



## Policy analysis

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

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## 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) as well as common crop raiding species such as baboons; (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 location, extent and magnitude of housing development in southwestern Ethiopia can limit the ability of several mammal species 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.

## 1. 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 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, and with 63% of the population currently residing 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 and Brook, 2014; Crist et al., 2017). Such demands

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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 and Laforsch, 2019), infrastructure (Torres et al., 2016), or housing development (Villaseñor et al., 2017).

In the rural areas of Sub-Saharan Africa, livelihoods are largely based on subsistence farming, and the effects of human population growth on biodiversity are often mediated by agricultural expansion (Perrings and 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; Caryl et al., 2016; Soga et al., 2014; 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 Sub-Saharan Africa.

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 Sub-Saharan Africa, 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 and 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 and 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. We did not formulate species by species hypotheses, but overall, we expected that (1) increasing housing density would be detrimental for species that are known to have high affinity with forest habitat (such as bushbuck and bushduiker) and (2) that species able to exploit human-dominated landscapes (such as baboons and bushpigs) could tolerate or even benefit from human settlements. Specifically, we asked: (i) how do different mammal species respond to increasing rural housing density? (ii) to what extent do different housing 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 coffee forests from housing development 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.

## 2. Methods

### 2.1. Study area

The study area encompasses an area of 3800 km<sup>2</sup> and is located in a coffee growing area in Jimma zone, in the Oromia region, southwest of Ethiopia (Fig. 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 and 1.5% (Hylander et al., 2013) and it is estimated that forest cover has decreased from 79% to 60% between 1973 and 2010 (Ango, 2016). The current proportion of forest in the study kebele 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<sup>2</sup>.

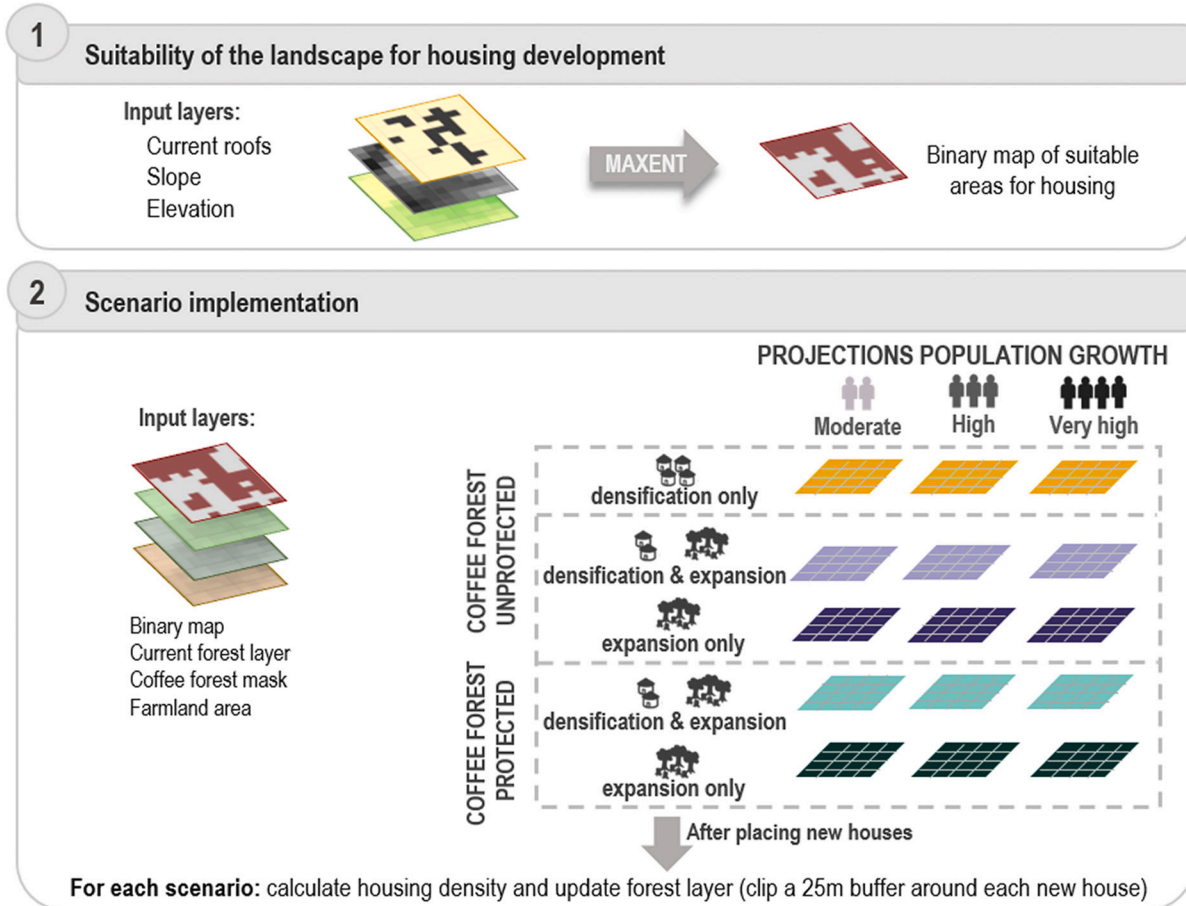
### 2.2. Sampling design and data collection

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 early January 2016 to the end of March 2017. Cameras were rotated to new sampling locations approximately every four months. We considered this rotation period to be a good compromise between battery duration, card capacity and the likelihood of cameras starting to malfunction due to water and moisture damage. All *kebeles* were surveyed in all the four main seasons of Oromia (with the exception of one *kebele* for which the short rainy season (*Arfaasaa*), was poorly covered). We used a map of forest cover derived from RapidEye satellite imagery (5 m 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 Fig. 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<sup>2</sup>) of herbs

**(a) SCENARIOS OF FUTURE HOUSING DENSITY**



**(b) PREDICTIVE MODELLING**

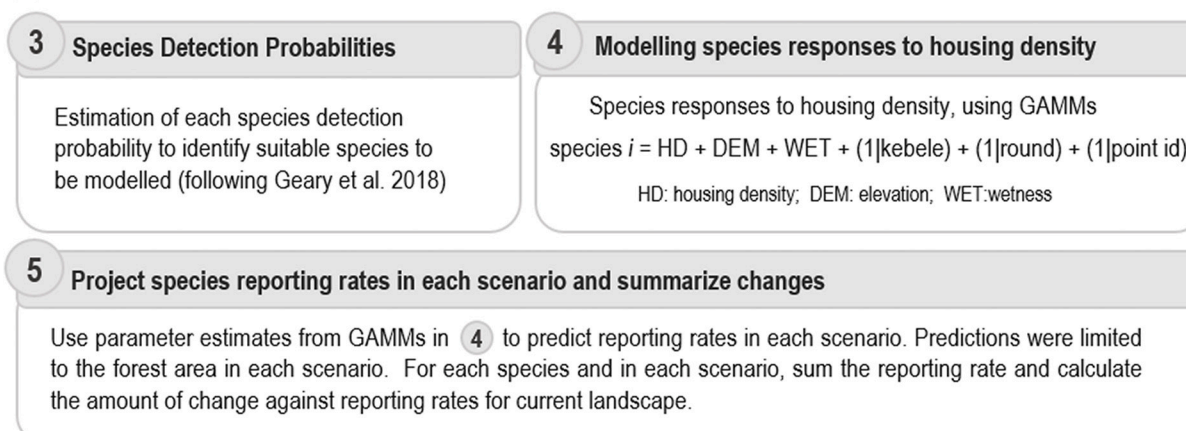


Fig. 1. Methodological workflow used in the development of scenarios of housing density and on the modelling approach.

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 h/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: 112 days), with premature deactivation resulting from camera failure or human interference. We manually classified all pictures using Exif-PRO™ 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 and Marshall, 2009). Identification at the species level was not always possible for some groups (hares, genets, mongooses, jackals and hyraxes), due to low image quality, and for these the group level was used in data analysis.

### 2.3. 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 (Fig. 1a).

#### 2.3.1. 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 (30 × 30 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).

#### 2.3.2. 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 (Fig. 1a). We used the current landscape configuration as a baseline scenario.

Housing 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 housing 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).

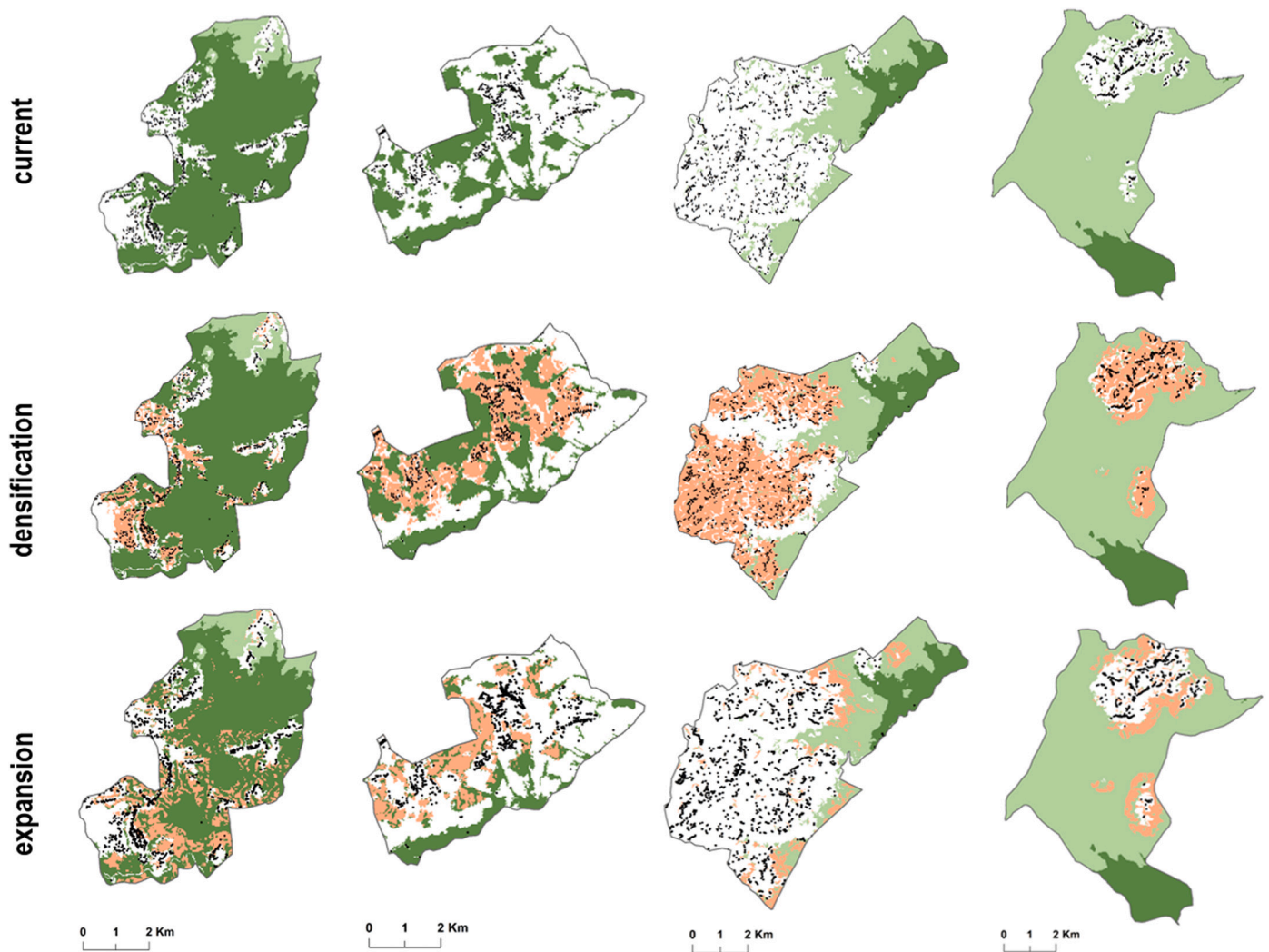
Finally, for the two housing development types that involved expansion, and for each of the three population projections of human population growth, we applied a final criterion related to the protection of coffee forest criteria (iii). This was comprised of two protection levels: “**coffee forest protected**”, where all suitable forest areas located within coffee altitude (1500–1950 m) were protected against development (i.e. coded as unsuitable for housing development), and “**coffee forest unprotected**”, where all suitable forest areas located 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 (Figs. 1a and 2).

We randomly placed the new houses in the landscape according to the three levels of human population growth and for each housing 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 (Fig. 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 housing development types, two coffee protection criteria and three levels of human population growth) (Fig. 2). Housing density was calculated for each cell, using Point Density toolbox in Arcmap (ESRI, 2018), within a buffer of 500 m. 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 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 × 30 m cell size.

### 2.4. 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 and 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





**Fig. 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 housing development type. Columns represent the four different surveyed *kebeles*. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

**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 housing development type criteria. % change is illustrated against current area of forest in the landscape (which encompasses 9429 ha).

	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

working camera days in the field.

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 (Fig. 1b). 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, number of nights not detected), combined using the *cbind* function in R.

We used Generalized Additive Mixed Models (GAMMs) to model each species’ reporting rate in relation to current housing density and wetness and elevation (Fig. 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 modelling 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 ( $\text{cor} = -0.70$ ), 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. Finally, and after conducting an exploratory analysis of our predictors, we excluded a sampling point that behaved as an outlier for housing density. All models were run using a total of 91 sampling points (i.e. after exclusion of the outlier and three points where cameras operated less than 30 days) and using package *gamm4* (Wood and Scheipl, 2017).

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  $\leq 0.05$ ). 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.

### 3. Results

#### 3.1. Overview of the mammal community

We identified 32 mammal species across the 95 survey sites sampled over 15 months (corresponding to 10,766 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 Bou-tourlini's blue monkey (*Cercopithecus mitis* spp. *boutourlinii*) are species of conservation concern, listed both as "vulnerable" on the IUCN red list (2019).

#### 3.2. Species responses to housing density

From the 32 species detected, 20 species met the detectability criteria for modelling (Fig. 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 (Fig. 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, 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).

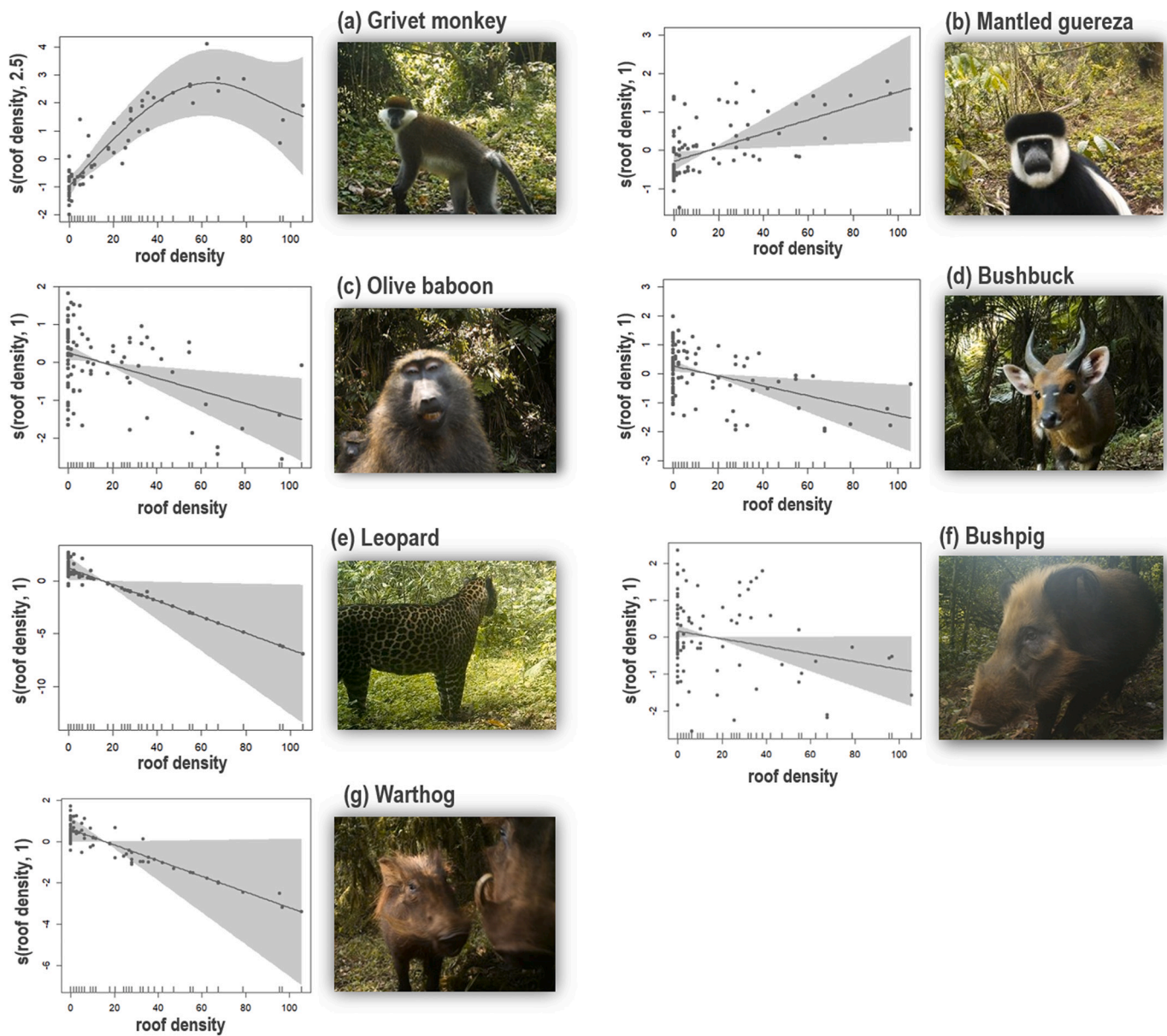
#### 3.3. Species responses to scenarios of future housing density

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 (Fig. 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 was predicted to decline with "very high" growth in human population when coffee forest was protected (Fig. 4a, b). 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 (Fig. 4c–g). For this group of species, "densification only" had the least detrimental impact on reporting rates (with declines between 6 and 11% for the bushpig 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 and 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, housing development type (i.e., "expansion only" versus "densification and expansion") (Fig. 4e) was the major differentiator in its response to future housing density, whereas for the warthog it was the protection of coffee forest (Fig. 4g).

### 4. 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., positive, negative and lack of responses observed), rural human population growth in Ethiopia is likely to negatively influence several species of mammals, including a threatened apex predator (the leopard) as well as some common raiding species (e.g. olive baboon); (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 these, two monkey species, the



**Fig. 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.

grivet monkey and the mantled guereza, were more commonly encountered in forests surrounded by higher housing density. These species are amongst those that can tolerate and even benefit from some level of human disturbance (Naughton-Treves, 1998). For instance, 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 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 undisturbed forest (Mertens et al., 2018). Areas of less disturbed forest were also important for the bushbuck, a species that depends on dense vegetation for refuge (Kingdon et al., 2013). Contrary to our initial expectations, olive baboons, bushpigs and warthogs - species known to use and exploit human dominated habitats (Hill, 2018) - responded negatively to housing density and to the different scenarios of housing development. A possible explanation for this lies in the strong context of human-wildlife

conflicts that characterizes the region. In the study area, crop-raiding is an important source of conflict between farmers and wildlife and olive baboons, warthogs and bushpigs are amongst the most renowned crop-raiding species in the region (Ango et al., 2017). Crop-raiding brings disbenefits to the local community (Ango et al., 2017; Dorresteijn et al., 2017) and leads to retaliation and persecution against crop-raiders. Thus, in a context of human-wildlife conflicts in the landscape, it is reasonable to expect that crop-raiding and retaliation and persecution might be driving species responses to housing density since these species need forest habitat to retreat to. Furthermore, the stronger negative responses of these species when coffee forest is unprotected against housing development may be related with species' preferences for forest areas that are more open and typically closer to settlements (such as coffee forest), from where it is easier to access food crops.

We did not observe responses of about two-thirds of the species to housing density. However, this does not mean that these species will be unaffected by housing development. The lack of responses likely results from a combination of two factors. First, it is possible that a potential



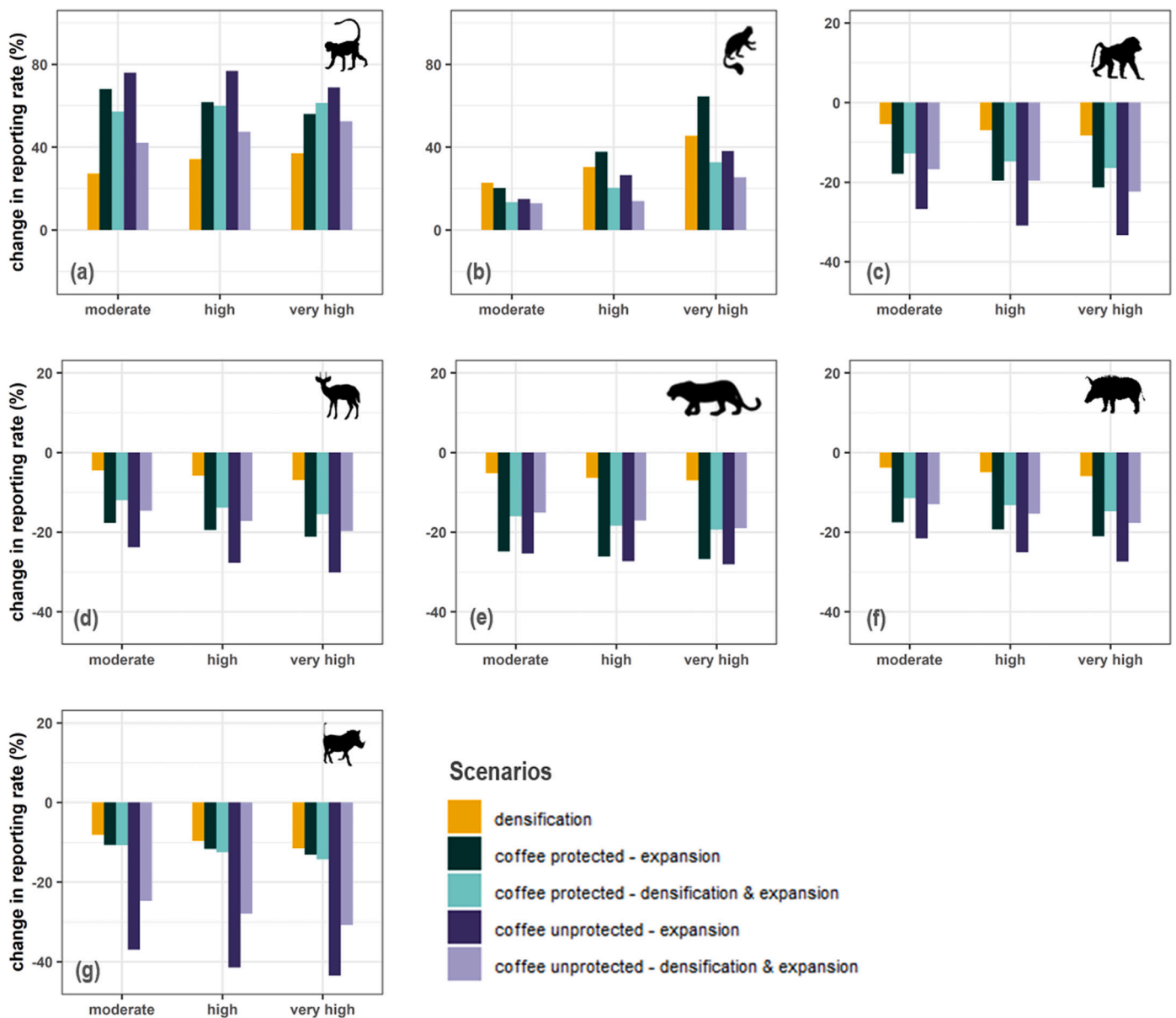


Fig. 4. Species responses to future scenarios of rural housing density, across the four study areas (*kebeles*). Response variable is the proportion of change in each species reporting rate for each scenario. Panels legend: (a) grivet monkey, (b) mantled guereza, (c) olive baboon, (d) bushbuck, (e) leopard,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

effect (either positive or negative) could not be detected due to few sites with records for some of the species (e.g. hares, buffalo). Second, some species such as small carnivores (i.e. mongooses, genets and civets) can tolerate some level of human disturbance and occasionally exploit livestock resources around human settlements (e.g. by stealing chickens from households, Dorresteijn et al. unpublished). However, such an occasional use of resources may not be enough to detect a positive response of these species to housing density.

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 and 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 (El-Sabaawi, 2018), introduction of invasive species (Gavier-Pizarro et al., 2010), increasing hunting pressure, amongst others (Benítez-López 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. (2020) 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, the location, extent and magnitude of development can influence species responses to housing and can limit their ability to persist in the landscape. Our results show that forest encroachment by housing expansion has the worst outcomes for mammals (as a combined result of habitat loss and degradation and human disturbance), 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.

#### Declaration of competing interest

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

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2021.109046>.

#### References

- Ango, T., 2016. Ecosystem services and disservices in an agriculture-forest mosaic. A study of forest and tree management and landscape transformation in southwestern Ethiopia. In: PhD Thesis. Stockholm University.
- Ango, T.G., Börjeson, L., Senbeta, F., 2017. Crop raiding by wild mammals in Ethiopia: impacts on the livelihoods of smallholders in an agriculture-forest mosaic landscape. *Oryx* 51, 527–537. <https://doi.org/10.1017/S0030605316000028>.
- Ango, T.G., Hylander, K., Börjeson, L., 2020. Processes of forest cover change since 1958 in the coffee-producing areas of Southwest Ethiopia. *Land* 9 (8), 278. <https://doi.org/10.3390/land9080278>.
- Benítez-López, A., Alkemade, R., Schipper, A.M., et al., 2017. The impact of hunting on tropical mammal and bird populations. *Science* 356, 180–183. <https://doi.org/10.1126/science.aaj1891>.
- Benítez-López, A., Alkemade, R., Verweij, P.A., 2010. The impacts of roads and other infrastructure on mammal and bird populations: A meta-analysis. *Biological Conservation* 143, 1307–1316. <https://doi.org/10.1016/j.biocon.2010.02.009>.
- Betts, M.G., Wolf, C., Ripple, W.J., Phalan, B., Millers, K.A., Duarte, A., Butchart, S.H.M., Levi, T., 2017. Global forest loss disproportionately erodes biodiversity in intact landscapes. *Nature* 547, 441–444. <https://doi.org/10.1038/nature23285>.
- Bradshaw, C.J.A., Brook, B.W., 2014. Human population reduction is not a quick fix for environmental problems. *Proc. Natl. Acad. Sci. U. S. A.* 111, 16610–16615. <https://doi.org/10.1073/pnas.1410465111>.
- Brown, M.L., Donovan, T.M., Schwenk, W.S., Theobald, D.M., 2014. Predicting impacts of future human population growth and development on occupancy rates of forest-dependent birds. *Biol. Conserv.* 170, 311–320. <https://doi.org/10.1016/j.biocon.2013.07.039>.
- Caryl, F.M., Lumsden, L.F., van der Ree, R., Wintle, B.A., 2016. Functional responses of insectivorous bats to increasing housing density support ‘land-sparing’ rather than ‘land-sharing’ urban growth strategies. *J. Appl. Ecol.* 53, 191–201. <https://doi.org/10.1111/1365-2664.12549>.
- Crawley, M.J., 2013. *The R Book, Second, edition*. ed. Wiley, Chichester.
- Crist, E., Mora, C., Engelman, R., 2017. The interaction of human population, food production, and biodiversity protection. *Science* 356, 260–264. <https://doi.org/10.1126/science.aal2011>.
- Dorresteijn, I., Schultner, J., Collier, N.F., Hylander, K., Senbeta, F., Fischer, J., 2017. Disaggregating ecosystem services and disservices in the cultural landscapes of southwestern Ethiopia: a study of rural perceptions. *Landsc. Ecol.* 32, 2151–2165. <https://doi.org/10.1007/s10980-017-0552-5>.
- El-Sabaawi, R., 2018. Trophic structure in a rapidly urbanizing planet. *Functional Ecology* 32, 1718–1728. <https://doi.org/10.1111/1365-2435.13114>.
- ESRI, 2018. ArcGIS Version 10.6.1. Environmental Systems Resource Institute, Redlands, CA.
- Fiske, I., Chandler, R., 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software* 43, 1–23. <https://doi.org/10.18637/jss.v043.i10>.
- Gagné, S.A., Fahrig, L., 2010. The trade-off between housing density and sprawl area: Minimising impacts to forest breeding birds. *Basic and Applied Ecology* 11, 723–733. <https://doi.org/10.1016/j.baae.2010.09.001>.
- Gavier-Pizarro, G.I., Radeloff, V.C., Stewart, S.I., et al., 2010. Housing is positively associated with invasive exotic plant species richness in New England, USA. *Ecological Applications* 20, 1913–1925. <https://doi.org/10.1890/09-2168.1>.
- Gaynor, K.M., Hohnowski, C.E., Carter, N.H., Brashares, J.S., 2018. The influence of human disturbance on wildlife nocturnality. *Science* 360, 1232–1235. <https://doi.org/10.1126/science.aar7121>.
- Geary, W.L., Ritchie, E.G., Lawton, J.A., Healey, T.R., Nimmo, D.G., 2018. Incorporating disturbance into trophic ecology: fire history shapes mesopredator suppression by an apex predator. *J. Appl. Ecol.* 55, 1594–1603. <https://doi.org/10.1111/1365-2664.13125>.
- Geschke, A., James, S., Bennett, A.F., Nimmo, D.G., 2018. Compact cities or sprawling suburbs? Optimising the distribution of people in cities to maximise species diversity. *J. Appl. Ecol.* 55, 2320–2331. <https://doi.org/10.1111/1365-2664.13183>.
- Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E., Sodhi, N.S., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478, 378–381. <https://doi.org/10.1038/nature10425>.
- Hill, C.M., 2018. Crop foraging, crop losses, and crop raiding. *Annu. Rev. Anthropol.* 47, 377–394.
- Hylander, K., Nemomissa, S., Delrue, J., Enkosa, W., 2013. Effects of coffee management on deforestation rates and forest integrity: coffee and deforestation. *Conserv. Biol.* 27, 1031–1040. <https://doi.org/10.1111/cobi.12079>.
- Jacobson, A.P., Gerngross, P., Lemeris Jr., J.R., et al., 2016. Leopard (*Panthera pardus*) status, distribution, and the research efforts across its range. *PeerJ.* <https://doi.org/10.7717/peerj.1974>.
- Kingdon, J., Happold, D., Butynski, T., Hoffmann, M., Happold, M., Kalina, J., 2013. *Mammals of Africa. Volumes I–VI*. Bloomsbury Natural History.
- Kinnaird, M.F., Sanderson, E.W., O’Brien, T.G., Wibisono, H.T., Woolmer, G., 2003. Deforestation trends in a tropical landscape and implications for endangered large

- mammals. *Conserv. Biol.* 17, 245–257. <https://doi.org/10.1046/j.1523-1739.2003.02040.x>.
- Manlosa, A.O., Hanspach, J., Schultner, J., Dorresteijn, I., Fischer, J., 2019. Livelihood strategies, capital assets, and food security in rural Southwest Ethiopia. *Food Sec.* 11, 167–181. <https://doi.org/10.1007/s12571-018-00883-x>.
- Mertens, J.E.J., Emsens, W.-J., Jocqué, M., Geeraert, L., De Beenhouwer, M., 2018. From natural forest to coffee agroforest: implications for communities of large mammals in the Ethiopian highlands. *Oryx* 1–8. <https://doi.org/10.1017/S0030605318000844>.
- Mutoko, M.C., Hein, L., Bartholomew, H., 2014. Integrated analysis of land use changes and their impacts on agrarian livelihoods in the western highlands of Kenya. *Agric. Syst.* 128, 1–12. <https://doi.org/10.1016/j.agry.2014.04.001>.
- Naughton-Treves, L., 1998. Predicting patterns of crop damage by wildlife around Kibale National Park, Uganda. *Conserv. Biol.* 12 (1), 156–168.
- OBFFED - Oromiya Bureau of Finance and Economic Development, 2012. *The National Regional Government of Oromiya Bureau of Finance and Economic Development Condensed Physical Geography of Oromiya*.
- Perrings, C., Halkos, G., 2015. Agriculture and the threat to biodiversity in sub-saharan africa. *Environ. Res. Lett.* 10, 095015 <https://doi.org/10.1088/1748-9326/10/9/095015>.
- Phillips, S.J., Dudík, M., Schapire, R.E. Maxent software for modelling species niches and distributions (version 3.4.1). Available from url: [http://biodiversityinformatics.amnh.org/open\\_source/maxent/](http://biodiversityinformatics.amnh.org/open_source/maxent/). (Accessed 27 May 2020) (Internet).
- Pidgeon, A.M., Flather, C.H., Radeloff, V.C., Lepczyk, C.A., Keuler, N.S., Wood, E.M., Stewart, S.I., Hammer, R.B., 2014. Systematic temporal patterns in the relationship between housing development and forest bird biodiversity. *Conserv. Biol.* 28, 1291–1301. <https://doi.org/10.1111/cobi.12291>.
- Powers, R.P., Jetz, W., 2019. Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. *Nat. Clim. Chang.* 9, 323–329. <https://doi.org/10.1038/s41558-019-0406-z>.
- Rodrigues, P., Shumi, G., Dorresteijn, I., Schultner, J., Hanspach, J., Hylander, K., Senbeta, F., Fischer, J., 2018. Coffee management and the conservation of forest bird diversity in southwestern Ethiopia. *Biol. Conserv.* 217, 131–139. <https://doi.org/10.1016/j.biocon.2017.10.036>.
- Rodrigues, P., Dorresteijn, I., Senbeta, F., Fischer, J., 2019. Living on the edge: rapid assessment of the mammal community in a coffee forest in south-western Ethiopia. *Afr. J. Ecol.* 57, 279–285. <https://doi.org/10.1111/aje.12588>.
- Rovero, F., Marshall, A.R., 2009. Camera trapping photographic rate as an index of density in forest ungulates. *J. Appl. Ecol.* 46, 1011–1017. <https://doi.org/10.1111/j.1365-2664.2009.01705.x>.
- Senbeta, F., Denich, M., 2006. Effects of wild coffee management on species diversity in the Afromontane rainforest of Ethiopia. *For. Ecol. Manag.* 232, 68–74. <https://doi.org/10.1016/j.foreco.2006.05.064>.
- Shumi, G., Rodrigues, P., Schultner, J., Dorresteijn, I., Hanspach, J., Hylander, K., Senbeta, F., Fischer, J., 2019. Conservation value of moist evergreen Afromontane forest sites with different management and history in southwestern Ethiopia. *Biol. Conserv.* 232, 117–126. <https://doi.org/10.1016/j.biocon.2019.02.008>.
- Soga, M., Yamaura, Y., Koike, S., Gaston, K.J., 2014. Land sharing vs. land sparing: does the compact city reconcile urban development and biodiversity conservation? *J. Appl. Ecol.* 51, 1378–1386. <https://doi.org/10.1111/1365-2664.12280>.
- Steibl, S., Laforsch, C., 2019. Disentangling the environmental impact of different human disturbances: a case study on islands. *Sci. Rep.* 9, 13712. <https://doi.org/10.1038/s41598-019-49555-6>.
- Sushinsky, J.R., Rhodes, J.R., Possingham, H.P., et al., 2013. How should we grow cities to minimize their biodiversity impacts? *Global Change Biology* 19, 401–410. <https://doi.org/10.1111/gcb.12055>.
- Torres, A., Jaeger, J.A.G., Alonso, J.C., 2016. Assessing large-scale wildlife responses to human infrastructure development. *Proc. Natl. Acad. Sci. U. S. A.* 113, 8472–8477. <https://doi.org/10.1073/pnas.1522488113>.
- UN, 2019a. United Nations, Department of Economic and Social Affairs, Population Division. *World Population Prospects 2019: Highlights (ST/ESA/SER.A/423)*. United Nations, New York.
- UN, 2019b. United Nations, Department of Economic and Social Affairs, Population Division. *World Urbanization Prospects: The 2018 Revision (ST/ESA/SER.A/420)*. United Nations, New York.
- Villaseñor, N.R., Tulloch, A.I.T., Driscoll, D.A., Gibbons, P., Lindenmayer, D.B., 2017. Compact development minimizes the impacts of urban growth on native mammals. *J. Appl. Ecol.* 54, 794–804. <https://doi.org/10.1111/1365-2664.12800>.
- Wood, S.N., 2006. *Generalized Additive Models: An Introduction With R*. Chapman and Hall/CRC Press.
- Wood, S., Scheipl, F., 2017. *Generalized Additive Mixed Models Using 'mgcv' and 'lme4'*. Version 0.2-5. CRAN Repository.
- World Bank, 2019. Rural population. Retrieved from. <https://data.worldbank.org/indicator/SP.RUR.TOTL.ZS>.
- Zuur, A.F. (Ed.), 2009. *Mixed Effects Models and Extensions in Ecology With R, Statistics for Biology and Health*. Springer, New York, NY.