PROSPECTS FOR TROPICAL FOREST BIODIVERSITY IN THE LANDSCAPES OF SOUTHWESTERN ETHIOPIA

conservation in a context of land use change and human population growth

LEUPHANA
UNIVERSITÄT LÜNEBURG

Doctoral thesis by Patrícia Rodrigues

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Para a Carolina
Anda cookie, anda com a mommy.
Vamos conhecer a floresta. É preciosa.

Para a avó Alda

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Preface

This cumulative dissertation is submitted for the degree of Doc. rer. nat. at Leuphana University. It consists of seven chapters based on empirical research in the southwest of Ethiopia, conducted between 2015 and 2020. The research described herein was part of an interdisciplinary and collaborative research project SESyP - *Identifying Social-Ecological System Properties Benefiting Biodiversity and Food Security,* funded by the European Research Council (FP7-IDEAS-ERC, ID 614278). Together, the empirical studies presented in this dissertation contribute to the understanding of the biodiversity patterns in the southwest of Ethiopia and were designed with a context of land use change and human population growth in mind. Three chapters (II, IIIa-b and IV) are published, one is in revision (V) and two are submitted (VI, VII). The content of each chapter or appendix is the same as the published journal article. A reference to the journal in which each chapter is published, submitted or in revision, as well as its status and contributing co-authors is presented at the title page of each chapter. A list of references is provided at the end of each chapter. Some chapters are followed by supporting information. Stylistic differences (e.g. British or American English and formatting of references) are possible between chapters. In Chapter I, the synthesis, I alternate between the pronouns “I” and “we”, to acknowledge the collaborative nature of the research. Due to the stand-alone nature of the chapters, some repetition in the text of this dissertation was unavoidable. Data collection for this dissertation was made after all the relevant working permits (from *kebele*, *woreda* and *zone* levels, and from the Ethiopian Wildlife Conservation Authority) had been obtained and after approval by the Ethics Committee of Leuphana University.

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Abstract

Tropical forests worldwide support high biodiversity and contribute to the sustenance of local people's livelihoods. However, the conservation and sustainability of these forests are threatened by land-use changes and a rapidly increasing human population. In this dissertation, I focused on the effects of land-use change on forest biodiversity in the rural landscapes of southwestern Ethiopia, against a backdrop of human population growth. These landscapes are being progressively degraded, encroached and fragmented as a result of different pressures, including the intensification of coffee production, farmland expansion, urbanization and a growing rural population. Understanding the drivers of biodiversity loss and the responses of biodiversity to such pressures is fundamental to direct conservation efforts in these tropical forests.

This dissertation aimed to characterize biodiversity patterns in the moist Afromontane forests of southwestern Ethiopia and to examine how biodiversity patterns are affected by land-use and land-use changes (mediated by coffee management intensity, landscape attributes and housing development) in a context of a rapidly growing rural population. To achieve this goal, I take an interdisciplinary approach where, first, I examined the effects of coffee management intensity on diversity patterns of woody plants and birds, spanning a gradient of site-level disturbance from nearly undisturbed forest interior to highly managed shade coffee forests. Results showed that specialized species of woody plants (forest specialists) and birds (forest specialists, insectivores and frugivores) were affected by coffee management intensity. The richness of forest specialist trees and the richness and/or abundance of insectivores, frugivores and forest specialist birds decrease with increasing levels of disturbance. Second, I investigated the effects of landscape context on woody plants, birds and mammals. Community composition and specialist species of woody plants and birds were sensitive to landscape context, where woody plants responded positively to gradients of edge-interior and birds to gradients of edge-interior and forest cover. Further results showed that a diverse mammal community, with 26 species, occurs at the forest edge of shade coffee forests and that the leopard, an apex predator in the region depended on large areas of natural forest. A closer examination of leopard activity patterns revealed a shift in the diel activity as a response to human disturbance inside the forest, further highlighting the importance of natural undisturbed forests for leopards in the region. Together, these findings demonstrate the value of low managed shade coffee forests for biodiversity, and importantly, emphasize the irreplaceable value of undisturbed natural forests for biodiversity. Third, I investigated the effects of prospective rural population growth (mediated by housing development) on the forest mammal community. Here, population growth was projected to negatively influence several mammal species, including the leopard. Housing development that encroached the forest entailed worse outcomes for biodiversity than a combination of prioritized development in already developed areas and coffee forest protection. Fourth, to understand the motivations behind high human fertility rates in the region, I examined the determinants of women fertility preferences, including their perceptions

on social and biophysical stressors affecting local livelihoods such as food insecurity and environmental degradation. Fertility preferences were influenced by underlying social norms and mindsets, a perceived utilitarian value of children and male dominance within the household, and were only marginally affected by perceptions of social and biophysical stressors. Results further indicated a mismatch between the global discourse on the population-environment-food nexus and local perceptions of this issue by women. My findings suggest the need for new deliberative and culturally sensitive approaches that engage with pervasive social norms to slow down population growth.

Overall, this dissertation demonstrates the key value of moist Afromontane forests in southwestern Ethiopia for biodiversity conservation. It indicates the need to promote coffee management practices that reduce forest degradation and highlights that high priority should be given to the conservation of undisturbed natural forests. It also suggests the need to integrate conservation goals with housing development in landscape planning. A promising approach to achieve the above conservation priorities would be the creation of a Biosphere Reserve and to promote the ecological connectivity between the larger forest remnants in the region. Finally, this dissertation demonstrates the importance of placed-based holistic approaches in conservation that consider both proximate and distal drivers of forest biodiversity decline.

Chapter I

Chapter I

Prospects for tropical forest biodiversity in the landscapes of southwestern Ethiopia:

conservation in a context of land use change and human population growth

> *The paramount need of post-exuberant humanity is to remain human in the face of dehumanizing pressures. To do this we must learn somehow to base exuberance of spirit upon something more lasting than the expansive living that sustained it in the recent past. But, as if we were driving a car that has become stuck on a muddy road, we feel an urge to bear down harder than ever on the accelerator and to spin our wheels vigorously in an effort to power ourselves out of the quagmire. This reflex will only dig us in deeper. We have arrived at a point in history where counter-intuitive thoughtways are essential.*
>
> William R. Catton, Jr. Overshoot. 1982. p.7

Introduction

Tropical forests worldwide typically support high biodiversity while sustaining local livelihoods. However, their conservation and sustainability are threatened by increasing rates of environmental degradation and human population growth. Understanding the drivers of biodiversity loss and the responses of biodiversity to such drivers is fundamental to direct conservation efforts in tropical forests. My PhD dissertation takes an interdisciplinary approach to examine the prospects for tropical forest biodiversity using a case study in the highlands of southwestern Ethiopia. The southwest of Ethiopia hosts the last remnants of moist tropical forests in the country and retains the world's last and unique wild *Arabica* coffee populations. These forest remnants are embedded in mosaics of smallholder-dominated rural landscapes and support both high biodiversity and local livelihoods. I start this introduction by scoping the human impacts on the biodiversity of terrestrial ecosystems. Next, I briefly review land-use and land-use changes as a proximate driver of biodiversity decline, followed by the examination of human population growth as a distal driver of environmental change. Then, I summarize the major challenges posed by both drivers for tropical forest ecosystems and narrow down the context to southwestern Ethiopia. Altogether, these sections provide a brief background to support the motivation for the research and the discussion of the findings.

Human impacts on terrestrial ecosystems

Humans have radically changed more than 75% of all terrestrial ecosystems (Ellis & Ramankutty, 2008). Indeed, our trajectory as a global civilization is engraved with landmarks of our impact on the planet. From the great megafauna extinction in the late Pleistocene (Broughton & Weitzel, 2018), to the transition from hunting-gathering to agriculture and herding some 10 000 years ago, humans have been changing the Earth's ecosystems, mostly through hunting, agriculture and the use of fire (Ehrlich et al., 1997; Pereira et al., 2012). However, back then human activities were localized and population density was relatively low (Malhi et al., 2016; Boivin et al., 2016). It was not until the onset of industrialization in the 18th century and the progress brought by technological development, that the impact of humans on ecosystems started to escalate. Since the Industrial Revolution, human population has grown seven fold and the global economy has grown 30 fold (WWF, 2018), inducing deep changes in the natural environment. The fast-pace of these changes has motivated the designation of a new geological epoch, the Anthropocene (Crutzen, 2002; Corlett, 2015). In the Anthropocene, human activities dominate the Earth and are exceeding planetary boundaries (Rockström et al., 2009), dramatically changing the climate, interfering in biogeochemical cycles and geomorphic processes and inducing large-scale environmental degradation (Vitousek et al., 1997; Syvitski & Kettner, 2011).

A notable consequence of this human-induced environmental degradation is the global loss of biodiversity and widespread defaunation (Dirzo et al., 2014; Young et al., 2016). Biodiversity, in a broad sense, encompasses the complexity of interactions between genotypes, species, communities, ecosystems and biomes (Leadley et al., 2010). The sustained decline of biodiversity over the last century and the current rates of species extinctions suggests that a six mass extinction might be under way (Barnosky et al., 2011; Ceballos et al., 2015). Despite increasing worldwide conservation efforts, for the most part, global goals to reduce biodiversity loss such as the 2020 Aichi Targets are not being met (Tittensor et al., 2014; Johnson et al., 2017; Díaz et al., 2019). This is particularly worrying not only because of biodiversity's own intrinsic value (Soule, 1985) but also because biodiversity is the foundation of ecosystems that support humankind and is essential for human well-being and for the sustainable development of societies (Naeem et al., 2016). Indeed, biodiversity underpins all the 2017 United Nations Sustainable Development Goals (SDGs) - goals that call for shared action towards *"peace and prosperity for people and the planet, now and into the future"* (https://sustainabledevelopment.un.org/sdgs). The loss of biodiversity affects ecosystem functioning and stability and leads to the loss of ecosystem resilience (i.e. the capacity ecosystems have to absorb and adapt to change) (Angeler et al., 2019), and can compromise the sustainable development of modern human societies. Biodiversity decline can be attributed to both proximate and distal drivers. Proximate drivers impact directly biodiversity and include, in the terrestrial realm, land-use changes, overexploitation of organisms, pollution, invasive alien species and climate change (Sala et al., 2000; Díaz et al., 2019). Underlying the proximate drivers are distal, indirect pressures to biodiversity, prompted by demographic, economic, political, institutional, and technological forces, all underpinned by societal values (Díaz et al., 2019). Thus, considering the importance of biodiversity for human welfare, it has never been so urgent to understand the forces driving biodiversity decline.

Proximate drivers of biodiversity change: a focus on land-use and land-use changes

Land-use change is the predominant proximate driver of biodiversity loss in the terrestrial realm (Pereira et al., 2012; Díaz et al., 2019), and is typically driven by human activities such as agricultural expansion and intensification, wood extraction and urbanization (IPBES, 2019). Notorious effects of these activities include the loss, degradation and fragmentation of natural habitats (Foley, 2005). In general, habitat loss implies the destruction of the existing habitat and the conversion to a new land-use, for instance deforestation through agricultural expansion or urbanization (Laurance et al., 2014a). Habitat degradation refers to a gradual reduction in habitat quality and in the capacity to deliver ecosystem services and can result from intensification of human use (Fischer & Lindenmayer, 2007), whereas habitat fragmentation results in the creation of small and more isolated fragments of natural habitat (Haddad et al., 2015). The effects of habitat loss, degradation and fragmentation on biodiversity have been extensively discussed (Fahrig, 2003; Fischer & Lindenmayer, 2007) and despite some scientific disagreement regarding the effects of fragmentation (Fahrig, 2017; Fletcher et al., 2018; Rybicki et al., 2020) it is generally agreed that these three processes are among the most pressing threats for terrestrial biodiversity.

Biodiversity responses to the effects of land-use change are multifaceted and dependent on mechanisms associated with the type of land-use change, species biological characteristics (e.g. body size, gestation periods and longevity) (Pereira et al., 2004), ecological requirements (e.g. feeding strategy, habitat affinity) (Violle et al., 2007; Vandewalle et al., 2010) and stochasticity (Måren et al., 2018). For instance, while some species (e.g. habitat specialists) may decline or even go extinct with habitat degradation and fragmentation, others may respond positively (such as edge species) (Henle et al., 2004; Rybicki et al., 2020). These differences in species responses to land-use change might also entail cascading effects on the entire biological community (Kurten, 2013; Barnes et al., 2017). The persistence of a species in a changing landscape will depend on the maintenance of habitat features and functional processes that are key for the species survival (Chesson, 2000). Furthermore, species responses to land-use change are also influenced by time lag effects (Jung et al., 2019) and are contingent on the spatial scales being considered (Gardner et al., 2009; Isbell et al., 2017). Current scientific evidence suggests that in the regions worst-affected by land-use change, biodiversity decline can reach 76% of local species richness (Newbold et al., 2015a), with mammals and birds among the taxa most impacted (Monastersky, 2014; Joppa et al., 2016; Tilman et al., 2017; Cooke et al., 2019). Moreover, the loss of biodiversity due to changes in land-use is expected to further increase during this century (Pereira et al., 2010; Powers & Jetz, 2019). Thus, both current and projected biodiversity declines underscore the need to understand how biodiversity responds to land-use change to improve conservation efforts.

Distal drivers of biodiversity change: a focus on human population growth

Human population growth is one of the most pressing distal drivers of change underpinning biodiversity decline and environmental degradation (Díaz et al., 2019). The interactions between human population, land-use changes, and biodiversity decline are complex and direct links remain difficult to establish. This is mainly because of the different dimensions of human population growth (i.e. size, consumption and footprint), mismatches in ecological and demographic data and in spatial and temporal scales and interactions with other drivers (Carr, 2004; Carr et al., 2005). However, despite indirect, different scholars have been cautioning about the effects of unregulated human population growth on life supporting systems. Most notably, the work of Thomas Malthus (1798) established one of the first analytical relationships between human population growth, resource use and food supply. Later, the works of Ehrlich & Holden (1971), Catton (1982), Ehrlich & Ehrlich (1991) and Meadows et al. (2004) have systematically linked human population, economic growth and technological progress to anthropogenic environmental change.

Alarmingly, as of the 1st of January 2020, the world's human population surpassed 7.76 billion, representing an increase by more than two-fold since 1970 (UN, 2019a). Worryingly, a quick reversal of this trend seems very unlikely. United Nations projections estimate that by 2050 human population will growth to 9-12 billion people (UN, 2019a), with most of this growth happening in Africa. Simultaneously, scenarios for biodiversity in a business-as-usual pathway indicate the persistence of biodiversity decline (Pereira et al., 2010; Newbold et al., 2015; Powers & Jetz, 2019). Even though human population size continues to increase, the annual world rate of human population growth has been consistently declining for the past 40 years (UN, 2019a). However, while most developed nations have total fertility rates (i.e. the average number of children per women) close or below the replacement level of 2.1 (Searchinger et al., 2013), many nations of the global South, the majority located in sub-Saharan Africa (SSA), have high fertility rates (4.77 on average, between 2.4 in South Africa and 7.0 in Niger) (World Bank, 2019). Projections of human population growth for SSA indicate that by the end of the century Africa may increase its population by five to seven fold, reaching six billion people by 2100 (Bradshaw & Minin 2019; UN, 2019a). Reasons for the persistence of high fertility in SSA include, at broad scales, a combination of lower socioeconomic and modernization levels (Bongaarts, 2017a), stalls in education (Kebede et al., 2019) and traditional values that support pronatalist behaviours (Caldwell & Caldwell, 1987), among others. However, local accounts of the relationships between fertility preferences that result in large family sizes and environmental degradation remain an important gap in the literature intersecting demography and the environment. The above described context is reason for concern because many nations of SSA are facing serious environmental problems and strong declines in biodiversity as well as major societal challenges (such as poverty, food insecurity and land scarcity) (Fisher & Christopher, 2007; Hoag & Svenning 2017), all likely to be exacerbated by a burgeoning population (IPBES, 2018). Therefore, it is vital to understand not only the likely impacts of human population growth on biodiversity, but also the motivations behind high fertility preferences in such contexts.

Tropical forest ecosystems: a blend of drivers

Tropical ecosystems worldwide are regions where land-use and demographic changes blend more obviously. Tropical forests in particular have been severely impacted by land-use changes due to the encroachment of human activities (Lewis et al., 2015). This is alarming because tropical forests are hotspots of biodiversity (i.e. areas that overlap high biodiversity with exceptional levels of threats, Myers et al., 2000), and are a vital ecosystem in the planet. They host two-thirds of the Earth's terrestrial biodiversity (Gardner et al., 2009), and provide many key ecosystem services, including carbon storage and sequestration, soil and watershed protection and climate regulation (Brandon, 2014). Tropical forests are also important sources of raw materials such as timber, medicinal plants and bushmeat, all key resources for poor rural communities (Byron & Arnold, 1999).

Deforestation and forest degradation represent the two main human disturbances threatening the ecological integrity of tropical forests (Gibson et al., 2011; Malhi et al., 2014; Barlow et al., 2016). In tropical systems, deforestation is mostly driven by agricultural expansion (including for commodity production such as oil palm in Southeast Asia) (Curtis et al., 2018), mining (Sonter et al., 2017), road expansion (Laurance et al., 2014b; Laurance et al., 2017) and urbanization (Rudel, 2013). In turn, forest degradation typically results from increasing human disturbance by intensification of forest use and management (e.g. production of shade crops such as coffee and cocoa), extraction of forest products (e.g. selective logging), as well as cattle grazing, fire, over-hunting or collection of non-timber forest products (Laurance et al., 2014a, Lewis et al., 2015; Watson et al., 2018). The effects of forest degradation vary with scale (Ghazoul et al., 2015). At the forest site level, human disturbance via, for instance, logging or selective removal of plant species can lead to the simplification of the forest structure (Phillips, 1997). This simplification is likely to entail the biotic homogenization (including taxonomic, functional and phylogenetic dimensions) (Olden & Rooney, 2006; Dornelas et al., 2014; Newbold et al., 2018) and reduction of ecological functions (Ghazoul & Chazdon, 2017; Mitchell et al. 2015), in which disturbance adapted species become prevalent and forest specialists decline (Laurance et al., 2006; Alroy, 2017). Changes in the structure and composition of plant assemblages as a result of forest degradation (Ghazoul & Chazdon, 2017) are also expected to have cascading effects for different forest animal groups (Alroy, 2017). The situation is particularly troublesome for bird species that are forest specialists (such as many insectivore and frugivorous species) that have high forest specificity and lower mobility (Sekercioglu et al., 2002; Beier et al., 2002).

At the landscape level, landscape attributes (such as the amount of remaining forest) and edge effects (i.e. biotic and abiotic processes that cause changes in composition, structure or function near the edge, between forest and non-forest habitat, Harper et al., 2005) can also have a profound influence on the local patterns of biodiversity and on the ability of species to persist in a landscape (Gascon et al., 2000; Solar et al., 2016; Pfeifer et al., 2017). For instance, Pfeifer and colleagues (2017) found that species from four vertebrate groups highly dependent on the forest interior (and highly sensitive to edges) were 3.7 times more likely to be listed as threatened on the IUCN Red List compared with species with some level of forest edge tolerance. Importantly, site- and landscape-level effects are expected to co-vary, yet their separate effects on biodiversity remain poorly understood (Harper et al., 2005).

Despite being strongholds of biodiversity, only 26% of global tropical forests are under some form of protection (Morales-Hidalgo et al., 2015) and much of the remaining tropical forest areas are embedded in mosaics of smallholder-dominated rural landscapes (Koh & Gardner, 2010). Recent estimates of the world's extant tropical forests suggest that only 24% are still intact, 46% are fragmented and 30% are in a degraded state (Lewis et al., 2015). In the particular case of SSA, studies assessing changes in tropical forest cover show that the central African forests have remained relatively stable. Yet, major forest declines have been occurring in the Western and Eastern parts of the continent (~83.3 and 93.0%, respectively, Brandt et al. 2017), and in areas overlapping with current and projected high human population growth (Brandt et al., 2017; Aleman et al., 2018). Population projections indicate that most of this growth will be accommodated in urban settings (UN, 2019a), but a large portion will also happen in rural areas of smallholder-dominated landscapes (UN, 2019b). However, it is still unclear how accommodating an increasing human population will unfold for biodiversity in these landscapes. A recent review by Mehring and colleagues (2019) showed a detrimental impact of demographic changes on biodiversity (although contingent on the setting, scale and ecological and demographic metrics considered). Further, at regional scales, an increasing human population density has been demonstrated to have a negative effect in species occurrence and abundance (Newbold et al., 2015). As the influence of human settlements expands and as human disturbance encroaches the natural habitat of many species (Estes et al., 2012), only those that can tolerate some levels of disturbance might persist (Newbold et al., 2014). Considering all of the above, it is of vital importance to improve the understanding of the simultaneous influence of proximate and distal drivers of change, to advance the conservation of tropical forest biodiversity. To do this, there is the need to jointly examine the impacts on biodiversity of different mediators of land-use change and human population growth, as well as to understand the motivations underpinning fertility preferences.

A closer look at the tropical forests on the rural landscapes of southwestern Ethiopia

Situated in the Horn of Africa, Ethiopia is an example of a country that closely intersects high biodiversity, rapid human population growth and accelerated environmental degradation due to land-use change. The highlands of the southwest in particular, are extremely diverse, belonging to a hotspot of biodiversity, the Afromontane Biodiversity Hotspot (Mittermeier et al., 2004). This region holds the last remnants of nearly undisturbed moist evergreen Afromontane forest of the country and of the Horn of Africa (Friis et al., 1982). The landscapes of the southwest (Figure 1.1) are home to a diverse community of plants (Senbeta et al., 2014), birds (Gove et al., 2013; Buechley et al., 2015) and mammals (Mertens et al., 2018), with several endemic species, including the *Arabica* coffee shrub (*Coffee arabica*) (Senbeta et al., 2014), an important global commodity (Petit, 2007).

These landscapes have been gradually evolving as a coupled social-ecological system (Liu et al., 2007), where people and nature have been interacting in strong and complex ways, probably for more time than in any other place (Bonnefille & Hamilton, 1986). The landscapes provide important goods and services that people depend on for their livelihoods (Dorresteijn et al., 2017; Shumi et al., submitted). Livelihoods are based on subsistence crops (such as maize, teff and sorghum) and cash crops (coffee and khat) (Manlosa et al., 2019), and are complemented with livestock breeding and different forest goods, including firewood, timber, spices, medicinal plants and honey (Manlosa et al., 2019). Food security is higher than in other parts of Ethiopia, but low by international standards (WFP, 2020), with many households facing food shortages during the lean season (Manlosa et al., 2019). Further, the majority of the population is poor and land scarcity for farming has become a relevant problem, especially for the younger generation (Bezu & Holden, 2014). Land, including farmland and forest, is own by the government with farmers retaining limited usufruct or customary rights for the use of farmland and of forest, including for coffee production (Stellmacher, 2007; Crewett & Korf, 2008).

The production of coffee has a strong cultural and economic importance, both for the region and for the country. It represented 34% of foreign income from all exports in 2017/18 (GAIN, 2019). Coffee is traditionally grown in the forest, under the shade of native trees, and within a specific elevation belt (1500-2100m) (Senbeta et al., 2014). Farmers apply different levels of management intensity in the shade coffee forests (Aerts et al., 2011). Management intensity varies in the degree of pruning and thinning of the canopy, in the clearing of the understory and in the planting of seedling and saplings to increase the density of coffee shrubs (Aerts et al., 2011). Despite the importance of these forests for coffee production, deforestation has been increasing in the region (Getahun et al., 2013; Ango et al., 2016). Ango and colleagues (2016) show that between 1973 and 2010, around 24% of forest area has been encroached and lost to farmland area, with most of forest loss located above coffee elevation. In addition to deforestation, these forests are also under threat of degradation, mostly from intensification of coffee production and timber extraction (e.g. Hundera et al., 2013; Tadesse et al., 2014a).

The Growth and Development Plan of Ethiopia (ENPC, 2016), currently in the second stage of implementation clearly incentivizes intensification and the transition from subsistence agriculture to more commercially oriented production, including coffee. In this particular context, coffee production can have mixed effects for biodiversity. On the one hand, it can represent an incentive to retain shade forest in the region (Getahun et al., 2013; Hylander et al., 2013; Tadesse et al., 2014b), but on the other hand, the push towards intensification can cause forest degradation with negative consequences for biodiversity. Indeed, when compared to other coffee-growing regions in the world, and despite holding the worlds' genetic reservoir of *Arabica* coffee, the southwest of Ethiopia has received considerably less research attention than for instance regions in Latin America (e.g. Perfecto, 1996; Komar, 2006; Philpott et al., 2008), and an important knowledge gap remains on the effects of coffee management intensification on the regions' forest biodiversity.

Along with deforestation and degradation, the region, like the rest of the country, is also under pressure from a burgeoning human population. Different national assessments, on biodiversity (CBD, 2014), food security (WFP, 2019) and sustainable development (EPA, 2012) recognize the rapid growth in the Ethiopian population as a major threat. Currently a young cohort dominates the population, with

47% of Ethiopians less than 15 years old. In Oromia, the regional state encompassing the southwest, the fertility rate is around 5.4 births per women (CSA, 2016), and the prevalence of child marriage is high (UNICEF, 2016; Wogon et al., 2019). Despite significant improvements in reproductive health in the last decade (Hailemariam, 2016; Assefa et al., 2019), the use of modern contraception is around 28% and the unmet need for family planning is estimated at 29% (CSA, 2016). In addition, about 89% of the population in the southwest resides in a rural setting (OBFED, 2012). Contrary to the global trend of decreasing rural population due to migration to urban centres (World Bank, 2019), a large increase in rural dwellers is projected at least until 2050 (UN, 2019b). This increase will likely be accompanied by a need for housing in the landscape. However, knowledge gaps remain regarding the implications of new housing developments for biodiversity in the region.

In addition to understanding the impacts, albeit indirect, of human population growth on biodiversity, it is also of key importance to understand the mechanisms behind such growth. Existing studies addressing the determinants of fertility preferences in the region focus mainly on demographic factors, education and social norms and religion (e.g. Beekle & McCabe, 2006; Hogan et al., 2008; Tadesse & Headey, 2010; Tilahun et al., 2014). For the most part, these factors are considered in isolation, and to date no study has included the role of perceptions of different social and biophysical stressors affecting livelihoods, on fertility preferences. Given the above context, the southwest of Ethiopia represents a unique opportunity to study the intersection of land-use changes, human population growth and biodiversity.

Figure 1.1: Photographs of the study area representing: (a-c) forests in the landscape, (d) coffee shrubs, (e) farmland mosaic with human settlement and (f) main road on a remote *kebele*.

The majority of fieldwork for this dissertation (with the exception of Chapter V) was carried out in a total of four or five *kebeles* (the smallest administrative unit in Ethiopia), belonging to three *woredas* (Gera, Setema and Gumay) in the Oromia region (Figure 1.2), where the Oromo people are the largest ethnic group and Amhara, Tigre and Kefficho people are minorities. Human population density in the *kebeles* ranged from 66 to 137 people/km^2, and the amount of forest cover varied between 37 and 84% (as of the year 2015). Elevation ranges from approximately 1500 to 3000 m above sea level. The forest complexes of the study area belong to two Forest Priority Areas, the Sigmo-Geba and the Belete-Gera Forest Priority Areas, both designated in the 1980s, but their legal enforcement remains poor.

Plants, birds and mammals as ecological focal taxa

Biodiversity has different dimensions (e.g. taxonomic, functional, genetic and phylogenetic) and can be measured using a wide variety of metrics (Magurran & McGill, 2011). Here, for the most part, I focus on diversity of taxonomic and functional groups. Also, because different taxonomic groups may respond differently to land-use changes, the use of a diverse set of taxa is likely to provide a more thorough picture of the effects of land-use changes on biodiversity. Therefore, in this dissertation, I use plants, birds and mammals as study models of biodiversity in the southwest of Ethiopia. These three taxonomic groups have important roles in the forest ecosystem, and all are facing critical extinction rates (WWF, 2018).

Woody plants are particularly diverse and abundant in the region (Senbeta et al., 2014), providing a diversity of resources such as habitat, food and shelter for birds and mammals. Birds, in turn, are key agents in forest regeneration, as seed dispersers, pollinators and ecosystem engineers (Sekercioglu, 2006; Whelan et al., 2015). In addition, birds are good indicators of the forest condition, since they depend on the different vertical layers of the forest, with species showing contrasting affinities to the canopy, understory or ground vegetation (O'Connell et al., 2000; Alexandrino et al., 2016). Extensive studies from Latin America (reviewed in Komar, 2006 and Philpott et al., 2008) have documented declines in bird diversity, due to intensification of coffee management. However, in the southwest of Ethiopia, less than a handful of studies have addressed the effects of coffee management on the forest bird community (but see Gove et al., 2013; Buechley et al., 2015) and to date, no study has systematically compared the value of undisturbed natural forest and managed coffee forest for this taxonomic group. Like birds, mammals also have important key ecosystem roles (Ceballos & Ehrlich, 2008; Morris, 2010; Davidson et al., 2012).

Mammals are important seed dispersers (Stoner et al., 2007; Brodie et al., 2009), some species have key roles as top predators (Ripple et al. 2014) and exert both top-down and bottom-up forces that structure the trophic community (Estes et al. 2011; Lacher et al., 2019). Some species also have important ecosystem engineering functions (Wilby et al., 2003). In the southwest of Ethiopia, the paucity of studies addressing land-use changes and its effects on biodiversity is even more notorious for mammals. To date, only Mertens and colleagues (2019) have systematically investigated the mammal community in both natural and coffee forests but very little is still known about the mammal community in the region. This is an important knowledge gap, because mammals are sensitive to changes in forest extent and forest quality. Furthermore, mammals strongly interact with people in the landscape causing significant losses to livelihoods due to crop raiding leading to persistent human-wildlife conflicts (Ango et al., 2017; Dorresteijn et al., 2017).

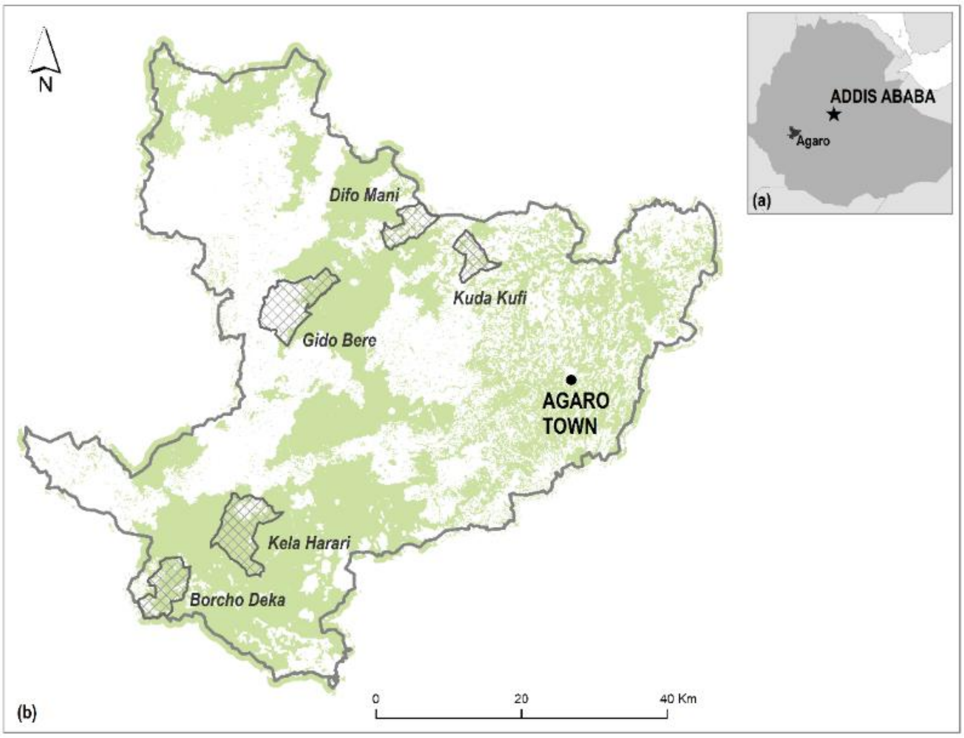


Figure 1.2: Study area location (a) in southwestern Ethiopia and (b) location of the main surveyed kebeles (hatched). Green area corresponds to forest cover, including both within and above coffee elevation areas.

Overarching goal

The overarching goal of this dissertation was to characterize the biodiversity patterns in the moist Afromontane forests of southwestern Ethiopia and to understand how these patterns may be affected by proximate and distal drivers of change. To this end, this thesis examined how biodiversity patterns are affected by land-use and land-use changes (a proximate driver) in the context of human population growth (a distal driver). By doing so, this thesis aimed to advance the understanding of how biodiversity can be best supported and conserved in the region.

This PhD dissertation was part of an interdisciplinary research project - SESyP (*Identifying Social-Ecological System Properties Benefiting Biodiversity and Food Security*) - that aimed to identify synergies between biodiversity conservation and food security. The project used a social-ecological system approach to integrate biodiversity conservation and food security in the southwest of Ethiopia (Manlosa et al., 2020). In social-ecological systems, livelihoods are strongly dependent on the biodiversity and ecosystem services provided by the landscape. In turn, people influence the ecological system through the different uses they make of the landscape (Folke, 2006). Whereas I do not take a social-ecological system approach *per se,* I do use the framework to ground the different empirical studies that constitute this dissertation. Thus, I focused my research on the ecological component of the social-ecological system (Rissman & Gillon, 2017) and on an underlying driver of change (Figure 1.3).

Research questions

To understand how land-use and land-use changes affect biodiversity in the tropical forests of southwestern Ethiopia, I specifically investigated how coffee management intensity, landscape context and future housing development may affect different biodiversity taxa, namely woody plants, birds and mammals. I further consider the context of human population growth by examining women perceptions of environmental change and the influence of perceptions in fertility preferences. Thus, this dissertation was guided by four main research questions (RQ):

- *RQ1: How does coffee management intensity affect biodiversity? (Chapters II, III)*
- *RQ2: How does biodiversity respond to landscape context? (Chapters II - V)*
- *RQ3: How may future housing development scenarios affect the forest mammal community? (Chapter VI)*
- *RQ4: What are the determinants of women fertility preferences in the region (Chapter VII)?*

Answering these questions is central to the understanding of how biodiversity may respond to different drivers of change and to advance the knowledge of the value of tropical forests to foster and support biodiversity conservation.

Brief overview of methods

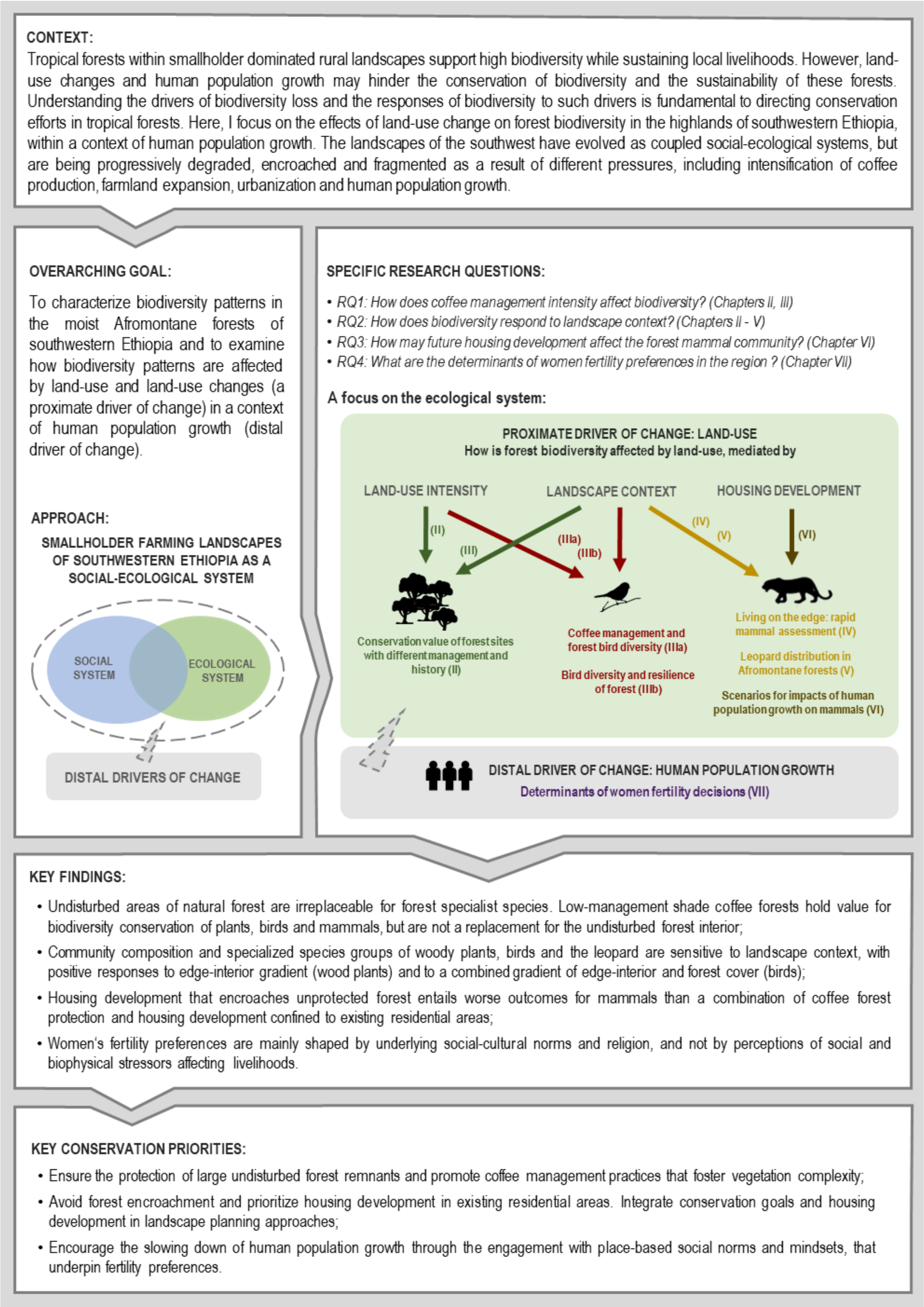
This thesis builds on a combination of a wide array of sampling and analytical methods, used in ecology and in the social sciences. Most of the empirical studies involved a series of spatial analysis using geographic information systems (ArcMap 10.2; ESRI, 2018). These included, for instance, the (i) supervised classification of RapidEye satellite imagery to derive the map of forest cover for the study area, (ii) a cost-distance analysis to guide sampling site selection, (iii) a Tasseled Cap approach to derive tin roofs in the landscape; (iv) digitizing grass roofs on the screen, among others. The surveys of the different taxonomic groups (i.e. woody plants, birds and mammals) were based on standard ecological survey methods, suitable for sampling in tropical forests (Sutherland et al., 2004; Sutherland et al. 2006; Rovero et al., 2016). Woody plants were surveyed using 20x20 m plots with measurement of standard features (such as diameter at breast height). Birds were surveyed using point counts of 15 minutes within 1 ha sites and mammals were surveyed using camera-traps with rotation. Sampling followed random and stratified random designs. A survey tool that included close- and open-ended questions was used to collect data on female fertility preferences.

Data analysis encompassed a range of methods that included: (i) ordination approaches (e.g. nonmetrical multidimensional scaling, principal component analysis, detrended correspondence analysis and constrained correspondence analysis) and (ii) indicator species analysis; both sets of methods used for the analysis of community composition patterns; (iii) generalized linear models and (iv) models that accounted for spatial autocorrelation (i.e. generalized linear mixed models and generalized additive mixed models) used for analysis of species richness and functional group responses; (iv) kernel density functions for examination of activity patterns and (iv) content analysis to resume interview texts. The specifics of the different sampling and analytical methods as well as their references are detailed in the individual chapters.

Thesis outlook

This thesis presents seven chapters grounded on empirical research. The first five empirical studies (Chapters II – VI) aim to understand the impacts of land-use and land-use changes on forest biodiversity, by assessing the effects of coffee management, landscape context and housing development on different taxonomic groups (RQ1-3), namely on woody plants (Chapter II), birds (Chapters IIIa and IIIb) and mammals (Chapters IV – VI). The last empirical study (Chapter VII) addresses the issue of human population growth, an underlying pressure in the study area, by examining the determinants of women fertility preferences in the region, including perceptions on social and biophysical stressors (RQ4). Figure 1.3 provides an overview of the dissertation, including its aims, approach, key findings and key conservation messages. Next, I provide a brief summary of each chapter.

Chapter II investigated the effects of site-level disturbance, landscape context and forest history on the diversity patterns of woody plants. To cover the gradient of disturbance, we stratified the forest in the study area according to accessibility, using a cost distance approach. We surveyed woody plants in randomly selected forest sites within our stratified sampling scheme. We assessed changes in community composition and in richness of different plant groups (forest specialists, generalist and pioneers species) along the gradients of site-level disturbance (mainly coffee management), landscape context (i.e. distance from the forest edge) and forest history (primary *vs.* secondary forests). We used coffee dominance as a proxy for coffee management intensity. Our results showed that woody plant community composition had high species turnover along the main compositional gradient, with different plant groups (i.e. generalists, pioneers and forest specialists) occupying different positions along the gradient, but with substantial overlap. Elevation, current distance to the forest edge, coffee dominance and forest history structured the community composition. Site-level coffee dominance affected negatively the total species richness and the richness of forest specialists, highlighting the negative effects of intensively managed coffee plots for woody plant diversity and composition as opposed to undisturbed forest sites. In addition, we found edge-mediated landscape effects on both community composition and species richness that were unrelated with coffee management. The richness of forest specialists significantly increased while the richness of pioneer species significantly decreased with increasing distance from the forest edge, in both primary and secondary forests. Secondary forests had lower species richness than primary forests. Our results highlight the value of undisturbed natural forests for woody plant diversity and the importance of considering site and landscape levels when devising conservation strategies. These should focus on maintaining areas of undisturbed interior forest to prioritize the protection of forest specialist species and the use of coffee management practices that reduce forest degradation.



CONTEXT:

Tropical forests within smallholder dominated rural landscapes support high biodiversity while sustaining local livelihoods. However, land-use changes and human population growth may hinder the conservation of biodiversity and the sustainability of these forests. Understanding the drivers of biodiversity loss and the responses of biodiversity to such drivers is fundamental to directing conservation efforts in tropical forests. Here, I focus on the effects of land-use change on forest biodiversity in the highlands of southwestern Ethiopia, within a context of human population growth. The landscapes of the southwest have evolved as coupled social-ecological systems, but are being progressively degraded, encroached and fragmented as a result of different pressures, including intensification of coffee production, farmland expansion, urbanization and human population growth.

OVERARCHING GOAL:

To characterize biodiversity patterns in the moist Afromontane forests of southwestern Ethiopia and to examine how biodiversity patterns are affected by land-use and land-use changes (a proximate driver of change) in a context of human population growth (distal driver of change).

APPROACH:

SPECIFIC RESEARCH QUESTIONS:

- *RQ1: How does coffee management intensity affect biodiversity? (Chapters II, III)*
- *RQ2: How does biodiversity respond to landscape context? (Chapters II - V)*
- *RQ3: How may future housing development affect the forest mammal community? (Chapter VI)*
- *RQ4: What are the determinants of women fertility preferences in the region ? (Chapter VII)*

A focus on the ecological system:

KEY FINDINGS:

- Undisturbed areas of natural forest are irreplaceable for forest specialist species. Low-management shade coffee forests hold value for biodiversity conservation of plants, birds and mammals, but are not a replacement for the undisturbed forest interior;
- Community composition and specialized species groups of woody plants, birds and the leopard are sensitive to landscape context, with positive responses to edge-interior gradient (wood plants) and to a combined gradient of edge-interior and forest cover (birds);
- Housing development that encroaches unprotected forest entails worse outcomes for mammals than a combination of coffee forest protection and housing development confined to existing residential areas;
- Women's fertility preferences are mainly shaped by underlying social-cultural norms and religion, and not by perceptions of social and biophysical stressors affecting livelihoods.

KEY CONSERVATION PRIORITIES:

- Ensure the protection of large undisturbed forest remnants and promote coffee management practices that foster vegetation complexity;
- Avoid forest encroachment and prioritize housing development in existing residential areas. Integrate conservation goals and housing development in landscape planning approaches;
- Encourage the slowing down of human population growth through the engagement with place-based social norms and mindsets, that underpin fertility preferences.

Figure 1.3: Overview of the dissertation structure. From top to bottom: a brief summary of the context is presented and is followed by the overarching goal and approach used. The specific research questions (RQs) are illustrated in italic and the chapters addressing each question are represented in brackets. The key findings and key conservation priorities are presented at the bottom.

Chapter IIIa examined the effects of coffee management intensity and landscape context on the forest bird diversity. It was built on the information generated in Chapter II, including a similar sampling scheme with overlapping survey sites and information on woody plant diversity. We used two rounds of point counts during the dry season to survey birds in forest habitat, covering two broad gradients of environmental conditions. One gradient represented site-level disturbance in terms of coffee management, spanning sites located in relatively undisturbed forest locations to sites highly managed for coffee production. The second gradient represented a landscape-level joint effect between the amount of forest cover surrounding sites and distance from the forest edge, covering sites with high forest cover and located towards the forest interior and sites closer to the forest edge and with less amount of forest cover. We assessed changes in the bird community composition along these two environmental gradients. Our results suggest that the forest supports a relatively diverse bird community, including some endemic species, with community composition being influenced by coffee dominance and amount of forest cover. In addition, we grouped bird species according to their diet, foraging strategy, migratory status, forest dependency and degree of endemicity, and examined group responses (in terms of richness and abundance) to the two environmental gradients. Our results showed that total species richness and abundance was not affected by either management or landscape context gradients but the richness of forest and dietary specialists (such as insectivores and frugivorous) increased with forest naturalness and with increasing distance from the forest edge and amount of forest cover. These findings indicate that vegetation complexity and set-aside areas of natural undisturbed forest promote bird diversity at both site and landscape scales.

Chapter IIIb further discussed these findings, expanding the discussion into implications for the provision of ecosystem services and for the resilience of the forest ecosystem, highlighting the importance of considering specific species assemblages that are based on ecological criteria or functional attributes when assessing effects of forest management on biodiversity. Together, these results strengthen the findings from Chapter II by highlighting the importance of undisturbed natural forests for forest specialist species and by reinforcing the need for coffee management practices that maintain forest structure complexity, for the conservation of forest bird community.

Chapter IV provided an account of the mammal community that occurs at the forest near the edge. Using camera-traps, we surveyed medium-large body sized mammals in sites located in the forest, near the forest edge (40m on average), both within and above coffee altitude (but mostly within). Our results showed that despite being frequently used by people for different purposes, the edge of these forests showed a diverse community of mammals, with up to fourteen species detected per site. Two top-predators were detected, the spotted hyena (*Crocuta crocuta*) and the leopard (*Panthera pardus*), a species of conservation concern. Our results also highlight that despite site location, the forest edge supported different species associated with human-wildlife conflicts, such as the baboon (*Papio anubis*), bushpig (*Potamochoerus larvatus*), warthog (*Phacochoerus africanus*), grivet monkey (*Chlorocebus aethiops*) and small carnivores such as the civet (*Civettictis civetta*) and the white-tail mongoose (*Ichneumia albicauda*). The diversity of mammal species found near the forest edge suggests that these forests hold promise for mammal diversity conservation and highlight the need to further explore how forest management and increasing disturbance of the forest edge may impact the mammal community.

In **Chapter V**, we focused on the effects of landscape context and human disturbance on the leopard, the top predator in the region and a species of conservation concern. We pooled datasets from four different camera-trap surveys conducted in Sheka and Jimma zones, and analyzed leopard reporting rates in relation to landscape context (i.e. amount of forest cover and distance to the forest edge). Our results showed that the leopard is a common resident in the study area, with evidence of mating behavior and recruitment. Our results also show that the leopard reporting rate was positively associated with the amount of natural forest cover. In addition, we analysed the leopard activity patterns in sites with and without recorded presence of people. Our findings suggest that leopard activity times shifted in response to human disturbance, with leopard activity being predominantly nocturnal (with two peaks, one at dawn and another at dusk) in sites with recorded presence of people, and mostly diurnal (with a peak around noon) in sites without recorded presence of people. This might indicate a possible mechanism for leopards and humans to coexist on fine-spatial scales. Given the leopard's ecological role as a top predator this temporal displacement of leopards by humans might also lead to cascading effects on lower-trophic levels, due to reduced predation risk. Together our results suggest that conserving large areas of natural forests is important for the conservation of the species.

Chapter VI considers the outcomes of scenarios of human population growth and housing development for the forest mammal community. We undertook an extensive camera trap survey of the mammal community in the forest using a stratified random design (based on total forest edge and amount of forest cover) that covered locations in both undisturbed forest areas and managed coffee forests. We modelled species responses to housing density and developed a set of scenarios that included alternative pathways of housing development (i.e. densification of houses within current village boundaries versus expansion of housing development into forest habitat), different levels of human population growth (i.e., moderate *cf.* high growth) and that considered the protection of coffee forest against development. Our results indicate that housing development is likely to have negative consequences for several mammal species, including the leopard. Results show that species responses to future scenarios of housing development varied with development type, coffee forest protection and level of human population growth. Overall, housing densification was less detrimental than the expansion of housing development into currently forested areas. Also, the negative impact of housing development on mammals was greater when coffee forest was unprotected from housing development and for higher levels of human population growth. The moist Afromontane forests of southwestern Ethiopia support a diverse mammal community, yet scenarios indicate that many of these species might be vulnerable to the effects of human population growth and housing development. Location, extent and magnitude of development can influence species responses and can limit their ability to persist in the landscape. From a conservation perspective, our results indicate that housing development strategies must be carefully planned to minimize the likely negative outcomes for biodiversity.

In **Chapter VII** we examined possible determinants of women fertility preferences (i.e. desired number of children and use of family planning methods), including perceptions of future trends in social and biophysical stressors that affect livelihoods (i.e. food security, environmental degradation, human population growth and land scarcity). We used a mixed-methods approach that included a household survey of women from rural areas, a survey of women attending higher education and qualitative interviews with health professionals. The surveys included a set of questions to elicit information about (i) household background, (ii) perceptions of future trends in the different stressors, (iii) the desired number of children, (iv) the use of family planning methods, and (v) aspirations and expectations for children. Our results indicate that perceptions about future trends in the different stressors had little influence on fertility preferences. Rather, fertility preferences appeared to be shaped by underpinning sociocultural norms and religion, a perceived utilitarian value of children, and male dominance within households. University respondents reported half of the desired number of children and a set of different social norms influencing fertility preferences. The different outlook on fertility preferences for rural and university respondents suggests that education may also have an effect on reducing the desired number of children and on the uptake of family planning methods. Our results have implications for the development of interventions aiming to encourage and promote the voluntary use of modern family planning methods and the slowdown of human population growth. They highlight the need to consider the specific socio-economic and cultural context in which fertility preferences are based and fertility decisions are taken.

Synthesis

This dissertation aimed to characterize biodiversity patterns in the moist Afromontane forests of southwestern Ethiopia and to understand how biodiversity may be affected by land-use changes in a context of a rapidly growing human population. The findings outlined here show that coffee management intensity, landscape context and future housing development (RQ1-3) impact biodiversity and are likely to continue to do so in the future if current threats affecting the landscape are maintained. Further, results from this dissertation show that the contexts in which fertility preferences are realized (RQ4) need to be better understood to slow down human population growth. Overall, the findings from this dissertation demonstrate the value of moist evergreen forests of southwestern Ethiopia for biodiversity conservation, while highlighting potential consequences that prospective land-use changes may entail for the forest biodiversity. Based on these findings, I discuss different insights that together pertain the prospects for forest biodiversity and call for the urgent protection of these unique forests. First, I discuss the conservation value of these forest complexes, by considering the irreplaceability of undisturbed natural forests as well as the potential of shade coffee forests for biodiversity conservation. Then, I reflect on human population growth as an issue of conservation concern and continue with considerations about the potential of biosphere reserves and connectivity approaches as tools for conservation. I conclude with broad reflections regarding the implications of my findings in light of current conservation discourses.

THE VALUE OF MOIST AFROMONTANE FORESTS FOR BIODIVERSITY CONSERVATION

The moist Afromontane forests of southwestern Ethiopia are part of the world's last primary forests (Potapov et al., 2017), but, as shown here, are vulnerable to the effects of land-use changes. Findings from this dissertation indicate the irreplaceable value of these forests for biodiversity conservation, especially for species that are dependent on undisturbed forest. For instance, the composition and richness of woody plants that are forest specialists was negatively affected by site-level disturbance (i.e. coffee management intensity) and landscape context (i.e. distance to the forest edge) (Chapter II). Likewise, bird groups such as insectivores, frugivores, and forest specialists showed strong associations with high forest naturalness, and with interior sites surrounded by high forest cover (Chapter III). Locations with low coffee management (i.e. with little or no pruning or thinning of the canopy and understory) tend to maintain a complex vegetation structure, providing a range of key resources for these bird groups, including foraging habitat, nesting and refuge. Importantly, many bird species within these functional groups are of current conservation concern (Sekercioglu et al., 2002), stressing the significance of natural undisturbed forests for biodiversity conservation.

In addition, findings from the leopard study (Chapter V) further support the importance of these forest remnants for species of conservation concern. Despite being a highly adaptable species, found in many different habitats throughout Africa (Jacobson et al., 2016) and able to shift activity times in response to human disturbance (Chapter V), the leopard in the study region seemed to be primarily associated with natural and interior undisturbed forests (Chapter V). While some adaptation in activity patterns could potentially support human-wildlife coexistence (Carter et al., 2012), increasing human disturbance of the forest habitat can lead to permanent displacements in the timing of leopard activity (Carter et al., 2015; Van Cleave et al., 2018). This diel shift can potentially lead to fundamental changes in the ecological role of the leopard, with likely repercussions for the entire mammal community and ecosystem functioning in general (Ordiz et al., 2013; Gaynor et al., 2018).

In addition to their value for biodiversity conservation, the natural forests of the study area also have a demonstrated value for the provisioning of different ecosystem services, both at local and regional levels (Ango et al., 2014; Shumi et al., 2019, Shumi et al., submitted). Since the Horn of Africa is becoming increasingly drier and hotter (Tierney et al., 2015), these last remnants of Afromontane forests may play a key role for regulating the region's climate and hydrological cycles and for stabilizing carbon storage, among other services (Abera et al., 2018). Furthermore, the remnants of natural forest are also of value for local livelihoods since the forests' core interior holds the genetic reservoir of *Arabica* coffee (a vital cash crop) (Anthony et al., 2002) and is an important source of seeds for forest regeneration, including for many plant species that have high local value (Shumi et al., 2019). Therefore, it can be anticipated that the loss of these natural undisturbed forests is likely to entail negative consequences for forest biodiversity and for the provision of key ecosystem services (Shumi et al., submitted). Once lost, the restoration of these forests and their associated biodiversity could turn out very difficult, if not impossible. Furthermore, their degradation and loss is likely to represent a decline in the natural capital available to support local livelihoods, a worrying social consequence, since many households in the region are highly dependent on forest resources for the realization of their livelihoods (Manlosa et al., 2019; Shumi et al., 2019).

On the other hand, the community of plants, birds and mammals that were found in the shade coffee forests, including at their edges, was relatively diverse, indicating that there is also value in conserving managed shade coffee forests. Many generalist and pioneer woody plant species were able to survive in coffee forests (Chapter II), and the community of forest birds was relatively stable along the gradient from near-natural forest to highly managed (coffee) forests (Chapter III). Furthermore, the rapid assessment of the forest edge (Chapter IV) showed that at least 26 mammal species occurred in managed shade coffee forests, although further examination is needed to understand the extent of coffee forest use by each species. Also, when examining the impacts for mammals of land-use changes mediated by future housing development (Chapter VI), the protection of coffee forests was beneficial for some mammal species such as the bushbuck, bushpig, olive baboon and warthog, illustrating their potential value for mammal conservation. However, the findings from this dissertation also indicate that as coffee management further intensifies different woody plants and bird groups become negatively affected (Chapters II and III). Management actions that contribute to intensifying coffee production, such as the complete clearance of understorey vegetation, increasing the density of coffee plants, and the elimination of native shade trees, progressively lead to the degradation of the forest structure (Senbeta & Denich, 2006; Hundera et al., 2013). This is worrying, because the degradation of the forest structure entails a subsequent biotic homogenization and ultimately compromises the resilience of the forest ecosystem, the capacity for forest regeneration and the ability of these forests to provide habitat, refuge and food resources for fauna (Tabarelli et al., 2012; Newton & Cantarello, 2015; Solar et al., 2015).

A further concern arises from the Growth and Development plan of Ethiopia that incentivizes a clear shift from subsistence towards more commercially oriented agriculture, including coffee production (ENPC, 2016). Given that coffee constitutes an important dimension of local livelihoods (Manlosa et al., 2019), this push towards intensification represents one of the most pressing threats to the ecological integrity of these forests (Aerts et al., 2017) due to an increasing risk, not only of biotic homogenization and simplification of the forest structure, but also of increasing human disturbance inside the forest. In light of the above, fostering coffee management practices that approximate traditional low-management and that maintain the structural complexity of vegetation are desirable if coffee forest biodiversity in this region of Ethiopia is to be protected. In summary, forests that are managed for coffee production have an important role in conservation but cannot be seen as a replacement for natural undisturbed forest.

HUMAN POPULATION GROWTH AS AN ISSUE OF CONSERVATION CONCERN

Adding to the susceptibility to land-use changes, the forest biodiversity of southwestern Ethiopia is also vulnerable to the effects of an increasing rural human population (Chapters V and VI). Projections for the country indicate that the rural population is expected to increase steadily at least during the next 30 years (UN, 2019a), and the southwest is no exception. This rapid rural growth raises not only a series of societal concerns (such as guaranteeing equitable access to basic needs) but also a series of environmental challenges, including how to best accommodate new dwellers in the landscape while minimizing the impacts for biodiversity. Scenarios of human population growth, mediated by land-use change through housing development (Chapter VI) showed that the forest mammal community in the region is susceptible to the effects of an increasing population and highlight the importance that land-use decisions can have for conservation outcomes. For instance, several mammal species, including a top predator (the leopard) were negatively affected by both housing development type (i.e. densification *cf.* expansion), and decisions regarding coffee forest protection (i.e. protected *vs.* unprotected). The negative effects for mammals were minimized when housing development was prioritized in areas within the existing human footprint. This prioritization prevented the encroachment of the forest habitat, avoiding the combined effect of forest loss and further human disturbance.

In addition, land-use decisions determining the protection of coffee forest lessened the likely negative impacts of housing development for some species, including the bushbuck, the bushpig and the olive baboon. Importantly, very high levels of human population growth led to worse outcomes for most species, compared to more moderate growth. Even the grivet monkey, a species that seemed to benefit from some level of human disturbance, decreased its tolerance with very high levels of human population growth. In addition, the leopard changed activity patterns to avoid human disturbance in the forest (Chapter V) and there is a need to understand the temporal dynamics of other species in response to human activity in the region. Mammals have become more nocturnal across the globe in response to increased human activity (Gaynor et al., 2018) with potential ecosystem-level consequences. Altogether, these findings suggest that from a conservation perspective, human population growth is a key issue, with lower levels of growth likely to conduce to better prospects for mammal diversity conservation in the region. However, slowing down human population growth hinges on declining fertility rates, which in turn are the result of reproductive preferences and behaviours subjective to a myriad of context dependent factors (Caldwell & Caldwell, 1987; Atake & Gnakou, 2019).

The examination of women's fertility preferences (Chapter VII) indicated that these appeared to be shaped by a combination of underpinning sociocultural norms and religion, a perceived utilitarian value of children, and by male dominance within the household. Results also showed that fertility preferences were little affected by perceptions about future trends in different stressors expected to affect livelihoods (i.e. environmental degradation, food insecurity, human population growth and land scarcity); they thus illustrate a disconnect between the global discourse on population-environment-food nexus (Crist et al., 2017) versus perceptions and preferences by local women. Engaging with social norms and mindsets not only has the potential to improve individual health (especially of women and girls) and household wellbeing (Cislaghi et al., 2019; Gupta et al., 2019) but such engagement would also be of principal importance to address social and environmental challenges posed by high fertility and human population growth (Kinzig et al., 2013). Likewise, the differences in women fertility preferences in the rural and university settings suggests that education might also be an avenue for reducing high fertility, as has been widely demonstrated in the literature (Bongaarts, 2003; Grown et al., 2005; Bongaarts et al., 2017). Given the above, new deliberative and culturally sensitive approaches (UNFPA, 2008), designed within the framework of human rights, are needed to engage with social norms that incentivize unsustainably large family sizes.

In summary, the competition over natural resources, including land, is likely to be exacerbated in biodiverse areas facing rapid human population growth, and the achievement of higher human welfare and environmental sustainability is likely to be facilitated by slower population growth (Dasgupta, 1995; Ehrlich et al., 1997; Ehrlich & Ehrlich, 2013). Therefore, from a conservation and sustainable development standpoint, fertility rates and human population growth are impactful factors, and their addressal should be a priority.

LANDSCAPE APPROACH TO CONSERVATION: A BIOSPHERE RESERVE

By separating the effects of site-level disturbance from landscape-level context, this dissertation demonstrates the independent effects of site- and landscape scale attributes on biodiversity and highlights the need for integrated conservation approaches. The community composition and specialized species groups of woody plants, birds and also the leopard were sensitive to the landscape context. Therefore, adding to the site-level conservation measures discussed above (i.e. the use of coffee management practices that reduce forest degradation), a landscape-level approach to conservation is essential, if the entire forest ecosystem is to be protected. A promising approach to integrating both site- and landscape-level conservation could be the creation of a UNESCO Biosphere Reserve (BR). Biosphere reserves aim to reconcile and balance the conservation of biodiversity with sustainable development, comprising a protected core area, and the zonation into buffer and transition areas of sustainable human use, and that incorporate human settlements (https://en.unesco.org/biosphere). A BR in the study area would have the potential to promote the protection of the undisturbed forest remnants, to foster the conservation value of low-intensity managed coffee forests, and to guide housing development in the landscape. Not only could it curb the encroachment of the forest and limit human disturbance in the forest interior (Beyene, 2014), but combined with tourism (Bires & Raj, 2020), participatory forest management (Ameha et al., 2014; Wood et al., 2019) and possibly with coffee certification schemes (Wiersum et al., 2012; Mitiku et al., 2018), it could support the sustainable development of human activities in the region.

A study on possible pathways of development for the southwest of Ethiopia, co-developed with key stakeholders, identified the establishment of a BR as a possible development trajectory for the region (Jiren et al., submitted). In this scenario, sustainable agriculture was combined with eco-coffee production and tourism opportunities and the forest was managed by the community and included an exclusion zone (Jiren et al., submitted). Importantly, insights from the final outreach of the SESyP project explained elsewhere (Manlosa et al., 2020; Fischer et al. submitted), indicate that local communities are open to discuss the possibility of a BR in their landscape, an encouraging sign that it may indeed be a viable option for the landscape. Furthermore, three established Biosphere Reserves already exist in the region surrounding the study area: Yayu (to the North), Kaffa (to the Southwest) and Sheka (to the West), all of which are important areas of coffee production (Aerts et al., 2017).

As extensive research in conservation biology has shown, the protection of isolated pockets of forest remnants, despite being useful may not guarantee the persistence of biodiversity in the distant future (Metzeger & Décamps, 1997; Mönkkönen & Reunanen, 1999; Grande et al., 2020). Therefore, an ambitious, but long-term landscape approach would be to promote the connectivity between the different BRs in southwestern Ethiopia, to foster the protection of the vital forest ecosystem in the region. Enhancing connectivity could contribute to maintain genetic exchange between forest remnants (Bennett, 2003) and facilitate immigration and counteract extinctions (Grass et al., 2019), especially under the additional threat of climate change (Senior et al. 2019). Importantly, it is likely that forests in the landscape will become increasingly fragmented (Hundera et al., 2013, Ango et al., 2016), especially if current deforestation trends remain unchanged (Manlosa et al., 2020). Moreover, climate change projections suggest that the coffee growing altitude may shift to higher elevations (Davis et al., 2012; Moat et al., 2017), leaving the forest at lower altitudes vulnerable to deforestation as it no longer harbours coffee. As presented here, continuing forest degradation and deforestation will cause important declines in the forest biodiversity in the region. Therefore, promoting the connectivity between remaining large forest blocks and between the different Biosphere Reserves in southwestern Ethiopia could greatly benefit forest biodiversity. It is important to recognize though that the above recommendations are not without challenges in their implementation, and the efficacy of BRs has been questioned (Coetzer et al., 2013). Nonetheless, given their potential to balance conservation with human needs the creation of a BR and the fostering of connectivity between reserves deserves further consideration as a conservation approach for the forests in the region.

SHIFTING CONSERVATION DISCOURSES

Reconciling biodiversity conservation with human needs and development is an ever-increasing challenge (UN, 2015). The challenge is particularly acute in tropical forest areas that are biodiversity-rich and where livelihoods highly depend on local natural resources (Gardner et al., 2009), as the case of southwestern Ethiopia illustrates. The moist evergreen forests of the southwest are embedded in a mosaic landscape of subsistence farming where people are an integral part of the landscape (Manlosa et al., 2020, Fischer et al., submitted). Recognizing these landscapes as continuously evolving social-ecological systems (Folke, 2006) implies acknowledging their inherent complexity (Liu et al., 2007). This complexity emerges from dynamic interactions between the social and ecological components of the system across different scales (Liu et al., 2007) and affects the forest system and its biodiversity (Filotas et al., 2014). However, conservation discourses on how to best conserve and protect tropical forest biodiversity often tend to dismiss the inherent complexity associated with landscapes that evolved as social-ecological systems. Examples of such conservation discourses include the old polarization around "single-large or several-small" reserves (Tjørve, 2010 and references therein), the ongoing debate on "land sharing - land sparing" (e.g. Green et al., 2005; Phalan et al., 2011; Fischer et al., 2008; Fischer et al., 2014; Kremen, 2015) and, to some extent, the recent "Half-Earth" - "Sustainable Half-Earth" - "Whole-Earth" propositions (Brüscher et al., 2017; Pimm et al., 2018; Schleicher et al., 2019). The findings from this dissertation demonstrate that conservation recommendations in landscapes such as those of the southwestern Ethiopia can combine both ends of the spectrum. Considering the debate on "land-sharing - land-sparing", the sparing of natural undisturbed forests ("land-sparing"), and the careful management of shade coffee forests ("land sharing") are not mutually exclusive conservation approaches for the region (Kremen & Merenlender, 2018; Grass et al., 2019), and as the findings of this thesis suggest, their combination should be considered to enhance tropical forest biodiversity conservation.

Similar to conservation discourses some conservation initiatives may also oversimplify their approach to conservation problems in social-ecological systems. Conservation initiatives, especially at local and regional scales, tend to typically target proximate drivers of biodiversity decline (such as deforestation and poaching)(Geist & Lambin, 2002), and underlying drivers are often overlooked (Díaz et al., 2019). However, as stated by Brewer and colleagues (2012) channelling the focus of conservation efforts to proximate drivers only, without considering underlying pressures can compromise conservation efforts and the protection of biodiversity in the long term (Kramer et al., 2009). Furthermore, the observed disconnect between what local women perceived and the global discourse on the population-environment-food nexus illustrates the need to conduce placed-based, social-ecological research (Balvanera et al., 2017a, 2017b) in order to address both proximate and distal drivers of biodiversity decline.

While this dissertation examined a distal driver of change (i.e. human population growth) in the region, it was not a goal *per se* to establish direct and causal links among these drivers. Rather, by considering possible future impacts of housing development on the forest mammal community and by examining women fertility preferences in the region, this dissertation aimed to create a space to discuss possible implications of both land-use change and human population growth for biodiversity in the southwestern Ethiopian context. From a conservation perspective, it would be beneficial to move past and beyond narrow and reductionists conservation discourses, towards more holistic conservation approaches (Chan et al., 2007; Chazdon, 2018; Kohler et al., 2019). Such holistic approaches should contemplate the biophysical and social components of the landscape but also the underlying geopolitical, demographic and economic contexts and value systems driving current threats (Kohler et al., 2019; Díaz et al., 2019). Only then can we navigate the conservation and sustainability of tropical forests to their full potential.

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Chapter II

Chapter II

Conservation value of moist evergreen Afromontane forest sites with different management and history in southwestern Ethiopia

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Forest is life, human being life.

Farmer from southwestern Ethiopia

Abstract

Tropical forest ecosystems harbor high biodiversity, but they have suffered from ongoing human-induced degradation. We investigated the conservation value of moist evergreen Afromontane forest sites across gradients of site-level disturbance, landscape context and forest history in southwestern Ethiopia. We surveyed woody plants at 108 randomly selected sites and grouped them into forest specialist, pioneer, and generalist species. First, we investigated if coffee dominance, current distance from the forest edge, forest history, heat load and altitude structured the variation in species composition using constrained correspondence analysis. Second, we modelled species richness in response to the same explanatory variables. Our findings show that woody plant community composition was significantly structured by altitude, forest history, coffee dominance and current distance from forest edge. Specifically, (1) total species richness and forest specialist species richness were affected by coffee management intensity; (2) forest specialist species richness increased, while pioneer species decreased with increasing distance from the forest edge; and (3) forest specialist species richness was lower in secondary forest compared to in primary forest. These findings show that coffee management intensity, landscape context and forest history in combination influence local and landscape level biodiversity. We suggest conservation strategies that foster the maintenance of large undisturbed forest sites and that prioritize local species in managed and regenerating forests. Creation of a biosphere reserve and shade coffee certification could be useful to benefit both effective conservation and people's livelihoods.

Introduction

Tropical forest ecosystems host the richest terrestrial biodiversity and provide important local, regional and global human benefits through provisioning, regulating, supporting and cultural ecosystem services (MA, 2005; Lewis et al., 2015). However, tropical primary forests, including strictly protected areas, are suffering from human induced degradation (Wittemyer et al., 2008; Gibson et al., 2011; Melo et al., 2013). While tropical deforestation has long received attention, forest degradation and its consequences are increasingly also considered to be important (Edwards et al., 2014; Edwards, 2016; Barlow et al., 2016).

In a context of gradual forest degradation, forest species diversity and composition (i.e. the various proportions of different species) are shaped by three major factors, namely (i) site-level disturbance (e.g., see Schmitt et al., 2010), (ii) landscape context, and (iii) forest history (e.g. primary versus secondary forest) (Chazdon, 2008; Barlow et al., 2016). Site-level disturbance includes recurrent and unsustainable logging, hunting, forest fire, fuelwood collection, livestock grazing, and forest management for coffee production (Hundera et al., 2013; Thompson et al., 2013). Such disturbance, in turn, is related to various socio-economic drivers from the level of households to global markets, and can take place legally or illegally (Lambin et al., 2001; Lewis et al., 2015). Forest landscape context influences forest composition via edge effects, which are the abiotic and biotic changes associated with boundaries between forest and non-forest habitats (Harper et al., 2005; Ewers and Didham, 2006; Laurance et al., 2006). Forest history can result in various legacy effects, including immigration credits (Shumi et al., 2018) that cause delays in species recovery within secondary forest (Foster et al., 2003; Chazdon, 2008).

Different woody plant species can be expected to respond differently to forest sites with different degrees of site level disturbance, landscape contexts and histories. Slow growing, shade-tolerant specialist species should persist primarily in relatively stable or less disturbed sites, whereas faster growing pioneer and generalist species may favor more disturbed sites (Sheil and Heist, 2000). For instance, Primack and Lee (1991) noticed a change in species composition from shade-tolerant to pioneer species in sites disturbed by logging in Bornean rainforests. Pioneer and generalist species should respond positively to edge effects, while forest specialist species should respond negatively and should be more abundant in sites deep within the forest (Harper et al., 2005). Species recovery in secondary forest should depend on the extent and intensity of past land use, as well as the surrounding vegetation – for example, most tropical secondary forests on post-agricultural land are dominated by fast-growing pioneer species (Foster et al., 2003; Chazdon, 2008). Although these mechanisms are intuitively appealing, relatively few studies have systematically compared largely undisturbed primary sites with disturbed sites, or have separately assessed the effect of site level disturbance, landscape context and forest history.

Here, we investigate woody plant species composition and richness in forest sites spanning gradients in site-level disturbance (especially coffee management, although we are aware of other disturbances such as firewood collection, logging and grazing), landscape context (distance from the edge) and forest history (primary versus secondary forest) in southwestern Ethiopia. The vegetation in the region is moist evergreen Afromontane forest (Friis et al., 2010). It is the center of origin and diversity of *Coffea arabica* L., still harbors the gene pool of wild coffee populations (Anthony et al., 2002), and is part of the Eastern Afromontane Biodiversity Hotspot (Schmitt, 2006). Over the last few decades, deforestation for agricultural land, settlements and timber extraction has been rapid in the area (Reusing, 2000; Tadesse et al., 2014b; Getahun et al., 2017). Moreover, local people use the forest to obtain fuelwood, construction wood, and farm tools, as well as for livestock grazing, medicine, spices, honey and coffee production (Ango, 2016; Dorresteijn et al., 2017).

Traditionally, coffee is grown and managed in Afromontane forests with varying intensity, ranging from relatively undisturbed wild forest coffee fruit collection to intensively managed semi-plantation coffee systems, where undergrowth plants including herbs, shrubs and trees are cleared; canopy trees are selectively thinned out; and additional coffee seedlings are planted to increase coffee yield (Schmitt et al., 2010; Hundera et al., 2013). In some instances, intensification also involves the removal and replacement of native trees with exotic species, use of herbicides, fertilizers and improved coffee varieties (Wiersum et al., 2008; Tadesse et al., 2014a). There are two divergent observations about coffee forest management. On the one hand, via providing an economic incentive, managing the forest for coffee production has historically helped to slow down deforestation rates (Hylander et al., 2013a). However, at the same time, increasingly intensive coffee production has been linked to forest degradation and loss of local biodiversity (Schmitt et al., 2010; Aerts et al., 2011; Hundera et al., 2013). Considering ongoing and historical site-level and landscape-level changes, as well as the global importance of moist evergreen Afromontane forests, we sought to investigate how woody plant species composition and richness vary along a gradient of (1) coffee management; (2) forest landscape context (from forest edge to deep inside the forest); and (3) forest history (secondary versus primary forest).

Methods

Study area

The study was conducted in five kebeles (the smallest administrative unit in Ethiopia) of three districts (woredas): Gera, Gummay and Setema of Jimma Zone, Oromia Regional State, southwestern Ethiopia (Fig. 1). The study area comprised a mosaic of land use types, with forest cover ranging from 37 to 84% in the five kebeles, while arable land, grazing land and settlements accounted for the rest. The region comprises undulating slopes and flat plateaus, with elevation ranging from 1500 to 3000m above sea level. The area has a warm moist climate, driven by the dynamics of the inter-tropical convergence zone, with 1500–2000mm of annual rainfall, and a 20 °C mean annual temperature. The area has unimodal rainfall patterns, with some rain throughout most of the year, and more substantial summer rain primarily from June to September (Friis et al., 2010; Schmitt et al., 2013; Ango, 2016).

The dominant tree species in moist evergreen Afromontane forest include *Olea welwitschii*, *Pouteria adolfi-friederici*, *Schefflera abyssinica*, *Prunus africana*, *Albizia spp*., *Syzygium guineense*, and *Cordia Africana* (Cheng et al., 1998). *Coffea arabica* is native to the forest and grows naturally at altitudes between 1000 and 2000m above sea level (Schmitt, 2006; Senbeta et al., 2014). Coffee and to a lesser degree honey are economically important non-timber forest products. Agriculture including crops and livestock is the main source of livelihoods, and can lead to degradation (e.g. via overgrazing) and encroachment of forested areas (Kassa et al., 2016).

Land cover mapping and study site selection

Our design sought to capture broad gradients in site-level conditions, landscape contexts and histories. To this end, first we generated a current map of woody versus non-woody vegetation, from RapidEye satellite images from 2015 (5m resolution) using an automatic image classification, based on Maximum Likelihood in ArcGIS. We also determined historical forest cover using supervised image classification of Landsat imagery from 1973 (Landsat 1-MSS, obtained from http://www.usgs.gov/).

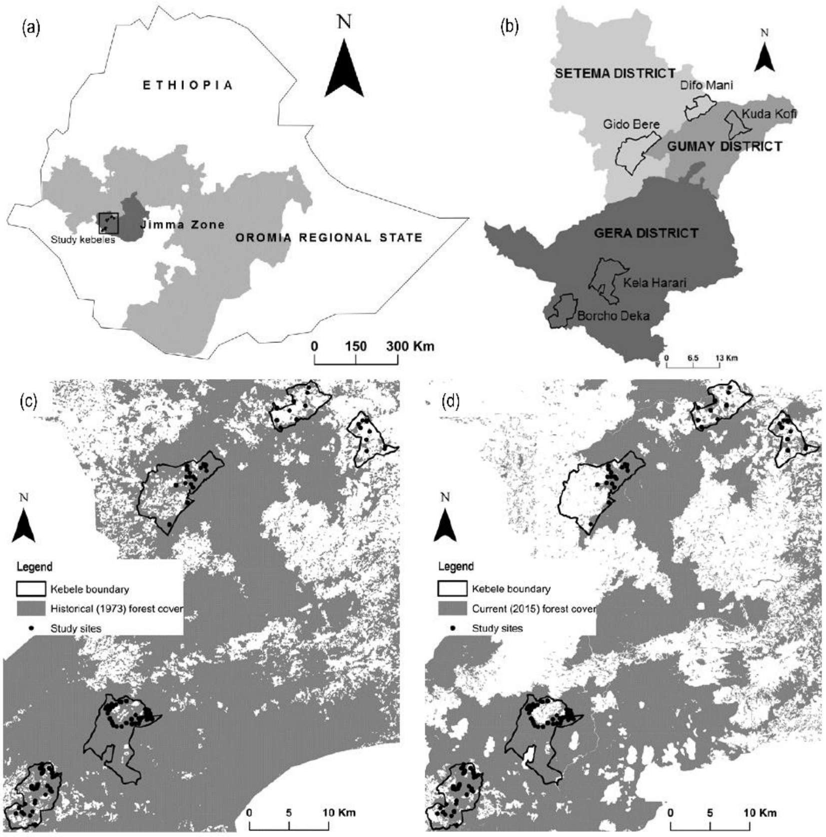

Figure 1. Overview of (a) location of the study area (square) in Ethiopia; (b) study area with the five study kebeles highlighted; (c) historical (1973) forest cover (grey color) and survey sites (black points); and (d) current (2015) forest cover (grey color) and survey sites (black points).

Then, using the current forest map, we stratified the forest in a way that most likely captured the expected full gradients of forest conditions, especially with respect to human disturbances. Here, we assumed that forest disturbances could be closely related with accessibility, as a proxy for the likely level of human interference – remote sites deep within the forest may be less disturbed than highly accessible areas. Based on this, we stratified the current forest into four cost distance classes (low, medium, high and very high cost distance), using the cost distance analysis tool in ArcGIS, which takes into account the distance to a given point and uses a penalty for steep slopes (which reduce accessibility). Then, we determined the proportion of forest cover and hence, the proportion of cost distance classes within each kebele using the above mentioned current land cover map. Finally, we randomly selected a total of 108, 20m by 20m sites, distributed across the five kebeles (ranging between 9 and 38 sites per kebele) and across the four cost distance classes (29 in low, 21 in medium, 20 high, and 38 very high cost distance). In general, such randomly located sites stratified by cost-distance have the advantage of being unbiased by subjective classification (but see Hundera et al., 2013; Tadesse et al., 2014a) and proximity to roads. The disadvantage is that our approach was not fully balanced with respect to other environmental or forest conditions; such as primary versus secondary forests (e.g. we actually got very few interior secondary forests, see below).

Woody plant surveys

We surveyed woody plants from November 2015 to January 2016, and from April to May 2017. At each of the 108 sites, we recorded all individuals of tree and shrub species with height≥1.5 m. As the existence of young trees is typically correlated with the presence of seedlings (recent regeneration) in a given site (e.g. Fischer et al., 2009), for logistical reasons, we chose not to count individuals < 1.5m in height for this study. We identified plants that were readily identifiable in the field. For species that were difficult to identify in the field, specimens were collected, pressed, dried and transported to the National Herbarium at Addis Ababa University for identification. Nomenclature followed the Flora of Ethiopia and Eritrea (1989–2006). Species were further segregated into forest specialist, generalist and pioneer species (Appendix A) based on relevant literature (Flora of Ethiopia and Eritrea, 1989–2006; Teketay, 1997; Tesfaye et al., 2002; Hundera et al., 2013). For each site, we quantified (1) total species richness, (2) forest specialist richness, (3) pioneer species richness, and (4) generalist species richness.

Forest and environmental parameters

To account for the actual coffee management intensity in situ at each site (Fig. 2), we quantified coffee dominance. Coffee dominance was measured as ranging from 0 to 1, and was determined as the ratio of the number of coffee plants to the total number of woody plants in each site (Rodrigues et al., 2018). This measure of coffee dominance was used because it is a countable, objective measure of how many stems of a given site are coffee, out of all stems. In undisturbed or unmanaged coffee forest, coffee plant density is very low, while in intensively managed coffee forest, it is much higher typically and constitutes>50% of all plants (Schmitt, 2006). The high dominance of coffee in intensively managed sites results from shrub and small tree species other than coffee being systematically removed by coffee growers (Hundera et al., 2013). Low values of "coffee dominance" therefore indicate a high likelihood of coffee occurring at natural densities, while high values of coffee dominance indicate human interference. To account for landscape context as distinct from cost distance (which was used only to guide site selection), we determined the current Euclidean distance of the center of the survey sites from the nearest current forest edge. We also compared the current (2015) forest map with the historical (1973) forest map to classify each site as primary forest (forested in both 1973 and 2015) versus secondary forest (forested in 2015, but farmland in 1973). This way, after our initial site selection, we classified 95 sites as primary forest sites and 13 as secondary forest. A summary of study sites by their cost distance classes and current distances from the nearest forest edge in both primary and secondary forests is provided in Table 1.

Table 1. Number of the surveyed 20 m by 20 m sites in terms of forest strata and current Euclidean distance from the nearest forest edge in primary and secondary forests (see Methods for details).

	Category	Sites in primary forest (forested in both 1973 and 2015)	Sites in secondary forest (forested in 2015, but farmland in 1973)	Total
Forest strata	Low cost distance	22	7	29
	Medium cost distance	19	2	21
	High cost distance	18	2	20
	Very high cost distance	36	2	38
	Total	95	13	
Current distance from forest edge	Edge sites (with < 100 m distance from edge)	26	9	35
	Interior sites (with > 100 m distance from edge)	69	4	73
	Total	95	13	

Finally, we quantified other environmental variables that we believed might affect woody plant composition and richness as covariates, namely altitude and heat load of the sites. The ASTER Digital Elevation Model (30m resolution; https://reverb.echo.nasa.gov/) was used to derive altitude; heat load was calculated following the procedures described by Olsson et al. (2009). An overview of all variables ultimately used for statistical analysis and their description is provided in Table 2.

Figure 2. Overview of forest disturbances and coffee management gradients in southwestern Ethiopia: (a) relatively undisturbed or unmanaged interior coffee forest site; (b) slightly managed interior coffee forest site; (c) managed semi-plantation coffee forest site; and (d) intensively managed semi-plantation coffee forest site.

Data analysis

First, we investigated which environmental variables drive community composition. Second, we modelled total species richness, richness of forest specialist, generalist and pioneer species in response to the explanatory variables (Table 2). Using the log-transformed abundance data of all species (except Coffea arabica) in all study sites, we conducted constrained correspondence analysis (CCA) to assess how environmental predictors could explain species composition. We tested if plant community composition and study site scores correlated with coffee dominance, current distance from the forest edge, forest type, heat load, and altitude, using the CCA from the 'vegan' package (Oksanen et al., 2018) in R Core Team (2018). Prior to this, we conducted a detrended correspondence analysis (DCA) to determine the length of the compositional gradient, which denotes the degree of species turnover in the community (Hill and Gauch, 1980). All explanatory variables except altitude were log-transformed, and all predictors were tested for significance ($p < 0.05$) using 999 permutations. We specified kebele to account for the non-independence of the samples within a kebele.

Table 2. Definition and description of the explanatory variables used to model plant species richness.

Type	Variable	Definition and method
Fixed effect	Current distance	The distance in m from the center of the site to the nearest current (2015) forest edge (Fig. 1c).
	Coffee dominance	The ratio of the number of coffee plants to total number of woody plants in a given site
	Altitude	Altitude above sea level derived from the ASTER DEM.
	Heat load	Measure of potential incident radiation and temperature, estimated from aspect and slope (Olsson et al., 2009)
	Forest type	Forest land use with two factors – primary forest since 1973 and secondary forest restored after 1973 from farmland.
Random effect	*Kebele*	Smallest administrative unit within which sites were nested.
	Dummy	Observation level random effect to account for overdispersion.

We then used generalized linear mixed effects models (GLMMs) with a Poisson error structure to investigate the effects of local and landscape level explanatory variables (Table 2) on richness of (1) total species, (2) forest specialist species, (3) generalist species and (4) pioneer species. In all cases, we specified kebele (to account for grouping in experimental units) and an observation-level dummy variable (to account for overdispersion) as random effects. Prior to modelling, we checked for possible correlations among explanatory variables. Most correlations were below 0.2, but there was a stronger correlation between coffee dominance and altitude (correlation coefficient $r=0.6$). In this case, we still included both variables in the regression models, but checked that all models had a variance inflation factor of<2. Furthermore, we log-transformed coffee dominance, current distance to the forest edge, and heat load to remove skew, and scaled all continuous variables to zero mean and unit variance to obtain directly comparable coefficients. Finally, to visualize local and landscape level effects, we predicted species richness in response to coffee dominance and current distance to the forest edge.

Results

Species composition analysis

A total of 113 (including one unidentified) species of trees and shrubs, representing 40 families, were recorded from all sites (Appendix A). Of these, 45 were forest specialist, 30 were generalist, and 38 were pioneer (including two planted) species. The most abundant species were *Coffea arabica* (a forest specialist occurring at 78 sites), *Maytenus arbutifolia* (generalist at 64 sites), *Chionanthus mildbraedii* (forest specialist at 55 sites), *Vernonia auriculifera* (pioneer at 50 sites), *Dracaena afromontana* (forest specialist at 37 sites), and *Justicia schimperiana* (generalist at 33 sites) (Appendix A).

The first DCA axis had a length of 3.89 standard deviations, indicating almost a complete species turnover along the main compositional gradient. The CCA ordination indicated that different groups of species occupied different locations but with substantial overlap (Fig. 3a). The CCA showed that woody plant community composition was significantly correlated with several explanatory variables (F=2.333, $p < 0.001$; Fig. 3b). Woody plant community composition was significantly associated with altitude (F=4.483, $p < 0.001$),forest history – secondary forest (F=2.342, $p < 0.001$), coffee dominance (F=2.959, $p < 0.001$) and current distance from forest edge (F=2.928, $p < 0.001$).

Species richness models

Total species richness and forest specialist species richness were negatively related to coffee dominance (Table 3; Fig. 4a, d). Richness of forest specialist species increased significantly in both primary and secondary forests with current distance from the forest edge (Table 3; Fig. 4e, f), while richness of pioneer species decreased significantly in both primary and secondary forests with current distance from the forest edge (Table 3; Fig. 4h, i). A lower richness of forest specialist species was found in secondary as opposed to primary forest (Table 3; Fig. 4f). In addition, richness of total species was negatively related to altitude and heat load, and richness of generalists and pioneer species declined with altitude (Table 3).

Discussion

Focusing on biodiverse moist evergreen Afromontane forest, we found evidence of site-level disturbance, landscape context, and forest history effects on woody plant species composition and richness. First, we observed significant negative effects of coffee management intensity on total species richness and forest specialist species richness. Second, we identified contrasting landscape context effects, namely a positive effect of distance from the current forest edge on forest specialist species richness, and a negative effect on pioneer species richness. Third, we found significantly lower forest specialist richness in secondary versus primary forest.

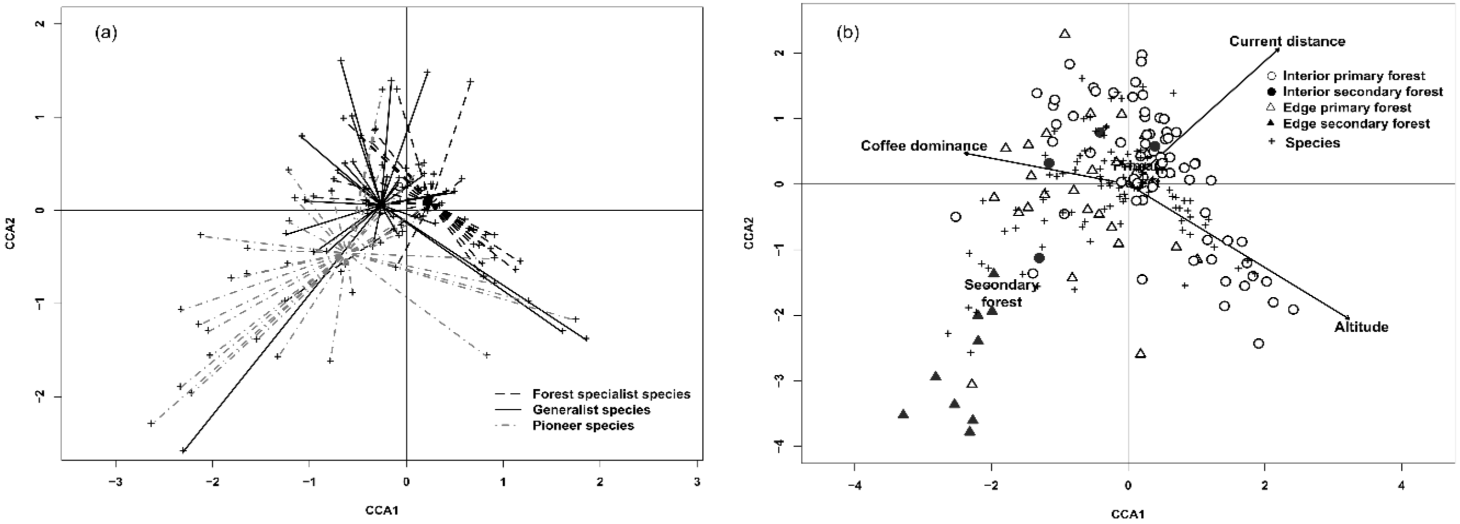

Fig. 3. CCA ordination. (a) CCA biplot showing woody plant species (indicated by "+" sign) (except *Coffea arabica*) based on log-transformed abundance data. Species were grouped and connected to their group's centroid by lines: forest specialist species (black long-dash lines), generalist species (black lines) and pioneer species (grey two-dash lines). (b) CCA biplot of all 108 study sites (indicated by circles and triangles), all 112 species (except *Coffea arabica*) (indicated by "+" sign) and the significant environmental variables. Study sites were classified by their current distance from the nearest forest edge, with >100 m edge distance as forest interior sites (circles), and <100 m edge distance as edge sites (triangles); and also by forest type: primary forest sites (unshaded circles and triangles), and secondary forest sites (black-shaded circles and triangles). Explanatory variables significantly correlated with plant community composition ($p < 0.001$) were altitude, current distance, coffee dominance and forest type- secondary forest.

Table 3. Results of generalized linear mixed effects models for total species richness, forest specialist species richness, pioneer species richness and generalist species richness. Explanatory variables were continuous except for forest type. The coefficient for forest type indicates the difference between primary and secondary forest, with primary forest being the reference level. Significance levels are indicated by: *P < 0.05; **P < 0.01; ***P < 0.001.

Response	**Term**	**Coefficient**	**Standard error**	***Z-value***	***P*-value**
Total species richness	Intercept	2.761	0.142	19.485	<0.001 ***
	Current distance	-0.000	0.031	-0.009	0.993
	Coffee dominance	-0.148	0.038	-3.908	<0.001 ***
	Heat load	-0.065	0.028	-2.284	0.022 *
	Altitude	-0.145	0.046	-3.188	0.001 **
	Forest type	-0.024	0.110	-0.220	0.826
Forest specialist species richness	Intercept	2.209	0.171	12.924	<0.001 ***
	Current distance	0.137	0.043	3.220	0.001 **
	Coffee dominance	-0.193	0.051	-3.766	<0.001 ***
	Heat load	-0.058	0.036	-1.609	0.108
	Altitude	-0.088	0.060	-1.466	0.143
	Forest type	-0.344	0.167	-2.067	0.039 *
Pioneer species richness	Intercept	0.765	0.071	10.774	<0.001 ***
	Current distance	-0.305	0.063	-4.825	<0.001 ***
	Coffee dominance	-0.146	0.079	-1.849	0.065
	Heat load	-0.024	0.063	-0.372	0.710
	Altitude	-0.163	0.082	-1.971	0.049 *
	Forest type	0.318	0.176	1.812	0.070
Generalist species richness	Intercept	1.377	0.203	6.780	<0.001 ***
	Current distance	-0.087	0.049	-1.772	0.076
	Coffee dominance	-0.046	0.059	-0.782	0.434
	Heat load	-0.065	0.052	-1.252	0.211
	Altitude	-0.260	0.078	-3.356	<0.001 ***
	Forest type	0.029	0.177	0.163	0.871

Unlike many other studies in the region (and elsewhere in the tropics)(e.g. Gole, 2003; Hundera et al., 2013; Tadesse et al., 2014a), using a spatially randomized design based on cost distance and a large data set, we were able to cover large gradients of forest conditions in relation to coffee management, landscape context and forest history. Our findings revealed independent effects of all three gradients, highlighting the importance of their recognition in developing appropriate conservation strategies. We discuss these findings and their implications for conservation in relation to other studies, particularly from Ethiopia and other tropical regions.

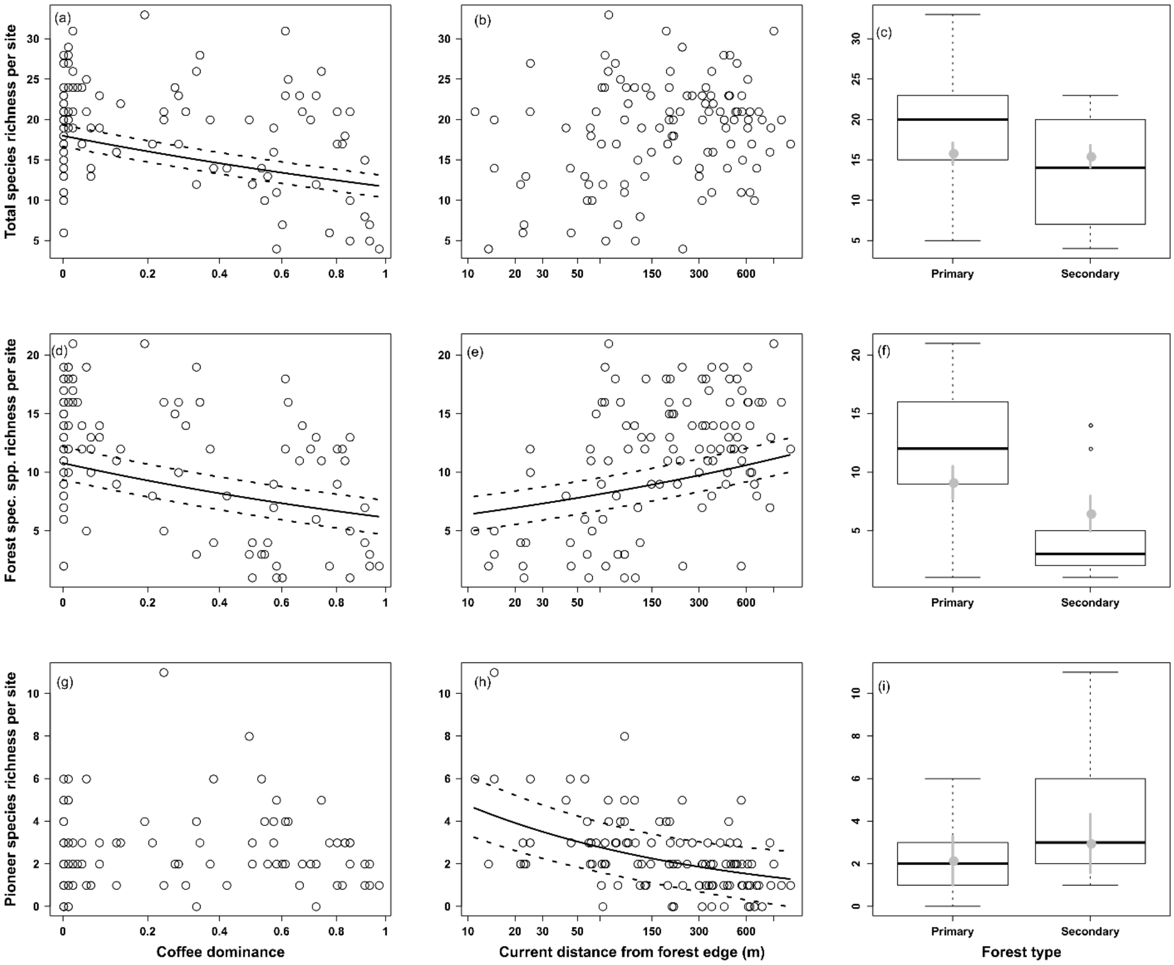

Fig. 4. Effects of coffee management, current distance from nearest forest edge, and forest type on richness of total species (panels (a), (b) and (c)), forest specialist species (panels (d), (e) and (f)), and pioneer species (panels (g), (h) and (i)) based on the generalized liner mixed effects models. Solid black regression lines indicate model predictions for primary forest while all other variables were held constant at their means; and dashed lines indicate 95% confidence intervals. The x-axes display original values but both coffee dominance and current distances were scaled and used on a logarithmic scale in the models. The box-and-whisker plots (c, f, i) illustrate the relationship between forest type and species richness, where the grey dot represents the predicted means and the grey lines the corresponding 95% confidence intervals.

The merit of shade coffee systems for biodiversity conservation and ecosystem services has received considerable attention globally (Jhaet al., 2014; Tadesse et al., 2014a; Rodrigues et al., 2018). Coffee is grown across southwestern Ethiopia (Senbeta and Denich, 2006;Schmitt et al., 2010; Hundera et al., 2013) as well as in Latin America and elsewhere in the tropics (Perfecto et al., 1996; Philpott and Dietsch, 2003; Hernandez-Martinez et al., 2009), often under the shade of native trees. However, a major difference in Ethiopia is that Arabica coffee is a native, primary component of forest ecosystems (Schmitt, 2006; Aerts et al., 2011). Here, traditional coffee management intensity ranges from very low disturbance forest systems to semi-plantation systems (Teketay, 1999; Wiersum et al., 2008; Tadesse et al., 2014a). Our findings revealed negative effects of intensively managed coffee systems on native species composition and diversity as opposed to undisturbed coffee forest sites. Several native tree species, such as *Cassipourea malosana*, *Chionanthus mildbraedii*, *Pouteria adolfi-friederici*, and *Trichilia dregeana* appeared to be affected by intensive coffee management. This is consistent with other studies in southwestern Ethiopia, which also found strong negative effects on native plant species (Gole, 2003; Schmitt et al., 2010; Hundera et al., 2013) and on forest and dietary specialist birds (Gove et al., 2008; Rodrigues et al., 2018), suggesting loss and homogenization of biodiversity in increasingly simplified forest coffee systems.

At a landscape level, edge effects are known to have negative consequences on native forest species (Murcia, 1995; Gascon et al., 2000; Wiens, 2002). However, landscape context and site effects are often confounded and therefore usually difficult to differentiate in their respective influences on biodiversity (Harper et al., 2005). Here, we found edge-mediated landscape effects on species composition and richness that were not related to coffee management. Our findings show that sites closer to the forest edge differ in native species composition from sites in the interior forest. Of the forest specialist species, for example, *Chionanthus mildbraedii*, *Pouteria adolfi-friederici*, *Podocarpus falcatus*, and *Schefflera abyssinica* appeared to be most strongly affected by edge effects. Furthermore, edge influence extended relatively deep into the forest, with forest species richness continuously increasing deep into the forest, strongly affecting up to 100 m from the edge but potentially reaching several hundred metres into the forest (Fig. 4e). Our empirical findings are consistent with earlier southwestern Ethiopian studies that showed forest and dietary specialist bird species diversity (Rodrigues et al., 2018) and understory epiphytic fern and epiphyllous bryophyte cover (Hylander et al., 2013b) to increase towards the interior of the forest. As to the distance of edge influence, the edge effect in our study area was comparable to edge effects reported elsewhere in the tropics (Harper et al., 2005), such as 100 to 300m in central Amazonian lowland rainforest (Laurance et al., 1998) and 500m in tropical forest in Queensland, Australia (Laurance, 1991). A possible driver for the edge effects in our study area may be the relatively intensive use of forest edges by local people, which includes but is not restricted to coffee growing. Local people in the region greatly depend on wood and non-wood forest products such as fuelwood, construction materials including poles and timber, farm and household tools, and honey (Ango, 2016; Dorresteijn et al., 2017). While forest edges may be hotspots of such human uses, people in the region further penetrate the forest to find and use resources from considerable distances(Hylander et al., 2013b), thereby potentially causing far reaching edge effects (Didham and Lawton, 1999; Gascon et al., 2000;Cadenasso et al., 2003). These findings highlight the general importance of maintaining largely undisturbed forest interior locations for native species conservation (Gibson et al., 2011; Barlow et al., 2007).

Secondary forests in our study area hosted significantly lower forest specialist species richness and differed in composition compared to primary, old-growth forests. At the species level, for example, *Cassipourea malosana* and *Trichilia dregeana* did not occur at secondary forest sites, and *Pouteria adolfi-friederici* and *Syzygium guineense* occurred at only one interior secondary forest site (noting that we had only four interior sites of secondary forest in total). Such decreases in native tree species richness in secondary forest have been noted consistently in the tropics (Chazdon, 2003; Lugo and Helmer, 2004; Wright, 2005). Possible reasons for lower native tree species richness in secondary forest are land use legacy effects of past agricultural land use (e.g. loss of individual trees or propagules, habitat change, inadequate seed dispersal, or loss of soil fertility; Shumi et al., 2018; Thompson et al., 2002; Arroyo-Rodríguez et al., 2017) coupled with the inherently slow natural restoration and restocking with slow-growing tree species. Our findings demonstrate that secondary forests, which we also found to differ in species composition from primary forests, may take up to 40 years (assuming that the oldest regrowth could have occurred immediately after 1973) and longer to attain a similar composition to remnant forest. This matches closely with other forest ecosystems, where recovery in species composition takes several decades – e.g. 30–40 years in Atlantic secondary forest in southern Brazil (Zanini et al., 2014), 80 years in south-eastern Puerto Rico (Marin-Spiotta et al., 2007), and 70–100 years in central Panama (DeWalt et al., 2003). Overall, while our results clearly underline the primary importance of safeguarding old growth native forests (see Gibson et al., 2011; Barlow et al., 2007), they also highlight the need for assisted and natural recovery of forests (Chazdon, 2008; Crouzeilles et al., 2017).

Conservation implications

Our study revealed a combination of site-level, historical and landscape-level effects on Ethiopian forest biodiversity. Because coffee is important for local livelihoods and Ethiopia's economy (Petit, 2007; Moat et al., 2017), pressure on forest biodiversity from coffee management intensification is potentially high (e.g. Hundera et al., 2013; Tadesse et al., 2014a). Further forest degradation could also result from an increasing number of local people heavily depending on forest products (Ango, 2016; Dorresteijn et al., 2017). Moreover, imperfect forest management and investment policies, and poorly defined property rights (e.g. Lemenih and Kassa, 2014; Tura, 2018) have also exposed Ethiopian forests to recurrent deforestation (e.g. Tadesse et al., 2014b; Getahun et al., 2017), particularly in areas above coffee altitude(e.g. Hylander et al., 2013a). Biodiversity conservation in southwestern Ethiopia and similar systems elsewhere requires integrated strategies that foster appropriate local and forest landscape management (Gardner et al., 2009; Edwards,2016; Chazdon, 2018). One option could be to further promote the biosphere reserve approach, which can integrate sustainable development and biodiversity conservation (Batisse, 1982; Bridgewater, 2002).Eco-friendly coffee certification schemes could additionally help to maintain specialist species in managed coffee forests (Perfecto et al.,2005; Takahashi and Todo, 2017). Given the high dependence of local livelihoods on forest products and the vulnerable biodiversity in southwestern Ethiopia, however, any approach must carefully weigh social and ecological costs and benefits.

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Supporting Information for Chapter II

Conservation value of moist evergreen Afromontane forest sites with different management and history in southwestern Ethiopia

Appendix A. List of tree and shrub species encountered in all 108 studied forest sites, their family and local names, guild (forest specialists, pioneers and generalists species) and habit, total abundance from all sites and the number of sites they occurred in. Sp.occ: species occurrence. Abund: abundance

Scientific name	Family name	Local name	Guild	Habit	Abund	Sp. Occ. (no. of sites)
Abutilon longicuspe Hochst. ex A. Rich	MALVACEAE	Inchinii dalacha	Pioneer	Shrub	6	2
Acacia abyssinica Hochst. ex Benth.	FABACEAE	Sondii adii	Pioneer	Tree	2	2
Acanthus eminens C.B.Cl.	ACANTHACEAE	Baalan-waraantee	Forest specialist	Shrub	903	22
Alangium chinense (Lour.) Harms	ALANGIACEAE	Daanissaa	Pioneer	Tree	11	7
Albizia gummifera (J. F. Gmel.) C.A. Sm.	FABACEAE	Ambabeessa	Generalist	Tree	311	33
Albizia schimperiana Olivo	FABACEAE	Ambabeessa adii	Generalist	Tree	92	29
Allophylus abyssinicus (Hochst.) Radikofer	SAPINDACEAE	See´o/Seehoo	Forest specialist	Tree	232	41
Allophylus macrobotrys Gilg	SAPINDACEAE	Saahoo	Generalist	Tree	8	4
Apodytes dimidiata E. Mey. ex Arn.	ICACINACEAE	Wandabiyyoo	Forest specialist	Tree	48	21
Bersama abyssinia Fresen.	MELIANTHACEAE	Lolchisiaa	Forest specialist	Tree	379	71
Bridelia micrantha (Hochst.) Baill.	EUPHORBIACEAE	Minaanduloo	Pioneer	Small tree	8	1
Brucea antidysenterica J. F. Mill.	SIMAROUBACEAE	Qomanyoo	Forest specialist	Shrub to tree	154	34
Calpurnia aurea (Ait.) Benth.	FABACEAE	Ceekaa	Pioneer	Small tree	122	5
Canthium oligocarpum Hiern subsp. Oligocarpum	RUBIACEAE	Baalsadii	Forest specialist	Shrub to tree	113	34
Cassipourea malosana (Baker) Alston	RHIZOPHORACEAE	Ilkee	Forest specialist	Tree	136	25
Celtis africana Burm. f.	ULMACEAE	Qayii	Generalist	Tree	125	25
Chionanthus mildbraedii (Gilg & Schellenb.) Stearn	OLEACEAE	Gagamaa	Forest specialist	Tree	1526	55
Clausena anisata (Willd.) Benth.	RUTACEAE	Ulmaayii	Generalist	Shrub to tree	766	56
Clerodendrum myricoides (Hochst.) Vatke	LAMIACEAE	Maraasisaa	Pioneer	Shrub	7	3
Coffea arabica L.	RUBIACEAE	Buna	Forest specialist	Small tree	10006	78
Cordia africana Lam.	BORAGINACEAE	Waddeessa	Generalist	Tree	102	29
Crossopteryx febrifuga (G.Don) Benth.	RUBIACEAE	Unknown/ kanhinbekkamine	Generalist	Tree	2	1
Crotalaria exaltata Polhill	FABACEAE	Bilbiilee	Pioneer	Shrub	1	1
Croton macrostachyus Del.	EUPHORBIACEAE	Bakaniissa/Makkanniisa	Pioneer	Tree	350	61
Dalbergia lactea Vatke	FABACEAE	Unknown	Pioneer	Tree	15	5
Deinbollia kilimandscharica Taub.	SAPINDACEAE	unknown	Forest specialist	Tree	2	2
Diospyros abyssinica subsp. abyssinica (Hiern) F. White	EBENACEAE	Lookkoo gurraacha	Forest specialist	Tree	58	12
Dombeya torrida (J. F. Gmel.) P. Bamps	STERCULIACEAE:	Daanissaa	Pioneer	Shrub to tree	13	5
Dracaena afromontana Mildbr.	DRACAENACEAE	Algee	Forest specialist	Shrub	1250	37
Dracaena fragrans (L.) KerGawl.	DRACAENACEAE	Eemoo	Planted	Shrub to tree	974	19
Dracaena steudneri Engl.	DRACAENACEAE	Bubiftuu/Yubdoo	Forest specialist	Shrub to tree	50	15
Ehretia cymosa Thonn.	BORAGINACEAE	Ulaagaa	Generalist	Shrub to tree	153	34
Ekebergia capensis Sparrm	MELIACEAE	Orooroo/Somboo	Forest specialist	Tree	22	8
Elaeodendron buchananii (Loes) Loes.	CELASTRACEAE	Lookkoo	Generalist	Tree	177	30
Entada abyssinica Steud. ex A. Rich.	FABACEAE	Ambaltaa	Pioneer	Tree	2	2
Erythrina brucei Schweinf.	FABACEAE	Beroo	Pioneer	Tree	2	2
Erythrococca abyssinica Pax	EUPHORBIACEAE	Agabaatee	Generalist	Shrub	71	13
Erythrococca trichogyne (Muell. Arg.) Prain	EUPHORBIACEAE	Qayii	Forest specialist	Small tree	212	22
Eucalyptus camaldulensis Dehnh.	MYRTACEAE	Baargamoo dimaa	Pioneer-planted	Tree	6	2
Eugenia bukobensis Engl.	MYRTACEAE	Unknown	Forest specialist	Small tree	2	1
Euphorbia abyssinica Gmel.	EUPHORBIACEAE	Adaamii	Pioneer	Tree	4	3
Fagaropsis angolensis (Engl.) Milne	RUTACEAE	Qomanyoo	Forest specialist	Tree	28	9
Ficus exasperata Vahl.	MORACEAE	Baalansofii	Pioneer	Small tree	10	3
Ficus glumosa Del.	MORACEAE	Anuunnuu (unknown)	Generalist	Tree	1	1
Ficus ovata Vahl	MORACEAE	Qelenxoo	Generalist	Small tree	1	1
Ficus sur Forssk.	MORACEAE	Harbu	Generalist	Tree	99	28
Ficus thonningii Blume	MORACEAE	Dambii	Generalist	Small tree	11	4
Ficus vasta Forssk	MORACEAE	Qilxuu	Pioneer	Tree	3	3
Flacourtia indica (Burm.f) Merr.	FLACOURTIACEAE	Akuukuu	Generalist	Small tree	17	9
Galiniera saxifraga (Hochst.) Bridson	RUBIACEAE	Mixoo-sare (Unknown)	Forest specialist	Small tree	675	65
Grewia ferruginea Hochst. Ex A. Rich.	TILIACEAE	Laanqanoo	Pioneer	Shrub	8	3
Hallea rubrostipulata (K. Schum.) J.-F. Leroy	RUBIACEAE	Anuunuu	Forest specialist	Tree	4	2
Hibiscus macranthus Hochst. ex A. Rich.	MALVACEAE	Inchinii daalacha	Pioneer	Shrub	1	1
Hypericum revolutum Vahl	GUTTIFERAE	Uleefonii	Pioneer	Small tree	1	1
Ilex mitis (L.) Radlk.	AQUIFOLIACEAE	Qetoo/Kofoo	Forest specialist	Tree	76	12
Justicia schimperiana (Hochst. ex Nees) T. Anders.	ACANTHACEAE	Dhuummupaa	Generalist	Shrub	1567	33
Lannea schweinfurthii (Engl.) Engl.	ANACARDIACEAE	Booqqoo	Generalist	Tree	6	5
Lannea welwitschii (Hiem) Engl.	ANACARDIACEAE	Anuunuu	Forest specialist	Tree	3	2
Lepidotrichilia volkensii (Giirke) Leroy	MELIACEAE	Seehoo	Forest specialist	Tree	139	20
Macaranga capensis (Baill.) Sim	EUPHORBIACEAE	Wongoo	Forest specialist	Tree	470	43
Maesa lanceolata Forssk.	MYRSINACEAE	Abbayyii	Generalist	Tree	270	51
Manilkara butugi Chiov.	SAPOTACEAE	Gawoo	Forest specialist	Tree	1	1
Maytenus arbutifolia (A. Rich.) Wilczek	CELASTRACEAE	Ombooroo/Kombolcha	Generalist	Shrub	1590	64
Maytenus senegalensis (Lam.) Exell	CELASTRACEAE	Ombooroo	Pioneer	Shrub	26	4
Maytenus sp.	CELASTRACEAE	Qooraatii	Generalist	Shrub	95	10

Maytenus undata (Thunb.) Blakelock	CELASTRACEAE	Qoolaatii	Generalist	Shrub	16	3
Millettia ferruginea (Hochst.) Bak.	FABACEAE	Astiraa	Forest specialist	Small tree	654	62
Mimusops kummel A. DC.	SAPOTACEAE	Qoolaatii	Generalist	Tree	29	9
Myrsine africana L.	MYRSINACEAE	Qacama	Generalist	Shrub	9	1
Nuxia congesta R.Br. *ex Fresen.*	LOGANIACEAE	Qacama	Forest specialist	Small tree	1	1
Ocimum lamiifolium Hochst. ex Benth.	LAMIACEAE	Damaakkase	Pioneer	Shrub	2	1
Olea welwitschii (Knobl.) Gilg & Schellenb.	OLEACEAE	Bayaa	Forest specialist	Tree	91	36
Oxyanthus speciosus subsp. stenocarpus DC	RUBIACEAE	Imbiraangoo	Forest specialist	Shrub	139	22
Pavetta abyssinica Fresen.	RUBIACEAE	Xumaanee	Forest specialist	Small tree	637	21
Pentas schimperiana subsp. schimperiana (A. Rich.) Vatke	RUBIACEAE	Simararuu	Pioneer	Shrub	2	2
Phoenix reclinata Jacq.	ARECACEAE	Meexxii	Pioneer	Tree	51	10
Phyllanthus mooneyi M Gilbert	EUPHORBIACEAE	Kechema	Pioneer	Shrub	20	3
Phyllanthus ovalifolius Forssk.	EUPHORBIACEAE	Qacama	Generalist	Small tree	58	5
Phyllanthus reticulatus Poir	EUPHORBIACEAE	Qacama	Pioneer	Shrub	65	6
Pittosporum viridiflorum Sims	PITTOSPORACEAE	Soolee	Forest specialist	Small tree	39	16
Plectranthus garckeanus (Vatke) J.K. Morton	LAMIACEAE	Yaryoo	Generalist	Shrub	5	1
Podocarpus falcatus Mirb.	PODOCARPACEAE	Birbirsa	Forest specialist	Tree	29	12
Polyscias fulva (Hiern) Harms	ARALIACEAE	Daraku/Kariyoo	Forest specialist	Tree	20	17
Pouteria adolfi-friederici (Engl.) Baehni	SAPOTACEAE	Qararoo	Forest specialist	Tree	181	41
Premna schimperi Engl.	LAMIACEAE	Maraasisaa	Pioneer	Small tree	4	2
Prunus africana (Hook. f.) Kalkm.	ROSACEAE	Oomoo	Forest specialist	Tree	66	12
Psidium goajava L.	MYRTACEAE	Zayitunaa	Pioneer-planted	Small tree	15	2
Psychotria orophila Petit	RUBIACEAE	Wandabiyyoo	Forest specialist	Small tree	806	34
Rhamnus prinoides L'Herit.	RHAMNACEAE	Geeshee	Pioneer	Shrub	37	7
Ritchiea albersii Gilg	CAPPARIDACEAE	Agabaatee	Pioneer	Small tree	3	2
Rothmannia urcelliformis (Hiern) Robyns	RUBIACEAE	Mixoo	Forest specialist	Small tree	169	35
Rytigynia neglecta (Hiern) Robyns	RUBIACEAE	Mixoo	Forest specialist	Shrub	596	42
Sapium ellipticum (Krauss) Pax	EUPHORBIACEAE	Bosoqa	Generalist	Tree	48	10
Sarcocephalus latifolius (Smith) Bruce	RUBIACEAE	Diboo	Pioneer	Small tree	25	1
Schefflera abyssinica (Hochst. ex A. Rich.) Harms	ARALIACEAE	Gatamaa/Bottoo	Forest specialist	Tree	28	19
Schefflera myriantha(Bak.) Drake	ARALIACEAE	Bottoo	Forest specialist	Small tree	3	1
Senna occidentalis (L.) Links	FABACEAE	Salaamakii dimaa	Pioneer	Shrub	226	16
Senna petersiana (Bolle) Lock	FABACEAE	Salaamakii adii	Pioneer	Shrub	199	19
Solanecio gigas (Vatke) C. Jeffrey	ASTERACEAE	Doomboorokoo	Pioneer	Shrub	70	11
Solanecio mannii (Hook. f) C. Jeffrey	ASTERACEAE	Haamitii-baloo	Forest specialist	Small tree	41	10
Solanum giganteum Jacq.	SOLANACEAE	Unknown	Generalist	Shrub	1	1
Syzygium guineense subsp. guineense F. White	MYRTACEAE	Baddeessa	Forest specialist	Tree	361	58
Teclea nobilis Del.	RUTACEAE	Hadhessaa	Forest specialist	Small tree	253	28
Trichilia dregeana Sond.	ASTERACEAE	Anuunuu	Forest specialist	Tree	146	20
Unidentified sp.1	RUBIACEAE	Mixoo	Generalist	Shrub	180	12
Vepris dainellii (Pichi-Serm.) Kokwaro	RUTACEAE	Hadhessaa babalaa	Forest specialist	Small tree	675	69
Vernonia adoensis Sch. Bip. ex Walp.	ASTERACEAE	Tuurujee	Pioneer	Shrub	8	2
Vernonia amygdalina Del.	ASTERACEAE	Ibicha	Generalist	Shrub	112	21
Vernonia auriculifera Hiern.	ASTERACEAE	Reejii	Pioneer	Shrub	1287	49
Vernonia hochstetteri Sch. Bip. ex Walp.	ASTERACEAE	Xasee	Pioneer	Shrub	16	5
Vernonia sp.1	ASTERACEAE	Reejii Arbaa	Pioneer	Shrub	3	1
Vernonia sp.2	ASTERACEAE	Sooyyama	Generalist	Shrub	12	4
Vernonia thomsoniana Olivo & Hiern ex Oliv.	ASTERACEAE	Sooyyama	Pioneer	Shrub	8	2

Chapter III

Chapter IIIa

Coffee management and the conservation of forest bird diversity in southwestern Ethiopia

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If a bird does not recognise a tree, it will not rest on it.

Proverb

Abstract

Moist evergreen forests of southwestern Ethiopia host high levels of biodiversity and have a high economic value due to coffee production. Coffee is a native shrub that is harvested under different management systems; its production can have both beneficial and detrimental effects for biodiversity. We investigated how bird community composition and richness, and abundance of different bird groups responded to different intensities of coffee management and the landscape context. We surveyed birds at 66 points in forest habitat with different intensities of coffee management and at different distances from the forest edge. We explored community composition using detrended correspondence analysis in combination with canonical correspondence analysis and indicator species analysis, and used generalized linear mixed models to investigate the responses of different bird groups to coffee management and landscape context. Our results show that (1) despite considerable bird diversity including some endemics, species turnover in the forest was relatively low; (2) total richness and abundance of birds were not affected by management or landscape context; but (3) the richness of forest and dietary specialists increased with higher forest naturalness, and with increasing distance from the edge and amount of forest cover. These findings show that traditional shade coffee management practices can maintain a diverse suite of forest birds. To conserve forest specialists, retaining undisturbed, remote forest is particularly important, but structurally diverse locations near the forest edge can also harbour a high diversity of specialists.

Introduction

Tropical forest biodiversity is rapidly declining due to the conversion of forests to agriculture and the intensification of traditional agricultural systems (Wright 2005). Between 1990 and 2010, the amount of deforested land across the wet tropics increased by 62% (Kim et al. 2015), coupled with a 40% increase in human population numbers (Edelman et al. 2014). For tropical biodiversity conservation to be successful, it needs to promote and ensure viable rural livelihoods. In this context, tropical agroecosystems and in particular shade coffee agroforests have received considerable attention, given their potential benefits for both conservation and livelihoods (Bhagwat et al. 2008; Reed et al. 2017).

Coffee is one of the world's major agricultural commodities grown in tropical areas (Jha et al. 2014) occupying an area of 10.5 million hectares worldwide (FAO 2014). The species *Coffea arabica* represents two thirds of the world's coffee market (Aerts et al. 2011), and is mostly produced in agroforests (Perfecto et al. 1996; Jha et al. 2014). To date, the vast majority of research investigating the implications of coffee production for biodiversity has focused on Latin America (Philpott et al. 2008 and references therein). However, coffee is also of particular relevance in East Africa, from where it originates (Senbeta and Denich 2006). The Arabica coffee shrub is native to the biodiversity hotspot of wet Afromontane forests of southwestern Ethiopia, where it naturally occurs at low densities (Labouisse et al. 2008). In Ethiopia, coffee is a highly valued cash crop, with significant economic and cultural value (Petit 2007).

Coffee in Ethiopia is traditionally grown in agroforests, under the shade of native trees but with varying degrees of management. Management can range from very little or no intervention, to the pruning and thinning of the canopy, coupled with the removal of understorey species that may compete with coffee (Aerts et al. 2011). In the last few decades, coffee growing areas of southwestern Ethiopia have experienced both high rates of deforestation (mainly for agriculture) and a push towards the intensification of coffee production in state and privately owned plantations (Tadesse et al. 2014a). Intensification is achieved through different management practices, including the reduction of shade tree cover and diversity; an increase in coffee density; the replacement of native shade trees with faster growing exotic species; the use of agrochemicals; and the use of improved coffee varieties (Tadesse et al. 2014b). Accordingly, coffee growing has mixed effects on biodiversity conservation in southwestern Ethiopia. On the one hand, coffee production can help to reduce deforestation, because it provides a source of revenue from remnant forest, thus creating an incentive to maintain it (Philpott and Bichier 2012; Hylander et al. 2013). On the other hand, a shift towards more intensively managed coffee plots can cause the homogenization and simplification of forest structure and diversity, with potentially negative effects on biodiversity (Aerts et al. 2011; Hundera et al. 2013).

Different species can be expected to respond in different ways to coffee management, and a mixture of positive, negative or null responses of species to coffee management practices have been reported (see Komar et al. 2006 and Philpott et al. 2008 and references therein). Typically, forest specialist species respond positively to systems with a high degree of naturalness, whereas generalist species tolerate more disturbed or simplified systems (Tejeda-Cruz and Sutherland 2004). The ability of species to persist in landscapes with different degrees of coffee management will depend on a variety of factors, including: (1) species life history traits and ecological attributes (such as breeding and feeding strategies and habitat affinity) (Newbold et al. 2013); (2) site-specific conditions (such as vegetation structure and composition) (Leyequién et al. 2010); and (3) landscape context (such as landscape configuration, natural forest cover surrounding a site and distance to edge) (Tejeda-Cruz and Sutherland 2004; Anand 2008). Site-specific conditions and landscape context, in turn, can be expected to co-vary, with sites near forest edges being more disturbed and structurally different from reference sites deep within the forest (Harper et al. 2005). Both the management of coffee sites and the landscape context are thus important for biodiversity outcomes, but because they often co-vary, their separate effects remain poorly understood. Therefore, and especially in the context of rapidly changing coffee management in Ethiopia, a better understanding of the effects of landscape context and site-specific conditions is urgently needed to inform appropriate management practices.

Here, we used birds as a focal taxon. Birds play important functional roles in ecosystems, as seed dispersers, pollinators, predators and ecosystem engineers, thereby providing a direct link between biodiversity and ecosystem functions and services (Şekercioğlu 2006). In Ethiopia, few studies have documented the effects of coffee management on bird diversity (but see Gove et al. 2008; Buechley et al. 2015; Engelen et al. 2016). Existing studies suggest that relatively intensively managed coffee systems had higher species richness than forests with more sparse coffee (Buechley et al. 2015), but that forest specialists may decline with increasing coffee density (Gove et al. 2008). Notably, to date, the value of undisturbed forest areas has not been systematically compared with locations managed at different intensities, and the effects of site-specific characteristics and landscape context remain poorly understood. To overcome these shortcomings, we investigated (*i*) how bird community composition changes along a gradient of coffee forest management; and (*ii*) how management intensification and landscape characteristics relate to the richness and abundance of different groups of birds, including functional groups and species with different range sizes.

Methods

Study area

Our study was conducted in an area of approximately 3800 km^2 in the Jimma Zone, Oromia (Fig. 1). It focused on three districts (*woredas*): Gera, Gummay and Setema. The region is undulating, with steep slopes and flat plateaus in some areas, and elevation ranges from 1900 to 3000 m above sea level. The climate is conditioned by the Inter-Tropical Convergence Zone (Schmitt et al. 2013), with 1500-2000 mm of annual rainfall (Friis et al. 2011), and a mean annual temperature of approximately 20°C (Cheng 1998). The region is part of the Eastern Afromontane Biodiversity Hotspot (Mittermeier et al. 2004), and natural vegetation is dominated by moist evergreen Afromontane forest (Friis et al. 2011). Common canopy tree species include *Olea welwitschii, Pouteria adolfi-friederici, Schefflera abyssinica, Prunus africana, Albizia spp.*, *Syzygium guineense*, *Croton macrostachyus* and *Cordia africana* (Cheng 1998). Coffee is native to the region and primarily occurs between altitudes of 1500 and 1900 m (Senbeta et al. 2014). Existing studies suggest a high richness of both trees (> 140 species; Senbeta et al. 2014) and birds (> 110 species; Gove et al. 2008; Engelen et al. 2016), including some endemics. Approximately half of the study area is covered by forest, while the remainder is used for smallholder farming. Human population density in the region has been steadily increasing for several decades (Teller and Hailemariam 2011). Consistent with this, since the 1970s, forest cover has been decreasing, mainly as a result of the conversion of forest to farmland (Cheng 1998; Hylander et al. 2013).

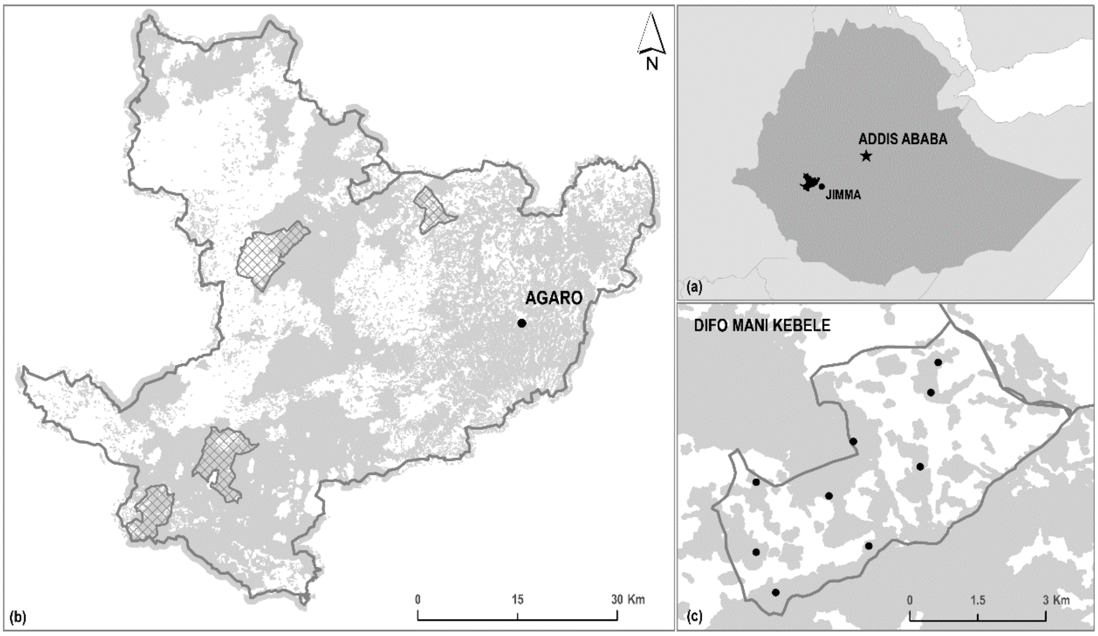

Figure 1. Location of (a) study area in Jimma zone, southwestern Ethiopia; (b) the five focal kebeles in Agaro/Jimma zone (hatched); (c) example of sampling design with survey points (black bullets) in one kebele. In (b) and (c) grey colour depicts woody vegetation.

Selection of survey sites and land cover mapping

We aimed to capture the entire gradient of available forest conditions, both in terms of coffee management and remoteness (Fig. 2). Unlike many other authors, we specifically avoided a priori categories such as "forest coffee", "semi-forest coffee", "semi-plantation", "plantation" and "garden coffee" (e.g. Hundera et al. 2013; Tadesse et al. 2014b; Worku et al. 2015). Despite their intuitive appeal, such classifications are not consistently defined across different studies and regions (Philpott et al. 2008; Moguel and Toledo 1999).

To establish survey sites, first, we selected five *kebeles,* which represent the smallest administrative unit in Ethiopia. *Kebeles* are meaningful units from both social and biodiversity perspectives. It is at the *kebele* level that important land use decisions are taken. Also, logistics, including research permits, are tied to the *kebele* level. From a biodiversity perspective, *kebeles* are also a relevant unit: they are relatively homogeneous units in terms of policy regime and their size is typically relevant as "landscape context" for organisms such as birds. *Kebeles* were selected to cover different social and landscape contexts: ranging from higher to lower dependence on coffee, from higher to lower levels of isolation from major towns, and from high to low levels of forest cover. Their size ranged from 19 km^2 to 52 km^2. We used RapidEye satellite images from 2015 (5 m resolution) to derive a map of woody versus non-woody vegetation, using an automatic classification routine, based on Maximum Likelihood in ArcGIS (ESRI 2013).

Second, we sought to stratify our sites in a way that most likely captured the full gradients of site-specific conditions and landscape context. To this end, and since we had no a priori knowledge of the survey sites, we created a map of the 'cost distance' to each point within the forest from the closest point of adjacent farmland. We assumed that management level (and consequently the naturalness of the site) would be closely related with people's accessibility to the forest, a proxy for the level of human interference. Therefore, remote sites would have a very low or no management for coffee, whereas more intensive management could be expected in more easily accessible areas.

We used the cost distance analysis tool in ArcGIS, which takes into account the distance to a given point and includes a penalty for steep slopes. A total of 66 survey sites were randomly distributed within the 5 *kebeles* (between 8 and 21 points per *kebele*) in four cost distance classes (low, medium, high and very high cost distance). Thus, our survey sites were located in forests varying in accessibility and in the degree of management for coffee production (Fig. 2). The gradient of environmental conditions thus spanned sites located in intact, remote forest to sites located in relatively intensively managed shade coffee forest. More intensively managed forest coffee sites were characterized by a higher level of understory clearing and canopy thinning and pruning. Despite their reduced diversity in woody species, these sites originated directly from patches of undisturbed forest and still contained relict trees of the original canopy cover.

Figure 2. Examples of southwestern Ethiopian forests with increasing coffee dominance: (a) deep forest interior without management for coffee production; (b) forest interior with low coffee management intensity; and (c) forest that is intensively managed for coffee production.

Data collection

Bird data

We sampled birds using two repeated 15 min point counts, within 1 ha circular sites (radius = 56 m) around each of the 66 previously identified locations, between November 2015 and February 2016. Sampling took place between 06h00 and 10h30 in the morning. All birds seen or heard within the sites were recorded. A recorder (Linear PCM Olympus LS-14) was used to aid post hoc identification of birds not identified in the field. Surveys were cancelled on rainy and foggy days and all birds flying over, plus raptors, swifts and swallows were excluded. Bird species were classified into different ecological groups according to (1) diet, (2) foraging strategy, (3) migration status, (4) forest dependency, and (5) degree of endemicity. Diet and foraging strategies described the use of forest resources in terms of major food sources and vertical strata explored, while migration status described the degree of seasonal movements and residency of birds. Forest dependency referred to the level of association with forest habitat. Diet and foraging strategy were gathered from the Elton Traits Database (Wilman et al. 2017). Forest dependency, migration status and the degree of endemicity were derived from Birdlife International's World Database (retrieved at http://www.birdlife.org/datazone) and complemented with data from The Handbook of the Birds of the World (del Hoyo et al. 2014). The degree of endemicity was calculated for each species as the inverse of their documented spatial extent of occurrence.

Vegetation and environmental data

We surveyed woody vegetation at each survey point, in a plot of 20 m by 20 m. In each plot we quantified three management-related variables: (1) woody plant species richness, (2) mean diameter at breast height of woody species (dbh), and (3) coffee dominance. Woody plant species richness was assessed for shrubs and trees with heights ≥ 1.5 m and dbh ≥ 5 cm. Mean dbh per plot was calculated as the average dbh of all woody plant species that met these criteria. Coffee dominance was assessed as ranging from 0 to 1, and calculated as the ratio of the number of coffee plants to the total number of woody plants in each plot. In addition to vegetation data, we considered three landscape-related variables: (1) distance to the forest edge, (2) a wetness index, and (3) proportion of canopy cover within a 200 m radius. Distance to the forest edge was calculated from the centre of the survey site to the closest edge. Here, we used Euclidean distance (ranging between 10 and 900 m) rather than the cost distance used for site selection because the two measures were highly correlated, and Euclidean distance had a more direct interpretation. The topographic wetness index was derived using the ArcHydro Toolbox in ArcGIS (ESRI 2013), based on the ASTER Global Digital Elevation Model v2 (30 m resolution; https://reverb.echo.nasa.gov/). Canopy cover within a 200 m buffer around each survey site was calculated from the map of woody vegetation derived from RapidEye imagery.

Data analysis

To investigate patterns in bird community composition and their relation with environmental variables we used detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA). We first used the DCA to explore the length of the environmental gradient and to determine the degree of species turnover in the community (a first axis length greater than 4 standard deviations represents a complete turn in species composition (Hill and Gauch 1980)). We then performed a CCA to explore the patterns of community composition in relation to the environmental variables (ter Braak 1986). Both DCA and CCA were performed on the bird community matrix of raw abundances, with rare species downweighted. For the CCA all vegetation and environmental predictors were scaled and tested for significance ($p < 0.05$) using 999 permutations (package *vegan* (Oksanen et al. 2013) in R (R Core Team 2016)).

For visualization purposes, we divided survey sites into two groups according to their degree of coffee dominance. Coffee occurs naturally at very low densities in unmanaged forest. Therefore, we adopted a cut-off value of coffee dominance to visualize relatively natural conditions as follows: sites with coffee dominance < 0.2 included minimal or no management for coffee ("without management"), whereas the remaining sites (coffee dominance ≥ 0.2) were considered to be managed for coffee production ("with management"). Indicator species analysis was used to explore the composition of bird assemblages at sites with and without coffee management. An indicator value (IndVal; varying between 0 and 1) was estimated for each species according to Dufrêne and Legendre (1997). Here, the maximum value (IndVal = 1) is attributed to a species when it is found in all sites of a group (maximum specificity) and exclusively within that group (maximum fidelity). A species was considered to be an indicator when its IndVal ≥ 0.5 for a $p < 0.1$ (randomization procedure based on 999 permutations). The analysis was performed using the function *multipatt* in the package *indicspecies* (De Cáceres and Jansen 2016) in R (R Core Team 2016).

To model the effects of predictors on richness and abundance of different groups of birds we used generalized linear mixed models (GLMM). We used a Poisson distribution with log-link function for count data response variables and a Gaussian distribution with identity link for endemicity (Zuur et al 2009). *Kebele* was used as a random effect to account for spatially nested survey sites. We inspected models for overdispersion by examining residual plots. Models did not show evidence of overdispersion. Given high variation and multicollinearity among environmental predictors, we performed a principal components analysis (PCA) with varimax rotation to summarize the variation in environmental variables. We then used the rotated axes of the PCA as fixed effects in all models. All variables were scaled and centred before the PCA. Richness and abundance of the different bird groups were used as response variables. Total species richness was derived based on pooled data from both survey rounds, and total abundance was calculated as the maximum of individuals observed in a single survey. Modelling was performed in R (R Core Team 2016) using packages *lme4* (Bates et al. 2015) and *DHARMa* (Hartig 2016).

Results

We recorded 1344 individual birds from 76 species and 32 families (Table S1). Orioles (*Oriolus monacha* and *O. larvatus*), montane white-eye (*Zosterops poliogastrus*), green-backed camaroptera (*Camaroptera brachyura*), Rueppell's robin-chat (*Cossypha semirufa*) and Ethiopian boubou (*Laniarius aethiopicus*) were the most frequently encountered species. Twenty-one species were endemic to the Horn and Eastern Africa (Table A1), six of which were endemic to the highlands of Ethiopia and Eritrea: the yellow-fronted parrot (*Poicephalus flavifrons*), black-winged lovebird (*Agapornis taranta*), Abyssinian slaty flycatcher (*Melaenornis chocolatinus*), thick-billed raven (*Corvus crassirostris*), Abyssinian woodpecker (*Dendropicos abyssinicus*) and wattled ibis (*Bostrychia carunculata*). The number of bird species ranged from 4 to 20 per site, and the number of individuals from 5 to 37. We recorded 92 woody plant species (4 to 31 per site).

Community composition

The first DCA axis suggested less than one complete species turnover (length of 2.18 standard deviations), indicating substantial species overlap between sites. The CCA showed that bird community composition significantly correlated with environmental predictors (F = 1.597, $p < 0.05$). Significant environmental predictors associated with bird community composition were "coffee dominance" (F = 2.064, $p < 0.01$; Fig. 3) and "canopy cover 200m" (F = 2.349, $p < 0.05$; Fig. 3). Four indicator species were found for sites without coffee management: the narina trogon (*Apaloderma narina*), white-cheeked turaco *(Tauraco leucotis)*, brown woodland-warbler (*Phylloscopus umbrovirens*), and African hill-babbler (*Pseudoalcippe abyssinica*). One indicator species, the paradise flycatcher (*Terpsiphone viridis*), was found for sites with coffee management.

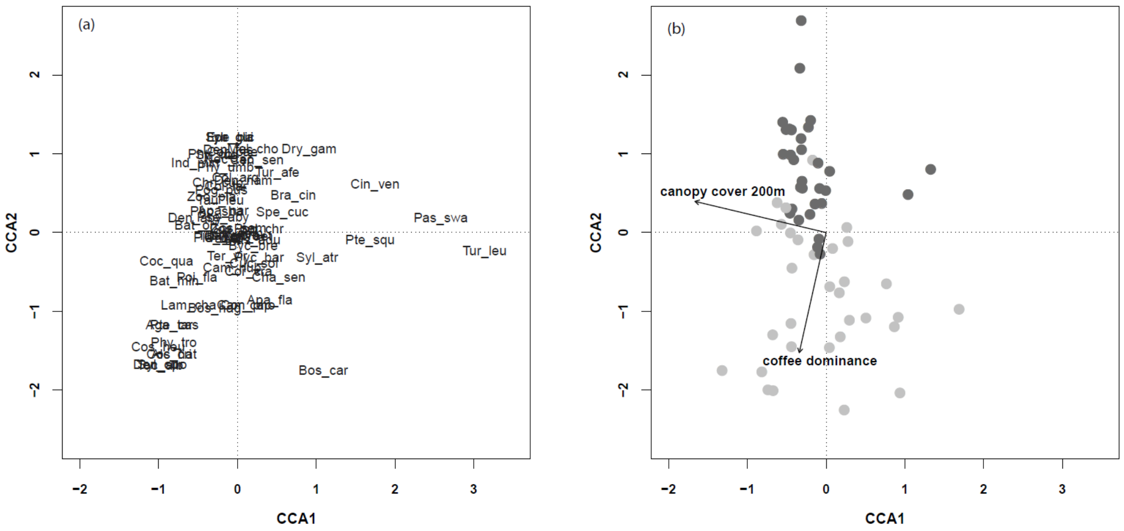

Figure 3. CCA ordination diagrams of bird community along the environmental gradients: (a) representation of species (species codes provided in Table A1); (b) representation of survey sites (dark grey correspond to sites "without coffee management" and light grey dots correspond to sites "with coffee management"); only variables with a significant relationship ($p < 0.05$) with bird community composition are represented by arrows. Labels of environmental variables: coffee dominance at the site ("coffee dominance"); proportion of tree canopy cover within a 200 m radius ("canopy cover 200m"). Note that the positive x-axis has been truncated to improve readability and one site (at x= 6.994 and y= -0.343) and six species (Vid_cal, Ser_str, Ser_cit, Cen_mon and Mel_edo, all with coordinates at x= 4.010 y= -0.121) therefore are not shown.

Bird responses to environmental gradients

The first two axes of the rotated PCA together explained 54% of variation in environmental data (Table 1). The first rotated axis (rPC1) explained 28% of the variation and represented a management gradient. Positive values of rPC1 indicated higher plant species richness and larger mean dbh values, whereas negative values indicated a higher dominance of coffee shrubs, lower plant species richness and smaller mean diameters. Thus, rPC1 represented a gradient from high naturalness (at high values) to intensive coffee management (at low values). The second rotated axis (rPC2) explained 26% of variation, and described a gradient of landscape context. Low values were assigned to sites closer to the forest edge, with little surrounding canopy cover, whereas high values described sites far from the edge, with more surrounding canopy cover (Table 1).

Table 1. Principal component analysis loadings after varimax rotation, and variance explained by the first two components (rPC1 and rPC2). Bold values represent the highest loadings on the positive and negative sides of the axes. Both components were used in the generalised linear mixed model analysis as predictor variables.

Variable	**rPC1**	**rPC2**
Plant species richness	**0.78**	0.15
Coffee dominance	**-0.65**	-0.27
Tree diameter (dbh)	**0.78**	-0.11
Distance edge	0.19	**0.84**
Canopy cover (200 m)	0.06	**0.86**
Wetness	0.11	0.03
% variance explained	28.0	26.0

In the mixed models, total species richness and total abundance did not respond to either gradient (Table A2). However, richness and abundance of highly forest dependent species, as well as richness of midhigh foragers responded positively to both lower intensity of management (rPC1) and higher canopy cover (rPC2) (Table 2, Fig. 4). Richness of insectivores responded positively to increasing canopy cover and distance from the edge. Both richness of frugivores and abundance of insectivores increased with less intensive management (Table 2, Fig. 4).

Discussion

The vast majority of studies assessing the effects of management for coffee production on biodiversity focus on the Neotropics. Although Ethiopian shade coffee may in fact be among the most bird-friendly coffee in the world (Buechley et al. 2015), prior to this study, little was known about bird distribution in the moist Afromontane forests of southwestern Ethiopia (but see Gove et al. 2008, Buechley et al. 2015, Engelen et al. 2016). More specifically, the effects of coffee production of different intensities, in different landscape contexts, and especially as compared to remote areas was virtually unknown in this biodiversity hotspot. In contrast to the common situation where landscape context and site-specific variables strongly co-vary, we found two independent gradients influencing community composition, richness, and abundance of bird groups. First, we identified a management gradient (from a high degree of forest naturalness to relatively intensive coffee management) to affect birds. Second, birds were influenced by a landscape context gradient (from the forest edge towards higher canopy cover in the interior). Our analyses highlighted that (1) despite considerable bird diversity, species turnover in the forest was relatively low; (2) total richness and abundance of birds were not affected by management or landscape context; but (3) the richness of forest and dietary specialists increased with higher forest naturalness, and with increasing distance from the edge and amount of canopy cover. We discuss these findings in relation to existing studies from Ethiopia and other tropical regions, and deduce implications for bird conservation.

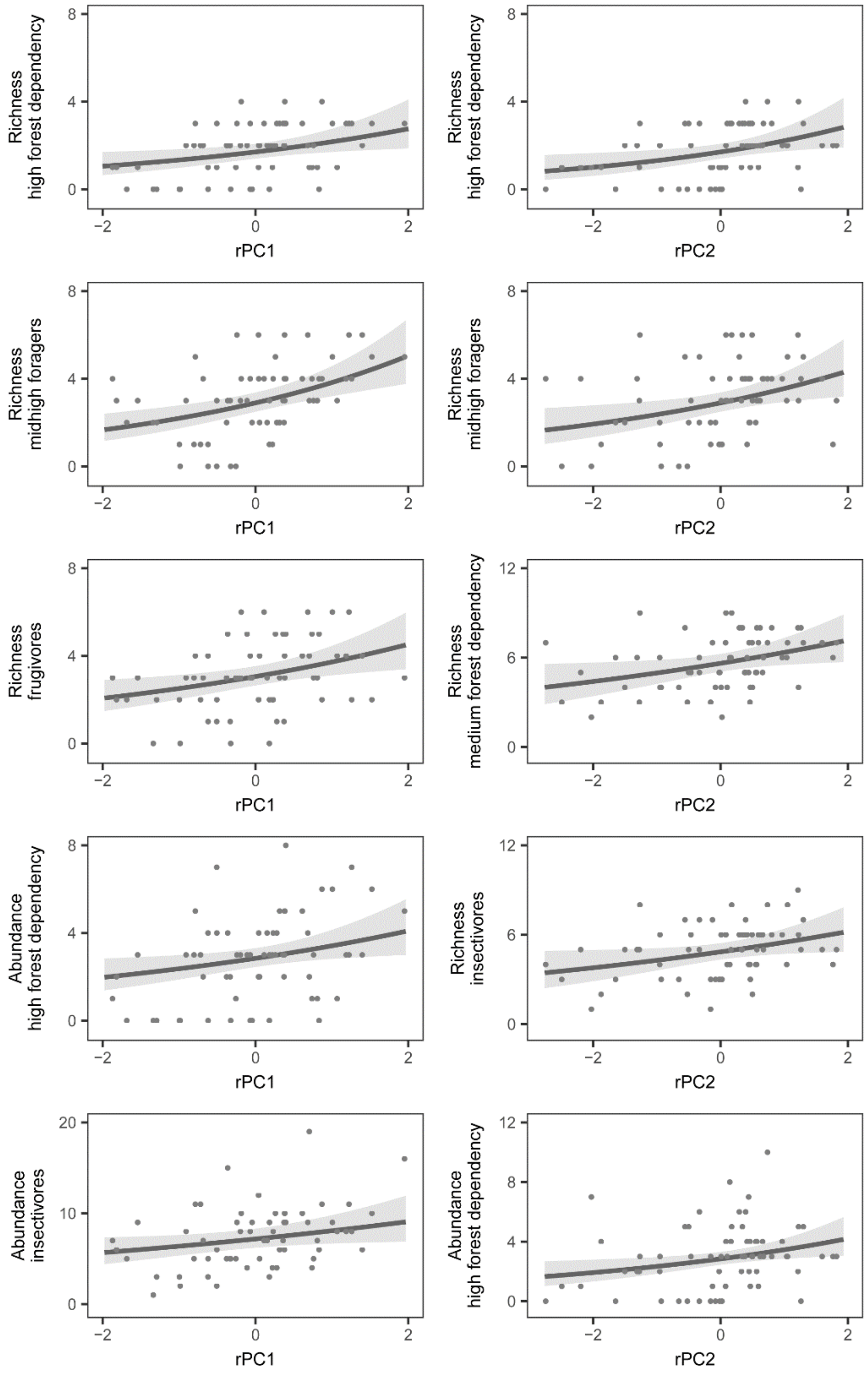

Figure 4. Responses of different bird groups to rotated PCA axes describing the environment. Only significant responses are represented. Data points are displayed in dark grey and light grey areas indicate 95% confidence intervals for the regression lines. rPC1 refers to the gradient of coffee management, with increasing values representing an increase forest naturalness and a decrease in coffee management intensity. rPC2 refers to a gradient of landscape context with high positive values describing sites further away from the forest edge and with higher proportion of forest cover.

Table 2. Results of generalized linear mixed models, assessing the effect of forest management on richness and abundance of bird groups. In all models kebele was included as a random effect. Only significant models are shown (n = 7 from a total of 21). rPC1 refers to the coffee management effect and rPC2 refers to the landscape context effect. Refer to Table A2 in Supplementary Material for the remaining models. Codes for the significance levels: *** p<0.001, **p<0.01, *p<0.05.

	Intercept [SE]	**rPC1 [SE]**	**rPC2 [SE]**	**Variance *kebele* [SE]**
Richness				
High forest dependency	0.531 [0.097] ***	0.242 [0.098] *	0.263 [0.101]**	0.000 [0.000]
Medium forest dependency	1.726 [0.052] ***	0.096 [0.053]	0.122 [0.054]*	0.000 [0.000]
Frugivores	1.117 [0.071] ***	0.197 [0.069] **	0.067 [0.071]	0.000 [0.000]
Insectivores	1.579 [0.056] ***	0.102 [0.057]	0.124 [0.058]*	0.000 [0.000]
Midhigh foragers	1.064 [0.074] ***	0.278 [0.073] *	0.204 [0.075]**	0.000 [0.000]
Abundance				
High forest dependency	1.045 [0.074] ***	0.183 [0.075] *	0.196 [0.077] *	0.000 [0.000]
Insectivores	1.971 [0.072] ***	0.118 [0.056] *	0.088 [0.056]	0.013 [0.114]

Findings in relation to existing studies from Ethiopia and other tropical regions

By using a spatially fully randomised design, with unbiased placement of survey sites away from roads and major tracks, we were able to cover a gradient of coffee production that was larger than the gradients covered in previous studies in the region. This approach yielded interesting findings. Unlike in most other studies, our data revealed independent effects of site-specific conditions and landscape context, with our results suggesting that both are important in determining richness and abundance of different bird groups.

Site-specific conditions and landscape context are shaped by environmental parameters and human interventions, and can influence species diversity and community composition (Clough et al. 2009). Bird diversity and composition are known to be affected by both local vegetation attributes (MacArthur and MacArthur 1961) and landscape context (Banks-Leite et al. 2010; Carrara et al. 2015). In most systems, site-specific effects and landscape context effects are confounded (and thus difficult to separate) because of an interplay of local and landscape processes via edge effects (Harper et al. 2005). In contrast, our analysis identified a clear separation of site-level, management-related attributes and landscape context. This unexpected finding suggests that some patches of forest are intensively managed, even though they are deep within the forest interior; while other patches remain relatively undisturbed, even though they are close to the forest edge. This, in turn, enabled us to assess whether birds responded primarily to management or to landscape context, a finding with important implications for conservation.

Total bird richness and abundance did not respond to either management or landscape context gradients. The lack of response to management is in line with a study from Tanzania, which found no effect of land-use intensification (from forest to coffee plantations) on the richness and abundance of birds and bats (Helbig-Bonitz et al. 2015). However, Buechley et al. (2015) found higher species richness in relatively intensively managed coffee systems than in forests with more sparse coffee, whereas many other studies have documented declines of overall richness and abundance of birds with coffee management intensification (reviewed in Komar et al. 2006 and in Philpott et al. 2008). The relatively small contrast between intensively and less intensively managed coffee forest sites in our study area may explain these differences.

Unlike for total richness and abundance, we observed responses to the forest management gradient for the richness and abundance of forest specialists, abundance of insectivores, and richness of midhigh foragers and frugivores. Homogenization of vegetation structure and composition has been reported to be detrimental for both forest specialists and insectivorous birds elsewhere (Şekercioğlu et al. 2002; Perfecto and Vandermeer 2008). Forest specialists are highly dependent on forest interior habitat and on specific microclimatic conditions. Insectivores, in particular, are known to benefit from high vegetation structural complexity, which is closely associated with food availability for this group (Mas and Dietsch 2003; Philpott et al. 2008). Management intensification therefore can have detrimental effects for these ecological groups: for example, pruning and thinning of the canopy and slashing of the understorey could reduce the availability and diversity of foraging sites (Waltert et al. 2005). Finally, landscape context also affected some ecological groups: highly and medium forest dependent species, insectivores and midhigh foragers were sensitive to the edge-interior gradient, with more species found in interior sites surrounded by high canopy cover. Species classified as highly dependent on forest showed an increase in both richness and abundance at sites that were located further from the forest edge, highlighting the importance of interior forest, irrespective of management, for some species.

Finally, with respect to bird community composition we found it to be relatively stable along the gradient of forest naturalness versus coffee management. While other studies have reported much higher turnover rates for birds in coffee systems, our results are broadly consistent with previous research in the region (Buechley et al. 2015). Discrepancies with other studies may be explained in two ways. First, many studies of bird communities in coffee growing areas have included homegardens (e.g. Gove et al. 2008; Helbig-Bonitz et al. 2015) or more intensive land uses such as sun coffee plantations (e.g. Greenberg et al. 1997a). This greatly increases the likelihood of finding high species turnover, by adding species that are associated with farmland habitats and open areas. Second, when compared with studies from the Neotropics (e.g. Tejeda-Cruz and Sutherland 2004; Greenberg et al. 1997b), community turnover in our study may be relatively low because evolutionary processes have led to a greater pool of species in the Neotropics (Jetz et al. 2012).

Conservation implications

There is a lively debate in the scientific community regarding the best approaches to retain biodiversity while securing livelihoods (Fischer et al. 2014, 2017). Two major discourses stand out: "land sparing" versus a focus on "countryside biogeography". The discourse on land sparing emphasises the supreme importance for conservation – especially of sensitive species – of maintaining large blocks of undisturbed forest (Green et al. 2005; Phalan et al. 2011, Hulme et al. 2013). On the other hand, countryside biogeography highlights the value of integrated management of conservation and production areas throughout the landscape "matrix", that is, areas outside natural forest (Daily 2001). Our findings show that these discourses need not be mutually exclusive (Kremen 2016).

One main finding of our study was the relative stability of community composition and richness and abundance of bird species along the gradient of coffee management. This suggests that under traditional shade coffee management practices, diverse forest bird communities can persist, as also observed elsewhere (e.g. Greenberg et al. 1996b). Our study thus underlines that appropriately managed forest ecosystems, where habitat complexity and plant species diversity are fostered, can serve conservation purposes while also contributing to rural livelihoods. Yet, our second major finding demonstrates that certain species (e.g. the Abyssinian ground-thrush and African hill-babbler) were primarily found in relatively remote areas with high naturalness. This supports existing evidence that conservation of sensitive species hinges on protecting areas that are largely free from human disturbance, for example via a strategy of "land sparing" (Gibson et al. 2011).

By separating the effects of site-specific conditions and landscape context on bird diversity we showed that both influence the richness and abundance of different bird groups – indicating that conservation measures need to consider both local and landscape scales. For instance, forest specialists and insectivores responded to the gradient of landscape context, implying that to assess only site-conditions would be insufficient. Yet, other species responded strongly to site level conditions, suggesting that looking exclusively at landscape context would ignore the potentially major benefits for conservation of retaining high structural complexity for local bird diversity. From a conservation perspective, we argue that the maintenance and protection of large undisturbed areas of natural forest should receive the highest priority, because many forest specialist are highly dependent on undisturbed areas. However, where the protection of large patches of remote forest is not possible, even fragmented forest managed at low intensities can support a diverse bird community. In the context of rapidly changing coffee production systems in Ethiopia, participatory forest management may help to achieve conservation goals on the ground. In our study area, three of the *kebeles* are within two Forest Priority Areas, the Sigmo-Geba and Belete-Gera areas (UNEP-WCMC 2016). These priority areas were established in the 1980s with the aim to protect and manage the remaining natural forests. To date none of these areas has been legally constituted and only Belete-Gera has a provisional forest management agreement between the government and the local community, which prevents the on-site enforcement of conservation provisions.

Conclusion

Traditional coffee agroforests in southwestern Ethiopia host a diverse community of birds. However, some uncertainty still remains regarding the potential of these systems to host sensitive species such as forest specialists. Thus, while coffee agroforests are valuable for bird conservation they should not be considered a replacement for natural undisturbed forests. The landscape of southwestern Ethiopia is vulnerable to the intensification of traditional coffee agroforest systems and to the conversion of natural forests into agricultural land. Because coffee production in the region is of great importance for rural livelihoods, guidelines for coffee production should both secure livelihoods as well as promote biodiversity. Management strategies and certification schemes that encourage traditional practices (i.e. that foster habitat complexity and heterogeneity) and the retention within the matrix of large undisturbed natural forests should be promoted in the region if conservation and rural livelihoods improvement are to be achieved together.

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Supporting Information for Chapter III (a)

Coffee management and the conservation of forest bird diversity in southwestern Ethiopia

Table A1: Species list, classification used and number of individuals recorded. The scientific nomenclature follows Birdlife International 2016. Diet and foraging strategy were gathered from Elton Traits Database (Wilman et al. 2014) and forest dependency, migration status and the degree of endemicity were derived from Birdlife International's World Database. Classification codes: Endemics (End): HA (Horn of Africa), EA (East Africa), EE (Ethiopia & Eritrea), ETH (Ethiopia); Diet: V (vertebrates), F (frugivores and nectarivores), O (omnivores), I (insectivores), P (plants and seeds); Foraging strategy (Forag.): gr (ground foragers), c (canopy foragers), un (understorey), g (generalists), mh (midhigh), gr/u (ground/understorey), mh/c (midhigh/canopy); Forest Dependency (For. Dep.): Low (low forest dependency), Med (Medium Forest dependency) and High (High forest dependency), NF (does not occur in forest). Migration status: non mig (non-migrant), full mig (full migrant), alt mig (altitudinal migrant); NA (not-applicable).

Family	Scientific Name	SpCode	Common Name	End.	Diet	Forag.	For. Dep.	Mig.	N. ind
Alcedinidae	*Alcedo cristata*	Alc.cri	Malachite kingfisher	-	V	water	Low	non mig	1
Bucerotidae	*Bycanistes brevis*	Byc.bre	Silvery-cheeked hornbill	EA	F	g	High	non mig	68
Bucerotidae	*Tockus alboterminatus*	Toc.alb	Crowned hornbill	-	O	c	High	non mig	2
Campephagidae	*Campephaga phoenicea*	Cam.pho	Red-shouldered cuckooshrike	-	I	g	Med	full mig	3
Campephagidae	*Coracina caesia*	Cor.cae	Grey cuckooshrike	-	I	mh/c	Med	non mig	2
Cisticolidae	*Apalis flavida*	Apa.fla	Yellow-breasted apalis	-	I	c	Med	non mig	1
Cisticolidae	*Camaroptera brachyura*	Cam.bra	Green-backed camaroptera	-	I	g	Low	non mig	96
Columbidae	*Columba arquatrix*	Col.arq	African olive-pigeon	-	F	g	Med	non mig	7
Columbidae	*Columba larvata*	Col.lar	Lemon dove	-	O	gr	Med	non mig	4
Columbidae	*Streptopelia lugens*	Str.lug	Dusky turtle-dove	EA	P	gr	Med	non mig	1
Columbidae	*Streptopelia semitorquata*	Str.sem	Red-eyed dove	-	P	gr	Med	full mig	26
Columbidae	*Turtur afer*	Tur.afe	Blue-spotted wood-dove	-	P	gr	Med	full mig	2
Columbidae	*Turtur tympanistria*	Tur.tym	Tambourine dove	-	P	gr	Med	full mig	70
Coraciidae	*Eurystomus glaucurus*	Eur.gla	Broad-billed roller	-	I	g	Med	full mig	2
Corvidae	*Corvus capensis*	Cor.cap	Cape crow	-	O	gr	NF	non mig	1
Corvidae	*Corvus crassirostris*	Cor.cra	Thick-billed raven	EE	O	gr	Low	non mig	6
Cuculidae	*Centropus monachus*	Cen.mon	Blue-headed coucal	-	V	g	Med	non mig	1
Cuculidae	*Centropus senegalensis*	Cen.sen	Senegal coucal	-	V	gr	Med	non mig	1
Cuculidae	*Centropus sp.*	Cen.sp	coucal	-	V	-	Med	non mig	1
Cuculidae	*Chrysococcyx cupreus*	Chr.cup	African emerald cuckoo	-	I	c	Med	full mig	8
Cuculidae	*Cuculus solitarius*	Cuc.sol	Red-chested cuckoo	-	I	g	Med	full mig	2
Estrildidae	*Coccopygia quartinia*	Coc.qua	Yellow-bellied waxbill	EA	P	g	NF	non mig	3
Estrildidae	*Spermestes bicolor*	Spe.bic	Black-and-white munia	-	P	gr/un	Low	non mig	2
Estrildidae	*Spermestes cucullatus*	Spe.cuc	Bronze munia	-	P	gr	Low	non mig	1
Fringillidae	*Serinus citrinelloides*	Ser.cit	Abyssinian citril	EA	P	gr/un	Low	non mig	2
Fringillidae	*Serinus striolatus*	Ser.str	Streaky seedeater	-	O	gr/un	Low	non mig	1
Indicatoridae	*Indicator minor*	Ind.min	Lesser honeyguide	-	F	un/mh	Med	non mig	1
Malaconotidae	*Dryoscopus gambensis*	Dry.gam	Northern puffback	-	I	mh	Low	non mig	1
Malaconotidae	*Laniarius aethiopicus*	Lan.aet	Ethiopian boubou	-	O	g	Med	non mig	80
Monarchidae	*Terpsiphone viridis*	Ter.vir	African paradise-flycatcher	-	I	c	Low	full mig	62
Muscicapidae	*Cossypha albicapilla*	Cos.alb	White-crowned robin-chat	-	I	gr	NF	non mig	1
Muscicapidae	*Cossypha heuglini*	Cos.heu	White-browed robin-chat	-	I	gr	Med	non mig	2
Muscicapidae	*Cossypha natalensis*	Cos.nat	Red-capped robin-chat	-	I	gr	Med	non mig	1
Muscicapidae	*Cossypha semirufa*	Cos.sem	Rueppell's robin-chat	-	I	gr/un	Med	non mig	80
Muscicapidae	*Melaenornis chocolatinus*	Mel.cho	Abyssinian slaty flycatcher	EE	I	gr	Low	non mig	7
Muscicapidae	*Melaenornis edolioides*	Mel.edo	Northern black flycatcher	-	I	g	Low	non mig	1
Muscicapidae	*Muscicapa adusta*	Mus.adu	African Dusky flycatcher	-	I	g	Low	non mig	22
Musophagidae	*Tauraco leucotis*	Tau.leu	White-cheeked turaco	HA	F	mh	Med	non mig	52
Nectariniidae	*Cinnyris venustus*	Cin.ven	Variable sunbird	-	O	g	Low	non mig	6
Nectariniidae	*Cyanomitra olivacea*	Cya.oli	Olive sunbird	-	F	un	Med	non mig	1

Nectariniidae	*Nectarinia tacazze*	Nec.tac	Tacazze sunbird	EA	O	g	Low	non mig	5
Nectariniidae	*Chalcomitra senegalensis*	Cha.sen	Scarlet-chested sunbird	-	O	g	NF	non mig	2
Oriolidae	*Oriolus sp (O. monacha & O. larvatus)*	Ori.sp	Orioles	NA	O	g	Low	non mig	125
Passeridae	*Passer swainsonii*	Pas.swa	Swainson's sparrow	HA	P	un	NF	non mig	2
Phasianidae	*Pternistis castaneicollis*	Pte.cas	Chestnut-naped francolin	HA	O	gr	Med	non mig	2
Phasianidae	*Pternistis squamatus*	Pte.squ	Scaly francolin	-	P	gr	High	non mig	1
Picidae	*Campethera nubica*	Cam.nub	Nubian woodpecker	EA	I	mh	NF	non mig	4
Picidae	*Dendropicos abyssinicus*	Den.aby	Abyssinian woodpecker	EE	I	mh/c	Med	non mig	3
Picidae	*Dendropicos fuscescens*	Den.fus	Cardinal woodpecker	-	I	g	Med	non mig	1
Picidae	*Dendropicos spodocephalus*	Den.spo	Eastern grey woodpecker	HA	I	g	Med	non mig	1
Picidae	*Dentropicos namaquus*	Den.nam	Bearded woodpecker	-	I	g	Low	non mig	1
Picidae	*Dendropicos sp.*	Den.sp	Woodpecker	-	I	NA	NA	non mig	3
Platysteiridae	*Batis minor*	Bat.min	Black-headed batis	EA	I	mh	Low	non mig	2
Platysteiridae	*Batis orientalis*	Bat.ori	Grey-headed batis	-	I	mh	NF	non mig	7
Platysteiridae	*Batis sp.*	Bat_sp	Batis sp.	-	I	mh	NA	non mig	4
Platysteiridae	*Platysteira cyanea*	Pla.cya	Brown-throated wattle-eye	-	I	mh	Med	non mig	7
Psittacidae	*Agapornis taranta*	Aga.tar	Black-winged lovebird	ETH	O	mh	Med	non mig	5
Psittacidae	*Poicephalus flavifrons*	Poi.fla	Yellow-fronted parrot	ETH	F	mh	Med	non mig	11
Pycnonotidae	*Pycnonotus barbatus*	Pyc.bar	Common bulbul	-	F	g	Low	non mig	70
Ramphastidae	*Lybius guifsobalitus*	Lyb.gui	Black-billed barbet	-	O	un/mh	Low	non mig	2
Ramphastidae	*Pogoniulus chrysoconus*	Pog.chr	Yellow-fronted tinkerbird	-	F	g	Low	non mig	23
Ramphastidae	*Pogoniulus pusillus*	Pog.pus	Red-fronted tinkerbird	-	F	g	Low	non mig	11
Ramphastidae	*Pogoniulus sp.*	Pog.sp	Tinkerbird	-	F	g	Low	non mig	8
Sturnidae	*Lamprotornis chalybaeus*	Lam.cha	Greater blue-eared glossy-starling	-	O	gr	Low	non mig	21
Sturnidae	*Lamprotornis sp.*	Lam.sp	Starling	-	NA	NA	NA	NA	15
Sturnidae	*Pholia sharpii*	Pho.sha	Sharpe's starling	EA	F	c	High	non mig	27
Sylviidae	*Bradypterus cinnamomeus*	Bra.cin	Bracken warbler	EA	I	gr	Low	non mig	12
Sylviidae	*Phylloscopus collybita*	Phy.col	Common chiffchaff	-	I	g	Med	full mig	12
Sylviidae	*Phylloscopus trochilus*	Phy.tro	Willow warbler	-	I	c	Med	full mig	2
Sylviidae	*Phylloscopus umbrovirens*	Phy.umb	Brown woodland-warbler	EA	I	mh	Med	non mig	45
Sylviidae	*Phylloscopus sp*	Phy.sp	-	-	I	NA	NA	NA	14
Sylviidae	*Sylvia atricapilla*	Syl.atr	Blackcap	-	O	mh	Med	full mig	28
Sylviidae	*Sylvia curruca*	Syl.cur	Lesser whitethroat	-	I	g	Low	full mig	1
Threskiornithidae	*Bostrychia carunculata*	Bos.car	Wattled ibis	EE	I	gr	NF	non mig	2
Threskiornithidae	*Bostrychia hagedash*	Bos.hag	Hadada ibis	-	I	gr	Low	non mig	5
Timaliidae	*Pseudoalcippe abyssinica*	Pse.aby	African hill babbler	-	I	mh	High	non mig	43
Timaliidae	*Turdoides leucopygia*	Tur.leu	White-rumped babbler	HA	O	gr	Low	non mig	4
Trogonidae	*Apaloderma narina*	Apa.nar	Narina trogon	-	I	mh	High	alt mig	41
Turdidae	*Turdus abyssinicus*	Tur.aby	Olive thrush	-	O	gr	Med	alt mig	14
Turdidae	*Zoothera piaggiae*	Zoo.pia	Abyssinian ground-thrush	-	O	gr	Hgh	non mig	13
Viduidae	*Vidua chalybeata*	Vid.cha	Village indigobird	-	P	mh	NF	non mig	1
Zosteropidae	*Zosterops poliogastrus*	Zos.pol	Montane white-eye	-	F	mh	Med	non mig	113

Table A2. Results of generalized linear mixed models, assessing the effect of forest management on richness and abundance of bird groups. In all models kebele was included as a random effect. Codes for the significance levels: *** p<0.001, **p<0.01, *p<0.05.

	Intercept [SE]	**rPC1** [SE]	**rPC2** [SE]	**Variance kebele** [SE]
Richness				
Total	2.433 [0.089] ***	0.008 [0.058]	-0.015 [0.057]	0.030 [0.174]
Low for dependency	1.426 [0.060] ***	0.026 [0.059]	-0.048 [0.059]	0.000 [0.000]
Ground foragers	1.083 [0.072] ***	-0.016 [0.073]	0.017 [0.072]	0.000 [0.000]
Non-migrants	2.126 [0.121] ***	-0.004 [0.065]	-0.061 [0.062]	0.059 [0.245]
Abundance				
Total	2.923 [0.095] ***	-0.003 [0.034]	-0.040 [0.039]	0.039 [0.198]
Low for dependency	1.995 [0.054] ***	-0.029 [0.049]	-0.028 [0.052]	0.001 [0.027]
Medium for dependency	2.117 [0.113] ***	0.032 [0.059]	-0.021 [0.059]	0.051 [0.225]
Frugivores	1.691 [0.113] ***	0.032 [0.078]	-0.096 [0.076]	0.042 [0.206]
Ground foragers	1.381 [0.119] ***	-0.054 [0.091]	-0.022 [0.091]	0.039 [0.199]
Understorey foragers	0.292 [0.107] **	0.169 [0.100]	-0.074 [0.102]	0.000 [0.000]
Midhigh foragers	1.511 [0.189] ***	0.134 [0.076]	0.007 [0.075]	0.151 [0.389]
Canopy foragers	0.335 [0.075]	-0.009 [0.121]	0.143 [0.126]	0.091 [0.303]
Non-migrants	2.650 [0.117] ***	-0.026 [0.046]	-0.081 [0.067]	0.061 [0.248]
(c) Endemicity	0.930 [0.202] ***	0.006 [0.063]	-0.053 [0.062]	0.193 [0.439]

Chapter IIIb

Bird diversity and the resilience of southwestern Ethiopian forests

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[Commentary]

Abstract

Coffee forests in southwestern Ethiopia host a diverse community of birds including some endemics. Different ecological bird groups respond differently to coffee management intensity, amount of forest cover and to distance to the forest edge. In this commentary we highlight the implications of these differential responses for the resilience of the forest ecosystem and outline research priorities for future studies of bird diversity in the region.

Commentary

Ethiopia's highlands are part of a biodiversity hotspot (Mittermeier et al., 2004), sustain large areas of continuous and undisturbed moist evergreen forest, and are where coffee (*Coffea arabica*) originates (Senbeta & Denish 2006). In the southwestern highlands, coffee is traditionally grown in the forest, under the shade of native trees, and management is implemented using traditional practices such as the pruning and thinning of the canopy and the clearing of the understorey (Aerts et al. 2011). However, high rates of human population growth and deforestation (mainly for cropland expansion) together with the intensification of the coffee production systems are currently threatening the forest ecosystems in the region (Tadesse et al. 2014). Forest coffee management, in particular, can have diverse outcomes for biodiversity conservation. On the one hand it provides a source of income from native forest, thus providing an incentive to help slow down deforestation (Hylander et al., 2013). On the other hand, a shift towards more intensively managed coffee, where vegetation structure and composition are simplified, most likely would be detrimental to biodiversity (Aerts et al. 2011).

In a recent study (Rodrigues et al. 2018), we assessed changes in the forest bird community along a gradient of coffee management intensity. We sought to understand how bird community composition, and richness and abundance of different ecological groups of birds responded to coffee management and landscape context. We surveyed birds at a total of 66 forest points that differed in their degree of coffee management and accessibility. The location of sampling sites ranged from the deep forest interior in nearly undisturbed forests, to locations close to the forest edge – which is often but not always where coffee is most intensively produced and managed (Figure 1). In this commentary, we expand the discussion of our study's results, highlighting implications for the resilience of the forest ecosystem and outlining research priorities for future studies of bird diversity in the region.

Figure 1. Southwestern Ethiopian forests: (a) view of continuous moist evergreen forests; (b) forest interior without management for coffee production; (c) forest intensively managed for coffee production.

Overall, we found a diverse community of forest birds (76 species, 6 of which were endemic to the highlands of Ethiopia and Eritrea), and we found no effect of coffee management and landscape context on total species richness and total abundance of birds. However, the richness and abundance of forest specialists and the richness of dietary specialists increased with higher forest naturalness (a local, management-related effect), and with increasing distance from the edge and amount of forest cover (a landscape context effect). As we explain below, these results have important implications for conservation measures, land management decisions, and the resilience of forest ecosystems (Figure 2).

One of our major findings, the lack of response of total bird richness and total abundance to both coffee management intensity and landscape context indicates that these two measures of diversity, when considered alone, may be insufficient to describe the diversity of an ecological community and can even mask changes in community patterns (Lewis 2009). Thus, this result highlights the importance of complementing total species richness and total abundance measures with guild-specific responses in the characterization of ecological communities undergoing environmental disturbance (Mac Nally et al., 2008).

Furthermore, the assessment of specific bird assemblages that are based on ecological criteria or functional attributes (such as feeding guilds or foraging strategies) allows the connection with specific functions and ecosystem services provided by birds. For instance, frugivorous birds are important seed dispersers and thus play a key role in forest regeneration, while insectivores play an important pest control function (Johnson et al., 2010). The decrease of both richness and abundance of different ecological groups thus may entail consequences for the ecosystem functions and services those groups provide (Clough et al. 2009; Şekercioğlu, 2006). Although a decline in richness alone might not compromise the delivery of a service (because few but dominant species may be able to maintain the function (Winfree et al. 2015), it can have a negative effect on the resilience of communities by reducing response diversity. Response diversity describes the diversity of responses different organisms exhibit to a particular disturbance or environmental change (Elmqvist et al., 2003). Reduced response diversity can undermine resilience because in a situation with low response diversity, a given change may negatively affect many species at the same time, thus compromising the capacity of the ecosystem as a whole to absorb and recover from disturbances (Mori et al., 2013).

Although our results do not allow us to draw conclusions regarding specific implications of declines of different ecological groups on ecosystem services and ecosystem resilience (see for instance Karp et al. 2011), they highlight the general importance of looking at responses of different ecological groups separately when addressing the effects and implications of forest management on biodiversity. For instance, our results suggest that forest naturalness benefits the richness of frugivores. However, since the abundance of frugivores was not affected by coffee management or landscape context, the service of seed dispersal might still be secured by the dominant frugivore species in the immediate term – but there might be a decline in response diversity and hence resilience to further changes in the future.

Possible scenarios for southwestern Ethiopian coffee forests span a wide range of possibilities. It is possible that coffee agroforests will expand into existing croplands, while traditional coffee is maintained in the forest. This would improve overall forest connectivity and reduce fragmentation, but could also lead to landscape and forest homogenization. At the other extreme, it is possible that farmland will further expand into currently forested areas, causing further fragmentation of natural forests, and accelerated biodiversity loss due to the intensification of coffee management in the remnant patches.

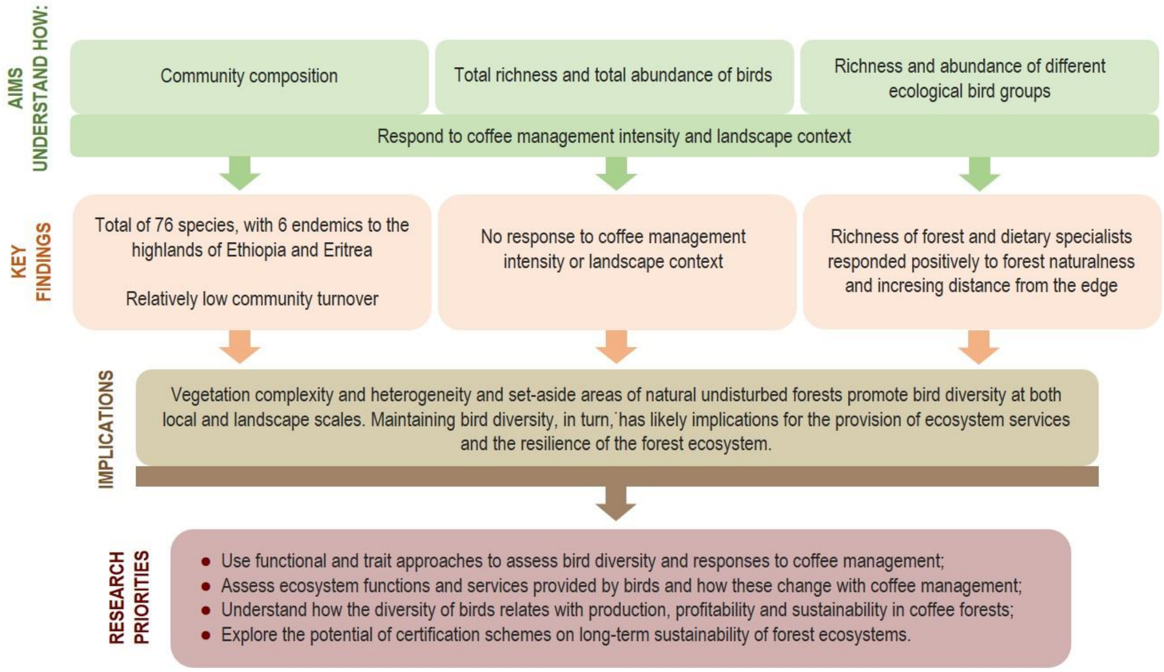

Figure 2. Aims of the study, major findings, implications for conservation and land management decisions, and research priorities for future studies on bird diversity in southwestern Ethiopia.

Despite the uncertainty associated with the future of southwestern Ethiopian forests, it is likely that coffee production will continue to be a major activity in the region. Therefore, understanding the extent to which coffee management affects different ecological communities and ecosystem services should be a priority for the region. Further research should focus on (1) the use of functional diversity and trait approaches to assess bird diversity and the responses to coffee management; (2) the assessment of ecosystem functions and services provided by birds and how these change with coffee management and landscape configuration; (3) understanding the relationships between bird diversity and the production and sustainability of coffee forests; and (4) the assessment of the potential of different coffee certification schemes (fair-trade, organic, bird-friendly) to improve the long-term sustainability of the forest ecosystem (Figure 2).

Ultimately, the resilience and sustainability of southwestern Ethiopian coffee ecosystems will rely on the how well the forests will be preserved and managed. Management and conservation measures should encourage traditional practices that promote the structural complexity of vegetation, as well as the maintenance and protection of large undisturbed areas of natural forest.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

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Chapter IV

Chapter IV

Living on the edge: rapid assessment of the mammal community in a coffee forest in southwestern Ethiopia

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[Short communication]

Introduction

The highlands of Ethiopia are within the Eastern Afromontane Biodiversity hotspot and contain some of the largest remaining patches of nearly undisturbed moist forest (Mittermeier et al., 2004). This region of Ethiopia is known as the evolutionary origin of coffee (*Coffea arabica*), and the production of the crop remains important to this day. Coffee is traditionally grown in forests, in the shade of native trees (Senbeta and Denish, 2006) and is managed mostly using traditional practices that maintain a diverse and complex forest structure (Aerts et al., 2011). Traditionally-managed coffee forests have the potential to benefit biodiversity by creating buffer areas, providing forest habitat for wildlife and plant species, and by slowing down deforestation rates for agricultural production (Hylander et al., 2013, Caudill et al., 2014). However, in recent decades, intensification of coffee production has been encouraged by national policies through the use of improved varieties, increasing coffee density, and reducing the diversity of shade trees, leading to simplification of forest structure and diversity (Tadesse et al., 2014a). In addition, despite the presence of coffee, ongoing expansion of agricultural land in the region increases deforestation rates, leading to forest fragmentation and increasing forest edge density (Tadesse et al., 2014b). Thus, while Ethiopia's coffee forests could potentially benefit biodiversity conservation, the combined threats of forest simplification and forest fragmentation can have severe impacts on species diversity (Hundera et al., 2013, Hylander et al., 2013).

To date, the conservation potential of Ethiopia's coffee forests has been assessed mostly for birds (Buechley et al., 2015, Rodrigues et al., 2018) and plants (Senbeta et al., 2014), including in the context of intensified coffee production (e.g. Gove et al., 2008, Aerts et al., 2011). Yet, very little information is available for mammals or other taxa. Mammals, however, are particularly sensitive to changes in forest extent and quality because many require large areas of near-natural forest habitat. At the same time, mammals can cause serious damage to people's livelihoods in terms of crop loss, livestock predation, and human injury, which may intensify as a consequence of changes to their habitat. Given the current threats facing coffee forest landscapes there is a critical need to assess which mammal species are still present in the region to inform future research and conservation priorities. Here, we present the first results of a rapid assessment of the mammal community present at the edge of coffee forests in southwestern Ethiopia. Rapid assessments of biodiversity are a useful approach to collect biodiversity data in poorly studied regions, when time and financial resources are limited (Silveira et al. 2003). Camera trapping is a widely used method to perform rapid assessments of the diversity of medium-sized and large mammals (Yasuda, 2004, Tobler et al., 2008). It is non-invasive and cost-effective, especially for cryptic species with elusive behavior and nocturnal habits (Munari et al., 2011). We recognize that a more comprehensive assessment, over longer periods of time, and including locations deep within the forest, would be desirable. Hence, we offer our findings as a starting point that can help inform future management and research priorities.

Methods

Study area

The study area encompasses an area of 3800 km² and is located in a coffee growing area in the Oromia region, southwestern Ethiopia (Fig. 1). Mammal communities were assessed in four *kebeles* (smallest administrative unit in Ethiopia) across three districts (*woredas*): Gera, Gumay and Setema. The region is undulating, with steep slopes and flat plateaus, and elevation ranging from 1500 to 3000 m above sea level. Wild coffee is usually found at elevations ranging between 1000 to 2000 m above sea level (Senbeta et al. 2014), although cultivated plants can be found between 900 and 2800 m (Hundera et al., 2013).

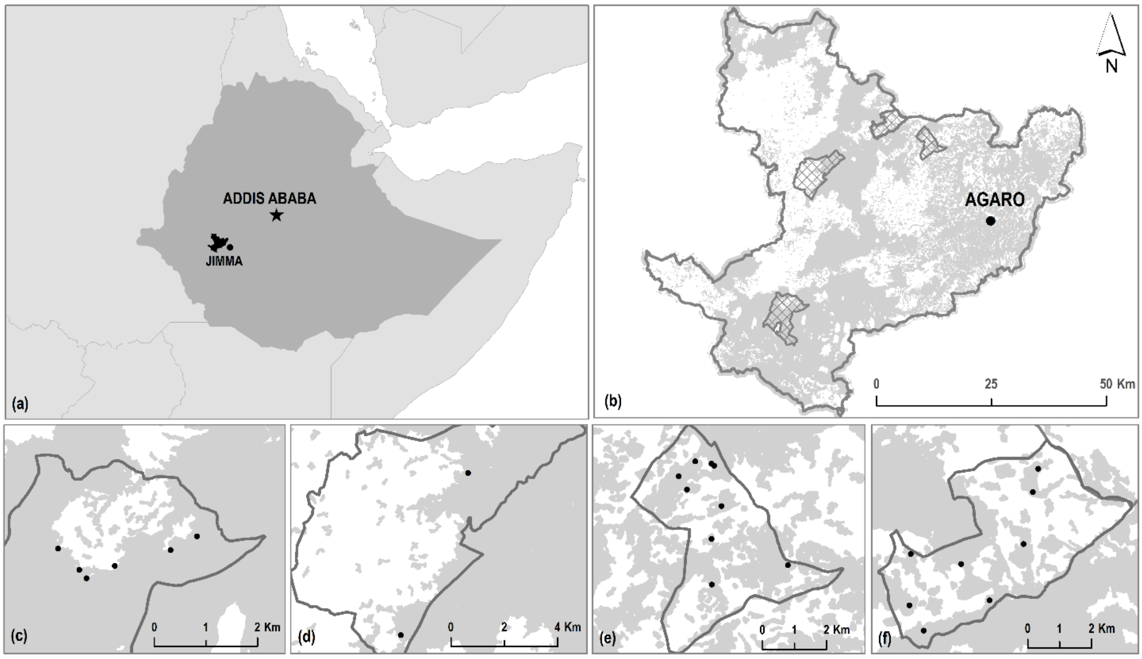

Figure 1. Study area and camera sites location: (a) study area in southwest Ethiopia; (b) selected *kebeles* (hatched) within the study area; (c), (d), (e), (f) camera sites in the different *kebeles*. Grey color in (b) to (f) depicts area of woody vegetation. Woody vegetation includes undisturbed natural forest and shade coffee forests, the latter being widespread near the forest edges in particular.

Data collection and data analysis

We randomly set-up twenty-five motion-triggered Bushnell Trophic Cam HD Max cameras, within forest near the forest edge, in the dry season from 8th November 2015 to 2nd February 2016. Although all of the kebeles have extensive coffee areas, and most of the cameras were placed within wild coffee altitude, seven cameras were placed in forest above wild coffee altitude. Cameras were placed along animal trails and in few cases on human trails. Cameras were tied to trees at knee height and no bait was used. The area in front of the camera was cleared of herbs and small shrubs to increase the potential for capture success and to prevent empty frame pictures triggered by wind. The clearance of vegetation can affect the detectability of species since some species can avoid open areas. Nonetheless, since the area cleared was relatively small (approximately 9 m^2) and the same procedure was applied to all of the cameras (n=25), we assume that its effect was minimal. Cameras were placed on average 40 m (SD± 26.95) from the forest edge, and were on average 1382 m apart from each other (minimum distance: 140 m; maximum distance: 6540 m). We focused on the forest edge because for this rapid assessment, it provided a logistically feasible entry point to learning about the regional mammal fauna; and because the forest edge is of major economic importance through the widespread production of coffee in this area. Technically, we defined the edge as the "interface between forested and nonforested ecosystems", which "appears as a belt of variable width" (Harper et al., 2005). Cameras were programmed to take photographs 24 hours/day, with sequences of three photographs at a time. Date and time of day were tagged in each photograph. Cameras were active between 13 and 60 days (average: 43 days), depending on logistical conditions beyond the control of the research team. No cameras were stolen, but two cameras stopped recording before the pick-up date, due to an unidentified equipment fault.

The pictures were manually classified using ExifPRO™ software. Empty frames and pictures with birds were excluded, and all pictures of humans were counted and then deleted from the database to comply with the ethics protocol approved by Leuphana University. All pictures triggered within a one hour period and for the same species were considered to be the same event (Rovero and Marshall, 2009). Species belonging to the families *Procaviidae*, *Leporidae*, *Canidae* and some species from *Herpestidae* and *Viverridae* could only be identified to genus level because of low image quality.

Given the scope of this research and the relatively small dataset, we opted for analyses that were suitable for a preliminary (rather than authoritative) assessment of the data. We therefore opted to use non-metric multidimensional scaling (NMDS), with Bray-Curtis distance measure, to investigate patterns in the mammal community. NMDS is a robust unconstrained ordination method commonly used in community ecology studies (Minchin, 1987). It runs on a distance matrix (or a matrix of dissimilarities) and attempts to represent the pairwise dissimilarity between objects (given by their rank order) in a low dimensional space defined beforehand (Bocard et al., 2011). In an NMDS diagram, sites that are similar in species composition are located close to each other, while sites that are less similar are placed further apart. The fit of the data is assessed by the stress value (low stress values indicate a good fit whereas stress values larger than 0.3 indicate a poor fit) (Zuur et al., 2007). For this analysis, we excluded the records of the Gambian squirrel and the crested-rat because camera-trapping is not the most appropriate method to survey these small-bodied species (for all scientific names, see Table 1). The NMDS was performed on the encounter rate matrix (number of independent events divided by sampling effort) and square-root transformed to decrease the influence of a small number of highly abundant species. NMDS was performed in R (version 3.3.1, R Core Team, 2016) using package vegan and function metaMDS (Oksanen et al., 2013).

Results and Discussion

Our sampling effort corresponded to 1075 camera trap days, retrieving a total of 101,435 pictures, of which 14% corresponded to wild mammal species (with 1292 independent events), 58% to people (59325 pictures) and 28% to empty frames. A total of 26 mammal species (including five congenerics) corresponding to 16 families were recorded (Table 1 and Figure 2). The order Carnivora was represented by eight species, Primates by six species and Artiodactyla by five species. The number of species detected per site varied between three and 14. Genets, baboons, bushduiker and bushbuck were the most common species (with more than 100 independent events and recorded at least in 15 sites; Table 1).

Importantly, the leopard was observed at the forest edge. This is a species of conservation concern (Vulnerable status on IUCN RedList, Stein et al. 2016), and one of the leopard records corresponded to a melanistic form of the species (Figure 2n) (da Silva et al., 2017). Mantled guereza and blue monkeys were documented together on the ground in a mixed-species group in two independent events, a behavior also observed elsewhere in Africa (e.g., Chapman and Chapman, 1995). Baboons were recorded feeding on coffee shrubs, which is in agreement with observations of local people who mentioned losses in coffee production due to baboons (Dorresteijn, personal communication). The crested-rat was detected at one site, in a highly fragmented coffee forest (in Kuda Kufi *kebele*, Figure 1e). This record complements findings by De Beenhouwer et al. (2016), who published a first observation of the crested-rat in the Afromontane rainforest in the nearby Belete-Gera forest. Our new record now expands the known distribution of this species to the north. Interestingly, while De Beenhouwer et al. (2016) observed the species in natural forest, and stipulated that low anthropogenic disturbance might have contributed positively to its survival, our record indicates that the species can also use more disturbed edge forest.

Table 1. Mammal species recorded by camera traps at the forest edge in southwestern Ethiopia, during a total of 1075 camera trap days. Nomenclature follows Wilson and Reeder (2005). NS: number of sites; NE number of independent events

ORDER & Family	Species	Common name	Species code	NS	NE
HYRACOIDEA					
Procaviidae	*Heterohyrax brucei* (Gray, 1868) and *Procavia capensis* (Pallas, 1766)	Hyrax	Hyraxes	12	27
TUBULIDENTATA					
Orycteropodidae	*Orycteropus afer* (Pallas, 1766)	Aardvark	Oryc_afer	3	3
PRIMATES					
Galagidae	*Galago senegalensis* (Saint-Hilaire, 1796)	Northern lesser galago	Gala_sene	2	3
Cercopithecidae	*Cercopithecus neglectus* (Schlegel, 1876)	De Brazza's monkey	Cerc_negl	1	1
Cercopithecidae	*Cercopithecus mitis* (Wolf, 1822)	Blue monkey	Cerc_miti	5	16
Cercopithecidae	*Chlorocebus aethiops* (Linnaeus, 1758)	Grivet monkey	Chlo_aeth	11	37
Cercopithecidae	*Papio anubis* (Lesson, 1827)	Olive baboon	Papi_anub	20	204
Cercopithecidae	*Colobus guereza* (Rüppell, 1835)	Guereza	Colo_guer	9	13
RODENTIA					
Sciuridae	*Heliosciurus gambianus* (Ogilby, 1835)	Gambian sun squirrel	Heli_gamb	1	1
Hystricidae	*Hystrix cristata* (Linnaeus, 1758)	Crested porcupine	Hyst_cris	14	42
Muridae	*Lophiomys imhausi* (Milne-Edwards, 1867)	Crested rat	Loph_imha	1	1
LAGOMORPHA					
Leporidae	*Lepus saxatilis* (Cuvier, 1823) and *L. capensis* (Petter, 1963)	Hare	Lepu_sp	5	64
CARNIVORA					
Felidae	*Panthera pardus* (Linnaeus, 1758)	Leopard	Pant_pard	2	3
Viverridae	*Civettictis civetta* (Schreber, 1776)	African civet	Cive_cive	14	67
Viverridae	*Genetta maculata* (Gray, 19830) and *G. genetta* (Linnaeus, 1758)	Genets	Gene_sp	21	305
Herpestidae	*Atilax paludinosus* (Cuvier, 1829)	Marsh mongoose	Atil_palu	3	3
Herpestidae	*Herpestes sanguinea* (Rüppell, 1835) and *H. ichneumon* (Linnaeus, 1758)	Mongoose	Herp_sp	5	7
Herpestidae	*Ichneumia albicauda* (Cuvier 1829)	White-tailed mongoose	Ichn_albi	9	41
Hyaenidae	*Crocuta crocuta* (Erxleben, 1777)	Spotted hyena	Croc_croc	6	39
Canidae	*Canis mesomelas* (Schreber, 1775) and *C. adustus* (Sundevall, 1847)	Jackals	Cani_sp	4	6
Mustelidae	*Mellivora capensis* (Schreber, 1776)	Ratel / honey badger	Mell_cape	3	4
ARTIODACTYLA					
Suidae	*Phacochoerus africanus* (Gmelin, 1788)	Warthog	Phac_afri	13	42
Suidae	*Hylochoerus meinertzhageni* (Thomas, 1904)	Giant forest hog	Hylo_mein	2	3
Suidae	*Potamochoerus larvatus* (Cuvier, 1822)	Bushpig	Pota_larv	17	45
Bovidae	*Tragelaphus scriptus* (Pallas, 1766)	Bushbuck	Trag_scri	18	128
Bovidae	*Sylvicapra grimmia* (Linnaeus, 1758)	Bushduiker	Sylv_grim	19	187

Figure 2. Some of the mammal species detected in the study area. (a) De Brazza monkey; (b) warthog; (c) bushpig; (d) African civet; (e) blotched genet; (f) aardvark; (g) Grivet monkey; (h) bushduiker; (i) spotted hyena; (j) colobus guereza; (k) blue monkey; (l) baboons; (m) porcupine; (n) leopard (melanistic form); (o) honey badger; (p) white-tail mongoose; (q) bushbuck.

The NMDS resulted in a two axis optimal solution (stress value: 0.194). In the ordination plot, the distribution of species across the sites indicated some clustering of species by ecological guild: carnivores clustered together at the right end of the first axis, horned ungulates at the left side of the diagram, and primates and wild pigs at the center (Figure 3). This result may indicate that regardless of site location, some species associated with human-wildlife conflicts, such as baboons, warthogs, bushpigs, grivet monkeys, hyenas, genets and civets, are always present at the forest edge. These species are commonly reported by locals to damage crops or attack domestic animals with major negative consequences for peoples' livelihoods (Lemessa et al., 2013, Ango et al., 2014, Dorresteijn et al., 2017). Because there appears to be no escape from potentially problematic mammals, there is a crucial societal need to understand the factors driving their distribution.

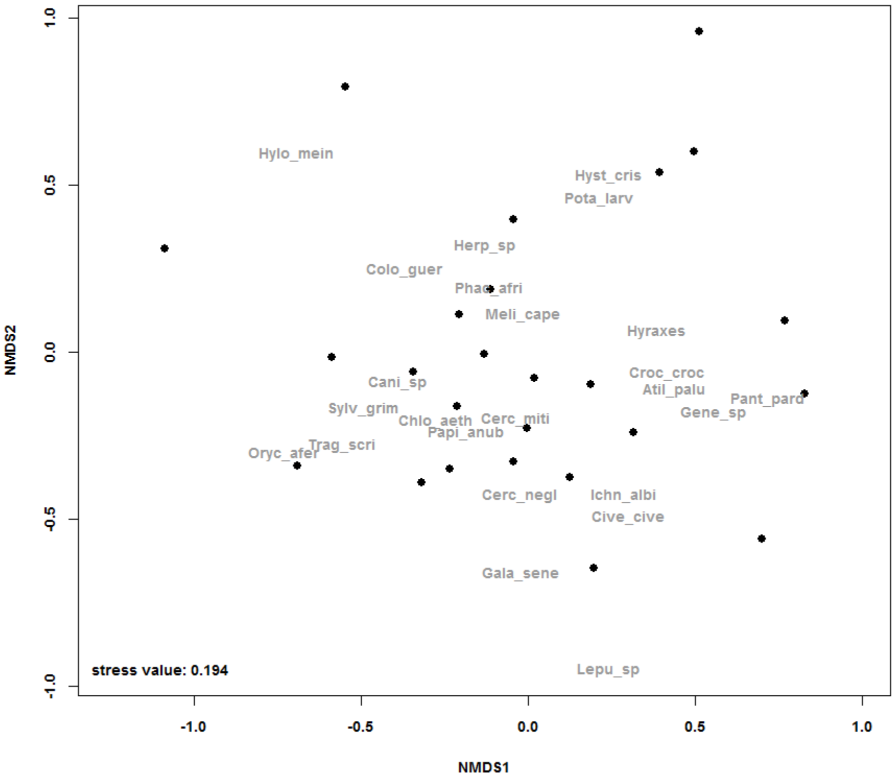

Figure 3. Ordination diagram using NMDS, showing some clustering of species by ecological guild: carnivores (Pant_pard; Gene_sp; Atil_palu; Croc_croc; Ichn_albi; Cive_cive) clustered together at the right end of the first axis, horned ungulates (Trag_scri and Sylv_grim) at the left side of the diagram and primates (Chlo_aeth; Cerc_miti; Papi_anub) and wild pigs (Phac_afri; Pota_larv) at the center. Black dots represent camera sites. Species codes are provided in Table 1. Only medium to large species were included.

Forest edges in the region are intensively used by local people for different purposes, including the collection of timber and firewood, as forage area for cattle, or to place beehives (Hylander et al., 2013, Dorresteijn et al., 2017). Furthermore, due to greater accessibility, the more intensively managed plots for coffee are also usually found at the forest edge. Perhaps surprisingly, despite this level of anthropogenic disturbance, many mammal species used the edges, including some typical forest interior species, such as the leopard and giant forest hog. Further research could compare the encounter rates of these species at forest edges with encounter rates in the forest interior, to better understand this finding. Key questions are whether forest edges are in fact sought out by these species because they offer access to useful resources (e.g. crops, livestock), or whether they represent spill-over or "sink" areas from core populations in the forest interior. Noting the potential of coffee forests for mammal conservation we highlight the need to further understand how these forests support mammal diversity. More research is especially needed to shed light on (1) the implications of coffee management intensification on the mammal community, and (2) the role of fragmentation on different mammal groups.

Central to answering these key priorities is to extend mammal research beyond the forest edge and into the poorly explored forest interior. Understanding mammal communities in the forest interior is needed as a baseline to assess the effect of different coffee management intensities on mammal communities. The possibility exists that different mammal groups respond differently to changes in forest structure and quality. For example, generalist species or species that draw on resources in the agricultural landscape may persist at the forest edge (Pfeifer et al., 2017), whereas more specialized species may be limited to interior areas with high forest cover and low fragmentation. Moreover, differential impacts of forest fragmentation on different mammal groups could potentially disrupt natural top-down trophic control of crop-raiding species (e.g. warthogs or baboons at the edge) by large predators (Estes et al., 2011), thereby further aggravating the problem of crop-raiding mammals for local people.

To summarize, coffee forests in southwestern Ethiopia hold promise for mammal conservation. However, a deeper understanding of mammal communities is needed to provide more complete insights for how to best manage the landscape for mammal conservation and for the mitigation of human-wildlife conflicts. In this context, gaining a better understanding of the dynamics between mammal distributions in the forest interior versus the forest edge should be prioritized.

Acknowledgements

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Chapter V

Chapter V

Leopard (*Panthera pardus*) distribution in the Afromontane coffee forests of southwestern Ethiopia

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[Manuscript in revision in Oryx]

> *The African leopard is an audacious animal, although it is ungrateful of me to say a word against him, after the way he has let me off personally ... taken as a whole, he is the most lovely animal I have ever seen; only seeing him, in the one way you can gain a full idea of his beauty, namely in his native forest, is not an unmixed joy to a person, like myself, of a nervous disposition.*
>
> Mary H. Kingsley. Travels in West Africa, Congo Français, Corisco and Cameroons. 2010. p.543

Abstract

The conservation status of the leopard *Panthera pardus* has been recently updated to “vulnerable” by the IUCN. In East and West Africa, leopard populations have declined by more than 50%. In the Horn of Africa, assessments are difficult to make given the scarcity of information regarding the species occurrence. In this study, we combined four systematic surveys using camera traps to assess leopard occurrence in two major coffee forest areas in the southwest of Ethiopia. We examined the relationships of leopard occurrence with forest cover and distance to the forest edge using generalized linear mixed models. Further, we used kernel density functions to examine leopard’s activity patterns in relation to human disturbance. Our study shows that leopards in the study area are fairly common residents, and more widely distributed than expected. Our results also show a strong positive relationship of leopard’s reporting rate with the amount of forest cover and shifts in leopard’s activity patterns in response to human disturbance. Our analysis suggests that the protection of remaining undisturbed forests is crucial for the conservation of leopards in the region. Since the leopard is considered the apex predator in this region, with cascading effects on lower trophic levels, an establishment of long-term monitoring protocols targeting the species and its prey would further support conservation efforts.

Introduction

Global biodiversity levels continue to decline and large carnivores are among the most impacted (Ripple et al. 2014, Wolf & Ripple 2017). Major threats to large carnivores include habitat loss, degradation and fragmentation, prey depletion, illegal hunting and human persecution (Wolf & Ripple 2016, 2017). Especially in Africa, a former stronghold of large carnivores, heavy range contractions and population declines have been recorded in the last decades (Bauer et al. 2015, Stein et al. 2016), with cascading effects on lower trophic levels (Atkins et al. 2019).

The leopard *Panthera pardus* is one of the species that have seen such a dramatic decline. Recent analyses indicate historical range contractions of 48-67% (Jacobson et al. 2016) and up to 80% according to Wolf & Ripple (2017). This has motivated a recent uplisting of the species from 'near threatened' to 'vulnerable' by the IUCN (Stein et al. 2016), as well as the listing as 'most endangered' on the CITES appendix I (2017). In East and West Africa, leopard populations are believed to have declined by more than 50% (Stein et al. 2016, Giordano et al. 2017). In East Africa, this reduction follows a general reduction in prey availability (estimated at 52%, Wolf & Ripple 2016). Other than prey decline, changes in habitat, poaching and human persecution are identified as the major ongoing causes for declines in leopard numbers and for the range contractions observed (Balme et al. 2010, Swanepoel et al. 2015, Stein et al. 2016, Rosenblatt et al. 2016, Ramesh et al. 2017).

These threats are further exacerbated in areas with high human population density, where the intersection of people and carnivores is strongest (Woodroffe 2000, Wolf & Ripple, 2017), especially because of the leopards' ecological requirements and behavioural traits. Leopards naturally occur at low densities, have low reproductive rates, and require large home ranges and prey biomass (Jacobson et al. 2016). Combined, these traits make leopards sensitive to anthropogenic pressures. On the other hand, it is a versatile species known to occur in a variety of habitats, with records even in urban metropoles (Brackzkowski et al. 2018).

Understanding the extent of range contractions, population declines and the impact of different threats is only possible when sufficient information on the species is available. In Ethiopia, the leopard remains poorly studied, and information regarding occurrence and distribution is mostly derived from studies that address human-wildlife conflicts based on interview data (e.g. Yirga et al. 2011, Gebresenbet et al. 2018). This is particularly so in the Southwestern highlands of Ethiopia, which are part of the Eastern Afromontane biodiversity hotspot and are home to some of the largest undisturbed patches of moist evergreen forest in the country (Gil et al. 2004). This is a region known as the evolutionary origin of Arabica coffee *Coffea arabica*, and the production of the crop is highly valued by locals and of high national importance (Petit 2007, Schmitt et al. 2010). People use the forest, and in particular the forest edge, for many different purposes, including for coffee cultivation and livestock grazing. In this forested part of the Ethiopian highlands, with very few confirmed lion records, leopards are considered the apex predator.

Using the largest dataset of leopard observations in the country, we contribute to fill the existing knowledge gap on leopard occurrence and distribution in Ethiopia. For this, we report leopard occurrence based on camera-trap surveys from two major forest areas in the southwest: Sheka and Jimma zones (where the leopard is currently classified as "possibly extinct", Stein et al. 2018). Since leopards are mostly associated to forest areas in this region (Myers 1976) and local livelihoods are highly dependent on forest resources (Shumi et al. 2019), we examined (1) the relationship of leopard occurrence with forest cover and distance to the forest edge, and (2) the extent to which the presence of people affects leopard activity patterns. We discuss our findings in light of the current knowledge of distribution and conservation of this species in the region.

Methods

Study area

The study area is located in southwestern Ethiopia and it covers two major zones (second-level administrative subdivision): Sheka and Jimma (Fig. 1). Both zones are within the Eastern Afromontane biodiversity hotspot and harbor large and continuous remnants of native moist evergreen montane forest. The topography of the region has undulating hills interspersed with steep slopes and flat plateaus, and the elevation ranges from 1500 to 3000 m above sea level. Arabica coffee plants are native to the area and occur naturally at low densities inside natural forests, usually between 1500 and 2000 m altitude (Schmitt et al. 2010). Coffee is cultivated by local residents in the forest with native shade trees and under different management intensities, and usually at the forest edge. For this study, a total of nine *kebeles* (smallest administrative unit in Ethiopia) (Fig. 1b) were sampled, using camera traps, in four different surveys, between 2014 and 2017 (Table 1).

Data collection

Jimma zone

Three systematic surveys, labeled as Survey 1, 2 and 3 (Table 1), were carried out in Jimma zone from August 2014 to March 2017, within two National Forest Priority Areas: the Belete-Gera forest and the Sigmo-Geba forest. Cameras were randomly placed in a total of 168 sampling sites, distributed in 9 *kebeles* (Table 1). Survey 1 aimed to compare mammal community composition in natural and coffee forests (Mertens et al. 2018). Cameras were programed to record 30-s videos and independent events for the same species were taken as observations separated by a minimum of 5 minutes, as described in Mertens et al. 2018. Cameras were active for 37 ± 16 days, on average. Survey 2 targeted the assessment of mammal community living at the forest edge (Rodrigues et al. 2019). Cameras were programmed to take pictures 24h/day, with sequences of three pictures at a time. Independent events for the same species were defined as records separated by one-hour period (Rodrigues et al. 2019). Cameras were active for 43 ± 10 days, on average. Survey 3 assessed mammal community composition at the forest edge and in the forest interior. Cameras were placed along two gradients: a gradient of forest cover and a gradient of edge amount, and were set in the field using the same settings described for Survey 2, and in Rodrigues et al. 2019. Cameras were active for 118 ± 34 days, on average.

Sheka zone

Survey 4 was carried out between February and June 2016 (Table 1), and encompassed the assessment of mammal communities in the Sheka Biosphere Reserve (De Beenhouwer et al. 2016). A total of 27 sampling sites across 2 *kebeles* were surveyed using camera settings as described above for survey 1. Cameras were active for 18 ± 8 days, on average. Details on location, duration and sampling effort for each survey are provided in Table 1.

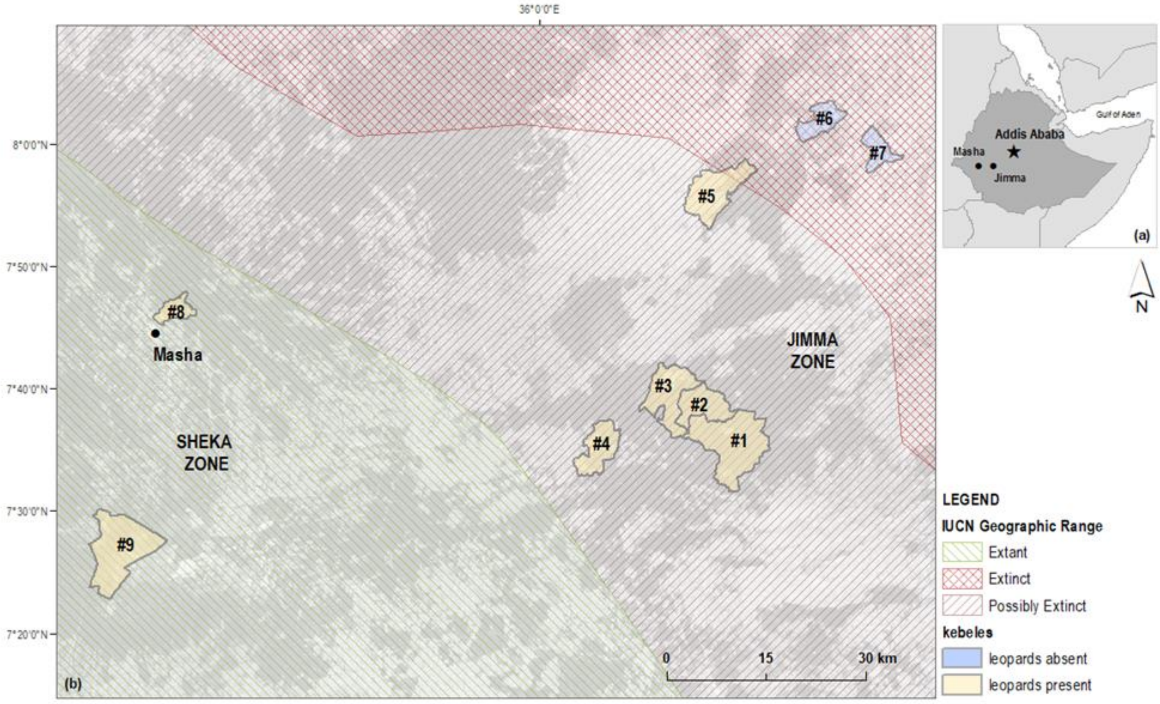

Figure 1. Location of (a) study area between the towns of Masha and Jimma, in southwestern Ethiopia; and (b) the 9 kebeles where camera trap surveys were carried out. Two kebeles were located in the Sheka zone, close to Masha town and 7 kebeles in the Jimma zone (right side of map). Dark grey shading represents forest areas. Kebeles numbers correspond to: #1 Afalo, #2 Gecho, #3 Kele Harari, #4 Boricho Deka, #5 Guido Bere, #6 Difo Mani, #7 Kuda Kefo, #8 Beto, #9 Anderacha.

Common features to surveys

We used motion-triggered Bushnell Trophy CamHD in all surveys. Cameras were placed at knee height (approximately 40 to 60 cm above the ground). Cameras were placed away from trails (except in Survey 2, where some cameras where located in trails), in small natural clearings or when these were not found in the sampling site, the area in front of the camera (approximately 9m^2) was cleared from emerging vegetation, to enhance a clear image of the species passing by, and to prevent empty frames triggered by wind. Bait was never used in any of the surveys. Date and time were recorded in the pictures and videos.

The videos and pictures were manually classified as described in Mertens et al. (2018) and Rodrigues et al. (2019), respectively. To standardize data across surveys, leopard observations were recorded as individual events only if one hour had passed between consecutive observations. Given the differences in the sampling design and length of the surveys we did not attempt to estimate leopard densities. However, since leopards' unique and distinctive coat patterns allow their individual identification, we counted the number of different individuals captured in the camera traps across the four surveys.

Table 1. Camera trap survey details (sampling period and effort) and summary of results (camera sites with presence and number of independent events) of leopard records in southwestern Ethiopia. *Kebele* names: #1 Afalo, #2 Gecho, #3, Kele Harari, #4 Boricho Deka, #5 Guido Bere, #6 Difo Mani, #7 Kuda Kefo, #8 Shato, #9 Anderacha.

	Jimma zone			**Sheka zone**
	Survey 1 Mertens et al. (2018)	**Survey 2** Rodrigues et al. (2019)	**Survey 3** Rodrigues et al. (this study)	**Survey 4** De Beenhouwer et al. (2016)
Period of survey	Aug 2014 - Jan 2015	Nov 2015 - Jan 2016	Jan 2016 - Mar 2017	Feb – June 2016
n. camera sites	48	25	95	27
n. camera trap days	1722	1075	10955	510
n. camera sites with presence	6	2	27	2
n. independent events	10	2	57	2
Total area surveyed (km^2)	121	142	158	94
Kebeles surveyed	#1, #2	#3, #5, #6, #7	#3, #4, #5, #6	#8, #9

Data analysis

Given the geographic separation between the two zones (Sheka and Jimma) and the low number of leopard records detected in Sheka we restricted data analysis to the Jimma zone, for which we pooled datasets from Surveys 1, 2 and 3. We used RapidEye satellite images from 2015 (5 m resolution) to derive a map of forest cover, using an automatic classification routine based on Maximum Likelihood in ArcGIS (ESRI 2013)(Rodrigues et al. 2018). We derived two forest related variables from the map: amount of forest cover and distance to the forest edge. The amount of forest cover was calculated for a buffer of 500m around each camera site and distance to the forest edge was measured from each camera location to the closest forest edge, using Euclidean distance derived using Spatial Analyst toolset in ArcMap (version 10.6.1, ESRI 2016).

We first examined leopard occurrence in relation to forest related variables. Our response variable was the leopard reporting rate, i.e. the number of camera days in which leopards occurred at a sampling site over the total number of days the camera at a sampling site remained operational (Geary et al. 2017). This allowed us to account for differences in sampling effort between sampling sites and differences between data types (video and pictures).

We used generalized linear mixed models, to account for spatially nested sampling sites within *kebeles* and we included *kebele* as a random effect in the model. Data points located in *kebeles* with absence of leopards (#6 and #7) were excluded from the model. The inclusion of "Survey" as a random effect to account for temporal autocorrelation, resulted in an overfitted model; therefore, this variable was not included in the model. We acknowledge this may be suboptimal, however since (1) the leopard is a long lived species, (2) the surveys span 3 years and (3) we do not aim to make model predictions, but rather focus on exploring relationships between leopard occurrence and forest variables, we built our full model using *kebele* as the only random effect. We limited our analysis to two fixed effects: distance from the forest edge and proportion of forest cover since we only had 21% of sites with leopard records. Proportion of forest cover describes forest extent and varied between 17 and 100% while distance to the forest edge was used as a proxy for human influence, by assuming that areas close to the forest edge are more accessible and therefore more likely to be disturbed than the forest interior. Distance to the forest edge varied between 5 and 1974 m. These fixed effects were not correlated (Pearson correlation = 0.54). We used a binomial distribution with logit link, from package *lme4* in R (Bates et al. 2015). We tested for overdispersion on binomial models as described in Zuur et al. (2013).

Finally, to explore the activity pattern of the leopard, we separated our sites according to recorded presence or absence of people in the camera traps. For each of the two groups of sites we created leopard activity plots by fitting a kernel density function of observed activity times given by independent events (separated at least by one-hour period). We implemented this analysis in R with package *overlap* (Ridout & Linkie, 2009).

Results

The total sampling effort across the four surveys comprised 14,263 camera trap nights, during which we collected a total of 71 independent leopard occurrences (Table 1). The relative abundance index of leopards during the entire study period was 0.49 leopards/100 camera trap nights. Leopards were found in seven out of the nine surveyed *kebeles* (Fig. 1), in two out of 27 sampling sites surveyed in Sheka zone and in 35 out of 168 sampling sites in Jimma zone (Table 1). Five of the *kebeles* were outside of IUCN current distribution range for the leopard (Fig. 1). Based on their unique coat patterns, we were able to identify 14 different individuals including two cubs, during the entire study period and for the two zones.

In Jimma zone, sites with recorded presence of leopards were on average 534 ± 295m from the forest edge and 69% had records of human presence. Our model results showed that leopards' reporting rate was positively associated with amount of forest cover (p=0.019) and only marginally (p=0.052) associated to distance from the forest edge (Supplementary Table 1, Supplementary Figure 1). The model was not overdispersed and the overall fit was $R^2 = 0.34$. Leopard activity patterns differed between sites with and without recorded presence of people (Fig. 2): leopard activity peaked around noon in sites without records of people (n=11), whereas in sites where people were recorded (n=24) activity peaked at dawn (between 05h00-06h00) and dusk (19h00)(Fig. 2).

Noteworthy records were three independent events of melanistic forms (Plate 1a, one previously reported in Rodrigues et al. 2019), in Kele Harari *kebele* (December 2015) and in Boricho Deka *kebele* (June and August 2016). However, we cannot determine if these records correspond to more than one individual. Evidence of mating behavior (Plate 1b) and a female carrying two cubs (Plate 1c) were recorded in December 2016. In addition to the camera trap occurrences, we recorded loose observations of leopard tracks (in Jimma town in 2014) and a snared leopard (Plate 1d) in 2017, also found close to Jimma town.

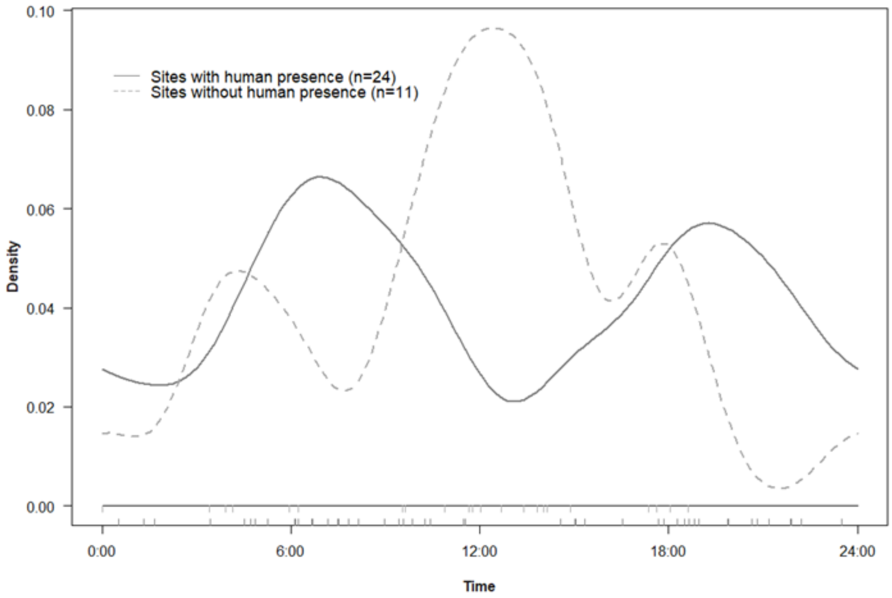

Figure 2: Distribution of leopard activity times in sites with and without recorded presence of humans, for Jimma zone.

Discussion

This study provides the best available knowledge on the occurrence and distribution of leopards in two major forest areas in southwestern Ethiopia, a region where information on the species is scarce. By pooling data from four different systematic camera-trap surveys, we were able to examine the leopard's relationship with forest cover and to investigate the influence of human disturbance on activity patterns. During our survey period, potential prey species for the leopard such as the bushduiker, bushpig and bushbuck (Hayward et al. 2006) were regularly detected in the camera traps (see Mertens et al. 2018 and Rodrigues et al. 2019 for details), suggesting the availability of wild prey, although we do not yet know at what densities. This information, together with the records of mating behavior, and of a female carrying cubs are an indicator of a resident population of leopards in the region, where melanistic forms also occur.

Our model results showed a strong positive relationship of the leopard reporting rate with the amount of forest cover, while the positive effect of distance to the forest edge was marginal at best. This is an important highlight of our study, for two reasons. First, it shows an association of the species with large and continuous blocks of natural forest. In Africa, leopards are known to be versatile predators in a variety of habitats (Jacobson et al. 2016, Stein et al. 2016), however, in this region of Ethiopia and despite the indication of leopards living close to Jimma town, their optimal habitat remains natural forest (Meyers 1974, Mertens et al. 2018). Second, the lack of a strong avoidance of the forest edge indicates that leopards can tolerate some level of disturbance, provided that large amounts of forest cover are available for the species to range. This finding is reinforced by our results on activity patterns.

Leopard activity was predominately nocturnal and peaked before sunrise and after sunset in sites with recorded presence of people, whereas in sites without human records, activity was mostly diurnal. This difference in activity times between sites with and without records of people seems to indicate a response to anthropogenic disturbance, suggesting that leopards can adapt to disturbance by shifting their activity times at fine-spatial scales (Woodroffe 2000, Carter et al. 2012; Van Cleave et al. 2018).

Plate 1: Camera trap pictures of (a) melanistic leopard, (b) mating behavior and (c) female carrying a cub. Panel (d) shows a photo of a snared leopard recorded near Jimma town in August 2017, considered a bycatch of bushmeat

Another important finding of our study is the need to update the distribution map of IUCN, which shows a large "possibly extinct" band in southwestern Ethiopia (Stein et al. 2016). Our data shows the species to occur and reproduce in this "possibly extinct" band, and our records for Jimma town extend their current distribution in the "extinct" band. Neighboring similar forest complexes in North and East of our study area are likely to contain suitable habitat and to also harbor the species. However, except for the Yayu Biosphere reserve, these are under no protection status, and monitoring in these areas should be prioritized. Similarly, monitoring should be implemented in our study area in the Jimma zone. Despite the designation of two Forest Priority Areas (Sigmo-Geba and Belete-Gera, UNEP-WCMC, 2016), in the 1980s, these areas have not yet been legally constituted, preventing the local implementation and enforcement of conservation measures.

The presence of the leopard as an apex predator adds to the conservation value of these forests and induces a myriad of cascading effects on prey communities and other forest components (Colman et al., 2015). Records of lions in the area are anecdotal and the only confirmed co-occurring predator is the spotted hyena (*Crocuta crocuta*), which forages mostly in the agricultural mosaic and around human settlements (Mertens et al., 2018, Foquet et al., 2019). As an apex predator the leopard can help to control the number of crop raiding species (such as baboons and bushpigs), either through direct predation or by creating a landscape of fear (Gaynor et al. 2018). This top-down control can bring benefits for local residents that are strongly affected by crop damage and crop loss (Dorresteijn et al. 2017). However, while some adaptation in activity patterns could potentially support human-wildlife coexistence (Carter et al., 2012), increasing human disturbance of the forest habitat can lead to permanent displacements in the timing of leopard activity (Carter et al. 2015; Van Cleave et al., 2018). This diel shift can potentially lead to changes in the ecological role of the leopard, with likely repercussions for the entire mammal community and ecosystem functioning in general (Ordiz et al., 2013; Gaynor et al., 2018).

In the southwest, deforestation and poaching are the primary threats to leopards (Tessema 2017), but their relative importance is not yet known. Trends in forest cover show that forest has been lost by 24% between 1973 and 2010 mostly due to encroachment and conversion to farmland (Ango et al. 2016). Given the importance of coffee in the region, it is likely that coffee production will remain an important activity, and thus to represent an incentive to maintain forest cover (Ango et al. 2016, Hylander et al. 2013). However, despite the contribution of coffee forests for supporting a diverse mammal community (Mertens et al. 2018, Rodrigues et al. 2018), maintaining large undisturbed natural forests is vital for the conservation of certain species, such as the leopard. Further, leopards are poached mostly for their skins (Tessema 2017), but to date it is unclear how leopard populations are affected by illegal trade, since no baseline population numbers exist. Therefore, considering all of the above, we suggest that future research in this region of Ethiopia should focus on (1) providing estimates of leopard density, to establish baseline data to inform conservation; (2) understanding the implications of increasing forest disturbance as a result of coffee management intensification and how it can affect human-leopard interactions; and (3) assessing the effect of forest fragmentation and how it can impact the persistence of leopards in the landscape.

Given the uncertainty that surrounds the future of forests in southwestern Ethiopia, and because the region is a hotspot of biodiversity, in which the leopard has an important function, we suggest that it is vital to establish long-term monitoring protocols targeting leopards and their prey and to promote the protection of the remaining undisturbed areas of forest. Nevertheless, given the increasing dependency of local livelihoods on forest resources (Dorresteijn et al. 2017), conservation measures should engage local communities by minimizing livestock predation and increasing awareness of pest control effects of predators. In light of this, this research was disseminated in the *kebeles* (including schools), *woreda* offices as well as federal authorities and non-governmental organizations in Ethiopia. Dissemination, both in English and Afaan Oromoo, took place in three major outreach events during the span of the surveys.

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Conflicts of interest

We have no conflicts of interest.

Ethical standards

The research was approved by the Ethics Committee of Leuphana University Lueneburg (EB-Antrag-201612-12), and it complies with the journal's ethical standards.

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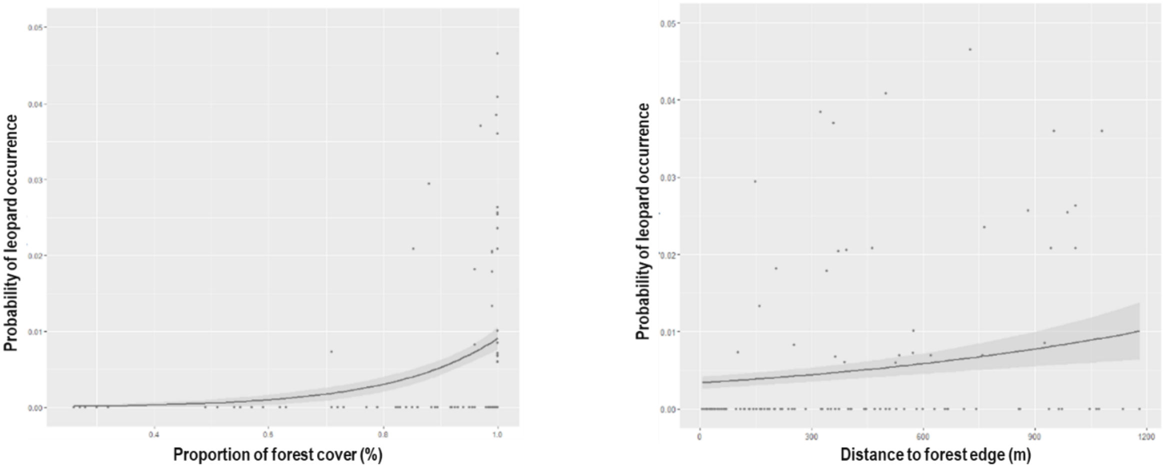
Supporting Information for Chapter V

Leopard (Panthera pardus) distribution in the Afromontane coffee forests of southwestern Ethiopia

Results

Supplementary Table 1. Results of a generalized linear mixed model, using distance to the forest edge and proportion of forest cover as predictors of leopard's reporting rate, as estimated from camera trapping surveys between 2015 and 2017, in southwestern Ethiopia. *Kebele* was entered as a random effect. Codes for significance levels: ***p < 0.001, **p < 0.01, *p < 0.05. Total number of sites (n= 127, excluded all of those where cameras were active less than 25 days).

	Coefficient Estimate	Standard Error [SE]
Intercept	-5.651	0.280 ***
Distance to edge	0.302	0.157 .
Proportion forest cover	1.122	0.478 **
Variance *kebele*	0.069	0.264



Supplementary Figure 1. Leopard responses to (a) distance to edge and (b) proportion of forest cover within 500m buffer, as determined by generalized linear mixed models.

Chapter VI

Chapter VI

Predicting the impacts of human population growth on mammals in southwestern Ethiopia

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They took all the trees
And put them in a tree museum
And they charged all the people
A dollar and a half to see 'em
Don't it always seem to go
That you don't know what you've got
'Till it's gone
They paved paradise
And they put up a parking lot

Big Yellow Taxi
Joni Mitchell 1970

Abstract

Projections of human population growth for 2050 indicate that Africa is expected to steadily increase its rural population, raising questions on how to best accommodate people while minimizing impacts on biodiversity. We explored the outcomes of scenarios of rural population growth mediated by housing development. We designed our scenarios based on (i) patterns of housing development (i.e. housing densification versus expansion), (ii) level of human population growth, and (iii) forest protection. Using camera traps, we surveyed mammals in the moist Afromontane forests of southwestern Ethiopia. We modelled mammals' responses to current and alternative housing development trajectories, using generalized additive mixed models. Our results suggest that (i) rural population growth is likely to negatively influence several mammal species, including a threatened predator (the leopard); (ii) negative impacts of population growth are likely to be exacerbated if new housing encroaches the forest (i.e., expansion), and likely to be less detrimental if houses are built within the existing human footprint (i.e., densification); and (iii) effects of human population growth can be modified by land-use decisions unrelated to biodiversity conservation, such as protection of economically important forest cover (native coffee forest in our study area). The forests of southwestern Ethiopia support a diverse mammal community, vulnerable to the effects of human population growth and housing development. The location, extent and magnitude of development can limit their ability to persist in the landscape. Our findings suggest that incorporating the ecological effects of housing development into landscape planning is fundamental to align conservation goals with development plans.

Introduction

In the next 30 years, the world's population is projected to grow by 2 billion, from current 7.7 to 9.7 billion (UN, 2019a). Half of this growth is projected for sub-Saharan Africa (SSA) alone (UN, 2019a). Here, fast increases in population numbers have been occurring since the mid-20th century, from roughly 200 million people in 1950 to more than one billion in 2017. Currently, 63% of the population resides in rural areas (UN, 2019a). By 2050, contrary to the global trend of decreasing rural population due to migration to urban centers (World Bank, 2019), African countries are projected to steadily increase their rural dwellers (with relative changes ranging from 24.5 % in Cameroon to 163 % in Niger, UN, 2019b). However, the implications of this projected rural increase for biodiversity conservation have been largely overlooked. With an increasing human population, it is reasonable to expect not only a growing demand for ecosystem goods and services and agricultural land for food production, but also a growing demand for housing and infrastructure (Bradshaw & Brook, 2014; Crist et al., 2017). Such demands can spur deforestation, forest fragmentation, and the erosion of biodiversity supported by natural forests (Gibson et al., 2011), and therefore it is vital to understand how rural population growth will unfold in biodiversity-rich areas. However, this is a challenging task because the links between human population growth and biodiversity are indirect and often oblique, as well as strongly dependent on scale (Pidgeon et al., 2014). A common approach in many scientific studies targeting regional and local scales is to decompose the effects of human disturbance, into more manageable proxies such as tourism (Steibl & Laforsch, 2019), infrastructure (Torres et al., 2016), or housing development (Villaseñor et al., 2017).

In the rural areas of SSA, livelihoods are largely based on subsistence farming, and the effects of human population growth on biodiversity are often mediated by agricultural expansion (Perrings & Halkos, 2015). Yet, for countries projected to significantly increase their rural population by 2050 (such as Ethiopia and Niger; UN, 2019b) an increasing demand for housing is also likely. However, the vast majority of studies to date have focused on the Global North and on urban and peri-urban development (Brown et al., 2014; Soga et al., 2014; Caryl et al., 2016; Villaseñor et al., 2017), whereas studies addressing the impacts of housing development in rural areas of the Global South remain scarce. This lack of knowledge is an important gap, especially in rural areas of Sub-Saharan Africa that host high levels of biodiversity, and where the impacts of housing development and associated human disturbance could be substantial.

The impacts of housing development on biodiversity are expected to vary with the type of development (e.g. housing density, location, and configuration) (Villaseñor et al., 2017). Two contrasting ways of development include (i) densification of houses concentrated in space and in existing residential areas ("housing densification") and (ii) expansion of residential areas into new locations ("housing expansion"). Densification results in high-density population centers, often with fewer natural features, whereas expansion results in low density—but more dispersed—population centers. Different outcomes for biodiversity can be anticipated from these contrasting patterns of housing development. Housing densification affects a smaller proportion of the landscape, but may require such dense housing that few species can occur within population centers. By contrast, housing expansion affects a much larger area, but could allow some species to occur throughout more sparsely populated centers (Geschke et al., 2018). For instance, while housing expansion through forest encroachment might approximate the effects of generic forest cover loss, the former may affect biodiversity without forest being cut, by increasing overall human disturbance in the landscape. Thus, it is important to understand the implications of different housing development strategies for biodiversity conservation in regions undergoing strong population increases such as SSA.

Here, we explore the ecological outcomes of scenarios of rural housing development for the southwest of Ethiopia. Both the country and the southwest in particular, are a good illustration of the persistent growth in rural populations in SSA, and of its accompanying challenges. About 89% of the southwestern population resides in a rural setting (OBFED, 2012), and according to UN projections, Ethiopia is the country in the world with the largest projected absolute increases in rural dwellers by 2050 (UN, 2019b). The southwest of Ethiopia is also highly biodiverse, belonging to the Afromontane Biodiversity Hotspot. It hosts large, continuous remnants of moist evergreen forests, where the genetic reservoir of Arabica coffee (*Coffea arabica*) is found (Senbeta & Denich, 2006). Coffee, in turn, is the single most important export commodity of the country, and much of it is grown in relatively biodiversity-friendly forest shade coffee contexts (Rodrigues et al., 2019). Local livelihoods strongly depend on subsistence farming and coffee production (Manlosa et al. 2019), and are constrained by land scarcity. Altogether, the interplay of these factors, combined with land inheritance mechanisms, can trigger farmland and coffee forest expansion and can result in a complex dynamic of forest loss across the landscape (Hylander et al. 2013). However, it is also possible that a shift towards more intensive agriculture might occur (e.g., by using improved varieties, fertilizers and pesticides) a response that has been observed in other regions of East Africa with a similar context (e.g. in the highlands of Kenya, Mutoko et al., 2014). Yet, it remains to be understood how a growing number of rural dwellers can be best accommodated in the landscape while minimizing impacts for biodiversity.

We investigated the effects of housing development on mammals. We focused on mammals for several reasons. First, mammals require large areas of near-natural forest habitat, with many species sensitive to changes in forest area and quality (Kinnaird et al., 2003). Deforestation and forest encroachment processes represent an increased risk in extinction for many mammal species (Betts et al., 2017; Powers & Jetz, 2019), and increasing anthropogenic disturbance can cause shifts in species activity times and trophic cascades (Gaynor et al., 2018). Second, southwest Ethiopia supports a diverse mammal community that includes top predators and threatened species such as the leopard (*Panthera pardus*) (Mertens et al., 2018; Rodrigues et al., 2019). Third, some mammal species in the region cause major damage to livelihoods (Ango et al., 2017; Dorresteijn et al., 2017), and human-wildlife conflicts could intensify as a consequence of changes in the forest habitat, entailing negative consequences for both people and wildlife.

We undertook a large-scale field survey of mammals, modelled their responses to housing and developed scenarios of how alternative housing development trajectories differed in their impacts on forest mammal diversity. Specifically, we asked: (i) how do mammal species respond to increasing rural housing density? (ii) to what extent different development types (i.e. densification versus expansion) and population growth projections (i.e., moderate *cf.* high growth) result in different outcomes for the region's mammal species? And (iii) how do decisions to protect from development economically important coffee forests affect the outcomes for the region's mammals? Answering these questions, in turn, is central for the successful conservation of mammal diversity in the region.

Methods

Study area

The study area encompasses an area of 3800 km^2 and is located in a coffee growing area in Jimma zone, in the Oromia region, southwest of Ethiopia (Figure S1). Mammal communities were assessed in four *kebeles* (smallest administrative unit) located in two districts (*woredas*). The southwest is a mountainous region with steep slopes and flat plateaus, and elevation ranges from 1500 to 3000 m above sea level. Coffee is native to the region and grows within 1500 – 1950 m (Shumi et al., 2019). The region is home to vast and nearly undisturbed areas of moist evergreen Afromontane forests. Annual deforestation rates in the region vary between 0.4 to 1.5% (Hylander et al., 2013) and it is estimated that forest cover has decreased from 79% to 60% between 1973 and 2010 (Ango et al., 2016). The current proportion of forest in the study *kebeles* varies between 33 and 88%. Livelihoods are based on subsistence farming of both food and cash crops (coffee and khat) and complemented by a diversity of forest products (Manlosa et al., 2019). *Kebele* area varied between 2345 and 5200 ha and population density between 66 and 137 people/km^2.

Sampling Design and Data collection

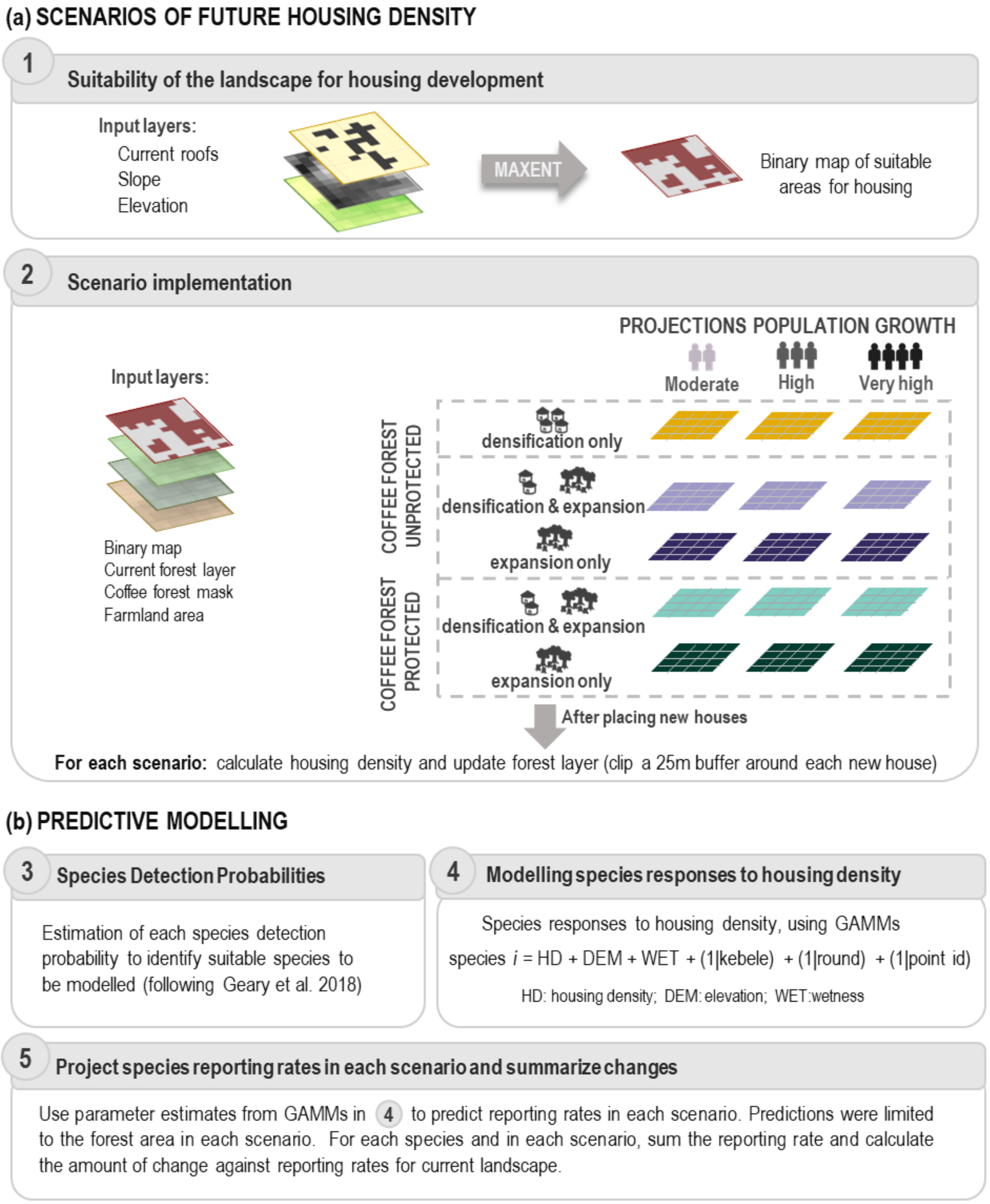
We surveyed mammals of medium to large body size at 95 sampling points using 39 remotely-triggered camera traps (digital Bushnell Trophy Cam). The survey lasted 15 months, from January 2016 to March 2017. Cameras were rotated to new sampling locations approximately every three months. We used a map of forest cover derived from RapidEye satellite imagery (5m resolution, 2015) (Rodrigues et al., 2018) to delineate our sampling design. We randomly placed cameras in the field using a stratified scheme that covered a gradient of forest cover and a gradient of total forest edge (see supporting information and Figure S2). Additionally, we tried to place cameras at least 500 m apart from each other in order to increase independence of observations for most species, but given very challenging terrain, in some instances, that was not possible due to access constraints. Cameras were on average 653 m apart and 300 m from the forest edge (between 5 and 1080 m). Cameras were attached to trees at knee-height and no bait was used. We cleared the area in front of the camera (approx. 9 m^2) of herbs and small shrubs to increase the potential for capture success and to prevent empty pictures triggered by vegetation moving in the wind. We programmed cameras to take photographs 24 hours/day, with sequences of 3 photographs at a time. Date and time of day were tagged in each photograph. Cameras were active between 2 and 180 days (mean: 114 days), with premature deactivation resulting from camera failure or human interference. We manually classified all pictures using ExifPRO™ software. Empty frames and pictures with birds were excluded, and all pictures of humans were counted and then deleted from the database. All pictures of the same species and triggered within a one-hour period were considered the same event (Rovero & Marshall, 2009). In some instances, species could only be identified to genus level (e.g. hares *Lepus sp.*) because of low image quality.

Scenarios of future housing density

We developed scenarios of rural housing density for the study area, for the period of 2017-2047. Scenario development followed two major steps: (1) assessment of landscape suitability for housing development, and (2) scenario implementation (Figure 1a).

(1) Suitability of the landscape for housing development

The landscape of the study area is hilly with steep slopes and flat plateaus, which means that not all areas are suitable for housing development. We used maximum entropy algorithm, in MAXENT software (version 3.4.1, Phillips et al., 2020), to identify areas potentially suitable for new houses. We used the location of the 4114 current roofs in the landscape as a response variable and slope and elevation as predictors. We produced a binary map of suitability for housing development. We then excluded from the binary map all grid cells (30x30 m unit) that corresponded to existing houses in the landscape (hereafter, current houses). This final binary map thus indicated which areas in the landscape are within slope and elevation values that are suitable for housing development, but are not currently populated (see supplementary information for more details).



For each scenario: calculate housing density and update forest layer (clip a 25m buffer around each new house)

Estimation of each species detection probability to identify suitable species to be modelled (following Geary et al. 2018)

Species responses to housing density, using GAMMs

species i = HD + DEM + WET + (1|kebele) + (1|round) + (1|point id)

Use parameter estimates from GAMMs in ④ to predict reporting rates in each scenario. Predictions were limited to the forest area in each scenario. For each species and in each scenario, sum the reporting rate and calculate the amount of change against reporting rates for current landscape.

Figure 1: Methodological workflow used in the development of scenarios of housing density and on the modelling approach.

(2) Scenario implementation

We designed a total of 15 future scenarios based on three general criteria (and combinations thereof), namely: (i) housing development type, (ii) projections of human population growth, and (iii) protection of coffee forest (Figure 1a). We used the current landscape configuration as a baseline scenario.

Development type (i) encompassed three possible pathways of rural development: **"densification only"**, **"expansion only"** and **"densification and expansion"**. In the "densification only" development type, new houses were accommodated in the landscape by increasing the density of already settled areas, usually within the existing footprint and adjacent farmland matrix. In "expansion only", new houses could encroach into the forest up to a distance of 400 m from the forest edge, reflecting the gradual spread of housing into nearby, forested areas that are suitable for housing. The "densification and expansion" development type was a combination of "densification only" and "expansion only". In this development type, new houses were equally distributed between "densification only" and "expansion only" (i.e. half in each), but only up to 200 m from the forest edge. To have a sense of which distances were reasonable to characterize "expansion only" development type in our kebeles, we visually examined satellite images from 1973 (Landsat images 1-MSS, obtained from http://www.usgs.gov/) and 2015 (using RapidEye satellite images), and compared forest extent and the extent of housing area within that period. This visual examination allowed us to determine 400 m as a reasonable distance to allow for encroachment of forest in "expansion only" development type over this time period.

For each of the three development types (i), we considered three projections of human population growth (ii) for the study area: **"moderate growth"**, **"high growth"** and **"very high growth".** To derive the number of new houses under each level of growth, the number of current households in the landscape (n=2347) was multiplied by a factor of 1.8 (moderate growth), 2.1 (high growth) and 2.4 (very high growth), and corrected for the average number of roofs in a household (i.e. a household has on average 1.8 roofs, corresponding to the house and its associated free-standing kitchen). This represented an addition of 3400, 4500 and 5700 new roofs in the landscape. These growth factors approximate the probabilistic projections of population growth in Ethiopia for the year 2047 (median, 85% and 95% upper intervals; UN, 2019a).

Finally, for the two development types that involved expansion, and for each of the three population projections of human population growth, we applied a final criterion related to the protection of coffee forest criteria (iii). This was comprised of two protection levels: **"coffee forest protected"**, where all suitable areas for housing located within coffee altitude (1500 – 1950 m) were protected against development (i.e. coded as unsuitable for housing development), and **"coffee forest unprotected"**, where forest areas within coffee altitude could be cleared and allow housing development. The former recognizes that people are unlikely to clear land suitable for coffee because of its importance to livelihoods (Figure 1a and Figure 2).

We randomly placed the new houses in the landscape according to the three levels of human population growth and for each development type and for both protection of coffee forest criteria. To guide the placement of the new houses according to each scenario, we used a combination of (i) the binary map of housing suitability; (ii) the area of farmland for the "densification only" and "densification and expansion" development type, (iii) the current area of forest for the "expansion only" and "densification and expansion" development types (a 400 m or 200 m band from the forest edge, respectively), and (iv) a mask of the forest within coffee altitude for the coffee protection criterion (Figure 2). Houses were placed using the Random Point toolbox in ArcMap with a 10 m minimum input distance between two new houses. Due to constraints in the area available to accommodate new houses we were unable to generate randomized repetitions of this procedure. We then merged new houses in each scenario with current houses in the landscape and generated 15 new raster maps of housing density scenarios for the landscape (resulting from the combination of three development types, two coffee protection criteria and three levels of human population growth) (Figure 2). Housing density was calculated for each cell, using Point Density toolbox in Arcmap (ESRI, 2018), within a buffer of 500m. Species responses to housing density are known to vary with the scale of analysis (Caryl et al., 2016). However, we used a fixed buffer of 500 m in order to achieve a compromise between the area of our study *kebeles* and the diversity of home-ranges within the mammal community (which included far-ranging species, such as the leopard, as a well as species with smaller home ranges, such as hares). As a last step, we created a buffer of 25 m around each new house (considering that each new house area is likely to encompass a small home garden) and updated the forest map in each scenario to reflect the forest loss associated with housing development (Table 1). All spatial analysis were performed in ArcMap 10.6.1 (ESRI, 2018), using both shapefiles and rasters of 30 x 30 m cell size.

Table 1: Changes in forest area in each scenario, i.e. for combinations of three levels of human population growth (moderate, high and very high), coffee forest protection and development type criteria. % change is illustrated against current area of forest in the landscape.

	moderate		**high**		**very high**	
	Area (ha)	**% change**	**Area (ha)**	**% change**	**Area (ha)**	**% change**
Densification	9326	-1	9295	-1	9266	-2
Coffee excluded						
Expansion	8393	-11	8305	-12	8235	-13
Densification & expansion	8785	-7	8695	-8	8624	-9
Coffee included						
Expansion	7963	-16	7708	-18	7537	-20
Densification & expansion	8552	-9	8376	-11	8236	-13

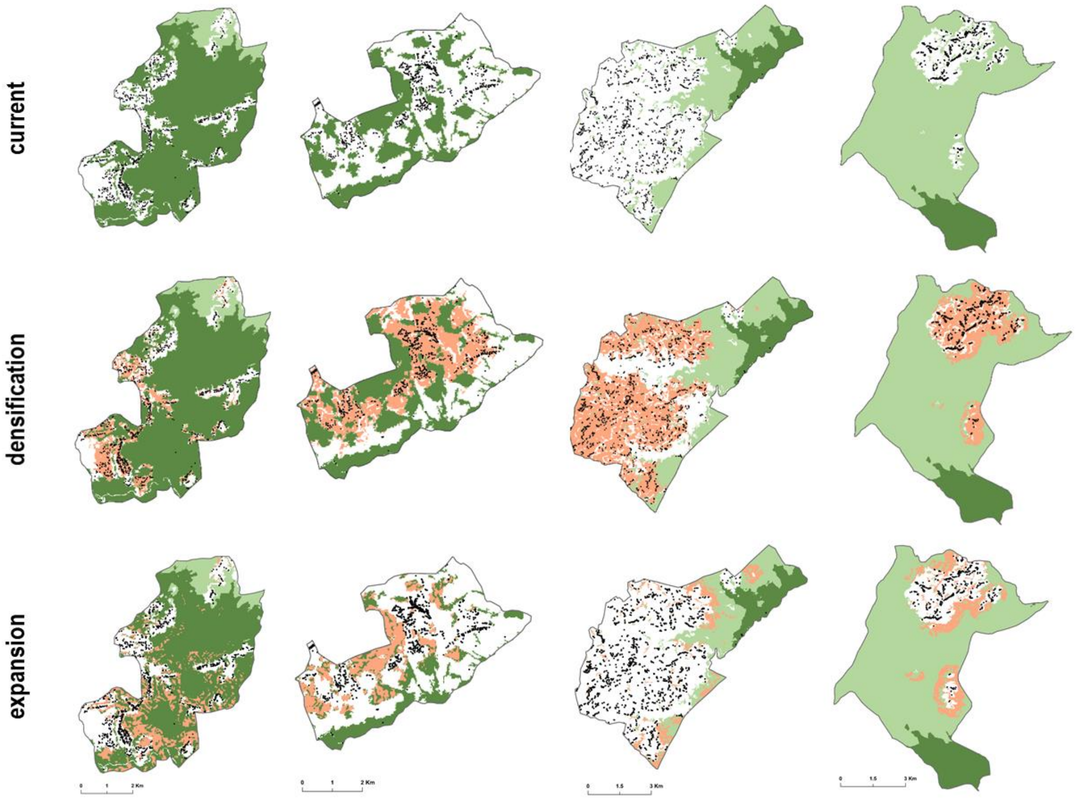


Figure 2: Spatial representation of the suitable area available for housing development under "densification" and "expansion" development types, combined with criteria of "coffee unprotected" against housing development. Light green corresponds to forest above coffee altitude and dark green to forest within coffee altitude. Suitable area for the "expansion" and "densification" development type scenarios is colored in orange. Black dots represent current roofs in the landscape. "Expansion" type of development spreads up to a distance of 400 m from the forest edge and towards the forest interior. A third type of development (not illustrated) was considered, combining "densification" and "expansion", up to a distance of 200 m from the forest edge and towards the forest interior. Current forest area is illustrated for comparison purposes. New dwellings are not represented to improve visualization of the area allocated to each development type.

Predictive models

Prior to the modelling procedure, and in order to assess how confident we could be that species absences from the cameras could be considered "true absences", we followed the approach in Geary et al. (2018) and calculated the survey-level detection probability for each species, using the package "unmarked" in R (Fiske & Chandler, 2011). This analysis indicated that we could be confident that our sampling effort was adequate for 20 species detected in our survey, when considering confidence levels of 90 to 95%. We restricted further analyses to these 20 species and to sites with a sampling effort above 30 working camera days in the field (n=91).

The modelling approach included two main steps: (1) modelling species responses to current house density and (2) prediction of species responses to scenarios of housing development. In the modelling of species responses to current house density, our response variable was each species' 'reporting rate', i.e. the proportion of nights that a species was detected at a survey site over the duration of the survey at the site (i.e. total number of nights the camera remained operational). Reporting rates serve as a surrogate of species' abundance and activity (Geary et al., 2018). Each species reporting rate was modelled as the number of successes (species detected) and failures (species not detected) over a fixed number (n = total number of nights that cameras remained operational) of (binomially distributed) Bernoulli trials (Crawley, 2013). The response variable used in the models was thus a combination of two vectors (number of nights detected, total number of nights), combined using the *cbind* function in R.

We used Generalised Additive Mixed Models (GAMMs) to model each species' reporting rate in relation to current housing density and wetness and elevation (Figure 1b). Wetness was included as a proxy for water accumulation and availability (since some species such as the marsh mongoose are associated with small streams) and elevation as a proxy for areas with potential for coffee production. We chose GAMMs over alternative modeling approaches such as occupancy modelling for two main reasons. First, GAMMs allow for non-normally distributed response variables that can be fitted with parametric and nonparametric smoothing terms. This means that both linear and highly nonlinear relationships between response and predictor variables can be modelled (Zuur, 2009). Second, we needed to incorporate the non-independence of our data points within each *kebele*, and GAMMs allow for the inclusion of random effects that can control for non-independence of observations. We included a smoothed term for modelling responses to housing density because responses to measures of population density are often non-linear (e.g. Geschke et al., 2018). Current housing density (i.e. the number of roofs within 500 m) was strongly and negatively correlated with the proportion of forest cover within 500 m of a survey point (cor = -0.70), indicating that as housing density increases, forest cover is reduced. Therefore, we did not include forest cover in our models but consider that mammals' negative responses to roof density also indicate a likely positive relationship with forest cover. Wetness and elevation were fitted as linear terms in the models. Elevation was derived from the ASTER Global Digital Elevation Model v2 (30 m resolution; https://reverb.echo.nasa.gov/), and the topographic wetness index was based on the digital elevation model and derived using the Wetness Index toolbox in ArcMap. As sampling sites were clustered within the four *kebeles*, and because there were three separate survey rounds, we included '*kebele*' and 'survey round' as nested random effects in all models (Geary et al., 2018). Sampling site was also included as a random effect to improve convergence of the models and to account for one sampling point where the camera could not be rotated. Models were run using package *gamm4* (Wood & Scheipl, 2020)

The second step of the modelling procedure was the prediction of species responses. To examine the effects of the different scenarios of housing density over time we focused on those species that significantly responded to housing density (i.e. species models with p values of smoothed term in GAMMs ≤ 0.05). For these species (seven in total), we projected each reporting rate across the four *kebeles* and within the forest area in each of the 15 scenarios, and for the current landscape as a baseline. Finally, in order to assess how species activity in the forest would change between 2017 and 2047, for each species we summed the projected reporting rates in each scenario and calculated the differences to reporting rates in the current landscape.

Results

Overview of the mammal community

We identified 33 mammal species across the 96 survey sites sampled over 13 months (corresponding to 10,955 camera trap nights of field effort and to a total 538,030 pictures retrieved) (Table S1). Common species included the baboon (*Papio anubis*), bushpig (*Potamochoerus larvatus*), bushduiker (*Sylvicapra grimmia*), bushbuck (*Tragelaphus scriptus*) and genets (*Geneta sp.*). Top predators included the leopard (*Panthera pardus*) and the spotted hyena (*Crocuta crocuta*). Our extensive field effort and the survey of the forest interior allowed the detection of rare species such as the caracal (*Caracal caracal*), African buffalo (*Syncerus caffer*) and African wildcat (*Felis lybica*). The leopard and the Boutourlini' blue monkey (*Cercopithecus mitis spp. boutourlinii*) are species of conservation concern, listed both as “vulnerable” on the IUCN red list (2019).

Species responses to housing density

From the 33 species detected, 20 species met the detectability criteria for modelling (Figure S3). Of the species that met the criteria, seven responded significantly to current housing density. The grivet monkey (*Chlorocebus aethiops*) and the mantled guereza (*Colobus guereza*) responded positively to housing density, with some evidence of a decline in areas of higher housing density beyond 60 roofs per 500 m for the grivet monkey. The remaining five species (i.e. the leopard, bushbuck, baboon, warthog (*Phacochoerus africanus)* and the bushpig) responded negatively to housing density (Figure 3, Table S2). Results for the warthog and the bushpig need to be considered with caution, because the p-value of the smoothed term was $p=0.05$ (Wood et al., 2006). The leopard and warthog reporting rates were also associated with elevation, positively for the first and negatively for the second (Table S3) and the mantled guereza was positively associated with the wetness index (Table S3).

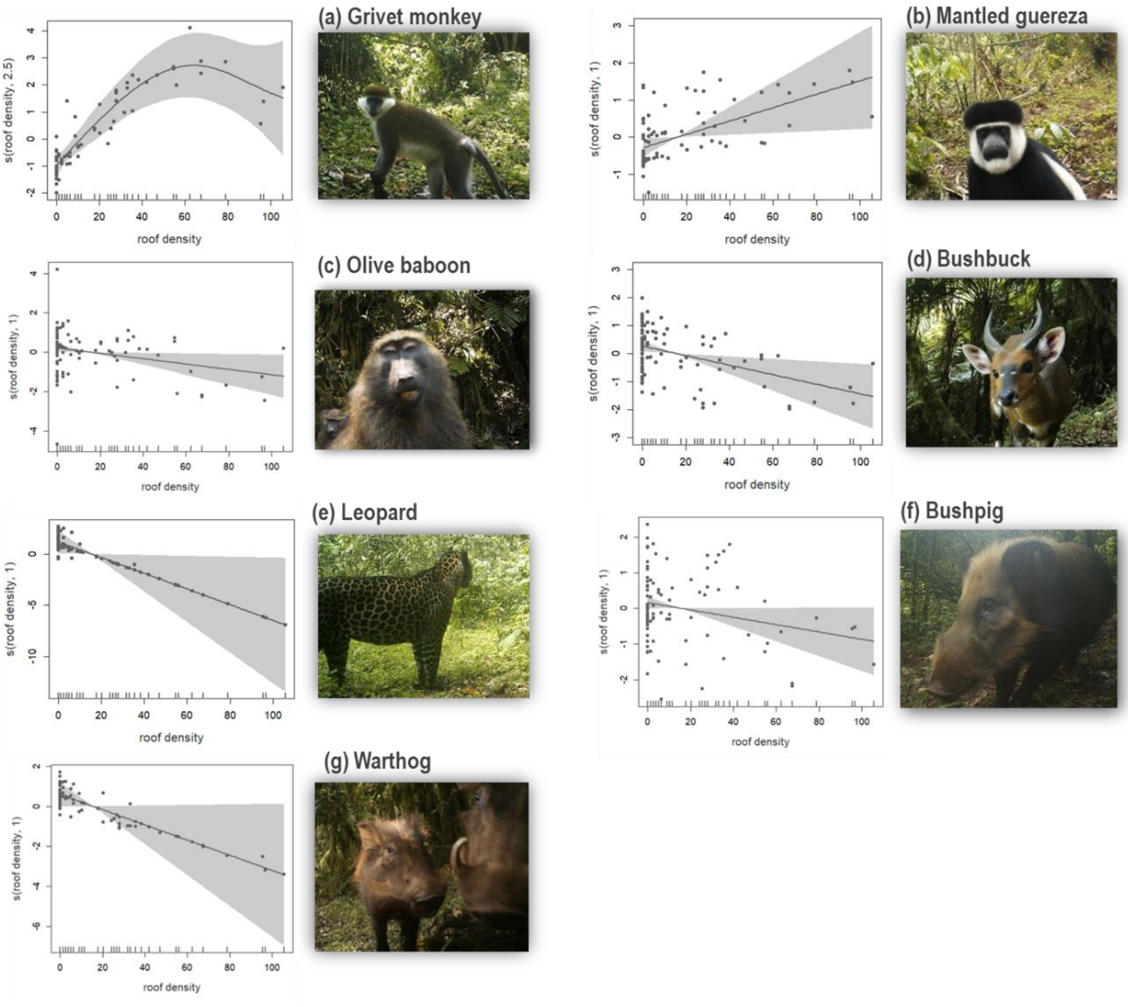


Figure 3: Mammal species responses illustrating the relationship between species reporting rate and current roof density. Grey areas indicate 95% confidence intervals. Grey dots correspond to model residuals. Warthog and Bushpig were on the limit of significance (Table S2). Roof density is used here as a proxy for the number of houses within a buffer of 500 m.

Species responses to scenarios of future housing density

Species responses to scenarios of future housing density were positive (i.e., increased reporting rate) for the grivet monkey and mantled guereza and negative for the leopard, baboon, bushbuck, warthog and bushpig (Figure 4). The reporting rate of the mantled guereza increased (compared to the current scenario) with increasing levels of housing density for all development types (i.e. "densification only", "expansion only" and "densification and expansion") and coffee forest protection criteria (i.e. "coffee protected" and "coffee unprotected"), whereas the grivet monkey exhibited mixed trends, depending on development type and coffee forest protection criteria (Figure 4a, b). When coffee forest was protected, the grivet monkey was predicted to decline with "very high" growth in human population. For the olive baboon, bushbuck, leopard, bushpig and warthog, increasing levels of human population growth (i.e. from "moderate growth" to "very high growth") led to stronger declines in reporting rates

(Figure 4c-g). For this group of species, “densification only” had the least detrimental impact on reporting rates (with declines between 4 and 11% for the baboon and warthog, respectively). The combination of “expansion only” and “coffee unprotected” criteria had the worst outcomes for these species, with declines in reporting rates between 27–43% (for the leopard and the warthog, respectively). Additionally, for this same group of species, and with the exception of the leopard, the protection of coffee forest against housing development (i.e., “coffee forest protected”) led to weaker declines in species reporting rate. For the leopard, development type (i.e., “expansion only” versus “densification and expansion”)(Figure 4e) was the major differentiator in its response to future housing density, whereas for the warthog it was the protection of coffee forest (Figure 4g).

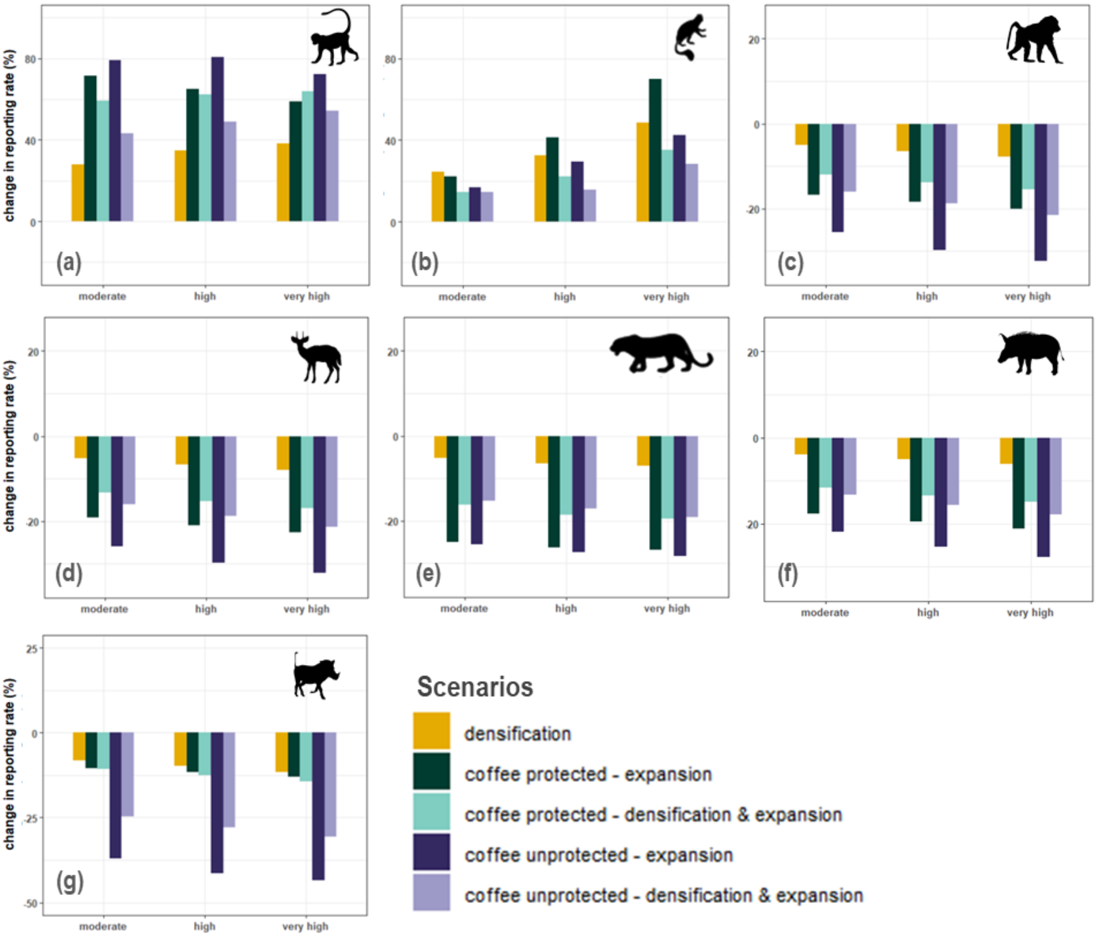


Figure 4. Species responses to future scenarios of rural housing density, across the four study areas (*kebeles*). Response variable is the proportion of change in each species reporting rate for each scenario. Panels legend: (a) grivet monkey, (b) mantled guereza, (c) Olive baboon, (d) bushbuck, (e) leopard, (f) bushpig, (g) warthog.

Discussion

Accommodating a growing population while conserving biodiversity is a challenge facing many biodiversity-rich rural landscapes in Sub-Saharan Africa. Here, we examined the broad implications of different scenarios of rural housing development for mammal diversity conservation. Our results highlight that (i) although species responses to housing density are not uniform (i.e., both positive and negative responses observed), rural human population growth in Ethiopia is likely to negatively influence several species of mammals, including a threatened apex predator (the leopard); (ii) the negative impacts of population growth are likely to be compounded if forest areas are cleared to make space for new housing (i.e., expansion), and likely to be more modest if new houses are built within the existing human footprint (i.e., densification); and (iii) the effects of human population growth can be modified by land-use decisions unrelated to biodiversity conservation, such as the protection of economically important forest cover.

Housing density was a significant predictor of the reporting rates of seven of the twenty species modelled. Of two monkey species - the grivet monkey and the mantled guereza - were more commonly encountered in forests surrounded by higher density housing. Both species are known to tolerate some human disturbance (Naughton-Treves, 1998). In the study area, the grivet monkey is considered a problematic species, often raiding food crops while the mantled guereza, despite being mostly folivorous, is known to steal fruits from homegardens (Ango et al., 2017). Hence, it is not surprising that these two species appear to favor forests in proximity to human settlements. The remaining five species were recorded less often in forest surrounded by higher densities of houses. In the study area, and despite being a highly adaptable species (Jacobson et al., 2016), the leopard seemed to be restricted to areas of natural and interior forest (Mertens et al., 2018). Areas of less disturbed forest were also important for the bushbuck, bushpig and warthog, species that depend on dense vegetation for refuge. Finally, the negative response of olive baboons to housing density may result from their gregarious behavior, requiring relatively large areas of forest for refuge, especially given the context of strong conflicts with farmers in the region (Ango et al., 2017).

One outcome of our study was the importance of considering the density and location of new dwellings. The magnitude of species responses to housing density depended on the combination of type of development, coffee forest protection and human population growth. For those species negatively affected by housing density, the "expansion only" type of development represented the worst outcome, whereas compact development (i.e "densification only") was the least detrimental. This result aligns with previous studies focusing on the effects of urban growth on biodiversity, showing less detrimental effects of compact over dispersed urban development for marsupial mammals (Villaseñor et al., 2017), bats (Caryl et al., 2016) and birds (Gagné & Fahrig, 2010; Sushinsky et al., 2013). This is because dispersed development occurs at a lower-density and covers a larger area, entailing the encroachment of the forest habitat resulting in the loss of forest area and forest disturbance through edge effects. However, the effects of expansion development in rural areas (such as in our landscape) are likely to be greater than in urban areas, since basic infrastructure (e.g. road network) is still incipient. The development of a road network to serve new dwellings is generally shown to further increase the degradation of the forest habitat and associated biodiversity (Benítez-López et al., 2010). Additionally, and apart from the obvious consequence of habitat loss and degradation that can impact the ability of species to persist in the landscape, housing expansion can interfere with a wide array of ecological features such as trophic relationships (Dobson et al., 2006), introduction of invasive species (Doherty et al., 2016), increasing hunting pressure, among others (Luskin et al., 2017). For those species sensitive to housing density, higher levels of human population growth are likely to entail worse outcomes than more moderate levels, a finding similar to other studies examining the impacts of an increasing human population on biodiversity (Villaseñor et al., 2017; Geschke et al., 2018).

Our study highlights the vital importance of land-use decisions for biodiversity conservation. In the southwest of Ethiopia, coffee forest is a cultural and economically important type of forest cover, and we found that its protection against housing development led to less detrimental outcomes for mammals. This approach adds a further element of realism to our scenarios, as locals are unlikely to remove forests that they, or their community, depend on for income. However, this should not be interpreted as coffee forests being a replacement for natural forests, since some species (such as the leopard and buffalo) are associated with largely undisturbed forests, including above coffee altitude (Mertens et al., 2018). Also, the possibility exists that when coffee forest is protected, areas of natural forest above coffee altitude will be converted instead; a dynamic that Ango et al. (2016) coined as a "deforestation leakage", i.e. the movement of people from areas with coffee forests to areas of natural forest, with the consequent deforestation of the latter. Coffee forest thus plays an important complementary role to largely undisturbed forest, but there are complex and potentially strong social-ecological interactions between the two types of forest cover. Anticipating combined effects of these drivers should be a priority in bridging land use and landscape planning with biodiversity conservation.

In summary, our results show that forest encroachment by housing expansion has the worst outcomes for mammals (as a combined result of habitat loss and degradation), that the protection of coffee forests can benefit some but not all mammal species and that increasing levels of human population growth further exacerbate negative outcomes for mammal diversity. From a conservation perspective, we argue that (i) housing development types that target already residential areas should be prioritized to avoid further forest loss; (ii) incorporating the ecological effects of housing development into landscape planning is fundamental to align conservation goals with development plans and (iii) programs that increase awareness of the rural community on the challenges posed by a growing human population should be supported. Finally, and despite the inherent uncertainty associated with scenario exercises, we argue that the moist Afromontane forests of southwestern Ethiopia are not only of high importance for mammal diversity conservation (Mertens et al., 2018), but are also of demonstrated value for birds (Rodrigues et al., 2018) and plants (Shumi et al., 2019), as well as of important value for local livelihoods (Manlosa et al., 2019), and therefore their conservation and management should be prioritized.

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Supporting Information for Chapter VI

Predicting the impacts of human population growth on a forest mammal community in southwestern Ethiopia

Methods

Study area

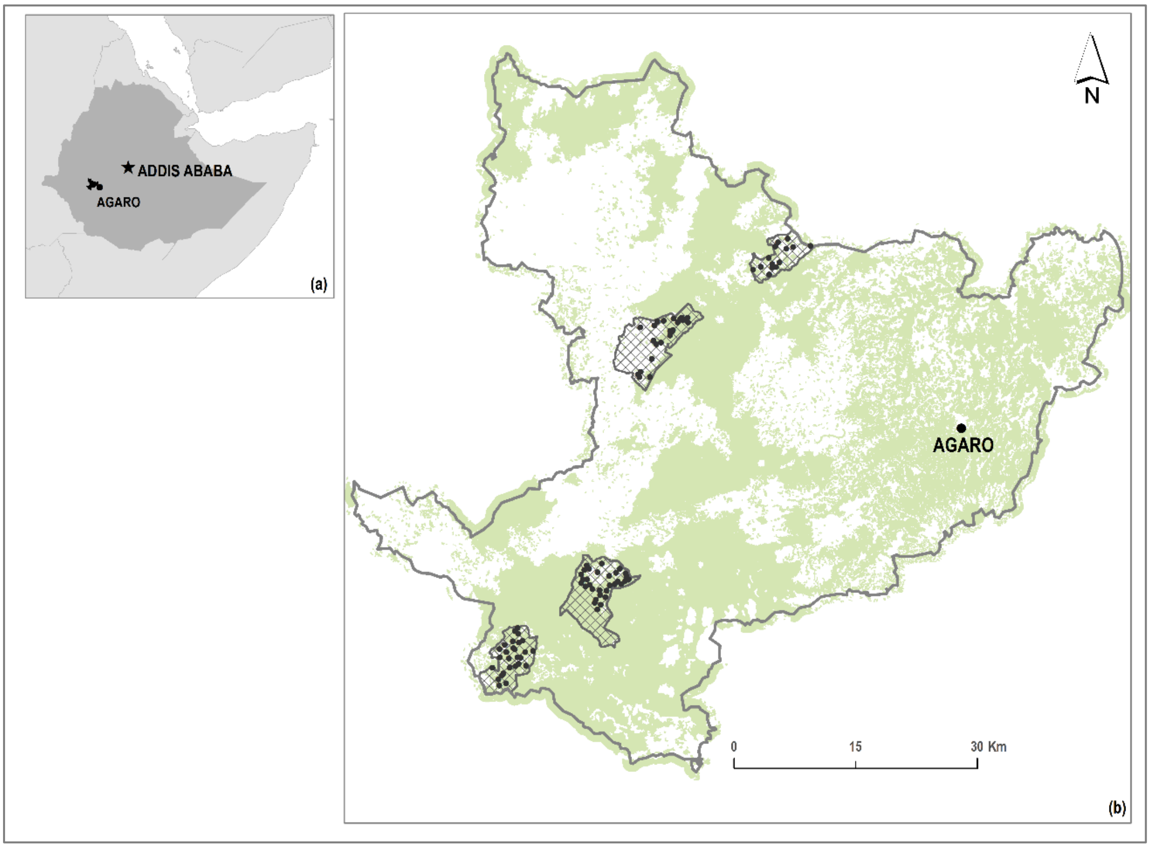

Figure S1: Study area location (a) in southwestern Ethiopia and (b) location of surveyed kebeles (hatched) and survey sampling sites. Green area corresponds to forest cover in the area.

Sampling Design and Data collection

We placed our cameras in the field according to a stratified scheme covering two gradients: a gradient of forest cover and a gradient of total forest edge. We initially tried to keep both gradients fully independent (Ethier & Fahrig, 2011; Trzcinski et al., 1999) but reality in the field meant that some combinations did not exist. Thus, our sampling scheme fully covered the two gradients, but with some correlation between them as illustrated below.

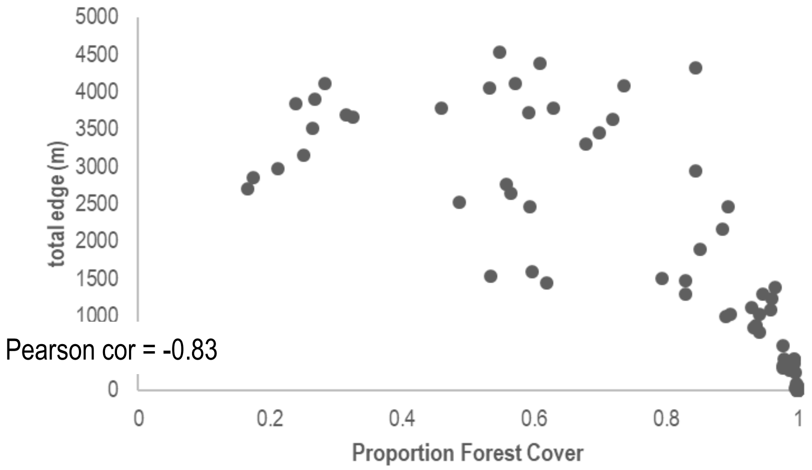

Figure S2. Distribution of sampling sites according to the gradient of forest cover and total forest edge, used to stratify the sampling design.

Scenarios of future housing density

(1) Suitability of the landscape for housing development

To assess which areas are potentially suitable for housing development, we used a maximum-entropy algorithm to model, implemented in MAXENT software (version 3.4.1, Phillips et al., 2020). We used the location of current houses as a response variable, and elevation and slope as predictors. We ran 10 replicates, and produced a binary map of suitability for housing (values of "1" corresponding to suitable areas for housing and values of "0" to unsuitable areas) based on the threshold of maximum training sensitivity plus specificity.

Current houses in the landscape we derived using a combination of classification and manual digitation on screen. Current houses with a tin roof were derived from a Tasseled Cap classification approach on RapidEye 2015 (5 m resolution) satellite imagery (Schönert et al., 2014). This created a raster of tin roofs for the region. Current houses with grass roofs were manually digitized using Bing Aerial images, 2015, in QGIS (QGIS, 2015). Tin and grass roofs were combined into a unique shapefile illustrating current roofs in the landscape. Housing density was approximated via roof density.

Results

Table S1. Mammal species recorded by camera traps at the forest edge in southwestern Ethiopia, in a total of 96 sampling sites and during a total of 10894 camera trap days. Nomenclature follows Wilson and Reeder (2005). NS: number of sites; NE number of unique events (given by total number of nights with detection.

ORDER & Family	**Species**	**Common name**	**NS**	**NE**	**IUCN status**
HYRACOIDEA					
Procaviidae	*Heterohyrax brucei, Procavia capensis*	Hyrax	42	144	LC
TUBULIDENTATA					
Orycteropodida	*Orycteropus afer*	Aardvark	3	4	LC
PRIMATES					
Galagidae	*Galago senegalensis*	Northern lesser galago	12	64	LC
Cercopithecidae	*Cercopithecus neglectus*	De Brazza's monkey	18	49	LC
Cercopithecidae	*Cercopithecus mitis ssp. boutourlinii*	Boutourlini Blue monkey	24	49	VU
Cercopithecidae	*Chlorocebus aethiops*	Grivet monkey	38	252	LC
Cercopithecidae	*Papio anubis*	Olive baboon	83	1325	LC
Cercopithecidae	*Colobus guereza*	Mantled Guereza	45	143	LC
RODENTIA					
Sciuridae	*Heliosciurus gambianus*	Gambian sun squirrel	11	29	LC
Hystricidae	*Hystrix cristata*	Crested porcupine	69	346	LC
Muridae	*Lophiomys imhausi*	Crested rat	8	16	LC
LAGOMORPHA					
Leporidae	*Lepus saxatilis, L. capensis*	Hare	15	101	LC
CARNIVORA					
Felidae	*Felis lybica*	African Wildcat	1	1	LC
Felidae	*Caracal caracal*	Caracal	2	2	LC
Felidae	*Panthera pardus*	Leopard	27	57	VU
Viverridae	*Civettictis civetta*	African civet	56	319	LC
Viverridae	*Genetta maculata, G. genetta*	Genets	82	936	LC
Herpestidae	*Atilax paludinosus*	Marsh mongoose	8	27	LC
Herpestidae	*Herpestes sanguinea, H. ichneumon*	Mongoose	17	35	LC
Herpestidae	*Ichneumia albicauda*	White-tailed mongoose	20	51	LC
Hyaenidae	*Crocuta crocuta*	Spotted hyena	17	31	LC
Canidae	*Canis mesomelas, C. adustus*	Jackals	9	19	LC
Mustelidae	*Mellivora capensis*	Ratel / honey badger	17	27	LC
ARTIODACTYLA					
Suidae	*Phacochoerus africanus*	Warthog	31	233	LC
Suidae	*Hylochoerus meinertzhageni*	Giant forest hog	46	217	LC
Suidae	*Potamochoerus larvatus*	Bushpig	85	870	LC
Bovidae	*Tragelaphus scriptus*	Bushbuck	85	868	LC
Bovidae	*Sylvicapra grimmia*	Bushduiker	83	1274	LC
Bovidae	*Syncerus caffer*	African buffalo	13	37	LC

Table S2. Results from generalized additive mixed models (GAMMs), illustrating the relationship between roof density within a 500m buffer and species reporting rate (i.e. the proportion that a species was detected at a survey site over the duration of the survey at the site). Only results for species present in more than 20 sites are illustrated. Species with significant and nearly significant p-values are illustrated in bold. edf: estimated degrees of freedom. Codes for significance levels: *** p<0.001, **p<0.01, *p<0.05.

Species name	Common name	edf	χ^2	p-value
Cercopithecus mitis	Blue monkey	1	0.043	0.835
Colobus guereza	**Colobus monkey**	**1**	**5.42**	**0.019***
Chlorocebus aethiops	**Grivet monkey**	**2.474**	**27.87**	**3.23e-6*****
Papio anubis	**Baboon**	**1**	**5.00**	**0.025***
Hystrix cristata	Porcupine	1	0.24	0.623
Hyrax sp	Hyraxes	1	0.19	0.665
Genetta sp	Genet	1	1.25	0.263
Civettictis civetta	Civet	1	0.004	0.951
Ichneumia albicauda	White-tail mongoose	1	1.09	0.296
Panthera pardus	**Leopard**	**1**	**4.48**	**0.034***
Hylochoerus meinertzhageni	Giant forest hog	1.752	3.1	0.239
Potamochoerus larvatus	**Bushpig**	**1**	**3.83**	**0.050**
Phacochoerus africanus	**Warthog**	**1**	**3.72**	**0.053**
Tragelaphus scriptus	**Bushbuck**	**1**	**7.29**	**0.007****
Sylvicapra grimmia	Bushduiker	1.507	0.80	0.361

Table S3. Estimates for wetness and elevation linear predictors. Random estimates are not presented. SE: standard error. Codes for the significance levels: *** p<0.001, **p<0.01, *p<0.05.

	wetness			**elevation**		
Common name	**coefficient**	**SE**	**p-value**	**coefficient**	**SE**	**p-value**
Blue monkey	-0.049	0.145	0.735	-0.001	0.001	0.245
Colobus monkey	0.191	0.075	**0.011***	-0.0006	0.000	0.43
Grivet monkey	-0.036	0.093	0.697	0.002	0.001	0.253
Baboon	0.069	0.056	0.215	-0.001	0.000	0.053.
Porcupine	0.082	0.06	0.206	0.000	0.000	0.503
Hyraxes	0.088	0.100	0.378	0.001	0.000	0.066
Genet	0.070	0.07	0.290	0.006	0.005	0.232
Civet	0.130	0.08	0.113	0.000	0.000	0.759
White-tail mongoose	0.052	0.15	0.733	0.001	0.001	0.303
Leopard	-0.1227	0.15	0.414	0.002	0.000	**0.002****
Giant forest hog	0.016	0.093	0.086	-0.001	0.000	**0.021***
Bushpig	-0.004	0.049	0.932	0.000	0.000	0.519
Warthog	-0.308	0.213	0.148	-0.005	0.002	**0.004****
Bushbuck	-0.032	0.060	0.587	-0.000	0.000	0.368
Bushduiker	0.0317	0.061	0.604	0.000	0.000	0.245

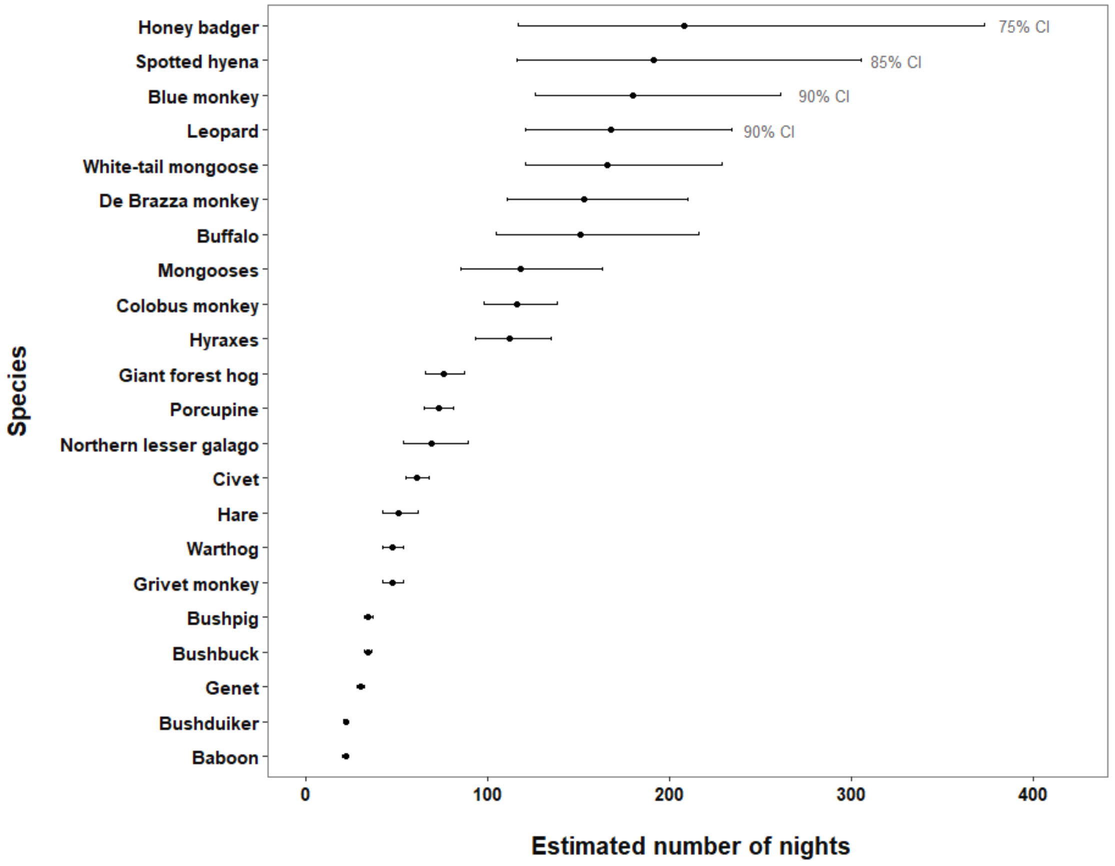

Figure S3: Results from detectability analysis assessing which species had enough sampling effort to be modelled. A total of 20 species could be modelled with confidence intervals between 90 – 95%.

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Chapter VII

Chapter VII

The role of perceptions, social norms and education in shaping women's fertility preferences: a case study from Ethiopia

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> *"(…) In a planet with limited resources and a sensitive climate, with most of its natural resources being overexploited and its economic systems overstressed, meeting the additional demands of a growing human population without destroying the Earth and our social systems will be one of the greatest tests to humanity in the years to come. (…) One can only hope that the issue of population growth rises from obscurity to the forefront of national and international concerns."*
>
> Camilo Mora, Ecology and Society 19(1).

> *"Suuta suuta anqaaqun lukaan demti"*
> Little by little, the egg begins to walk.
>
> (Ethiopian saying)

Abstract

The population-environment-food nexus is a serious sustainability challenge for the Global South, and for Africa in particular, where rapid human population growth typically overlaps with high levels of food insecurity and environmental degradation. In the context of sustainable development, it is important to understand the reasons driving high fertility in these challenged regions. Here, we examined possible determinants of women's fertility preferences, including perceptions of social and biophysical stressors, in southwestern Ethiopia. We considered four key stressors, namely food insecurity, environmental degradation, human population growth, and land scarcity. We examined to what extent perceptions of future trends in key stressors can explain women's fertility preferences towards the desired number of children and the use of family planning methods. We focused primarily on female respondents from a rural setting and complemented our research with findings from university respondents. Our results indicate that perceptions of future trends in the key stressors had little effect on fertility preferences of both rural and university respondents. Rather, fertility preferences appeared to be shaped by underpinning sociocultural norms and religion, a perceived utilitarian value of children, and male dominance within households. Our results have implications for the development of interventions aiming to encourage the use of modern family planning methods and the slowdown of human population growth, suggesting the need for deliberative approaches that engage with social norms, religion, education and society at large.

Introduction

Human population growth is a key driver underlying environmental degradation and food insecurity (Crist et al. 2017). The indirect influence of human population growth on the degradation of natural resources (through deforestation, overexploitation or pollution) is well established (IPBES, 2019; Marques et al., 2019). It also exacerbates food insecurity and poverty (Hall et al., 2017). The population-environment-food nexus is especially challenging in the Global South and in Africa in particular. Vulnerabilities to food insecurity here are high (FAO 2019), environmental degradation strong and ongoing (Laurance et al. 2014) and fertility rates are the highest worldwide (Bongaarts 2017). Compared to Latin America and Asia, the decline in fertility rates in Africa has been much slower (Korotayev et al. 2016; Bongaarts 2017), and despite improvements in family planning services (Ahmed et al. 2019), African women have on average twice as many children as their Latin American and Asian counterparts (Bongaarts and Casterline 2013). In the context of sustainable development, it is therefore important to understand the reasons behind women's fertility preferences, and for high fertility in particular.

Women's fertility preferences (including the use of family planning and the desired number of children) are influenced by social, economic, political and cultural contexts, operating at multiple scales with feedbacks that can balance or reinforce one another. Demographic factors (such as age and geographic context), educational attainment (Martin 1995; Bongaarts 2003; Bongaarts 2010; Smith et al., 2012; Marphatia et al., 2020), religion (Adsera 2006), social norms, and cultural beliefs (Munshi and Myaux 2006) are well known to influence women's fertility preferences. For instance, urban women typically have considerably lower fertility rates than rural women (Lerch 2019). Also, as the educational attainment of girls increases, marriage and the timing of the first child tend to be delayed (Martin 1995; Bongaarts 2003; Smith et al., 2012; Marphatia et al., 2020), and the uptake of family planning methods increases (Bongaarts 2010). Far less research attention, though, has been placed on women's perceptions of various social and biophysical stressors, and on the role such perceptions can play in influencing fertility preferences and behavior. This constitutes an important research gap, because perceptions represent the way in which people organize and interpret information – as such, they have a key influence on decision-making processes and behavior (Pyhälä et al. 2016). Perceptions may be particularly important in contexts of subsistence livelihoods and severe resource constraints, where households are vulnerable to both environmental degradation and food insecurity, such as in many settings in Africa.

Throughout much of Africa, many households' livelihoods depend primarily on subsistence farming and the collection of natural resources, such as firewood, fodder and water. These are time-consuming activities for the household unit, and thus children can have a utilitarian value as a source of labor (Leibenstein 1975; Robinson 1997). Especially as natural resources deteriorate or become scarcer, the perceived need to increase family sizes may therefore rise (Dasgupta 1995; Filmer and Pritchett 2002).

On the other hand, in situations of resource scarcity, it may be more difficult to support a household with many children (Abernethy 1997; Brauner-Otto and Axinn 2017), and individuals might perceive a future in which their livelihoods are troubled by food insecurity. Such perceptions of resource scarcity could then contribute to a smaller desired number of children, or even to the desire to have no children at all, out of concern of not having enough means to adequately provide for all family members. Furthermore, in subsistence economies where access to land is a critical determinant of food security, land scarcity can represent an additional source of concern, and may motivate a preference for a smaller family size.

Existing studies that examine perceptions of different stressors and fertility preferences are either grounded in the social-psychological Theory of Planned Behavior (Ajzen 1993; Ajzen & Klobas, 2013) or for the most part, explore in isolation the relationships between proxies for a given stressor (such as environmental degradation or human population growth) and fertility preferences (e.g Rovin et al., 2013; Biddlecom et al., 2005; Ghimire & Mohai, 2005). However, studies that jointly examine perceptions of different stressors and fertility preferences are missing, hampering our ability to fully understand the complexity of underlying drivers shaping these preferences. Furthermore, the majority of studies to date that look into determinants of women's fertility preferences are derived from cross-sectional studies such as demographic health surveys, while detailed local accounts of how women perceive different social and environmental stressors are typically lacking.

Ethiopia is an interesting area to study within the context of environmental degradation, food insecurity and human population growth. Ethiopia is the second most populous country in Africa, and its population has doubled from nearly 50 million people in 1990 to 100 million in 2015 (UN 2019a). Since the 1990s, family planning campaigns have been run, leading to a decrease in fertility rates to 2.6 children per woman in urban areas (Teller et al., 2011; CSA 2016). Nonetheless in rural areas, where the vast majority of people reside (ca. 81%, World Bank 2016), women have on average 5.5 children (CSA 2016). In these areas, per capita average farm size is declining, and high fertility rates pose challenges not only for environmental conservation, but also for food security and the general welfare of households (Manlosa et al., 2019a; Manlosa et al., 2019b).

Here, we examine possible determinants of women's fertility preferences, including perceptions of numerous social and biophysical stressors, in southwestern Ethiopia. We considered four key stressors, namely food (in)security, environmental degradation, human population growth, and land scarcity. We examine to what extent these stressors can explain women's fertility preferences in terms of desired number of children and use of family planning methods. Specifically, we (1) explore women's perceptions regarding future trends in local environmental conditions, food security and human population growth and perceptions on current land scarcity; (2) examine whether these perceptions influence women's fertility preferences; and (3) compare our findings between two different settings in southwestern Ethiopia, which strongly differ in the level of educational attainment of women. Our findings suggest that awareness of the investigated stressors on its own does not lead to a desire for smaller families, partly because of strong socio-cultural preferences for large families.

Methods

Study area

The study area is located in Jimma zone, Oromia, in southwestern Ethiopia. We collected data in four *kebeles* (smallest administrative unit) located in three *woredas* (districts, namely *Setema*, *Gumay* and *Gera*), as well as at Jimma University. The landscape in southwestern Ethiopia typically consists of a mosaic of agricultural land interspersed with scattered trees, live fences, homegardens and small to large fragments of natural forests and shade coffee forests. Livelihoods are characterized by subsistence agriculture based on food crops and cash crops (coffee and khat) (Manlosa et al., 2019a). Food security is higher than in other parts of Ethiopia, but low by international standards (WFP 2020). Forests in the region support high biodiversity (Rodrigues et al. 2018, 2019; Shumi et al. 2019) and provide many important ecosystem goods and services (Dorresteijn et al. 2017), but have been progressively encroached by farmland since the 1970s, leading to a decrease in forest cover from 79% to 60% between 1973 and 2010 (Ango et al., 2016). Environmental degradation is also apparent on agricultural land through for example increased erosion and soil depletion (Bishaw 2001). Human population in Jimma *zone* has increased by 26.6% from 1994 and 2007 (CSA 2007). In Oromia, the fertility rate is 5.4 children per woman, and the percent of married women using modern methods of family planning is around 28%, whereas the unmet need for family planning is estimated at 29% (CSA 2016). Children under the age of 15 years represent 47% of the Ethiopian population (CSA 2016). The median age at first marriage is 17.4 years, and of 17.8 at first birth. About half of the population in Oromia is Muslim, and social organization reflects a male dominated society with patriarchal values. Within the study area, polygamy is common. Since the 1990s, the government has implemented a series of interventions in order to slow down human population growth, including an increase in the availability of family planning methods (Olson and Piller 2013) and legislation against underage marriages, along with efforts to expand access to education and health care in rural areas (Hailemariam 2016).

Sampling and survey tool

The data for this study is based on a mixed methods approach, including a household survey with randomly chosen women in four k*ebeles* (n=122), a survey at Jimma University (n=149) and qualitative interviews with local health experts (n=5). The surveys were conducted in the local Oromo language in the *kebeles*, and in Oromo and Amharic at the university, by two trained female enumerators with backgrounds on health issues. The answers were translated into English by the enumerators. The interviews with health professionals in the *kebeles* were conducted in Oromo, and in English in the *woredas* (by choice of the interviewed health workers). Data collection took place in two periods: data for a pilot study were collected during July 2016, and the main survey was conducted between February and April 2017 (in the *kebeles* and at Jimma University).

For the household survey, we used a face-to-face questionnaire for data collection. An initial pilot questionnaire was developed and tested in the rural setting with 22 women. This pilot survey helped to train the enumerators and allowed the fine-tuning of questions for the survey tool, especially regarding the wording in Oromo. We used proportional cluster sampling, meaning that the number of women surveyed in each *kebele* was proportional to the *kebele* total population, and we used a spatial map of all the roofs in the *kebeles* to randomly select our households. One woman was interviewed per household. This resulted in a survey of 122 women aged between 18 and 49 years.

We used the desired number of children and the use of family planning as indicators of fertility preferences, since the desired number of children gives an idea about future-oriented aspirations and use of family planning indicates a present-view of actions. Our questionnaire had both open and closed items regarding women's perceptions of different stressors and their fertility preferences. The questionnaire consisted of eighteen questions structured into five sections: (*i*) household background, (*ii*) perceptions, (*iii*) desired number of children, (*iv*) family planning use, and (*v*) aspirations and expectations for children (see Supporting Information Tool S1). Section *i* elicited the age of marriage, age at first child, education level, marital status, religion, current number of children and their education. Section *ii* assessed a respondent's perceptions regarding future trends (i.e. in the forthcoming ten years) in food security, environmental conditions, human population, and current perceptions of land scarcity. Questions on perceptions of future trends were asked on a Likert scale, from 1 to 5 ("“much better” to “much worse”, or, in the case of human population growth, “decreasing a lot” to “increasing a lot”), and were followed by an open-ended question (“why?”) aimed at collecting a justification for the reported perceptions (see supporting information for details). Section *iii* focused on the desired number of children. Women were asked to report their desired number of children, why they would like to have more or less children than they already had, and about the benefits and disadvantages of having many or few children. Section *iv* asked about the use of contraceptives, and the frequency of use, as well as about women's views on the advantages and disadvantages of contraceptive use. This section also included questions to understand spousal communication and fertility preferences. Section *v* examined women's aspirations for their daughters and sons in terms of age of marriage. We included this section because (1) it could provide hints on the type of information and knowledge women will pass on to their children, and (2) it helped to assess if concerns emerging from perceptions would be raised when reflecting on what they aspire for their children.

To gauge the influence of education on perceptions and fertility decisions we conducted a second survey, with 149 women at Jimma University. We randomly selected respondents from a list of female students at the Jimma University College of Agriculture and Veterinary Medicine. We used the same questionnaire as in the household survey, but because most university students were unmarried and had no children, the wording was changed for some questions and in some instances the reference was the household of their parents (see Supporting Information Tool S2).

Finally, we interviewed five rural health extension workers to assess (1) local availability of family planning methods; (2) acceptance and reasons for the uptake of family planning methods; and (3) outreach activities regarding family planning. Informants included both female and male nurses from both *kebele* and *woreda* levels: three female nurses were interviewed in the *kebeles* of *Difo Mani* and *Kuda Kefo* (in *Setema* and *Gumay woredas*, respectively), two male nurses at *Gatira* town (in *Setema woreda*), and one female nurse in *Gera woreda* (see Supporting Information Tool S3).

Data analysis

The quantitative data analysis followed three main steps. First, we summarized respondents' socio-demographic characteristics, perceptions and aspirations for their children using descriptive statistics. Second, we modeled the relationships between women's perceptions, their background characteristics and two response variables, i.e. the desired number of children and the use of family planning. We used generalized linear models with a Poisson distribution to model the desired number of children, and a binomial distribution to model the use of family planning (use versus non-use). A set of different variables entered the models depending on (a) the response variable of interest and (b) the dataset (i.e. rural versus university respondents) (see Table S1). For instance, age and current number of children entered the models as predictors in the rural dataset, but were excluded from the university dataset, because 98% of university respondents were younger than 25 years old and none had children. We used AIC_c criteria (corrected for small sample size) to select the best model describing the data; but we also provide alternative models based on delta AIC_c values and model weights (Burnham and Anderson 2002). Notably, given the substantial differences between both datasets (i.e. rural and university respondents) in terms of age, religion and education, we deliberately avoided statistical comparisons between these datasets. The number of complete cases varied between questions and we therefore report the total and the partial number of respondents along with percentages. The final step in our data analysis consisted of a content analysis of the qualitative data from open-ended questions of the rural and university surveys, to assemble emerging information not captured by the quantitative data. Specifically, qualitative data was analyzed using a content reduction approach, based on summarizing content analysis (Mayring 2014).

Ethical considerations

Prior to our surveys, we obtained permission from *kebele* leaders, *woreda* officials and Jimma University to conduct the research. We then sought voluntary informed consent from each participant in the surveys. Consent was given verbally in the presence of a witness. All respondents were informed of their right to terminate the interviews at any time. Anonymity was granted to all respondents during the period of study and in all outputs from the research. Respondents were differentiated using an alphanumeric ID. Research was approved by the Ethics Committee of Leuphana University.

Results

Socio-demographic characteristics of respondents

Approximately 82% of rural respondents were at least 25 years old. The vast majority was Muslim (97%) and illiterate (66%) or had only attended primary education (27%) (Table 1). Rural households had on average seven members (adults and children), and women had on average 4.7 ± 2.2 children (Table 2). Approximately 98% of rural respondents were married, and the average age at marriage was 15.7 ± 3 years (Table 2). By contrast, nearly all university respondents were younger than 25 years old (98%) and the majority was Christian (84%) (Table 1). Only two respondents were married, and none had children.

Table 1. Socio-demographic characteristics of female respondents in SW Ethiopia, in rural and university contexts.

Characteristics	**Rural**		**University**	
	Frequency	Percent	Frequency	Percent
Age respondents (n_{rural}=120, n_{uni}=147)				
15-19	6	5	31	21.1
20-24	15	12.5	113	**76.9**
25-29	21	17.5	2	1.3
30-34	21	17.5	1	0.7
35-49	57	**47.5**	0	0
Religion (n_{rural}=118, n_{uni}=149)				
Muslim	114	**96.7**	22	14.8
Orthodox	3	2.5	93	**62.4**
Protestant	1	0.8	33	22.2
Others			1	
Education attainment (n_{rural}=102, n_{uni}=149)				
No education	67	**65.7**	0	0
1 to 6th grade	28	27.4	0	0
7 to 12th grade	7	6.9	0	0
College	0	0	149	100

Perceptions of food security trends

The majority of rural respondents (74% of n=122) expected an overall improvement in the food security of their household within the next ten years (Figure 1a). Reasons given for expected improvements were associated with the notion of "working hard", reported by 70% of rural respondents. The idea of "hard work" is represented by a strong dedication in terms of time commitment and diversification of activities that can lead to the increase of farm production and future investment. Respondents often mentioned the importance of sowing and harvesting on time, sharecropping, diversifying products and the performance of off-farm income generating activities, as forms of hard work: *"Through hard work. There is a shortage of land but we try to improve our production by intercropping crops like maize, coffee and sorghum together, by trading khat and coffee"* [R43]. The use of improved varieties, fertilizer and access to knowledge and technology were also perceived to contribute to future improvements in rural food security. Respondents who expected a deterioration of food security (16%) identified crop raiding by wild animals and land scarcity as the main reasons for such deterioration. The overall perceived trend for future food security was similar in university respondents (n=149), with 80% of respondents expecting an overall improvement (Figure 1a) within the next ten years. Like rural respondents, university students identified "hard work" (75%) as the main reason for this expectation. The use of improved crop varieties, and availability of knowledge and technology were also mentioned as contributing to better food security (Figure 1a).

Table 2. Reproductive history of female respondents in the rural context

Characteristics	Frequency	Percent
Age at first marriage (n=117)		
<15	68	58.1
15-18	29	24.8
≥18	20	17.1
Age at first birth (n=116)		
<15	15	13.0
15-18	47	40.5
≥ 18	54	46.6
Number of live children (n=122)		
≤ 2	21	17.2
3 - 5	50	40.9
≥ 6	51	41.8
Family size (n= 122)		
≤ 4	19	15.5
5-9	86	70.5
≥ 10	17	14

Rural respondents (n=122) were then asked if there was any effect of household size on the amount of food that each individual was able to consume. Perceptions varied among respondents. About 39% of rural respondents perceived no relationship between household size and the food available for consumption, reporting that their family size was small relative to their assets, and instead mentioning problems with damages to crops due to wild animals, climate instability, lack of rain and soil degradation, as illustrated by the following statement: "*No, the size of the family doesn't affect the intake of our food. The problem is we cannot harvest our expected yield due to wild animal damage. Therefore our family size doesn't matter for our food intake but we eat less or skip meals due to loss by animals*" [R121]. Nearly 30% of rural respondents perceived a negative effect of household size on food availability, explaining that the harvest was insufficient, leading to adults and children skipping meals or consuming a reduced amount of food per meal: *"Yes it [household size] has a negative effect on food … because our production is not enough for my family, sometimes they consume less due to shortage of food in the house"* [R38]. 31% of respondents were uncertain about the existence of such a relationship, but often reported that skipping meals or eating smaller meals was common among adults and children during periods of food shortage.

Approximately 71% of university respondents (n=149) reported no effect of household size on the amount of food each individual was able to consume. However, nearly 64% of all university respondents reported that in the future they would consider their assets when deciding the number of children to have, as illustrated by the following statement: "*No, they will not have an effect because I will determine my family size depending on my economy"* [R296].

Perceptions of environmental trends

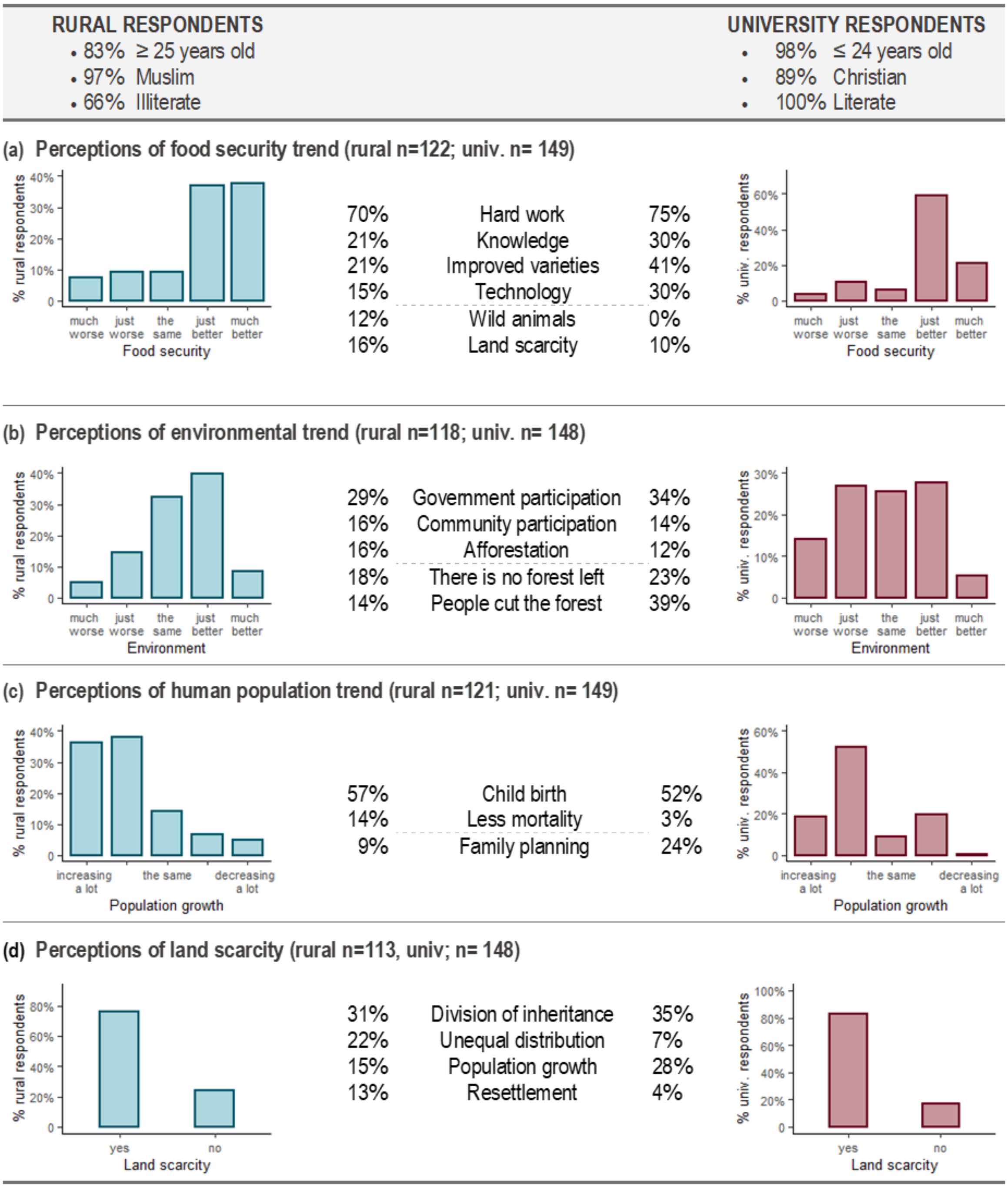
About half of the rural respondents (48% of n=118) expected improvements in the environmental conditions of their *kebele*, whereas about 32% expected no changes. Government afforestation initiatives and regulation of the use and extraction of forest products, together with increasing community participation in forest protection were identified as key factors underpinning improvements in the environment (Figure 1b): "*Because most people need to plant coffee in the forest and need shade trees, and government made a law for forest protection and if someone cuts the forest they will receive punishment"* [R41]. Respondents expecting no change in the environment commonly reported the lack of forest in the area around their house. Among the respondents who perceived some level of deterioration in their environment (ca. 20%), the destruction of forest was reported as the main reason for the degradation of environmental conditions, as well as a lack of clean water for drinking. Deforestation was perceived to be the result of the need to expand farmland area and to build new houses: "*Because people start clearing land to build their home and for their farming, to increase their land, for production; forest is decreasing rapidly"* [R45]. University students (n=149) had similarly mixed expectations regarding environmental degradation with some expecting a deterioration due to deforestation (41%), others expecting no change in environmental conditions (25.5%), and others identifying an overall improvement of natural resources due to afforestation initiatives led by the government with the engagement of the community (33%).

Perceptions of human population growth

Most rural respondents (74% of n=121) expected an overall increase in the regional population (Figure 1c). Childbirth (reported by 57% of respondents) was identified as the main reason for such an increase, combined with low child mortality (Figure 1c). Other reasons, mentioned by 19% of respondents, included early marriage, no use of family planning methods, polygamy and the Sharia law. Two respondents mentioned: "*95% of people in our kebele abide by Sharia law. Girls and boys are getting married at an early age*" [R139]; "… *the women are giving birth quickly and the people who migrate to another place are too few"* [R26]. Like rural respondents, most university participants (71%) expected an overall increase in the human population, mostly due to high rates of childbirth, immigration, and the lack of use and knowledge of contraceptives.

Perceptions and influence of land scarcity

Most rural respondents (76% of n=113) perceived that land available for farming was scarce in their *kebele*, especially for the younger generation. Inheritance of land combined with large family sizes and limited options for acquiring new land were identified as main reasons: *"In our area one husband can have three wives, from three wives he gets many children and during division, some children cannot get land"* [R84]. Respondents also noted the unequal distribution of land during the Derg regime (after 1975), human population growth and resettlement of people (Figure 1d) and issues related with land transactions (e.g. when people migrate and lend their land). Respondents who perceived no land scarcity (24%) commonly reported the lack of will to "work hard": "*There is enough land in our area but people don't want to work hard on it"* [R10]. Perceptions of current land scarcity were similar among university respondents, with the vast majority (80% of n=149) reporting that they perceived land for farming to be scarce. Like rural respondents, university students identified inheritance rules combined with large family sizes as the main reason for land scarcity, followed by human population growth (Figure 1d).



RURAL RESPONDENTS
- 83% ≥ 25 years old
- 97% Muslim
- 66% Illiterate

UNIVERSITY RESPONDENTS
- 98% ≤ 24 years old
- 89% Christian
- 100% Literate

(a) Perceptions of food security trend (rural n=122; univ. n= 149)

70%	Hard work	75%
21%	Knowledge	30%
21%	Improved varieties	41%
15%	Technology	30%
12%	Wild animals	0%
16%	Land scarcity	10%

(b) Perceptions of environmental trend (rural n=118; univ. n= 148)

29%	Government participation	34%
16%	Community participation	14%
16%	Afforestation	12%
18%	There is no forest left	23%
14%	People cut the forest	39%

(c) Perceptions of human population trend (rural n=121; univ. n= 149)

57%	Child birth	52%
14%	Less mortality	3%
9%	Family planning	24%

(d) Perceptions of land scarcity (rural n=113, univ; n= 148)

31%	Division of inheritance	35%
22%	Unequal distribution	7%
15%	Population growth	28%
13%	Resettlement	4%

Figure 1. Summary of perceptions on future trends in (a) food security, (b) environmental conditions, (c) human population growth and (c) land scarcity, for rural (blue) and university (red) respondents. The middle panel lists the main topics reported by respondents as contributing to the perceived trends. The proportion of respondents mentioning each topic is given on the left (rural) and right (university). Dashed lines in between topics separates reasons for "better - worse" and "increasing - decreasing" gradients.

Asked about the relationship between perceived land scarcity and fertility decisions, 61% of rural respondents (of n=121) reported no perceived relationship, with nearly half of them (43%) mentioning religious motivations for having children: "*Because in our religion having children does not depend on having land or wealth, it is Allah's will*" [R18]. The possibility of having other jobs, especially of sharecropping when lacking land was also noted by some respondents: "*Because if people desire many children they can work and get produce by working together with other people to get a share of the production through their labour and by cattle production and raise their children properly, so the size of land doesn't affect the desired family size*" [R25]. A similar share (40%, of n=122) of rural respondents reported a perceived positive effect of the amount of available farming land on fertility, with land availability seen as an important asset for food production and for children's future security through inheritance of land. This effect was also acknowledged by the majority of university students (70% of n=149) who perceived land to be a general source of income.

Desired number of children and use of family planning methods

Rural respondents reported six children on average as their desired number (Figure 2). The desired number of children of rural respondents was significantly and positively associated with the respondent's current number of children and with a perception of increasing human population growth (Table 3). Most rural respondents identified the utilitarian value of children (e.g. children helping in the fields or with household chores) and happiness as benefits of having more children, together with insurance at old age, and children being a result of Allah's or God's will (Table 4). Disadvantages of many children included the lack of material resources (e.g. clothes and school materials), parents being frequently tired, and a lack of time to look after children (Table 4).

Less than half of rural respondents (43% of n=122) reported to have used family planning methods at some point in their lives. The frequency of contraceptive use varied between "rarely" (34% of users) and "sometimes" (26% of users) to "often" (26% of users), with hormonal injections and contraceptive pills being the most frequently used methods. The unmet need for family planning (calculated as the difference between the desired number of children and the current number of children) was around 19%. In terms of advantages and disadvantages of using family planning methods, rural women reported benefits for the health of mother and child, benefits for taking care of children (less time being pregnant and breastfeeding), and benefits for the family economy (Table S2). Also, women who desired fewer children ($p < 0.05$) and women who discussed fertility preferences with their husbands ($p < 0.01$) were more likely to use family planning compared to those who desired more children and did not discuss fertility preferences with their husbands (Table 3).

Table 3. Summary of best generalized linear models, assessing the relationships between perceptions and fertility preferences. P_{ENV}: perceptions on environment; P_{FOOD}: perceptions on food security; P_{POP}: perceptions human population growth; P_{LS}: perceptions on land scarcity; AIC: Akaike Information Criteria. Codes for the significance levels: ***p < 0.001, **p < 0.01, *p < 0.05. n.a.: non-applicable, variables that were not included in the model.

BEST MODELS										
	Intercept	**Age**	**Current children**	**Desired children**	**Discuss husband (yes/willing)$^{\#}$**	**P_{POP}**	**P_{FOOD}**	**P_{LAND}**	**P_{ENV}**	**Explained deviance**
Rural										
Desired n. of children (n=108)	0.793***	0.011	0.044*	n.a.		0.101**				24%
Use of family planning (n=101)	0.067			-0.1803*	1.182**					9%
University										
Desired n. of children (n=143)	0.893***	n.a.	n.a.	n.a.		0.079				3%
Use of family planning (n=143)	-6.765***	n.a.	n.a.	0.437*	3.976***				0.5862*	47%

$^{\#}$Discuss fertility preferences with the husband: rural respondents reported *yes* or *no*, and university respondents reported *willing* or *not willing* to discuss (since the vast majority was not married). Reference level in the models is *no* and *not willing* for rural and university respondents, respectively.

University respondents desired three children on average (Figure 2). For university respondents, the best model had very little support in explaining the data, and no predictor variable seemed to have a significant influence on their desired number of children. The majority of university students reported they wanted to have fewer children than their parents. Reasons were the difficulty to provide food and material items for many children, an ability to provide only for a small family size, and benefits for mother and child health (Table 4), whereas disadvantages were the lower availability of child labour and having fewer relatives (Table 4). Around 28% of university respondents reported using or having used family planning methods. The frequency of use varied between "sometimes" (69%), "often" (12%) or "rarely" (12%). University respondents highlighted, among others, the health benefits for mother and child, more time to take care of children, and the ability to decide on the family size as advantages of using family planning (Table S2). Disadvantages were the health-related side effects associated with hormonal family planning methods (Table S2). Alternative models but with lower explanatory power for both datasets and response variables, are provided in Table S3(a-b).

Women's aspirations for their children

Figure 3 presents women's aspirations for their children in terms of age of marriage. Aspirations differed according to setting (rural versus university) and child gender. Around 45% of women in the rural setting aspired for their daughters to be married before the legal age of 18 years, whereas at university, 84% of respondents reported ages between 18 and 25 years. Respondents explained aspirations for underage marriage of daughters in terms of culture and of following Sharia law. In both rural and university settings the aspired age of marriage for sons was higher than for daughters, with women reporting that prior to entering marriage, sons needed to have work and savings to support their new family.

Table 4. Summary of benefits and disadvantages of having more or less children than the reference point. The reference level for rural respondents is their current number of children; whereas the reference number for university students refers to the number of children their parents have. Numbers refer to absolute counts of women that reported each benefit or disadvantage.

	Rural	**University**
Benefits and disadvantages of having more children than the reference		
Benefits	**n=83**	**n=33**
Children bring happiness	42 (51%)	19 (58%)
Substitution in case of death – “if one child dies we have more”	23 (28%)	3 (9%)
Children help in the fields and help with money	65 (78%)	28 (85%)
It is God‘s / Allah‘s will	24 (29%)	3 (9%)
Children increase the number of relatives	12 (14%)	5 (15%)
Children represent insurance at old age	9 (11%)	4 (12%)
Children are a sign of respect in the community	5 (6%)	1 (3%)
Others	4 (5%)	1 (3%)
Disadvantages	**n=90**	**n=51**
There is not enough money to buy clothes, school materials	67 (74%)	46 (90%)
There is no time to take care of children (e.g. give bath)	35 (39%)	12 (24%)
There is land competition between children	20 (22%)	5 (10%)
Children make parents tired	42 (47%)	42 (82%)
It is difficult to provide food	21 (23%)	28 (55%)
It negatively impacts the health of the mother and the child	11 (12%)	9 (18%)
Benefits and disadvantages of having less children than the reference		
Benefits	**n=30**	**n=98**
It is God‘s / Allah‘s will	1 (3%)	2 (2%)
I know I have enough to provide only for few children	17 (57%)	52 (53%)
It is good for the children and mothers health	14 (47%)	33 (34%)
It is difficult to provide goods for many children	22 (73%)	55 (56%)
Difficult to provide enough food and to raise children well	0 (0%)	46 (47%)
Disadvantages	**n=39**	**n=112**
Decreases the amount of relatives	6 (15%)	19 (17%)
Decreases the amount of labor	16 (41%)	62 (55%)
There are no disadvantages	25 (64%)	44 (39%)

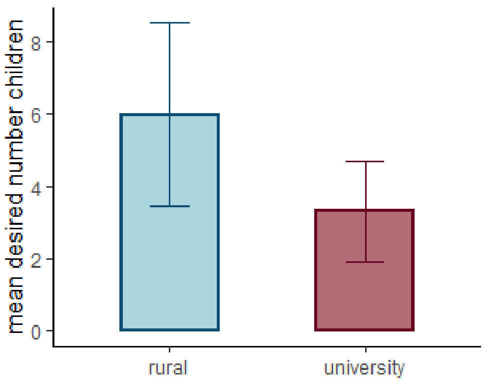
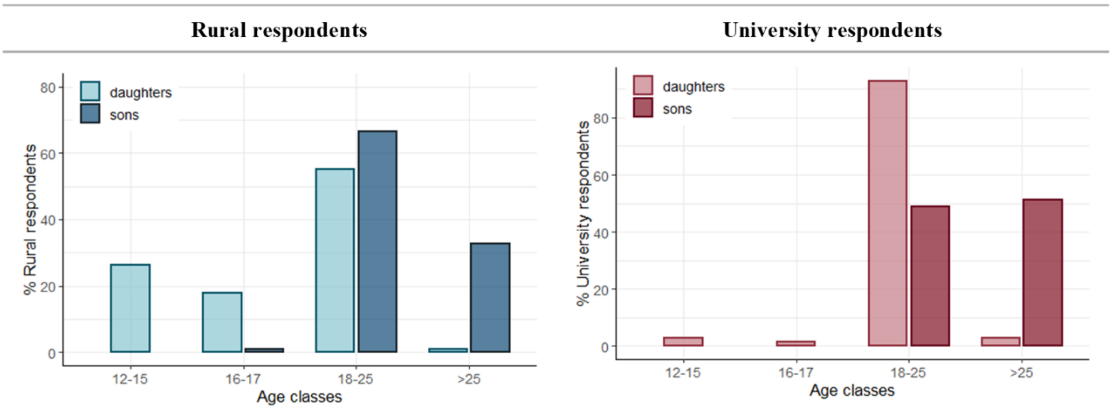


Figure 2. Mean desired number of children and standard deviation for rural (blue) and university (red) female respondents.

Availability of family planning services and social norms in rural communities

Health workers indicated that family planning methods had been available at the *kebeles'* health clinics since the late 2000s, at no cost to women. Two nurses from one *woreda* identified the compliance with religious rules as one of the main constraints to the use of family planning methods, in addition to fear and misinformation about side effects. A health worker from another *woreda* identified male dominance and lack of women's agency as factors limiting the uptake of contraception. The absence of engagement with reproductive health issues among community and religious leaders were also reported as obstacles to the uptake of family planning methods. At the *kebele* level, nurses reported both the influence of religion and husbands on the uptake of contraception. Notably, *kebele* nurses suggested that unsupportive social norms appeared to be changing, and that the community and its leaders were beginning to gain a better understanding of the side effects and of the advantages of family planning.

The inconsistency in use, especially regarding short-term methods (e.g. injections and pills), was reported as a challenge in the effectiveness of contraception. Healthcare providers connected this inconsistency with illiteracy, which prevented women from reading their health schedule and thus missing their appointments at the clinic. Outreach activities differed between *woredas*. *Setema* health workers reported outreach interventions that included engaging with community and religious leaders, and the use of school media at elementary education and high school levels to disseminate information regarding family planning. Furthermore, nurses from *Setema* and *Gumay woredas* reported regular visits to the *kebeles'* households. A health worker from *Gera* mentioned the absence of outreach activities engaging with community and religious leaders and stressed the need to include men in interventions that target family planning use.



"According to sharia law women should get married starting at 12 to 15 years and for men, starting at 20 he can get married." [R25]

"For her it is a shame to marry later than 15-20 years old. For him no problem to marry at whatever age." [R64]

"For our daughter, she should get married at this age [15 or 16 years] according to Sharia rule and our culture. For my son, after he completes his education and has his own work and after he helps me." [R92]

"It can happen for the future or not I advise them to get married at this age [18 years] but they can decide by themselves without my expectation." [R237]

"They can get married late but I will not allow for my child to get married early." [R261]

"I want to be a role model for my children and advise and guide them to get married after they complete their education and have an income." [R285]

Figure 3. Female aspirations for their children in terms of age of marriage, disaggregated by child gender and respondent setting.

Discussion

This study examined fertility preferences of rural women in relation to perceptions of future trends of key stressors that affect local livelihoods (i.e. environmental degradation, food insecurity, land scarcity and human population growth). Figure 4 synthesizes our findings. We discuss our results in detail for the rural dataset, and use the findings from university respondents to complement key points. Overall, our results indicate that perceptions of future trends in the different stressors had little effect on fertility preferences. Rather, fertility preferences appeared to be shaped by underpinning sociocultural norms and religion, a perceived utilitarian value of children, and male dominance within households. Our results have implications for the development of interventions aiming to encourage and promote the voluntary use of modern family planning methods and the slowdown of human population growth.

Perceptions on proximate and distal livelihood stressors

Previous research in our study area shows that rural households experience numerous stressors that can impede their livelihoods. For instance, during food shortages in the lean season, households often reduce the intake of food (Manlosa et al., 2019a). Findings from this study confirm perceived land scarcity for farming activities. However, despite this, the majority of rural respondents expected an improvement in food security in the next ten years. This perception rests not only on a prevailing ethic to "work hard" (either by devoting more effort to farming activities or by diversifying livelihoods), but also on the use of technology and improved crop varieties, irrespective of environmental constraints.

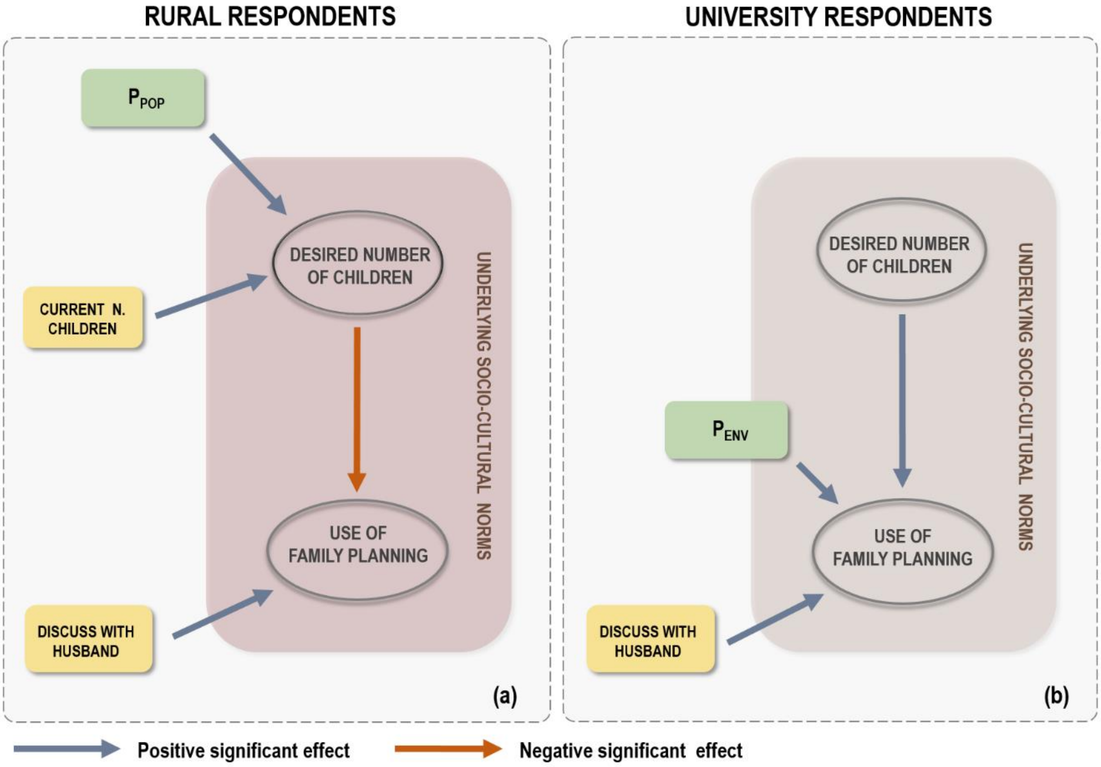


Figure 4. Synthesis of the variables influencing fertility preferences (i.e. the desired number of children and the use of family planning) by rural (a) and university (b) female respondents. The set of underlying socio-cultural norms differs between rural and university respondents and is represented by different shadings.

Similar patterns emerged for perceived environmental trends. Past trends in forest cover show progressive deforestation and degradation of natural forests at least since the 1970s (Ango et al., 2016; Hylander et al., 2013). However, many rural respondents perceived an improvement in forest cover in their *kebeles*. This perception was based on afforestation initiatives promoted by the government, on the enforcement of forest protection laws and training and awareness campaigns directed to the community, as well as community engagement in forest protection activities. Our findings suggest a disconnection between what is perceived locally versus global discourses on human population growth and the environment; and arguably a disconnection between local perceptions and measurable indices of environmental degradation, such as forest clearing. Whereas human population growth is seen as an underlying pressure on the natural environment and likely to exacerbate food insecurity globally (Dasgupta 1995; Crist et al. 2017), locally, many women expect improvements in their food security and in the future state of natural resources, despite acknowledging ongoing human population growth.

Determinants of fertility preferences

We discuss three potentially important determinants of women's fertility preferences – perceptions about future stressors, social norms and education. Generally speaking, the perception of future stressors seemed to only poorly explain fertility preferences. Indeed, the influence of perceptions on fertility preferences of rural women was limited to the perception of future trends in human population growth. Rural respondents who expected ongoing human population growth were more likely to desire more children than women who did not share this expectation. Similarly, the current number of children had a positive effect on the desired number of children of rural respondents. Among various possibilities, both relationships can be the result of social norms incentivizing large family sizes and the cultural value attributed to large families. This approximates what Barrett et al. (2020) described as "conformist" reproductive behaviour, that is, "when the family size that a household desires is positively related to the average family size in the community", so that it conforms with the community norm. Also, households where most members are children have access to more labour, better possibilities of future security (in some dimensions) and enjoy high social status in the community (Atake and Gnakou Ali 2019). Furthermore, in the rural context of southwestern Ethiopia, where gendered social norms are still strong (Manlosa et al., 2019a), with men as the primary decision-makers and mainly responsible for the farm and the production of food and women responsible for household chores and attending to children, narratives on environment and agricultural production may not be rationales on which the majority of women would base their fertility preferences.

Social norms and mindsets appeared to be strong underlying forces influencing fertility decisions in the rural setting. Local mindsets around the utilitarian value of children (i.e. extra labour contributes to the household economy) and around children as a divine will, were frequently mentioned, and are consistent with other studies in sub-Saharan Africa (e.g. Caldwell & Caldwell, 1987). Some respondents also held the traditional view that once being born, a child "*grows up by taking its chances or opportunities*", meaning that if children have good luck they will grow and be successful, a finding also reported in other studies in Ethiopia (Sahleyesus et al., 2009; Newmarch & Bekere, 2017). Another important and pervasive social norm elicited from rural women statements was the support for underage marriage of girls. Almost half of rural respondents expected their daughters to get married before the age of 18 years, and about a fourth preferring an age between 12 and 15 years. Different studies demonstrate that younger marriage ages in girls result in earlier motherhood and larger families (Efevbera et al. 2017, 2019; McClendon et al. 2018). Besides, early marriage and maternity undermine the rights and livelihood opportunities of girls by leaving them vulnerable to the health risks of early pregnancy and childbearing, and by prematurely ending their schooling (Delprato et al. 2015, 2017). Furthermore, a key determinant in the use of family planning methods by rural respondents was whether women discussed family planning with their husbands – a topic identified as important in many sub-Saharan African countries (reviewed in Blackstone et al., 2017). In our study, rural women who reported discussing family planning with their husbands were more likely to use family planning methods than those who did not. The use of contraception thus is not only the result of free choice by a given woman, but is mediated by underlying social-cultural community norms and gender-power relations within the household (Kane et al. 2016). Considerable research in sub-Saharan Africa confirms that the inclusion of husbands in the process of decision-making increases the consistent use of family planning (Terefe and Larson 1993; Bawah, 2002; Tilahun et al. 2014; Ezeanolue et al. 2015).

The different outlook on fertility preferences for rural and university respondents suggests that (post-primary) education may also have an effect on reducing the desired number of children and on the uptake of family planning methods. Indeed, education has long been regarded as one of the most effective drivers of fertility and social change (Bongaarts, 2003; Bongaarts et al. 2017). Not only does it delays marriages and first pregnancies, but it also contributes to improved gender equity (UNFPA 2012). Our results show that the average number of children desired by university respondents was half of that reported by rural women, with many students intending to use family planning. Among the most frequently mentioned advantages of family planning elicited from university respondents were the power to decide on the family size and the positive impact it brings to the family economy. More than half of university respondents indicated they intended to consider their future income when planning on having a family. Similar to the findings by Sahleyesus et al. (2009) for urban areas in Ethiopia, university respondents were weighting the available resources with the desired family size and balancing the trade-offs of having smaller or larger families with their "economy status". There were also major differences between the two groups of respondents in terms of preferred age of marriage of daughters. Unlike in the rural setting, underage marriage was rarely preferred by university students.

Notably, the contextual differences of the two groups of respondents in our study limited our ability to single out the effect of education from possible effects of religion and age. Nonetheless, expanding our analysis to the group of university respondents allowed us to highlight the complexity that underlies fertility preferences within a region, where the consideration of two different contexts (i.e. educated urban women and rural uneducated women) evidenced similarities (mostly regarding perceptions on stressors) but also differences in motivations and behaviours regarding fertility preferences.

Implications

The findings from our study are of significance for policy and practice. Here, we found a mismatch between the global discourse on the population-environment-food nexus (Crist et al. 2017) and local women's perceptions. This mismatch can have implications for the implementation of policies relating to demography, sustainable use of natural resources and livelihoods. This is because policies are typically developed at the national scale but implemented locally, and such mismatches can thus result in the design of inappropriate policies and the misallocation of resources. Understanding and tackling underlying paradigms (such as “hard work”) that contribute to the disassociation of knowledge among scales is therefore critical for the design and prioritization of appropriate interventions.

Likewise, our study highlights the need to consider the socio-economic and cultural context in which fertility preferences are based and fertility decisions taken. Ethiopia’s cultural background is extremely diverse, with more than 80 ethnic groups and more than 80 languages, five widespread religions and many traditional faiths (Adamu, 2013). Such a diversity of cultures implies that many different views, motivations and desires can be held regarding fertility preferences. Despite significant improvements in education and access to reproductive health care in the study area (Assefa et al. 2019), the desired number of children (currently 6.0) is well above the replacement rate of 2.1 (Searchinger et al. 2013) while the unmet need for family planning (currently at 28%) is still high. These indicators suggest that the transition from high to low fertility rates will require more than technical interventions – such as improving the availability of family planning methods. In the presence of strong and deep forces such as social-cultural norms, technical interventions alone are unlikely to trigger and sustain profound changes in fertility preferences and fertility outcomes (Abson et al. 2017).

Given the important role of social norms demonstrated in this paper and elsewhere (Nyborg et al. 2016), new deliberative approaches are needed to engage with those social norms that currently incentivize unsustainably large families sizes, to the possible detriment of both children and women (Bayisenge 2013). Such deliberative approaches should recognize that fertility and family welfare are a general social responsibility (not only one of women), and should involve all actors and institutions through which social norms are perpetuated. Transformative approaches that promote dialogue among men and women, couples, and the community and society at large should be encouraged (Kane et al. 2016); these should engage with topics such as education, family planning and adolescent health services, and with social norms and cultural beliefs. Importantly, as cautioned by Boyden and colleagues (2012), such approaches should identify and address social concerns and the underlying logic of prevailing norms as well as the potential outcomes for those involved, in order to avoid undesired adverse outcomes. Carrying on with business as usual, it seems, will not be a sustainable path for the region.

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Supporting Information for Chapter VII

The role of perceptions, social norms and education in shaping women's fertility preferences: a case study from Ethiopia

Table S1: List of variables included in the modelling of perceptions, demographic factors and response variables of interest. P_{ENV}: perceptions on environment; P_{FOOD}: perceptions on food security; P_{POP}: perceptions human population growth; P_{LS}: perceptions on land scarcity.

Datasets & Response variables	Predictor variables
Rural dataset	
Desired number of children	Age, Current n. children, P_{ENV}, P_{POP}, P_{FOOD}, P_{LS}
Use of family planning	Age, Current n. children, Desired n. children, Discuss husband, P_{ENV}, P_{POP}, P_{FOOD}, P_{LS}
University dataset	
Desired number of children	P_{ENV}, P_{POP}, P_{FOOD}, P_{LS}
Use of family planning	Desired n. children, Discuss husband*, P_{ENV}, P_{POP}, P_{FOOD}, P_{LS}

*Will discuss with a future husband.

Table S2. Summary of advantages and disadvantages of family planning methods, as perceived by rural women and university students.

	rural		**university**	
Advantages of family planning	**n=119**		**n=149**	
Good for the health of mother and child	92	(77%)	118	(79%)
Gives a rest to the family if they have no money	9	(8%)	6	(4%)
It is good to take care of children	32	(27%)	56	(38%)
Good for the family economy	14	(12%)	49	(33%)
To decide the family size	9	(8%)	77	(52%)
To prevent pregnancy	9	(8%)	22	(15%)
No advantages	8	(7%)	2	(1%)
I don't know	12	(10%)	3	(2%)
Disadvantages of family planning	**n=115**		**n=148**	
Can cause diseases	22	(19%)	20	(14%)
Causes continuous bleeding	42	(37%)	24	(16%)
Causes gastric problems	15	(13%)	20	(14%)
Causes headaches	35	(30%)	32	(22%)
Disrupts menstruation cycle	2	(2%)	14	(9%)
Needs balanced diet	15	(13%)	15	(10%)
Causes weight variation; anemia; skin and behavioural problems	17	(15%)	50	(34%)
No disadvantages	27	(23%)	37	(25%)
I don't know	20	(17%)	5	(3%)

Table S3a: Summary output of the model selection process assessing the relationships between perceptions and demographic factors and the desired number of children for rural respondents. The best model is highlighted in light grey. Alternative models with delta AICc < 2 are illustrated.

Rural dataset	Desired n. children (n=108)											
	intercept	**age**	**Current n. children**	**P_{POP}**	**P_{FOOD}**	**P_{LAND}**	**P_{ENV}**	**df**	**Loglik**	**AICc**	**delta AICc**	**weight**
Best model	0.793	0.011	0.044	0.101				4.0	-235.89	480.2	0	0.158
m2	1.048		0.066	0.102				3.0	-237.45	481.1	0.96	0.097
m3	0.869	0.011	0.044	0.101		-0.095		5.0	-235.327	481.2	1.07	0.092
m4	0.809	0.011	0.044	0.105	-0.019			5.0	-235.71	482	1.84	0.063
m5	0.753	0.019		0.105				3.0	-237.913	482.1	1.89	0.061
m6	1.123		0.066	0.101		-0.099		4.0	-236.835	482.1	1.89	0.061

Table S3b: Summary output of the model selection process assessing the relationships between perceptions and demographic factors and the use of family planning methods for rural respondents. The best model is highlighted in light grey. Alternative models with delta AICc < 2 are illustrated.

Rural dataset	Family planning use (n=101)													
	intercept	**age**	**Current children**	**Desired children**	**Discuss husband**	**P_{POP}**	**P_{FOOD}**	**P_{LAND}**	**P_{ENV}**	**df**	**Loglik**	**AICc**	**delta AICc**	**weight**
Best model	0.067			-0.180	+					3	-63.13	132.5	0	0.067
m2	0.543			-0.177	**+**		-0.225			4	-62.345	133.1	0.6	0.05
m3	0.701			-0.171	+				0	4	-62.451	133.3	0.81	0.045
m4	-0.429	0.002		-0.203	+					4	-62.924	134.3	1.76	0.028
m5	1.040			-0.170	+		-0.198		0	5	-61.866	134.4	1.85	0.027
m6	-1.030				+					2	-65.179	134.5	1.97	0.025
m7	-0.066		0.046	-0.196	+					4	-63.035	134.5	1.98	0.025

Table S3c: Summary output of the model selection process assessing the relationships between perceptions and demographic factors and the desired number of children for university respondents. The best model is highlighted in light grey. Alternative models with delta AICc < 2 are illustrated.

University dataset	Desired n. children (n=143)									
	intercept	**P_{POP}**	**P_{FOOD}**	**P_{LAND}**	**P_{ENV}**	**df**	**Loglik**	**AICc**	**delta AICc**	**weight**
Best model	0.8931	0.080				2	-254.684	513.5	0	0.195
m2	1.192					1	-256.106	514.2	0.79	0.132
m3	0.973	0.085	-0.047			3	-254.178	514.5	1.07	0.114
m4	0.945	0.079		-0.059		3	-254.563	515.3	1.84	0.078
m5	0.843	0.078			0.018	3	-254.584	515.3	1.89	0.076

Table S3d: Summary output of the model selection process assessing the relationships between perceptions and demographic factors and use of family planning methods for university respondents. The best model is highlighted in light grey. Alternative models with delta AICc < 2 are illustrated.

University dataset	Use of family planning (n=143)											
	intercept	**Desired n children**	**P_{POP}**	**P_{FOOD}**	**P_{LAND}**	**P_{ENV}**	**Will discuss husband**	**df**	**Loglik**	**AIC**	**delta AICc**	**weight**
Best model	-6.765	0.437				0.586	+	4	-43.647	95.6	0	0.211
m2	-5.95	0.399		-0.397		0.619	+	5	-42.797	96	0.45	0.168
m3	-6.445	0.424			-0.339	0.581	+	5	-43.535	97.5	1.92	0.081

TOOL S1 – RURAL SURVEY

Household Survey Questionnaire: Population growth and Family Planning

Kebele: ____________________ *Respondent ID:* _______________ *GPS Coordinates:* _______________

Interviewer ID: ____________________ *Date:* _______________ Marital status: _________________

INTRODUCTION ABOUT THE STUDY:

We are part of the team from Addis Ababa University and Leuphana University in Germany studying food security and biodiversity. You might have seen us before or heard from your neighbors that we have been in the kebele before, some months ago. The student doing this research seeks to understand the links between household perceptions on food security and environmental degradation and their fertility decisions. I would like to gather information from four kebeles in this region, and your household is one of those that were randomly chosen *(explain a bit more about why selection was random and how they were randomly selected)*. If it is alright with you, I would like to ask you to be part of this survey. It will include some general questions about your household, especially questions regarding your fertility decisions (e.g family size) and your awareness and opinion on family planning methods. The whole survey will take about 45 minutes. If there are questions that you don't want to answer, you are free not to answer them. Also, you are free to end this interview anytime you wish to, although I would really appreciate hearing your thoughts about all the questions I have. I would like to assure you that we will not use your name or the name of your community in any future publication coming out of this study. We cannot say that you or your community will directly benefit from the results of this study, but the study can generate information that may help us understand issues of food security and livelihoods better. Do you have any questions before we start? If not, we can start.

Witness (*write who else is present as witness that the respondent gave his/her consent to do the survey*):
____

Household profile

1. Can you provide us with some more information about household members?:

	ad1 (interv.)	ad2	ad3	ch1	ch2	ch3	ch4	ch5	ch6
Gender	O m O f	O m O f	O m O f	O m O f	O m O f	O m O f	O m O f	O m O f	O m O f
Age									
Completed education	O no, O 1-6, O 7-12, O college+	O no, O 1-6, O 7-12, O college+	O no, O 1-6, O 7-12, O college+	O no, O 1-6, O 7-12, O college+	O no, O 1-6, O 7-12, O college+	O no, O 1-6, O 7-12, O college+	O no, O 1-6, O 7-12, O college+	O no, O 1-6, O 7-12, O college+	O no, O 1-6, O 7-12, O college+
Current enrolment				O no, O 1-6, O 7-12, O college+	O no, O 1-6, O 7-12, O college+	O no, O 1-6, O 7-12, O college+	O no, O 1-6, O 7-12, O college+	O no, O 1-6, O 7-12, O college+	O no, O 1-6, O 7-12, O college+
*Age marriage									
*Age first birth									

Other members (ad = adult, ch = child):

2. What is your religion? O Muslim O Orthodox O Protestant O Catholic O Other, _____________

Aim 1: Perceptions regarding food security

3) How do you think the food security of your household will be in the next 10 years (future):

○ better ○ the same ○ worse

3a) How much better/worse: ○ much better ○ just better ○ just worse ○ much worse

4) Why?

BETTER	**WORSE**	
○ Technology	○ Soil degradation	**DO NOT READ!** **Just mark when applies**
○ Knowledge	○ Wild animals	
○ Soil fertility	○ Population growth	
○ Hard work	○ Land Scarcity	
○ Improved varieties	○ Others	
○ Others		

5a) How does the size of your family affects the amount of food you produce?

5b) How does the size of your family affects the amount that every individual is able to consume?

Aim 2: Perceptions regarding land scarcity

6) In some places people complain about land scarcity, when they don´t have enough land to farm and to feed their families, or when they don´t have enough land to have the livelihood they want or wish. Do you think that there is there land scarcity in your kebele? ○ yes ○ no

(If yes) Why is there land scarcity?

7) Do you think the amount land available to farm affects peoples decisions regarding the number of children they would like to have? ○ yes ○ no

7a) How?

Aim 3: Perceptions regarding environmental degradation

8) Will the environment in your kebele get better, the same or worse in the next 10 years (future)? (e.g. will be more or less drinking water or medicinal plants available, etc ….) ○ better ○ the same ○ worse

8a) How much better/worse: ○ much better ○ just better ○ just worse ○ much worse

9) Why do you think that will happen?

Aim 4: Perceptions regarding population growth

10) During the next 10 years (future), the population in your kebele will be growing, will be the same or will be decreasing?

○ increasing ○ the same ○ decreasing

10a) How much: ○ increasing a lot ○ increasing a bit ○ decreasing a lot ○ decreasing a bit

10b) Why do you think that will happen?

Aim 5: Desired family size

11) What is your desired family size (children + adults)? ______________________

(Alternatively "If you could go back in time would you have the same number of children?")

(Ask questions 12a and 12b or 13a and 13b depending on desired family size including more children than the current number)

12a) Explain why would you like **more** children than the ones you have now:

O God´s will O children bring happiness to the house; O if one children dies we have more; O children can help with money when they grow and become adults; O children can help in the fields (e.g guarding against wild animals, building fences); O Others	**DO NOT READ!** **Just mark when applies**

12b) Are there disadvantages of having **many** children?

O no money to buy clothes, school materials, O no time to give bath, O land competition between children O make parents tired, many children give headache O difficult to provide food for all children O others	**DO NOT READ!** **Just mark when applies**

##

13a) Explain why would you like **fewer** children than the ones you have now:

O God´s/Allah´s will O because I know I have enough to provide only for few children; O it is difficult to provide clothes, school materials for many children; O it is good for the children and mothers health; O Others	**DO NOT READ!** **Just mark when applies**

13b) Are there disadvantages of having **few** children?

O if I have few children I don´t get benefit from them; O decreases the amount of relatives; O decreases the amount of labor force available; O Others	**DO NOT READ!** **Just mark when applies**

Aim 6: Family Planning

14) Do you use any family planning method? O yes O no

15) How often? O Never O Rarely O Sometimes O Often O Always

15a) If yes, which method? O Tablet (pill); O condom; O injection; O patch; O pill of day after

O others ____________

16) In your opinion, what are the benefits of using family planning? And disadvantages?

a) Advantages	b) Disadvantages	
O No advantages	O No disadvantages	**DO NOT READ!** **Just mark when applies**
O gives a rest to family if they have no money	O if a women uses it for many years it can cause diseases	
O good for health of mother and children, a gap between births	O continuous bleeding after using patch for 3 years	
O good to take care of children (we have more time)	O gastric problems (injection and tablets)	
O good for family economy	O headaches (injection and tablets)	
O others	O Others	

17) In your household, do you and your husband discuss about the options together, for example did you discussed the use of family planning methods?

(if yes, don´t ask next questions 18, 18a and 18b.)

18) If no, would you like that to happen, to discuss things together? O Yes O No

18a) do you think that is better for the household?

Aim 7: Aspirations (what you would like to happen?)

19) At what age would you like your daughters to get married? And your sons?

TOOL S2 – UNIVERSITY SURVEY

Household Survey Questionnaire: Population growth and Family Planning

Kebele: ____________ *Respondent ID:* ____________ *GPS Coordinates:* _________________

Interviewer ID: _____________ *Date:* ______________ Marital status: _____________________

Academic program: ______________ *Year level:* ___________ *Home place:* _________________________

INTRODUCTION ABOUT THE STUDY:

We are part of the team from Addis Ababa University and Leuphana University in Germany studying food security and biodiversity. You might have seen us before or heard from your neighbors that we have been in the kebele before, some months ago. The student doing this research seeks to understand the links between household perceptions on food security and environmental degradation and their fertility decisions. I would like to gather information from four kebeles in this region, and your household is one of those that were randomly chosen *(explain a bit more about why selection was random and how they were randomly selected)*. If it is alright with you, I would like to ask you to be part of this survey. It will include some general questions about your household, especially questions regarding your fertility decisions (e.g family size) and your awareness and opinion on family planning methods. The whole survey will take about 45 minutes. If there are questions that you don't want to answer, you are free not to answer them. Also, you are free to end this interview anytime you wish to, although I would really appreciate hearing your thoughts about all the questions I have. I would like to assure you that we will not use your name or the name of your community in any future publication coming out of this study. We cannot say that you or your community will directly benefit from the results of this study, but the study can generate information that may help us understand issues of food security and livelihoods better. Do you have any questions before we start? If not, we can start.

Witness (*write who else is present as witness that the respondent gave his/her consent to do the survey*):
____

Household profile

1. Can you provide us with some more information about household members?

(If student is married/divorced/widowed, ask for information for her own family. If she's single, ask for information about her mother, father, and siblings but do not include children of her own siblings.)

Other members (ad = adult, ch = child):

	ad1 (interv.)	ad2	ad3	ch1	ch2	ch3	ch4	ch5	ch6
Gender	○ m ○ f	○ m ○ f	○ m ○ f	○ m ○ f	○ m ○ f	○ m ○ f	○ m ○ f	○ m ○ f	○ m ○ f
Age									
Completed education	○ no, ○ 1-6, ○ 7-12, ○ college+	○ no, ○ 1-6, ○ 7-12, ○ college+	○ no, ○ 1-6, ○ 7-12, ○ college+	○ no, ○ 1-6, ○ 7-12, ○ college+	○ no, ○ 1-6, ○ 7-12, ○ college+	○ no, ○ 1-6, ○ 7-12, ○ college+	○ no, ○ 1-6, ○ 7-12, ○ college+	○ no, ○ 1-6, ○ 7-12, ○ college+	○ no, ○ 1-6, ○ 7-12, ○ college+
Current enrolment				○ no, ○ 1-6, ○ 7-12, ○ college+	○ no, ○ 1-6, ○ 7-12, ○ college+	○ no, ○ 1-6, ○ 7-12, ○ college+	○ no, ○ 1-6, ○ 7-12, ○ college+	○ no, ○ 1-6, ○ 7-12, ○ college+	○ no, ○ 1-6, ○ 7-12, ○ college+
*Age marriage									
*Age first birth									

2. What is your religion? ○ Muslim ○ Orthodox ○ Protestant ○ Catholic ○ Other, _____________

Aim 1: Perceptions regarding food security

3) How do you think the food security of your household will be in the next 10 years (future):

○ better ○ the same ○ worse

(If married/divorced/widowed, keep the question as it is. If single, ask about the household with her parents.)

3a) How much better/worse: ○ much better ○ just better ○ just worse ○ much worse

4) Why?

BETTER	WORSE	
○ Technology	○ Soil degradation	**DO NOT READ!** **Just mark when applies**
○ Knowledge	○ Wild animals	
○ Soil fertility	○ Population growth	
○ Hard work	○ Land Scarcity	
○ Improved varieties	○ Others	
○ Others		

____

____

____

5a) How does the size of your family affects the amount of food you produce?

(If married/divorced/widowed, keep the question. If single, ask about their perception for the family that they will have in the future. Rephrase as: When you get married in the future, how do you think the size of your family will affect the amount of food that your future household will produce?)

____

____

____

5b) How does the size of your family affects the amount that every individual is able to consume?

(If married/divorced/widowed, keep the question. If single, ask about their perception for the family that they will have in the future. Rephrase as: When you get married in the future, how do you think the size of your family will affect the amount of food that every individual in the family will be able to consume?)

____

____

____

Aim 2: Perceptions regarding land scarcity

6) In some places people complain about land scarcity, when they don´t have enough land to farm and to feed their families, or when they don´t have enough land to have the livelihood they want or wish. Do you think that there is there land scarcity in your kebele? ○ yes ○ no

(For this question, refer to the kebele which the student considers as her home before moving to Jimma to study in university.)

(If yes) Why is there land scarcity?

7) Do you think the amount land available to farm affects peoples decisions regarding the number of children they would like to have? ○ yes ○ no
(For this question, refer to the kebele which the student considers as her home before moving to Jimma to study in university.)

7a) How?

Aim 3: Perceptions regarding environmental degradation

8) Will the environment in your kebele get better, the same or worse in the next 10 years (future)? (e.g. will be more or less drinking water or medicinal plants available, etc ….) ○ better ○ the same ○ worse
(For this question, refer to the kebele which the student considers as her home before moving to Jimma to study in university.)

8a) How much better/worse: ○ much better ○ just better ○ just worse ○ much worse

9) Why do you think that will happen?

Aim 4: Perceptions regarding population growth

10) During the next 10 years (future), the population in your kebele will be growing, will be the same or will be decreasing?

○ increasing ○ the same ○ decreasing

(For this question, refer to the kebele which the student considers as her home before moving to Jimma to study in university.)

10a) How much: ○ increasing a lot ○ increasing a bit ○ decreasing a lot ○ decreasing a bit

10b) Why do you think that will happen?

____

____

____

Aim 5: Desired family size

11) What is your desired family size (children + adults)? ______________________________
(If married/divorced/widowed, keep the question. If single, ask about their perception for the family that they will have in the future. Rephrase as: When you get married in the future, what is the family size that you would like to have?)

(Ask questions 12a and 12b or 13a and 13b depending on desired family size including more children than the current number reported)

12a) Explain why would you like **more** children than the ones you have now:
(If married/divorced/widowed, keep the question. If single, rephrase as: Why do you want to have more children than what your parents have?)

O God´s will O children bring happiness to the house; O if one children dies we have more; O children can help with money when they grow and become adults; O children can help in the fields (e.g guarding against wild animals, building fences); O Others	**DO NOT READ!** **Just mark when applies**

____

____

____

12b) Are there disadvantages of having **many** children?

O no money to buy clothes, school materials, O difficult to provide food for all children O no time to give bath, O land competition between children O make parents tired, many children give headache O others	**DO NOT READ!** **Just mark when applies**

____

____

____

##

13a) Explain why would you like **fewer** children than the ones you have now:
(If married/divorced/widowed, keep the question. If single, rephrase as: Why do you want to have less children than what your parents have?)

O God´s/Allah´s will O because I know I have enough to provide only for few children; O it is difficult to provide clothes, school materials for many children; O it is good for the children and mothers health; O Others	**DO NOT READ!** **Just mark when applies**

____

____

____

13b) Are there disadvantages of having **few** children?

O if I have few children I don´t get benefit from them; O decreases the amount of relatives; O decreases the amount of labor force available; O Others	**DO NOT READ!** **Just mark when applies**

____

____

____

Aim 6: Family Planning

14) Do you use any family planning method? O yes O no

(If they respond yes, proceed to question 15. If they respond "No because I'm not yet married", ask: In the future when you get married, do you plan to use any family planning method?)

Note their explanation:

____

____

15) How often? (If respondent says she plans to use it in the future, ask **How often do you think you will be using it?**)

O Never O Rarely O Sometimes O Often O Always

15a) If yes, which method? O Tablet (pill); O condom; O injection; O patch; O pill of day after O others ____________________

16) In your opinion, what are the benefits of using family planning? And disadvantages?

Advantages	**Disadvantages**	
○ No advantages	○ No disadvantages	**DO NOT READ!** **Just mark when applies**
○ gives a rest to family if they have no money	○ if a women uses it for many years it can cause diseases	
○ good for health of mother and children, a gap between births	○ continuous bleeding after using patch for 3 years	
○ good to take care of children (we have more time)	○ gastric problems (injection and tablets)	
○ good for family economy	○ headaches (injection and tablets)	
○ others	○ Others	
____ ____ ____ ____	____ ____ ____ ____	

17) In your household, do you and your husband discuss about the options together, for example did you discussed the use of family planning methods?

(If married/divorced/widowed, keep. If single, ask: In the future when you are married, do you think you and your husband will discuss about options for family planning together?

____

____

(if yes, don´t ask next questions 18, 18a)

18) If no, would you like that to happen, to discuss things together? ○ Yes ○ No

____

____

18a) do you think that is better for the household?

____

____

____

Aim 7: Aspirations (what you would like to happen?)

19) At what age would you like your daughters to get married? And your sons?

(If married, keep. If single, ask: In the future when you have your own daughters and sons, at what age would you like your daughters to get married? And your sons?)

____

____

____

TOOL S3 – HEALTH SURVEY GUIDE

Kebele: ______________________ Name health extension worker: ____________________

Interviewer ID: ___________________ Date: _____________________

INTRODUCTION ABOUT THE STUDY:

We are part of the team from Addis Ababa University and Leuphana University in Germany studying food security and biodiversity. The student doing this research seeks to assess the determinants of women's fertility decisions in this region of Ethiopia. We have conducted survey questionnaires to women in this kebele/woreda last year to understand their reasoning for the use or non-use of family planning methods. Now, we would like to gather information regarding the availability of family planning methods in the health extension, how is the interaction with the community made, as well as to collect official statistics regarding the number of users of the services available. The information you provide will remain anonymous, and will be used by researches, for scientific purposes only.

A. About the health extension clinic and workers

1. When was the health extension established?

____

2. How many people does the health extension serve?

____

3. How many health extension workers work in this clinic?

____

4. What is the education of health extension workers (e.g. high school, university degree?)

____

____

5. Which are your main functions as a health extension worker (e.g provide health information, treat minor injuries, provide medical supplies, assist in birth deliveries.

____

____

6. Did you get pre-service training regarding family planning counseling? ○ Yes ○ No

6a. If yes, how long was the training?

____

6b. What type of training e.g was the training given by a doctor at the hospital?

____

B. About family planning

1. Do you provide family planning methods in the health extension clinic? ○ Yes ○ No

1a. Which? ○ Tablet (pill); ○ condom; ○ injection; ○ patch; ○ pill of day after ○ others ______________

1b. Since when?

2. Is there a cost for family planning methods (how much does it cost?), or is it free?

3. Do women that use family planning method, use it in a consistent way? ○ Yes ○ No

3a. Do they follow their schedule, e.g don’t miss any injectable session?

4. Is the clinic open every day? ○ Yes ○ No

4a. How many hours a day is it open?

4b. How many women visit the clinic in a day, specific for family planning related issues?

5. Does the clinic ever run out of family planning supplies (e.g. injectable, condoms …) ○ Yes ○ No

5a. How long was the clinic without supplies?

5b. How often did the clinic run out of supplies in the last year?

5c. Which method do you most often run out?

6. Are there outreach activities to the population regarding family planning methods? ○ Yes ○ No

6a. What type of information is covered in the outreach? Availability of FP, their side-effects, the periodicity...

6b. What type of outreach (e.g. visits to the households, visits to schools …)?

6c. Is the outreach focused on women and men or just women?

6d. How often do these outreach activities happen?

7. From your experience, do you think family planning is generally accepted in this region?

8. From your experience what are the reasons women use family planning?

9. From your experience, do you think there are social or religious norms that do not support it? (e.g. religious prohibition, husband disapproval, community perception).

10. Are there signs that unsupportive norms are changing?

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I hereby declare that I have never taken any doctoral examination or applied for admission to such examination.

I further affirm that the dissertation with the title "*Prospects for tropical forest biodiversity in the landscapes of southwestern Ethiopia: conservation in a context of land use change and human population growth*" has not been submitted to any representative of any faculty and that I am submitting the dissertation only in this and in no other Doctoral procedure and that no other definitely fail has been achieved in any previous Doctoral procedure.

I furthermore declare, that I composed the submitted Dissertation "*Prospects for tropical forest biodiversity in the landscapes of southwestern Ethiopia: conservation in a context of land use change and human population growth*" independently and without having recourse to prohibited means. I have not used any aids or texts other than those I indicated. All passages taken in verbatim or substance from other works have been identified.

Lisbon, 1st July 2020

Patrícia Rodrigues