Spatial variation in human disturbances and their effects on forest structure and biodiversity across an Afromontane forest

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Abstract

Context Human disturbances can have large impacts on forest structure and biodiversity, and thereby result in forest degradation, a property difficult to detect by remote sensing.

Objectives To investigate spatial variation in anthropogenic disturbances and their effects on forest structure and biodiversity.

Methods In 144 plots of 20 × 20 m distributed across a forest area of 750 km² in Southwest Ethiopia, we recorded: landscape variables (e.g., distance to forest edge), different human disturbances, forest structure variables, and species composition of trees and epiphyllous bryophytes. We then first assessed if landscape variables could explain the spatial distribution of disturbances. Second, we analysed how forest structure and biodiversity were influenced by disturbances.

Results Human disturbances, such as coffee management and grazing declined with distance to forest edges, and penetrated at least a kilometer into the forest. Slope was not related to disturbance levels, but several types of disturbances were less common at higher elevations. Among human disturbance types, coffee management reduced liana cover and was associated with altered species composition of trees. The presence of large trees and basal area were not related to any of the disturbance gradients.

Conclusions Although most anthropogenic disturbances displayed clear edge effects, surprisingly the variation in the chosen forest degradation indices were only weakly related to these disturbances. We suggest that the intersection between edge effects and forest degradation is very context specific and relies much on how particular societies use the forests. For example, in this landscape coffee management seems to be a key driver.

Keywords Coffee management · Coffea arabica · Edge effects · Epiphyllous bryophytes · Forest degradation · Human-inhabited landscapes · Liana · Trees

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Introduction

Forest ecosystems are often rich in biodiversity (Wilson 1988) and store large quantities of carbon (Bustamante et al. 2016). To explain the spatial variation in species richness, composition, and forest structure it is necessary to map the variation in environmental factors as well as to understand local disturbance regimes (Thom et al. 2013). In many forested landscapes, human disturbances dominate over natural disturbances (Senf et al. 2017) and are the dominant driver of forest structure and biodiversity. Much focus on human impacts on forest systems has been on habitat loss. However, human disturbances that do not imply conversion of forests to open habitats are widespread and are better analysed within the framework of habitat degradation (FAO 2011; Ghazoul et al. 2015). Although habitat loss is certainly detrimental to biodiversity and carbon storage, forest degradation is often forgotten, although it is often as important (Mertz et al. 2012; Alroy 2017). One reason is that habitat degradation is a much more complex term to define (Ghazoul et al. 2015) and different kinds of disturbances cause different types and levels of habitat degradation (Barlow et al. 2016). Moreover, forest degradation can often be difficult to detect using remote sensing (Dupuis et al. 2020; Ahrends et al. 2021) and should be assessed at a landscape scale, due to the variability in the distribution of anthropogenic disturbances (Rodrigues et al. 2014). Understanding the distribution of various human disturbances causing habitat degradation can help to better predict future changes in biodiversity and forest structure that is crucial for example to identify forest areas of particularly high conservation priority (Chiarucci and Piovesan 2019) or to model carbon storage capacities (Qin et al. 2021).

The spatial distribution of human disturbances across a given landscape may vary from edges to interior forests (often denoted as edge effects, Laurance and Yensen 1991; Ries et al. 2017), but is often modified also by slope and accessibility (Turner and Gardner 2015). For example, in Azerbaijan and Iran, the intensity of livestock grazing decreases with terrain steepness, and grazing ceases 100 m into deciduous temperate forests (Noack et al. 2010). In contrast, in tropical rainforest of Queensland in Australia, logging of large trees was found to be more prevalent in the interior forests than at forest edges (Laurance 1991), and in the Anavilhanas park in the Amazon, the incidence of illegal logging did not correlate with distance to nearest settlements (Scabin et al. 2011). Thus, the spatial variation of human disturbances might be context-specific, even if proximity to edges in general is a strong predictor of higher levels of habitat degradation (Laurance and Yensen 1991; Banks-Leite et al. 2010). One important quantitative feature of edge effects is the depth of edge influence (Harper et al. 2005). This property is easy to study and model when it comes to physical processes such as flows of energy across edges causing gradients in for example microclimate (Hylander 2005; Ries et al. 2017). However, when it comes to edge effects that are caused directly or indirectly by human management it is likely that patterns such as the variation in the depth of edge influence will be related to local management practices by people from the surrounding settlements, and thus highly context specific.

Forest degradation is a very general term (Ghazoul et al. 2015), and different kinds of disturbances have different drivers as well as different impacts on biodiversity. Examples are selective logging, where only certain valuable tree species are extracted (Scabin et al. 2011), and grazing or browsing, which hampers not only the growth of seedlings and saplings but also the diversity of large trees in the long run (Galleguillos et al. 2018). Moreover, human disturbances often have indirect negative impacts on forest biodiversity (Barlow et al. 2016). For instance, opening up of continuous forests by roads causes fragmentation and increases edge effects, which threatens interior species (Young 1994), facilitates illegal hunting (Benítez-López et al. 2010), and exposes interior forests to wind storms, besides the direct effect of the removal of trees during the road construction (Laurance et al. 2009; Dissanayake et al. 2019). Still, the mere presence of humans in forest landscapes may not necessarily lead to biodiversity loss (Posey 1985), suggesting the importance of understanding the impacts of different types of human disturbances (Alroy 2017; Ahrends et al. 2021).

In Ethiopia, human presence is ubiquitous as both smaller and larger forest patches are surrounded by inhabitants. Local communities extract multiple products from forests including firewood, trees for construction (Shumi et al. 2019b) and spices (Furo et al. 2019), and also use forest areas for livestock grazing.
In Southwest Ethiopia, a major additional disturbance factor is coffee production under a canopy of shade trees, especially in forest margins (Lemessa et al. 2013; Dorresteijn et al. 2017). How deep into the forest coffee is produced is largely unknown, although its negative impact on biodiversity (especially forest specialists) is well documented (Senbeta and Denich 2006; Gove et al. 2008; Beenhouwer et al. 2015; Rodrigues et al. 2018; Shumi et al. 2019a). However, even if coffee management substantially changes forest species composition, coffee production under the forest canopy also reduces the deforestation rate in the landscape because it adds to the economic value of the forests (Hylander et al. 2013a).

In this paper, we studied anthropogenic disturbances and indicators of forest degradation across a moist Afromontane forest landscape in Southwest Ethiopia. Since different disturbances might penetrate to different depths into the forest and little is known on how they affect forest structure and biodiversity, we designed a study across a district with a large remaining forest area. We documented different types of disturbances as well as different indicators of forest degradation such as forest structure variables and biodiversity (trees and epiphyllous bryophytes) from the forest edges up to 3.5 km into the forest. We asked two specific, interrelated questions (Fig. 1): (1) How are different human disturbances distributed across the forest in relation to position in the landscape such as distance to agricultural land, slope, and elevation (hereafter called ‘landscape variables’)? (2) How do human disturbances influence forest structure and biodiversity?

For the first question, we hypothesized that forest sites with less human disturbance are located further from agricultural edges or roads and in steep areas; that the spatial extent of edge effects would differ among different types of disturbances, and that coffee management would decline with elevation (as a proxy for climate). For the second question, we hypothesized that the least disturbed sites would have denser forests with larger trees and higher biodiversity values. To test these hypotheses, we collected data on disturbances, forest structure and biodiversity (trees and epiphyllous bryophytes) from 144 plots that were randomly distributed across the 750 km$^2$ of forested land in the Gera district of Southwest Ethiopia. We specifically designed the study to include plots deep within the forest, since most studies of tropical forests are biased towards easily accessible sites close to edges and roads.

**Methods**

**Study area**

The study was undertaken in Gera district in Southwest Ethiopia (Fig. 2). The landscape has a varying topography from flat to rough terrain with an elevation between 1400 m and 3000 m a.s.l. and a dense stream network. About half of the Gera district (1388 km$^2$) is covered by forest. This area belongs to the remaining moist Afromontane forests in southwestern Ethiopia (Hundera et al. 2013). Characteristic species in this forest are for example *Pouteria adolfi-friedericii*, *Olea welwitschii*, *Syzygium guineense*, and several *Albizia* species (Friis et al. 2010). The region also has a rich bryophyte diversity, not least associated with the trees and shrubs (including coffee) both as a substrate and benefitting from the microclimate they create (Hylander and Nemomissa 2008; Hylander et al. 2017). The border between forested and non-forested land is generally very distinct both in satellite imagery and in the field.

The non-forested areas of the district are inhabited by smallholder farmers who cultivate annual crops and keep livestock (Lemessa et al. 2015; Shumi et al. 2018), which mean that the land-use at the forest edge most often is annual crops or open pastures. However, also the non-forested land has plenty of scattered trees and small woodlots. Coffee production from home gardens in the non-forested part of the landscapes as well as from semi-natural forest and unmanaged natural coffee forest is common in the district. Coffee production mostly occurs at elevations below 2000 m a.s.l. due to the physiological limitation of the coffee shrub (Damatta 2004). As additional sources of income, local people seasonally collect honey and spices from the forest (Kumsa and Takele 2014). Both species composition of birds (Rodrigues et al. 2018) and woody plants (Shumi et al. 2019a) are negatively affected by coffee dominance in the area, but also by unrelated edge effects up to 900 m from the agricultural land edge into larger forest areas (Rodrigues et al. 2018; Shumi et al. 2019a). However, even more remote forest areas had not been investigated to date, and the spatial extent of different types of disturbances...
(e.g. collection of fuelwood or logging) also remains poorly understood.

Study design

To capture how human disturbances were distributed across the forest landscapes and test their effects on basal area, distribution of large trees, liana cover, tree diversity, and epiphyllous bryophyte diversity, we randomly selected 200 points across the larger forest tracts in a satellite image from Google Earth (accessed on 2019-07-18). Due to time constraints, we finally used only 144 plots, which we assume to be representative of the pre-selected random plots (Fig. 2). Data was collected from January 31 to April 6, 2019. From each plot (20 × 20 m) we collected data on landscape variables, human disturbances, forest structure and biodiversity (Table 1).

We extracted several landscape variables that we expected to drive variation in human disturbances. From a RapidEye satellite image (from 2015) we calculated forest cover within a radius of 500 m surrounding each plot, and calculated the cost distance (i.e. the distance to a given point and includes a penalty for steep slopes) from adjacent agricultural land to each plot and elevation (see Rodrigues et al. 2018; Shumi et al. 2019a). To determine whether the plots were located in forest or open habitats in the past, we studied a Landsat image from 1973. Only one plot was located just at the forest edge in 1973, which now is located inside the forest; it was retained in the analyses (Supplementary data 1). From an ASTER-derived digital elevation model of 30 m resolution, we derived elevation and heatload (see Rodrigues et al. 2018; Shumi et al. 2019a). From the satellite image in Google Earth (2019) we measured distance to the closest agricultural field, distance to nearest home, and distance to the nearest road (defined as an all-weather road usable by cars). Finally, in the field we estimated for each plot the distance to the closest stream, the
slope, and the distance to the closest foot path (Table 1).

In the field we collected data on the following human disturbances: coffee management, stumps, burnings, signs of human presence, spices occurrence and grazing (for methods see Table 1). Signs of human presence is an aggregate variable derived from a few less frequent disturbance variables that all indicate human activities additional to those captured by the other disturbance variables, namely presence of: tree debarking, fire wood collection, beehives and footpaths. We further collected data on the following forest structure variables: canopy cover, tree circumference, natural dead trees, decomposing trees, walkability, thickets, longest moss, non-coffee woody species, tree abundance, liana cover and computed tree basal area and Shannon index of tree circumferences (for methods see Table 1). For assessing biodiversity, we identified all trees > 60 cm circumference in the plots and the occurrence of epiphyllous bryophytes on leaves of shrubs and low trees up to three meters. This data was used for analyses of species richness and species composition (for details see Table 1). Most of the tree species were identified in the field, but for difficult taxa we collected samples that were identified with the help of the Flora of Ethiopia and Eritrea (1989–2006) at the National Herbarium of Ethiopia, Addis Ababa University. All epiphyllous bryophytes were collected and dried and later identified by Kristoffer Hylander based on previous experience (see e.g. Hylander et al. 2010). Voucher specimens of both trees and bryophytes were deposited in National Herbarium of Ethiopia, Addis Ababa University (see also Appendix S4).

Data analysis

We first checked collinearity by running pair-wise correlation tests between all landscape variables (Appendix S1). Based on this, we selected the following landscape variables that were not correlated (r < 0.5) as explanatory variables in the first set of models: (1) forest cover in a 500 m buffer, (2) elevation, (3) heat load, (4) distance to agricultural field, (5) distance to road, (6) distance to stream, (7) slope, and (8) distance to closest foot path.

The main disturbance gradients were selected after pair-wise correlation tests among all human
Table 1 List of major variables with their method of collection, unit of measurement and data type. The final column indicates the transformation of the data used in the statistical analyses

| Variables                        | Methods used in field to collect the variables                                                                 | Unit   | Type           | Transform |
|----------------------------------|----------------------------------------------------------------------------------------------------------------|--------|----------------|-----------|
| **(a) Landscape variables**      |                                                                                                              |        |                |           |
| Distance to stream               | Distance to nearest stream or river from plots, as 1 (crossing), 2 (< 50 m), and 3 (> 50 m)                   | Meter  | Categoricala  |           |
| Closest footpath distance        | Presence of footpath in and around plot and the estimated distances from the plot, as 0 (if in plot/crosses plot), 30 (30–99 m), 100 (100–499 m), and 500 (> 500 m) | Meter  | Categoricala  |           |
| Distance to agricultural edge    | Distance measured on Google map from plot to nearest agricultural forest edge                                  | Meter  | Continuous     |           |
| Distance to road                 | Distance measured from Google map for each plot to the nearest all-weathered road                               | Meter  | Continuous     |           |
| Slope                            | Slope of the plot visually estimated as flat (1), gentle (2), steep (3) or very steep (4)                     | Categoricala |           |
| Forest cover                     | Percentage of forest cover in 2015 within 500 m buffer, done in ArcMap -neighbourhood and focal statistics     | Continuous |           |
| Heatload                         | Measure of potential incident radiation and temperature, estimated from aspect and slope derived from ASTER-digital elevation model by using gradient metrics toolbox-headload index in ArcMap | Continuous |           |
| Cost distance                    | The distance to a given point in the forest, from the closest adjacent farmland to each plot, which accounts for accessibility by introducing a penalty for steep slopes. It was calculated using the forest cover map of 2015 derived from RapidEye satellite image and the cost distance tool in ArcGIS | Continuous |           |
| Distance to home                 | Distance measured from Google map from plot to nearest home in adjacent agricultural land                       | Continuous |           |
| **(b) Human disturbance variables** |                                                                                                              |        |                |           |
| Coffee occurrence                | Presence of coffee within the plot (yes / no)                                                                 | Categorical |           |
| Coffee management                | Coffee management practices observed in plot like pruning, mulching, slashing or clearing understory and planting new coffee seedlings in plot (yes / no) | Categorical |           |
| Coffee dominance                 | Number of coffee shrubs above 1.5 m in height divided by the total number of woody plants (including trees) above 1.5 m (i.e., including the coffee shrubs) | Continuous |           |
| Stumps                           | Observed fresh or older (cut last year) stumps in plot (yes / no)                                           | Categorical |           |
| Burnings                         | Observed forest burnings in the plot (yes / no)                                                             | Categorical |           |
| Signs of human presence          | Presence of tree debarking, footpath, beehives (in and around plot) and signs of firewood collection in plot (yes / no) | Categorical |           |
| Grazing                          | Grazing signs observed in the plot (yes / no)                                                               | Categorical |           |
| Spices                           | Presence of spices (i.e., *Piper capense* and *Aframomum corrorima*) in the plot (yes/ no)                    | Categorical |           |
| **(c) Forest structure variables** |                                                                                                              |        |                |           |
| Canopy cover                     | Mean of canopy cover taken at four corners and center of each plot by using digital camera at 3.5 m above height from forest floor. Calculated with the software Image J | Continuous |           |
| Tree circumference               | The circumference of all trees per plot above 60 cm was measured at about 1.3 m above ground                   | Meter  | Continuous     |           |

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Before doing so, we removed variables related to burning since this occurred only in seven plots and we log-transformed some variables that had a skewed distribution (Table 1). The selected, uncorrelated (r < 0.5) disturbance variables chosen were: (1) coffee management, (2) stumps, (3) signs of human presence, (4) grazing, and (5) spices.

To examine the first question (Fig. 1), namely how landscape variables drove human disturbances we ran generalized linear models (GLM), with each of the five selected disturbance gradients as response variables (presence/absence), and the selected landscape variables as explanatory variables. We used a backward selection approach to select a final model using a threshold of $P < 0.1$ (Crawley 2007) using logit link function (binomial family). All explanatory variables were standardized to zero mean and unit variance to facilitate comparison of effect sizes between predictor variables. For all final models residual plots were examined. To illustrate the results for a selected number of significant relationships from the GLMs we...
plotted fitted lines of new GLMs with only the selected predictor variable in XY-plots for these relationships. We then helped the reader to compare the results, by calculating values on the x-axis for a certain probability on the Y-axis (e.g. we visualized the depth of the edge effect as the predicted distance to agricultural edges at 20% probability of occurrence of the focal disturbance).

To examine the second question (Fig. 1), namely how human disturbances explained forest structure and our selected biodiversity variables, we first reduced the 13 forest structure variables (besides liana cover) to three main forest structure gradients using a principal components analysis (PCA; Appendix S3). Then we separately modelled the three forest structure gradients, liana cover and the two biodiversity variables (tree species richness and epiphyllous bryophyte richness) as a function of the five disturbance variables using GLMs as described above.

Finally, we analysed how species composition of trees related to the five major disturbances using the adonis2 function in the vegan package with backward selection of non-significant variables (Oksanen et al. 2019). To illustrate how the different tree species responded to the main human disturbances we ran a Canonical Correspondence Analysis (CCA) ordination with the significant variables from the adonis2 analyses as explanatory variables and with default settings (R 2.5-6 vegan package; Oksanen et al. 2019). For the species compositional analyses, we only included plots containing three or more tree species per plot (Appendix S5). The data of epiphyllous bryophytes were insufficient to run species compositional analyses. All analysis were run using the statistical program R 3.6.0 (R Core Team 2019).

**Results**

Spatial variation of human disturbances across afro montane forest

Four of the five disturbance types were more common close to agricultural edges or in plots with less surrounding forest cover, while none of the disturbance types were reduced due to steep terrain (Table 2). Defining depth of edge influence as the point where there was a 20% probability of occurrence of the focal disturbance type (see Methods, Fig. 3), coffee management penetrated 1300 m into the forests from agricultural edges, the aggregate variable ‘Signs of human presence’ penetrated 1500 m, while grazing only penetrated 550 m (Fig. 3a, b, c). Both grazing and signs of human presence decreased with distance from footpaths in the forest, in addition to the general decrease with distance from agricultural edges, whereas coffee management was more common further away from streams (Table 2). The presence of stumps decreased with forest cover in the surrounding landscape (Fig. 3d). Yet, stumps were still common also in sites with high forest cover. Based on a fitted line of a single variable model there was 40% incidence of stumps already in sites with only 10% forest cover loss in a buffer of 1 km radius around the predicted point (Fig. 3d). Further, coffee management, stumps and spices decreased with elevation and coffee management increased, but presence of spices decreased, with heatload (Table 2). The adjusted R² varied from 0.08 for stumps to 0.21 for coffee management (Table 2).

Effects of human disturbances on forest structure and biodiversity

Twelve forest structure variables were reduced to three gradients with a PCA analysis: (1) a canopy cover gradient with high loadings also for walkability, (2) a large tree gradient with high loadings besides circumference of largest tree also for mean tree circumference and tree basal area, and (3) a dead wood gradient with high loadings also for number of natural standing dead trees, decomposing trees, non-coffee woody plants and thicket cover (Appendix S3).

In general, the disturbance gradients were weak predictors of the different forest structure and biodiversity variables (Table 3). The canopy cover gradient was positively related to presence of spices (Table 3) and amount of dead wood was negatively related to coffee management and grazing (Fig. 4b, c). However, the large tree gradient was unrelated to any of five human disturbance gradients (Table 3). The decrease of liana cover with coffee management was the strongest relationship in this set of analyses (Table 3, Fig. 4d). In total we found 42 tree species with a circumference of > 60 cm (0 to 7 per plot) (Appendix S4). Species richness of trees was slightly higher where there were many stumps, but lower at sites with grazing (Table 3, Fig. 4f, g). In total we found 20
### Table 2: The impact of landscape variables on five metrics of human disturbance

| Variables         | Distance to streams<sup>a</sup> Beta coef | Closest footpath distance<sup>a</sup> Beta coef | Distance to agricultural edge<sup>b</sup> Beta coef | Distance to road<sup>b</sup> Beta coef | Slope<sup>c</sup> Beta coef | Forest cover in 2015<sup>c</sup> Beta coef | Elevation<sup>c</sup> Beta coef | Heatload<sup>c</sup> Beta coef | Adjusted R<sup>2</sup> | Deviance |
|-------------------|------------------------------------------|------------------------------------------------|-------------------------------------------------|-----------------------------------|---------------------|-----------------------------------|---------------------|---------------------|---------------------|---------|
| Coffee management | + 0.59<sup>*</sup>                       | -0.60<sup>*</sup>                                | -0.49                                            | -1.12<sup>***</sup>             | + 0.52<sup>*</sup> | 0.21                              | 130.68              |                     |                     |         |
| Stumps            |                                          | -0.48<sup>**</sup>                                | -0.46<sup>*</sup>                                |                                   | 0.08                | 159.70              |                     |                     |                     |         |
| Signs of human presence | -0.71<sup>***</sup> | -0.70<sup>**</sup> | | | | | | | | |
| Grazing           | -0.48<sup>*</sup>                       | -1.29<sup>**</sup>                                |                                                   |                                   | 0.16                | 100.29              |                     |                     |                     |         |
| Spices            |                                          |                                                   |                                                   |                                   | -0.74<sup>***</sup> | -0.41<sup>*</sup> | 0.13                | 174.03              |                     |         |

Shown are standardized coefficients (Beta coef.) from backward-selected generalized linear models with a binomial error structure, with associated significance levels, where * = P < 0.05, ** = P < 0.01, *** = P < 0.001, and no asterisk indicates p < 0.1. A few relationships are illustrated in Fig. 3.

<sup>a</sup>Recorded in the field
<sup>b</sup>Measured from Google map
<sup>c</sup>Extracted from RapidEye [for forest cover] and ASTER [for elevation and Heatload] satellite image
epiphyllous bryophytes (0 to 14 per plot) (Appendix S4). Species richness of epiphyllous bryophytes was lower when there were signs of human presence (Table 3, Fig. 4h).

The tree species composition was affected by coffee management ($r^2 = 0.029$, $F = 2.62$, $p = 0.008$) and the presence of spices ($r^2 = 0.031$, $F = 2.85$, $p = 0.009$) (adonis2). As illustrated by the location of the different tree species scores in the CCA ordination diagram different tree species were differently related to the different human disturbances (Fig. 5). *Vernonia amygdalina*, *Ehretia cymosa* and *Millettia ferruginea* occurred in locations with more intensive coffee management; *Celtis africana* and *Ficus thomningii* are distributed in sites with more spices and low to intermediate coffee management (Fig. 5). Both the big forest tree *Pouteria adolfi-friederici* and the small disturbance loving *Maesa lanceolata* were located in sites with both less spices and coffee management (Fig. 5).

Fig. 3 Selected human disturbances as a function of landscape variables: a Coffee management, b Signs of human presence, c Grazing in relation to distance to agricultural edge, and d Stumps as a function of forest cover. Circles represent 144 randomly-distributed forest plots. Fitted line from a binomial model with only one predictor variable. All depicted relationships are statistically significant ($p < 0.05$) in GLMs where other variables are included (for details see Table 2). Red lines show (in a–c) the predicted depth of edge effects at 20% probability of occurrence of the disturbance, and (in d) the probability of occurrence of stumps at 90% forest cover. (Color figure online)

Discussion

A critical challenge in densely populated tropical landscapes is to balance people’s demand for ecosystem services with biodiversity conservation (Sayer et al. 2003), since we know that not only habitat loss but also habitat degradation are major threats to both biodiversity and carbon sequestration (Barlow et al. 2016; Qin et al. 2021). To address this challenge, an understanding of the spatial variation of anthropogenic disturbances and their effects on forest structure and biodiversity is essential. Here, we demonstrated that various disturbances such as coffee management, grazing, selective logging, and signs of human presence were, as expected, strongest at forest edges, but the predictive functions for the different edge effects differed in their rate of decay with distance from the edge. Surprisingly, forest biodiversity variables, such as species richness of trees or presence of large trees were only partly explained by human disturbances, suggesting possibilities for
finding viable combinations of human utilization and biodiversity conservation. In other words, to fully understand forest habitat degradation (Ghazoul et al. 2015) we need a combined understanding of both the distribution of various kinds of human disturbances, as well as their impact on forest structure and biodiversity. In this landscape coffee management seems to be key to understand the intersection between forest degradation and edge effects (see also Hylander et al. 2013a; Rodrigues et al. 2018; Shumi et al. 2019a). That leads to the conclusion that edge effects that are driven by human utilization of the forests may be very context specific and rely on how local societies value and use different forest resources.

Spatial variation in human disturbances

We found clear edge effects with many kinds of human disturbances being more pronounced closer to agricultural edges. This was expected since people in these landscapes are largely dependent on the forest for provisioning ecosystem services such as wild coffee (Hundera et al. 2013; Lemessa et al. 2013), spices (Furo et al. 2019), honey and firewood (Shumi et al. 2019b). Coffee management intensity decreased with distance from agricultural fields. Even more than a kilometer from the forest edge there was >20% probability of finding coffee management. In addition, our results also suggest that there is a tendency for coffee management to be more common closer to roads, even in locations that are far from agricultural edges. This finding indicates that roads can act as facilitators of accessibility, as demonstrated for other types of disturbances worldwide (Young 1994; Bennett 2017). However, in fact, coffee was present in almost all inventoried random plots at elevations below 2000 m where coffee can grow (Hylander et al. 2013a), and often in high densities, which might indicate a long history of promotion of coffee also deep into the forest in this landscape. Yet, the strongest impacts of human disturbances are closer to edges, which correspond to about 70% of the forest area if we assume a depth of edge influence of 1 km in this landscape, and include all small forest fragments as forest and include all edges even from roads and small agricultural clearings inside wider forest areas.

The intensity of grazing decreased towards the interior forest, which is congruent with evidence from temperate forests that showed a decreasing trend of grazing intensity into interior forest (Noack et al. 2010). Many previous studies show that the intensity of human disturbance decreases with slope or terrain variation in human disturbances.

### Table 3 Variation in forest structure and biodiversity variables as a function of five human disturbance gradients across the forest

| Variables                  | Coffee management (Beta coef.) | Stumps (Beta coef.) | Signs of human presence (Beta coef.) | Grazing (Beta coef.) | Spices (Beta coef.) | Adjusted R² | Deviance  |
|----------------------------|-------------------------------|---------------------|--------------------------------------|----------------------|-------------------|-------------|----------|
| Canopy cover gradient      | -0.17                         | + 0.18              |                                      | + 0.31***            | 0.24              | 100.95      |
| Largest tree gradient      |                               |                     |                                      |                      |                   |             |          |
| Dead wood gradient         | -0.29**                       |                     | -0.26*                               | 0.12                 | 110.11            |
| Liana cover                | -0.44***                      | -0.17*              | + 0.26*                              | 0.12                 | 119.89            |
| Tree species richness      |                               |                     |                                      | -0.32*               | 0.24              | 334.41      |
| Epiphyllous bryophyte richness | -0.52*                      |                     |                                      | + 0.41               | 0.04              | 988.99      |

Separate GLMs were run for each of six forest structure and biodiversity variables with five disturbance gradients as explanatory variables. Standardized coefficients (Beta coef.) are given from a backward selection GLM and significance levels are indicated by: *= P < 0.05, ** = P < 0.01, *** = P < 0.001, and no asterisk indicate p < 0.1

*aBased on PCA of 12 forest structure variables. The gradients go from low to high canopy cover, small to large trees and little too much dead wood (see Appendix S3)
ruggedness (Basnet 1992; Turner and Gardner 2015). However, this does not seem to be an important mechanism in our focal landscape, since areas that were steep were equally disturbed. Apparently, despite the rugged terrain people easily cross the landscape using small footpaths. Yet, forest disturbances were more common when there was a nearby footpath, as seen for grazing and the aggregate variable ‘signs of human presence’.

The presence of more stumps at lower elevation and in the sites with less forest cover might indicate a higher pressure for timber in areas with coffee management or that trees are removed in a process of coffee management intensification (Cheng et al. 1998; Geeraert et al. 2019). Often stumps are found deep into the forest (>1 km), despite the trouble it implies to transport the timber out of the forest. However, it should be noted that many stumps are small (<20 cm DBH) and the selective logging observed by us is not targeting the large trees (personal observations).

Even if the two focal species of spices (Piper capense and Aframomum corrorima) are wild species we assumed that their occurrence pattern would reflect human intervention since they are promoted. The fact that the spices were more common at low elevation might indicate that they are simultaneously managed together with coffee. However, they seem to have a slightly different niche since coffee management was positively, and the presence of species was negatively, related to heatload and spices were not common in plots where the coffee was managed. Interviews with farmers would allow to cast some light on this finding and elucidate if these patterns are due to active management towards the separation of the two
resources between slopes of different heatload across the landscape.

When scrutinizing each disturbance type it is clear that their pattern of occurrence is driven by how humans use the landscape in combination with environmental constraints (e.g. terrain roughness, climate etc.). Thus, it will be extremely difficult to make predictions of, for example, depth of edge influence of different disturbance types between landscapes, because it is likely that either the environmental constraints or the local cultural usage of forest resources or both factors differ between the landscapes. We believe that this aspect is generally neglected in the current understanding of edge effects (Ries et al. 2017), but links to the discussion on direct and indirect edge effects (Ruffell and Didham 2016) and how the land-use composition could alter edge effects (García-Romero et al. 2019).

Effects of human disturbances on forest degradation indicators such as forest structure and biodiversity

Forest structural gradients such as canopy cover and the number of large trees were affected by human disturbances to only a minor extent. This was a surprising finding given that people use these forests in many ways including coffee management, selective logging and grazing their cattle as shown in our results.

The most prominent negative effects on forest structure and biodiversity were the strong and negative effect on liana cover and the change in species composition of trees by coffee management. The negative impact on liana cover may be due to the removal of lianas to facilitate penetration into the forest for collection of resources such as spices, honey and wild coffee beans, in addition to regular clearing of lianas during coffee management activities. This interpretation seems to be in line with other findings in Ethiopia showing that liana diversity is negatively affected by human disturbances like selective logging (Senbeta et al. 2005) and coffee management (Senbeta and Denich 2006). However, in tropical forests in northeast Australia liana cover was higher at more disturbed areas such as forest edges (Laurance 1991) and fragmented areas (Campbell et al. 2018) than in interior intact forest, which contradicts with our findings. The lack of effect of human disturbances on large trees might be due to the fact that people tend to select smaller trees for logging, due to a combination of that they need the large trees for shading,

Fig. 5 Tree species distribution along presence of coffee management and spices illustrated with species scores from an CCA ordination analysis of the 88 forest plots (see line 288–289 for statistics). Blue arrows represent the gradient in coffee management and spices. (Color figure online)
prohibition of cutting wild trees, and finally logistic
costains of cutting, transporting and using large trees
(Shumi et al. 2019b). Alternatively, variation in
densities of large trees might reflect historical natural
disturbances or, in a few areas, old commercial
logging quotas (Ango et al. 2020).

Our observations suggest that tree species richness
was little affected by human disturbances across the
Gera forest landscape, even if it was slightly nega-
tively related to the grazing gradient. This is in stark
contrast to most studies of similar forest types in
southwestern Ethiopia (Senbeta and Denich 2006;
Senbeta et al. 2014; Shumi et al. 2019a) and elsewhere
(Ambinakudige and Sathish 2009), which found that
different types of anthropogenic disturbances reduced
tree species richness. Also, other biodiversity values
such as interior bird species richness have been shown
to decline towards the forest edges in this landscape
(see Rodrigues et al. 2018). A likely explanation for
this discrepancy may be that the other studies have
included a wider management gradient including more
samples very close to edges and in smaller remnant
patches than we did in this study where we focused on
the larger forest areas, as our study is one of the few
that made a survey deep into the larger forests of this
area. In our case the tree species richness was actually
slightly positively related to presence of stumps,
which might indicate that gaps created due to logging
of some trees increased the possibilities of establish-
ment for shade intolerant and pioneer tree species
(Bongers et al. 2009; Aguilar-Santelises and del
Castillo 2013). However, even though tree species
richness was not negatively affected by coffee man-
agement the species composition of trees changed (see
also Hundera et al. 2013; Shumi et al. 2019a).
For example, some trees occurring in sites with more
coffee management, such as Vernonia amygdalina and
Millettia ferruginea, are known to be preferred for
shade (Aerts et al. 2011; Hundera et al. 2013) while
trees with dense shade like Pouteria adolfi-friederici
seemed to be removed in sites managed for coffee
production. The small tree Measa lanceolata is
common in edges and newly disturbed sites. It thus
represents a species that reacts to other disturbance
gradients than coffee management and occurrence of
spices, which are driving the main compositional
pattern in our analyses. Thus, it illustrates the com-
plicity of the impact of various human disturbances on
the distribution of biodiversity across this forest
landscape. Epiphyllous bryophyte richness was
slightly negatively affected by the aggregate variable
‘Signs of human presence’, which is in line with a
study investigating edge effects in a similar landscape
where ferns and epiphyllous bryophyte richness
decayed closer to forest edges (Hylander et al. 2013b).
In a separate model for the variable ‘longest moss’ (see Table 1) as a function of distance to
agricultural edges we found a significant negative
effect ($p < 0.010$), which could indicate that forest
degradation negatively affects the moist microclimate
needed by bryophytes. To get more insights into how
forest structures and biodiversity are distributed across
these forests, we suggest investigating the legacies of
the historical distribution of both anthropogenic and
natural disturbances. Our choice of indicators for
forest degradation are only a few of many potential
proxies, and Ghazoul et al. (2015) suggest that future
assessment of forest degradation needs to have a more
functional approach (cf. Makelele et al. 2021). Future
studies could for example focus on how dispersal and
regeneration of woody species are distributed. The
focus on species composition instead of only species
richness is one way in that direction that is suggested
by Ries et al. (2017) for the development of edge effect
studies.

Implications for conservation and sustainability
of the landscape

The spatial variation in anthropogenic disturbances
across the Gera forest landscape showed a complex
pattern with different landscape variables related to
different disturbances types. However, the general
pattern was a distance decay in the imprint of human
management of the forests with less coffee manage-
ment, grazing and other signs of human presence
towards the core of the forests, even if the penetration
depth of various edge effects differed. Interestingly, in
the next step of our analyses the variation in many of
the variables related to forest degradation such as
species richness of trees, species richness of epiphyll-
ous bryophytes, presence of large trees and canopy
cover were not or only weakly related to the distur-
bance gradients across the forests. If our choices of
forest degradation indices are representative, this
might suggest that the level of present forest utilization
by people is compatible with biodiversity conserva-
tion across these forests. However, disturbance from
coffee management might be an exception, since it decreased liana cover and was related to a change in the species composition of trees (see also Nigatu et al. 2017).

Strict protection of the forests is not likely and will be detrimental to people’s livelihoods. However, this study demonstrates that high biodiversity values seem to occur across the forest and with clear policy and engagement from people, sustainable utilization of forest resources without compromising conservation values too much seems to be possible for the Gera forest landscape. In such multi-functional human-inhabited landscapes the goal should be to balance the protection and management of forest while also taking into account local people’s livelihoods (e.g. the approach of Yayu biosphere reserve, see Gole 2003). The utilization and management of the forest edges can sometimes protect the interior of the forests (Hatfield et al. 2019). Such a mechanism has been suggested for coffee in this landscape, where deforestation rates have been higher at elevations above the coffee growing zone (Hylander et al. 2013a). Yet, it is apparent that coffee management is a major disturbance factor in this landscape, with the capacity to strongly modify forest structures and biodiversity if going on for long time with more intensive management than now seen in the large forests that we focused on in this study (Geeraert et al. 2019). Thus, how coffee cultivation will develop will be critical for future biodiversity in this particular landscape. In other countries and continents, where coffee is not a native plant, the mere presence of coffee shrubs under the forest canopy could be a sign of forest degradation (Tejeda-Cruz et al. 2010). Thus, one cannot directly compare coffee management under a canopy of indigenous trees in Ethiopia with the rustic coffee system of Latin America where farmers plant coffee inside forests (Toledo and Moguel 2012). The trade-off between coffee production and biodiversity values may be stronger in Ethiopia than in other agroforestry systems around the world when the full gradient from more of less wild coffee to commercial coffee plantations is considered (Clough et al. 2017; Zwedie et al. unpublished). Some restrictions on intensification of coffee production also in Ethiopian forests are likely necessary in order to maintain the high biodiversity that currently exists in the Afromontane forests in Southwest Ethiopia, while other human disturbances seem less problematic when implemented at the current levels. However, as pointed out earlier it will be difficult to extrapolate the details of our findings to other areas, since the drivers of disturbances are so context specific involving the interaction between people and nature (see also Yesuf et al. 2019, who has a similar conclusion). Thus, to understand all aspects, including the spatial distribution, of forest loss, forest degradation as well as forest regrowth and restoration a socio-ecological systems framework is useful (Budiharta et al. 2016; Harvey et al. 2021).

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Declarations

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