction between landscape and the presence of Napier grass had a significant effect on the abundance of generalist predators, with the highest abundance in the simple landscape when Napier grass was present ($P < 0.01$; Table 2; Fig. 4A). In general, sole maize supported a low abundance of predators ($P < 0.05$), however, the interaction

Table 1
Determinants of log(x + 1)-transformed length of tunnelling in maize plants using a linear mixed model. Landscape complexity (simple, intermediate, complex), napier (presence or absence), cropping system (sole maize, maize-bean and maize-*Desmodium*) were fixed variables while farm was nested in landscape and year was taken as a random variable. The diverse landscape, the maize-*Desmodium* cropping system, and the presence of Napier, were reference variables. Significant effects ($P < 0.05$) are shown in bold.

	Estimate	Std. Error	*P*-value
Intermediate	0.562	0.403	0.188
Simple	1.647	0.402	**0.001**
Napier absence	−0.030	0.099	0.760
Sole maize	−0.166	0.140	0.238
Maize-bean	0.181	0.142	0.206
Intermediate *Napier absence	0.119	0.143	0.406
Simple *Napier absence	−0.013	0.141	0.928
Intermediate *Sole maize	0.512	0.200	**0.012**
Simple *Sole maize	0.158	0.197	0.425
Intermediate *Maize-bean	−0.475	0.202	**0.020**
Simple *Maize-bean	−0.195	0.199	0.329
Napier absence * Sole maize	−0.081	0.140	0.561
Napier absence * Maize bean	0.140	0.142	0.326
Intermediate *Napier absence *Sole maize	0.008	0.200	0.967
Simple *Napier absence * Sole maize	0.029	0.197	0.885
Intermediate *Napier absence * Maize-bean	−0.121	0.202	0.552
Simple * Napier absence * Maize-bean	−0.141	0.199	0.482

between cropping system and landscape had a significant effect on predator abundance, with higher predator abundance in sole maize plots located in the landscape of intermediate complexity. The generalist predator community was dominated by ants (Formicidae), followed by spiders (Araneae). The abundance of ants was high in the three landscapes, but relatively higher in the maize-*Desmodium* cropping system with Napier in the complex landscape (Fig. 5). However, the observed differences in predator abundance did not affect egg predation rates. In fact, egg predation was mostly affected by maize development stage with higher predation at maturity ($P < 0.01$; Fig. 4B) and was lower in maize-bean cropping system ($P < 0.05$, Table 2). In the landscape of intermediate complexity egg predation rates were highest in the maize-*Desmodium* cropping system (Fig. 4B), but differences were not significant.

3.3. Crop productivity

Maize yield was not significantly influenced by landscape, presence or absence of Napier grass and intercropping (Appendix C.1). Common bean grain yield in the maize-bean cropping system was 0.64 ± 0.10, 1.03 ± 0.10 and 1.15 ± 0.18 t DM ha^{-1} in the simple, intermediate and complex landscape, respectively (Appendix C.2); with significantly higher yield in the complex and intermediate landscape compared to the simple landscape (Appendix C.3). In the maize-bean-Napier cropping system, bean grain yield was 0.76 ± 0.09, 1 ± 0.18 and 1.4 ± 0.17 in the simple, intermediate and complex landscape, respectively (Appendix C.2), with significantly higher bean yield in the complex landscape compared to the intermediate landscape (Appendix C.3).

4. Discussion

While the push–pull system is relatively well studied and promoted in East Africa as a practice that can suppress stemborer and Striga infestations (Khan et al., 2008a), improve soil fertility (Khan et al., 2011) and generate higher economic returns than sole maize (Kipkoech et al., 2006; Khan et al., 2008b), this is the first study – to the best of our knowledge – that examines the performance of the push-pull system in farmers' field conditions along a gradient of landscape complexity. In addition, we assessed the effects of the "push" (*Desmodium*/bean) and "pull" (Napier) effects separately to explore opportunities to adjust the system to farmers' realities by changing companion crop species. Trap crops and repellent crops occupy space that many farmers would preferably allocate to food crops. We tested the impact of replacing *Desmodium* by common bean and removing Napier grass on the performance of the push-pull system (stemborer and natural enemy abundances). We observed that stemborer infestation levels were negatively associated with landscape complexity, while crop diversification (including or not a legume intercrop and Napier grass) did not influence stemborer infestation in both the simple and the complex landscapes. Yet, intercropping decreased stemborer infestation in the landscape of intermediate complexity. Generalist predator abundance tended to be lower in sole maize as compared to maize intercropped with legumes, but this was not the case in the landscape of intermediate complexity. Generalist predator abundance was positively associated

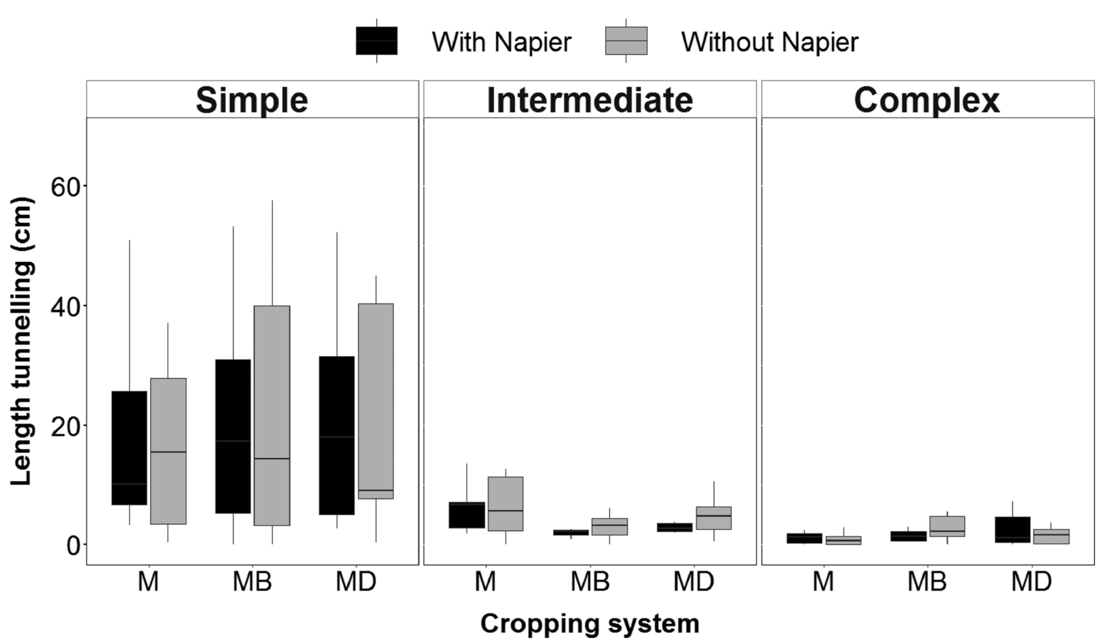

Fig. 3. Boxplots of length tunnelling per cropping system (sole maize (M), maize-common bean (MB), maize-Desmodium (MD)) and per landscape (simple, intermediate and complex) in the absence or presence of Napier grass.

Table 2
Estimates of the model for the abundance of generalist predators with negative binomial distribution and egg predation with logit link function. The variables landscape diversity (diverse, intermediate, simple), napier (presence or absence), cropping system (sole maize, maize-bean and maize-*Desmodium*) and maize development stage (grain filling and maturity) were fixed variables. Farm was taken as a random variable nested in landscape. The diverse landscape, the maize-*Desmodium* cropping system, the presence of Napier, and the maize development stage maturity were reference variables. Significant effects ($P < 0.05$) are shown in bold.

	Generalist predators				Egg predation		
	Estimate	Std. Error	p-value		Estimate	Std. Error	p- value
Intermediate	−0.473	0.257	0.066	.	1.680	5.238	0.7484
Simple	−0.073	0.256	0.775		0.815	0.518	0.1158
Napier absence	0.094	0.071	0.187		0.395	0.340	0.2445
Sole maize	−0.255	0.102	**0.013**	*	0.259	0.469	0.5813
Maize-bean	−0.062	0.101	0.541		−1.067	0.499	**0.0325**
Maturity	−0.113	0.085	0.185		1.390	0.428	**0.0012**
Intermediate * Napier absence	−0.175	0.106	0.098	.	−1.959	5.234	0.7082
Simple * Napier absence	−0.304	0.102	**0.003**	**	−0.739	0.476	0.1201
Intermediate * Sole maize	0.337	0.148	**0.023**	*	−1.219	5.254	0.8165
Simple * Sole maize	0.161	0.145	0.268		−0.318	0.662	0.6311
Intermediate * Maize-bean	−0.106	0.149	0.477		−2.079	5.262	0.6929
Simple * Maize-bean	−0.075	0.145	0.605		0.900	0.679	0.1849
Napier absence * Sole maize	−0.129	0.103	0.209		0.126	0.470	0.7884
Napier absence * Maize bean	0.037	0.102	0.715		−0.368	0.493	0.4552
Intermediate * Napier absence * Sole maize	0.148	0.148	0.317		0.894	5.254	0.8649
Simple * Napier absence * Sole maize	0.025	0.146	0.863		−0.408	0.663	0.5386
Intermediate * Napier absence * Maize-bean	−0.072	0.150	0.633		1.312	5.262	0.8031
Simple * Napier absence * Maize-bean	−0.100	0.145	0.493		0.641	0.678	0.3441

with the presence of Napier grass in the simple, maize-dominated, landscape. Although the impact of stemborer infestation on maize yield was not significant, the yield of bean, *Desmodium* and Napier grass in the push pull plots represented net gains in terms of food and feed production. These findings provide new insights on the performance of the different components of push-pull in different landscape contexts and can guide the design of ecologically intensive agroecosystems. Underlying mechanisms are explored below.

4.1. Stemborer infestation decreases with increasing landscape complexity

Stemborer infestation rates were higher in the simple, maize-dominated, landscape of Hawassa Zuria than in the intermediate and complex landscapes (Figs. 1 and 3). Midega et al (2014) reported that increased grassland ratios within a radius of 400 m around push-pull and sole maize fields led to lower stemborer infestation and higher maize yields. Since grasslands are potential host habitat of stemborers, they may attract stemborers that would otherwise infest maize plant, and thus may reduce infestation in maize crops. However, maize remains the favourite host plant for stemborers and the positive association between proportion of maize in the landscape and stemborer infestation is demonstrated in this study.

4.2. Push-pull is only effective in landscapes of intermediate complexity

The ‘intermediate complexity landscape hypothesis’ postulated by (Tscharntke et al., 2005) predicts that biodiversity-based management actions are more effective in landscapes of intermediate complexity than in simple or complex ones. In simple landscapes, there is too little habitat to support effective natural enemy densities, such that management actions are not effective because of the lack of colonization of natural enemies from the surrounding landscapes. In complex landscapes, the densities of natural enemies may already be high, such that further improvement by habitat management does not lead to further improvement in natural pest regulation. In this study, in the simple and complex landscapes, both the trapping and repellent effects exerted by Napier grass and legume intercrops were not effective. In the simple landscape with a high stemborer abundance, female stemborers were easily able to locate maize plants for egg deposition, independent of the presence of legumes or Napier grass nearby. In contrast, in the complex landscape with few stemborer host plants, stemborer populations and the associated egg deposition were likely to be low, masking potential effects of crop diversification strategies. These findings suggest that further research and implementation of push-pull system should consider the composition of the surrounding landscape for an effective control of stemborer.

4.3. Effect of companion crops on the abundance of generalist predators

The presence of Napier grass increased the abundance of generalist predators (mostly ants) in the simple, maize-dominated landscape. The presence of Napier in the landscape of intermediate complexity tended to increase the abundance of generalist predators ($P = 0.098$). Given the limited amount of semi-natural habitats in the simple landscape, Napier grass could be acting as a physical trap providing shelter for natural enemies (Shelton and Badenes-Perez, 2006). Generalist predators were less abundant in sole-maize crops. These findings are corroborated by previous studies, which showed higher abundance of generalist predators in a push-pull system compared to sole maize (Midega et al., 2004). Such higher abundance of predators is believed to be a result of the presence of associated crops (Midega and Kahn, 2003) and hamper host finding in the system (Eigenbrode et al., 2016), and not only a response to high stemborer abundance.

Egg predation rate was influenced by the development stage of maize. Females of *B. fusca* lay eggs in the leaf sheaths where they are less vulnerable to predation. In the study area, two to three generations per cropping season can occur (Azerefegne and Gebre-Amlak, 1994). The position at which the eggs are found correlates with the developmental stage of the plant (Van Rensburg et al., 1987). With increasing plant age, leaf sheaths fit more loosely around stems making egg batches more visible and accessible to predators, which can explain the higher egg predation rate at maturity compared to grain filling maize development stage (Fig. 4B).

Moreover, in the intermediate complexity landscape the presence of *Desmodium* increased egg predation rates slightly as compared to sole-maize or maize-bean cropping systems (Fig. 4B). Common bean is harvested about three months after simultaneous planting with maize, leaving the ground bare in between maize rows, while *Desmodium* is a perennial plant that covers the maize inter-row throughout the season. Thus, at maize maturity, maize-*Desmodium* cropping systems present a

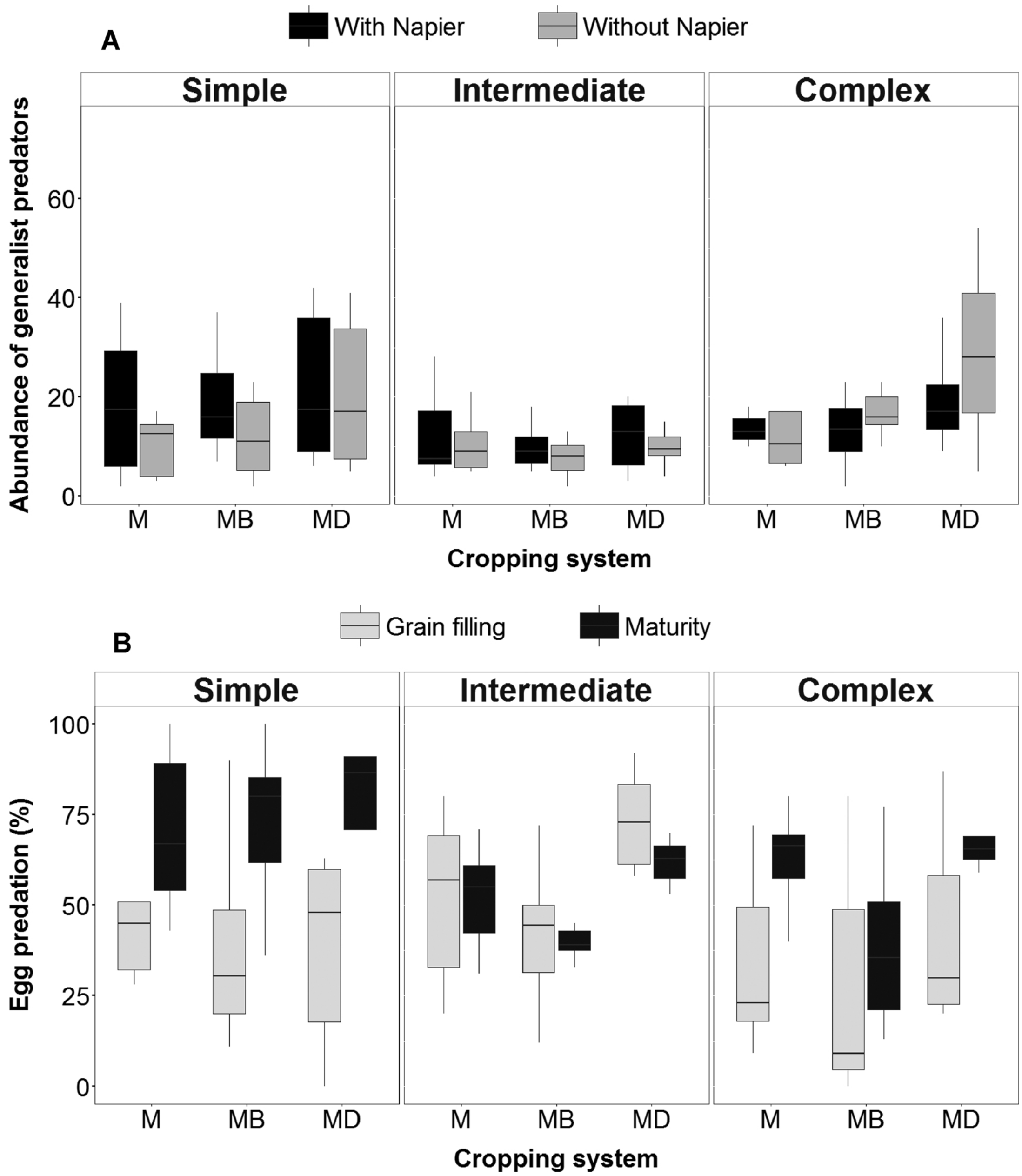

Fig. 4. Boxplots of total predator abundance in the absence or presence of Napier grass (A) and egg predation at two maize stages, grain filling and maturity (B), per cropping system (sole maize (M), maize-bean (MB), maize-*Desmodium* (MD)) and per landscape (simple, intermediate and diverse).

comparative advantage for generalist predators, due to the stable and undisturbed shelter that *Desmodium* plants offers. In the simple landscape, sole Napier (i.e., trap crop only) was effective in reducing stemborer infestation, corroborating the findings by Van den Berg and Van Hamburg (2015) who demonstrated that Napier planted along two contours of maize fields (in order not to hamper mechanical operations in maize fields) was effective in the control of stemborers. These findings show the specific effect and contribution of the companion crops in the push-pull system in terms of supporting predator abundance and egg predation in contrasting landscapes, and demonstrate the merit of further context-specific optimisation of the design of push-pull systems.

4.4. Push-pull had no effect on maize yield, but generated other benefits

Maize grain and stover yields were not significantly influenced by stemborer infestation. This result contrasts with previous research in Ethiopia which reported average yield losses due to *B. fusca* between 12%–40% of the total production depending on agro-climatic zone, maize variety, cropping system, and soil fertility level (Kfir et al., 2002, Mgoo et al., 2006). The limited impact of stemborer on maize yield in our study can be explained in two ways. First, in our experiment, all plots received the recommended fertilisation for the region (100 kg ha^{-1} of urea and 100 kg kg^{-1} of DAP), which is higher than typically applied by smallholder farmers. The higher maize vigour may have allowed maize plants to compensate for crop injury caused by stemborers. Second, 2014 and 2015 were low infestation years with mean stemborer densities of less than 0.6 larvae per plant (Kebede et al. in prep). The low infestation level has most likely obscured the negative association between stemborer infestation level and yield.

The adoption of the push-pull system by farmers has been limited in Kenya (Fischler, 2010), possibly due to farmers´ reluctance to replace food crops, such as common bean, by a fodder crop, and the reluctance to reduce maize production area in favour of a companion trap crops. Our study shows that push-pull systems did not reduce maize grain

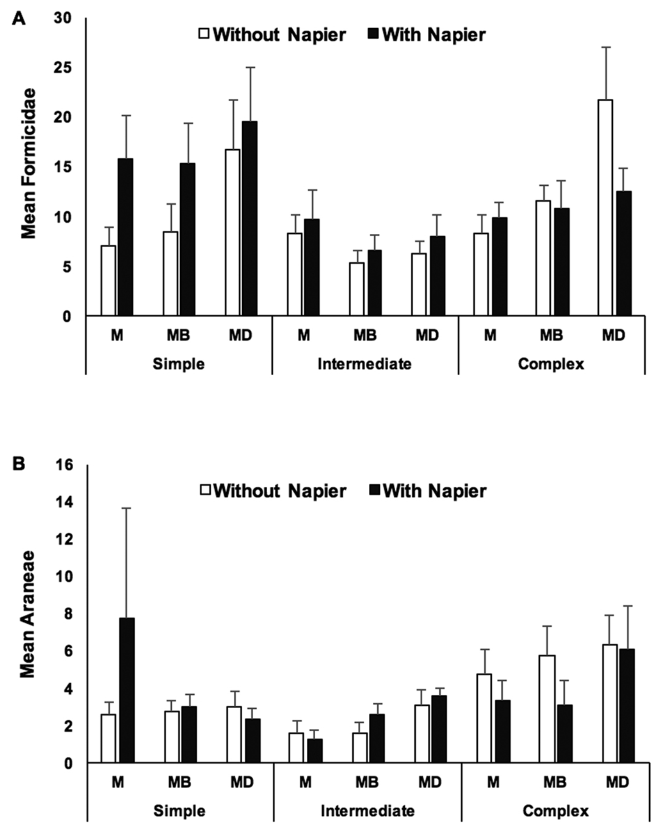

Fig. 5. Mean abundance of ants (A) and spiders (B) per cropping system (sole maize (MB), maize-bean (MB) and maize-*Desmodium* (MD)) with (black bars) or without (white bars) Napier grass along a gradient of decreasing annual/perennial crop ratio represented by the simple, intermediate and complex landscapes. Error bars indicate standard error of the mean.

yield, but rather increased the overall productivity of the system over two years (Appendix C). In the simple landscape, common bean was associated with a similar or higher generalist predator abundances and egg predation rates than *Desmodium*. However, in contrast to common bean, *Desmodium* produces highly effective inhibitory compounds against Striga (Hassanali et al., 2008). Therefore, a push-pull system with *Desmodium* may be advantageous in areas with Striga infestations, which was not the case of the study area.

Farming systems in Ethiopia and most of Africa are small-scale integrated crop-livestock systems. However, feed production in these systems is often not sufficient to feed the animals throughout the year and the nutritional quality of the feed is often less than optimal (Tripathi et al., 2006). Napier grass can be very productive with 35–40 t DM ha^{-1} per year when nitrogen is not a limiting factor (Oliveira et al., 2014). Integrating Napier grass and *Desmodium* in farming systems can increase feed supply to support livestock production (Tittonell et al., 2009). This is even more pertinent for our study area where farm sizes are small (less than 1 ha) and communal grasslands waning (Kebede et al., 2018). Push-pull systems may not only impact stemborers, but also other lepidopteran pests of maize and other cereals (Hassanali et al., 2008). This is particularly relevant for the control of the invasive fall army worm *Spodoptera frugiperda*, which recently invaded Africa and poses a major threat to food security and livelihoods in large parts of the continent (Day et al., 2017). Our study suggests that Napier grass can potentially stimulate generalist predators, such as ants, but that this effect depends on landscape context. Since ants can be predators of fall army worms in Latin America (Perfecto and Sediles, 1992), diversified maize cropping systems which support ants may be less prone to fall army worm infestations.

4.5. Limitation of the study

While experiments under farmers' fields aim at reflecting reality, the 5 m distance between the two Napier grass sub-treatments in our study (i.e., with or without Napier grass) may have been a limitation of the experimental design, since semiochemical interferences are plausible in the field within such short distances (Eigenbrode et al., 2016). However, since farmer's fields were often smaller than 1 ha, between block distances of more than 5 m were unacceptable for farmers as this would compromise food production and household income. Napier grass showed different levels of growth between the three landscapes due to differences in soil fertility and rainfall distribution. While in the diverse and intermediate landscape Napier grass reached up to 3 m or higher acting as a physical barrier to flying pests, it seldom exceeded 2 m in the simple landscape. In general, farmers were hesitant to provide land for the experiment. Farmers perceived the establishment of Napier grass in the middle of the field as a constraint due to the reduction of the area for their food crops and because Napier grass develops a dense and deep root system that can make ploughing more difficult (Van den Berg and Van Hamburg, 2015).

5. Conclusion

Our study demonstrates the importance of the landscape context on the effectiveness of the push-pull system. Push-pull did not have an effect at decreasing stemborer infestation levels in simple or complex landscapes. However, push-pull contributed to decrease stemborer infestation in the landscape of intermediate complexity where neither host plants nor perennial plants providing habitat to natural enemies were predominant. In addition, we demonstrated that common bean was as efficient as *Desmodium* in repelling stemborer and may replace it in areas where *Striga* infestations is not a constraint. Common bean also offered additional benefits in the simple landscape, by increasing the abundance of general predators and egg predation rate (regardless of the presence or absence of Napier) compared with sole maize or maize intercropped with *Desmodium*. To the best of our knowledge, this is the first study demonstrating that landscape complexity can have an overriding effect on the different semiochemically-mediated components of the push-pull system, which has been so far mainly tested at plot level and as a package.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi: https://doi.org/10.1016/j.agee.2018.09.012.

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