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ORIGINAL RESEARCH

Small forest patches in Ethiopian highlands uniquely support high plant biodiversity

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Abstract
Habitat fragmentation is one of the main causes of the global loss of plant biodiversity. It is also one of the major challenges in Ethiopia, where fragmented forest patches of different sizes have been observed. These patches of forest, especially in the highlands of northern Ethiopia, are mainly confined to churches. These remnant forest patches have long been said to have negative impacts (habitat amount hypothesis). Recently, however, there is evidence that these small patches of remnant forest may harbour more species than relatively large patches of the same area. We tested this hypothesis in the remnant church forests of the Ethiopian highlands using different plant growth forms. Ten church forests of different sizes were selected in which transects were established from the forest edges to the interior. A total of 56 20×20 m plots were used for plant sampling. All trees, shrubs and herbs within the plots were recorded, collected and identified. We found that the effects of forest fragmentation on plant diversity, abundance and composition varied with plant growth forms. In contrast to the habitat amount hypothesis, small forest fragments were found to support more tree species than relatively large forest fragments, suggesting the role of small forest fragments in maintaining species diversity. We found that soil moisture changes with fragment size but has no significant effect on plant abundance and diversity of plant growth forms. Our results indicate that a shift in conservation priorities may be needed to recognize the value of small fragmented patches of forest for biodiversity conservation, as a lack of protection of small patches of forest can lead to high cumulative impacts on biodiversity loss.

Keywords Church forests · Dry afromontane forest · Edge effects · Environmental factors · Forest fragmentation · Habitat amount hypothesis · Plant growth forms

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Introduction

Habitat fragmentation is one of the major drivers of biodiversity loss (Fahrig 2003). The East African region, centered on Ethiopia, is known for its plant diversity and endemism. The two global biodiversity hotspots, the East African Afromontane region and the Horn of Africa, are located in East Africa, where habitat fragmentation is a widespread phenomenon (Mittermeier et al. 2004). In Ethiopia, a significant change from closed canopy forests to mixed wooded grasslands and open grasslands has been observed over the last 30 million years (Jacobs 2004). Recently, many researchers have shown that Ethiopia's natural and semi-natural Ethiopian forests continue to be fragmented, mainly by humans, resulting in isolated patches of forest in the landscape (Daye and Healey 2015; Belay and Mengistu 2019; Negassa et al. 2020). By altering the pattern of habitat configuration at the landscape scale, forest fragmentation can increase the number, isolation and edges of forest patches, but decrease the size of forest patches (Fahrig 2003; Wang et al. 2014). This ultimately alters plant diversity, composition, and abundance in the landscape (Fahrig 2017).

The remaining fragmented forests in the Ethiopian highlands mostly left around churches, are referred to as 'church forests' and play an important role in conserving the biodiversity of national forests (Wassie et al. 2010). However, despite the ongoing debate on the impact of habitat fragmentation on plant biodiversity (Chase et al. 2020; Riva and Fahrig 2023), there is consensus that the size of fragmented remnant forests is gradually decreasing and affecting the distribution, diversity, and abundance of plant species (Ewers and Didham 2006). While the protection of large forest areas has long been a conservation priority, the contribution of small forest areas to the conservation of remaining plant diversity has been largely ignored. In the face of the unprecedented global habitat fragmentation, it is, therefore, crucial to assess the relative importance of small fragmented remnant forests for plant conservation (Tulloch et al. 2016). Despite the widespread remnant forests in the Ethiopian highlands, it is not yet fully understood how fragmentation interacts and influences different plant growth forms.

Fragmentation of forests leads to multiple small habitat patches, which have long been considered to have negative effects on plant communities (Villard and Metzger 2014; Hanski 2015). Diamond (1975) proposed the Habitat Amount Hypothesis according to which small habitat patches harbour a lower number of species compared to large habitat patches demonstrating the low value of small habitats for plant conservation. This hypothesis of single large or several small (SLOSS) compares fragmented habitat patches of different sizes in terms of their ability to support species diversity. The SLOSS hypothesis addresses the question of whether species diversity is higher in several small habitat patches or in a single large habitat patch. Recently, it has been reported that sets of small habitat patches can support more species than one or a few larger patches with the same total area, suggesting that the conservation of small habitat patches is disproportionately valuable (Riva and Fahrig 2022). Several small patches of forest may have high species richness compared to a few large patches if the disturbance is less likely to spread over the many small patches (Simberloff and Abele 1982). To promote the conservation of large contiguous forests, conservation agencies have used the concept that a single large habitat patch contains more species than several small patches with the same total area (Fahrig 2020). However, several small patches of habitat have been found to support more species than a single large patch (Fahrig 2020), raising the question of whether biodiversity conservation is better achieved with a single large patch or several small patches (SLOSS). The process of forest fragmentation in Ethiopia has left several patches of forest of different sizes, providing an important natural experimental design to test this hypothesis, which is crucial to effectively address the challenges of plant conservation. Although this study emphasizes the importance of small patches of forest for maintaining high plant diversity, it also aims to show that we need to re-evaluate our plant conservation strategies, as most biodiversity conservation policies are mainly focused on protecting large contiguous forests, and ignore the value of small patches of forest for effectively conserving biodiversity in the landscape.

Forest fragmentation may not have the same impact on all plant growth forms due to differences in species characteristics (slow growth vs. fast growth, woody vs. herbaceous) (Ewers and Didham 2006; Rodríguez-Loinaz et al. 2012). Herbaceous and woody species are not expected to be equally sensitivity to fragmentation due to their different life-histories. Woody species grow more slowly and should invest a lot to survival. In contrast, herbaceous plants have a rapid life-history (grow and die faster) with large investments in reproduction and rapid turnover. These life-history differences between different plant growth forms essentially cause them to respond differently to habitat fragmentation (Ewers and Didham 2006). Forest fragmentation can accelerate biotic homogenization by replacing shade-tolerant species with light-demanding species and/or replacing short-lived species with long-lived species through edge effects (Arroyo-Rodríguez et al. 2013). Previous studies have primarily used trees to understand the effects of fragmentation on plant communities based on the assumption that tree species largely contribute to carbon storage, biomass production, nutrient cycling, and microclimate regulation (Barbier et al. 2008; Slik et al. 2013; Tuff et al. 2016). As a result, other plant growth forms such as shrubs and herbs have been less studied although they contribute greatly to species richness, density, and biomass production (Ruokolainen et al. 2018). Pasion et al. (2018) reported that different plant growth forms vary with the effects of fragmentation, suggesting that tree species cannot be representative of other growth forms to quantify the effects of fragmentation on plant communities. Assessing the effects of fragmentation on different plant growth forms can, therefore, help to effectively address biodiversity conservation strategies.

Although edge effects are the result of forest fragmentation, little is known about how they alter the species composition, abundance, and diversity of different plant growth forms. Edge effects are thought to alter microclimatic conditions such as light, soil temperature, soil moisture, humidity, litter decomposition, and nutrient dynamics by changing the structural complexity of the forest, which in turn alters species diversity, composition, and abundance (Bennett and Saunders 2010). Edge effects could lead to different plant communities forming at the edge and in the interior of the forest (Lin and Cao 2009). Alien species, weedy species, disturbance-tolerant forest species, and colonizing plants might dominate at forest edges, but these species traits might not be common in forest interiors (King and Buckney 2001; Honnay et al. 2002), suggesting that species composition, diversity and abundance might differ between forest edges and interiors. Ruwanza (2019) found that the abundance of woody species increased with proximity to the forest edge, while this was not the case for herbs and grasses showing that the effects of forest edges vary according to plant growth form. On the other hand, edge effects can lead to biotic homogenization across edge-interior habitat gradients that exhibit similar species richness, abundance, and composition (Parra-Sanchez and Banks-Leite 2020). These mixed results show that edge effects can have different impacts on plant diversity depending on the study system, climate, and/or degree of disturbance. Further research is needed to better understand the complex impacts of forest fragmentation and edge effects on plant biodiversity.

We, therefore, aim to understand the effects of forest fragmentation on the distribution of different plant growth forms in the remnant church forests of the Ethiopian highlands. We specifically asked the following questions: (i) Does forest fragmentation have the same effect on the species diversity, composition, and abundance of different plant growth forms? (ii) To what extent does forest fragmentation change environmental conditions in small forest patches compared to large forest patches? (iii) Do the environmental factors in fragmented forests affect all plant growth forms in the same way? (i) We hypothesized that forest fragmentation and edge effects should influence plant diversity, composition, and abundance with different plant growth forms responding differently. Low diversity and abundance of trees and shrubs is expected in small forest fragments and forest edges due to low habitat quality, compared to relatively large forest fragments and forest interiors. For herbs, on the other hand, a higher diversity and abundance is expected in small forest fragments and forest edges than in large forest fragments and forest interiors. A different species composition between small and large forest fragments and between forest edges and forest interiors is also expected for all plant growth forms. (ii) Microenvironmental conditions would change with forest fragments and habitat types (forest edges vs. forest interiors), with the differential response of plant growth forms to environmental conditions due to differences in their growth strategies, habitat requirements, and sensitivity to disturbance.

Materials and methods

Study area

This study was conducted in Chilga district, in Central Gondar Administrative Zone, Amhara National Regional State, northwest Ethiopia (Supplementary Material Fig. 1). Chilga district is one of the areas in northwestern Ethiopia where remnants of Ethiopian Church forests exist. These remnant church forests represent the dry Afromontane forest of Ethiopia which is the largest vegetation type in the country after the Acacia-Commiphora woodland. Climatically, the study area is characterized by unimodal rainfall patterns as rainy and dry seasons. With a mean annual rainfall between 995 and 1175 mm, the temperature of the study area ranges from 11 in the rainy season to 32 °C in the dry season. The major soil types in Chilga district are 45% Cambisols, 40%Vertisols, and 15% Nitosols (CDOA 2020).

The Ethiopian dry Afromontane vegetation type is mainly dominated by human settlements where agriculture, urbanization, grazing, and fuel wood harvest have long been extensively practiced (Asefa et al. 2020). It contains vegetation ranging from legume-rich grasslands to shrubs, small and large trees with a closed canopy (Friis et al. 2010). The Ethiopian highlands with their mountainous topography are primarily covered with this type of vegetation and deforestation occurred for many centuries in the northern highlands of Ethiopia and resulted in forest patches around churches (McCann 1997). The fragmented forests of different sizes observed in the northern highlands of Ethiopia are mainly confined to Ethiopian churches (Wassie et al. 2010) showing that church forests are refugia for Ethiopian plant biodiversity. We selected ten church forests with different sizes ranging from 2.5 to 6.7 ha (Supplementary Material Table 1). We selected the 7 church forests as sets of several small forest patches while the other 3 church forests as few large forest patches so that the total area between the two sets of church forests is almost the same. We also included the ages of these forest patches that are given based on the ages of churches, otherwise the historical ages of the patches could be older than these (Supplementary Material Table 1).

Sampling method

We collected vegetation and environmental data in our study area. Transects in all selected Church forests were established from the forest edges to the interiors. A total of 56 20×20 m plots (28 for sets of several small church forests and 28 for sets of a few large church forests) were established for woody plants' (Trees and shrubs) sampling along the transect lines at the forest edges and interiors in which the distance between the plots was 100 m. The plots at the forest edge were 5 m away from the edge of the forest while plots at the forest interior were 100 m far from the forest edge. We established two plots, one at the edge and one at interior, along each transect line which has 200 m in length. For understory vegetation sampling (herbs), 2×2 m sub-plots were established at the center and corners of the main plots (20×20 m). All trees, shrubs, and herbs that were found within the sampling plots were recorded, collected, and identified at the Botanical Herbarium of Gondar University, Ethiopia. We counted the abundance of each species in each sampling plot. We also measured elevation, soil moisture, and soil pH at each 20×20 m sampling plot using, respectively, GPS, moisture probe meter, and soil pH meter. We measured the soil moisture and soil pH for the sampling plots at 20 cm depth with replicated measurements at the center and each corner of the plot and took the average for the final report.

Data analyses

The first aim of this study was to address how forest fragmentation affects the abundance, diversity, and composition of different plant growth forms. We used an analysis of variance (ANOVA) of generalized linear model (GLM) to estimate the effect of forest fragments (patch size), habitat types (forest edges vs. forest interiors), growth forms, forest patch ages, and their interactions on the species diversity (Shannon-Wiener diversity), abundance and species richness. We used Poisson distribution for abundance and richness and normal error distribution for Shannon-Wiener diversity. Since species diversity and species richness have been used interchangeably to test the Habitat amount hypothesis, we also used species richness to test the hypothesis (pooling species richness for several small forest patches vs. pooling species richness for a few large forest patches). Not only individual forest patches were compared to each other to address the question of how forest patch size influences plant diversity, but we also compared sets of several small patches to sets of a few large patches of the same total area. We applied this for all plant growth forms. We used PERMANOVA for differences in community composition between forest fragment sizes, and between habitat types, and their interactions using 'adonis' function in the vegan package (Oksanen et al. 2022). Non-metric Multi-Dimensional Scaling (NMDS) was used to visualize differences in community composition between those categorical variables and associated them with environmental factors. We used 'ggplot2' package in R for data visualization throughout our analyses (Wickham 2016).

The second aim was to test whether fragmentation has changed environmental conditions in the study area. Whether patch size, habitat type, forest patch age, and their interactions influence environmental factors, we used an analysis of variance (ANOVA) of generalized linear model (GLM) with Poisson distribution. The third aim of this study was to test the effect of environmental factors on diversity, abundance, and composition and whether the effects differ between plant growth forms. Linear mixed effect models with species diversity and abundance as response variables, while environmental factors (soil pH, soil moisture, and Altitude), plant growth forms, and their interactions as fixed factors with a random factor of habitat type were used to address this question. 'lmer' function in the 'lme4' package of R, was used to run this analysis (Bates et al. 2015). Soil moisture and abundance were log-transformed for the mixed effect model analysis and environmental factors were also standardized using a z-score for ease of comparison and interpretation.

Results

Effect of forest fragmentation on species abundance, diversity, and composition

Forest fragment size (patch size) was found to interact significantly with plant growth forms for species diversity but not for abundance (Table 1). While tree diversity showed a negative relationship with patch size, shrub diversity showed a positive relationship (Fig. 1b). We also used species richness as a complement to species diversity, and found a similar result that habitat patch size interacted with plant growth forms to determine species richness (Supplementary Material Table 2). Shrub richness increased but tree richness did not change with forest patch size (Fig. 1c). However, herb diversity and richness did not differ between forest patch sizes (Fig. 1b and c). We also compared how species richness differed between sets of small patches and sets of a few large patches and found that patch size and growth form interactively determined species richness (Supplementary Material Table 3). Several small forest patches support more tree species than a few large forest patches (F value = 5.72, $p = 0.0218$; Fig. 1d). However, the small forest patches support less shrub species than a few large forest patches (F value = 14.63, $p = 0.0004$; Fig. 1d).

Habitat type (forest edges vs. forest interiors) showed consistent and significant effects on species abundance and diversity. While effects of habitat type did not interact with growth forms to determine diversity, effects on abundance were found to vary with plant growth forms (Table 1). We found interior habitats to support more species abundance than edge habitats for all growth forms (Fig. 2). i.e., for trees ($\chi^2 = 26.6$, p value = < 0.00001), shrubs ($\chi^2 = 10.32$, p value = 0.001) and herbs ($\chi^2 = 97.35$, p value = < 0.0001). Species diversity was not varied significantly between edge and interior habitats for trees ($\chi^2 = 3.06$, p value = 0.08), shrubs ($\chi^2 = 4.16$, p value = 0.041), and herbs ($\chi^2 = 2.55$, p value = 0.1102) (Fig. 2). Age of forest patches interacted with plant growth forms to determine plant diversity but not abundance (Table 1). The diversity of trees and shrubs decreased with the age of forest patches while the diversity of herbs increased (Supplementary Material Fig. 2).

We also used PERMANOVA to test differences in species composition between forest patch sizes and between habitat types. We found significant differences in community composition of trees, shrubs and herbs between the small and big patch sizes (Fig. 3). Similarly,

Table 1 Results of the ANOVA of generalized linear model showing the effects of patch size, habitat type, growth forms, forest age and their interactions on plant abundance and diversity

Community metrices	Predictors	df	F value	*P* value
Abundance	Patch size	1	10.5	0.001534**
	Habitat type	1	98.04	2.2e-16***
	Growth form	2	32.8	5.5e-12***
	Age	1	9.9	0.002100**
	Patch size × Habitat type	1	2.15	0.14533
	Patch size × Growth form	2	2.12	0.124586
	Habitat type × Growth from	2	9.6	0.000142***
	Patch size × Age	1	0.009	0.923763
	Habitat type × Age	1	0.19	0.662681
	Growth form × Age	2	2.17	0.118307
	Patch size × Habitat type × Growth form	2	1.11	0.332102
	Patch size × Habitat type × Age	1	0.15	0.695566
	Area × Growth form × Age	2	0.52	0.597934
	Habitat type × Growth form × Age	2	1.14	0.322054
	Patch size × Habitat type × Growth form × Age	2	0.23	0.794044
Diversity	Patch size	1	0.008	0.92723
	Habitat type	1	4.7	0.03242*
	Growth form	2	10.6	5.98E-05***
	Age	1	2.6	0.11155
	Patch size × Habitat type	1	0.016	0.89758
	Patch size × Growth form	2	11.4	3.16E-05***
	Habitat type × Growth from	2	0.39	0.6768
	Patch size × Age	1	2.00	0.15979
	Habitat type × Age	1	0.17	0.6799
	Growth form × Age	2	3.6	0.03125*
	Patch size × Habitat type × Growth form	2	1.72	0.18276
	Patch size × Habitat type × Age	1	1.4	0.24176
	Area × Growth form × Age	2	0.68	0.50872
	Habitat type × Growth form × Age	2	0.002	0.99808
	Patch size × Habitat type × Growth form × Age	2	0.15	0.85945

***$P<0.001$; **$P<0.01$; *$P<0.05$

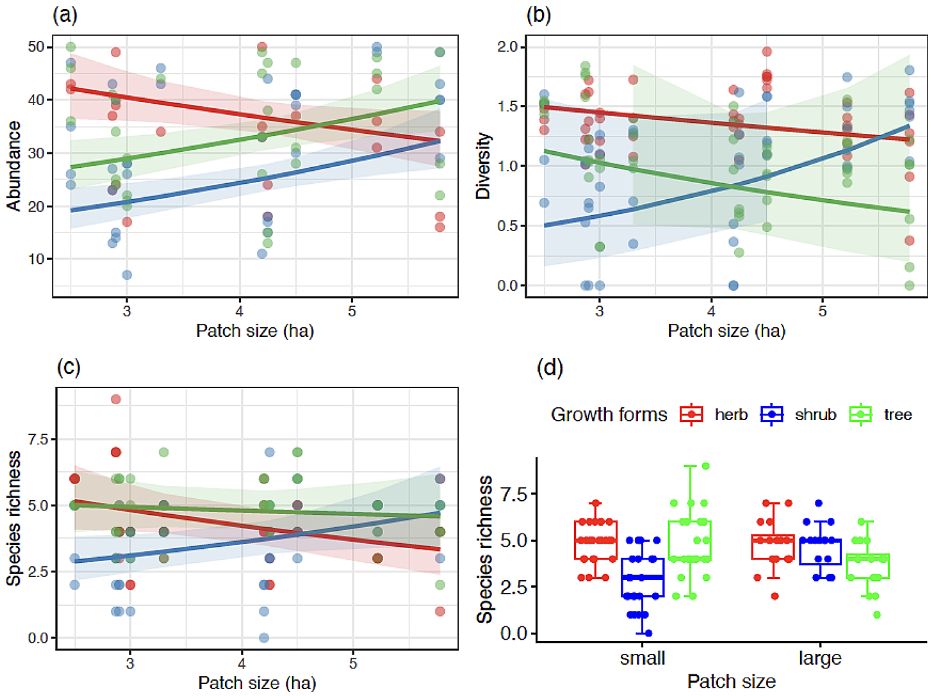

Fig. 1 The effect of forest patch size on (**a**) species abundance, (**b**) diversity, and (**c**) species richness across plant growth forms. Panel (**d**) shows the comparison of species richness between sets of several small forest patches and a few large forest patches

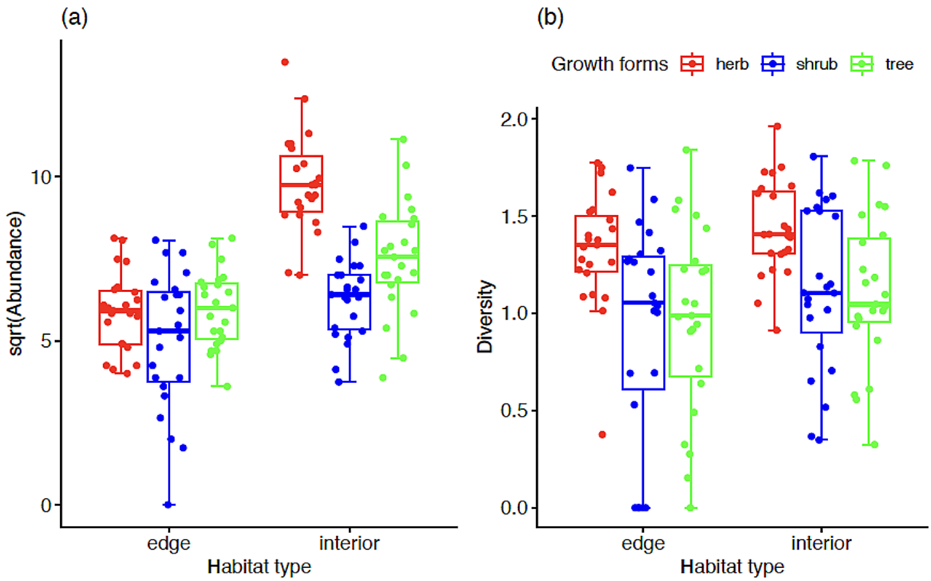

Fig. 2 The effect of habitat type on the (**a**) abundance and (**b**) diversity of different plant growth forms

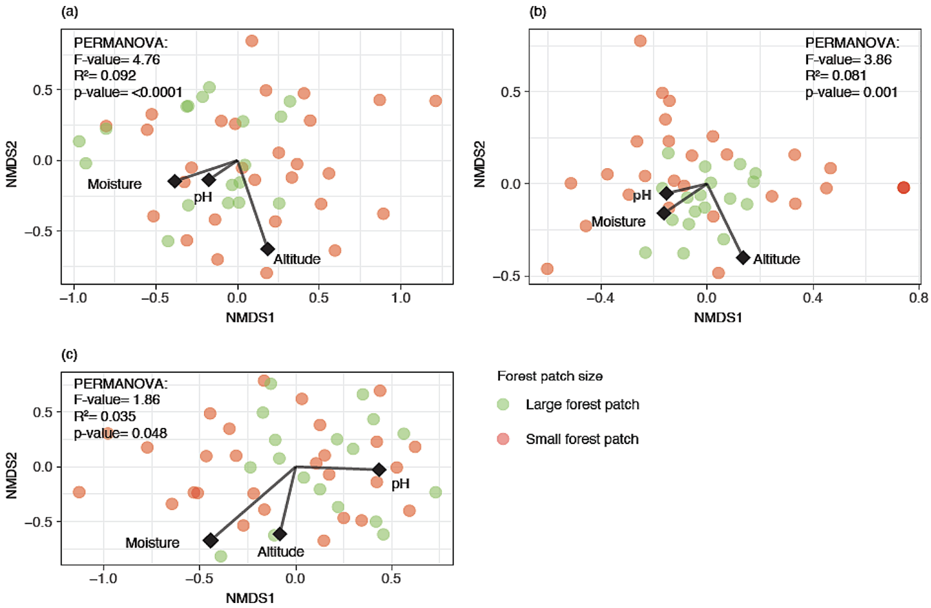

Fig. 3 Differences in community composition between small and large forest patches of (**a**) trees, (**b**) shrubs, and (**c**) herbs

differences in community composition between edge and interior habitats were found for trees and herbs but not for shrubs (Fig. 4).

Effect of forest fragmentation on environmental factors

We have investigated how microenvironmental conditions change with forest fragmentation. Soil moisture and Soil pH showed no significant differences across forest patch size, patch age, and between habitat types. Although only marginally significant, soil moisture was higher in the interior habitat than edge habitat (Table 2; Supplementary Material Fig. 3). Forest patch size, patch age, and habitat type did not interact with each other to determine environmental factors.

Effects of environmental factors on species abundance, diversity, and composition

We quantified the effects of environmental factors on species abundance and diversity using linear mixed-effects models. We found that altitude, but not soil pH and moisture, had a significant effect on species abundance and diversity (Table 3). Altitude has interacted with plant growth forms to determine species abundance but not species diversity. The abundance of trees and shrubs, but not herbs, decreased with increasing altitude. Similarly, tree and shrub diversity declined with increasing altitude (Supplementary Material Fig. 4).

We also estimated the effects of environmental factors on species composition. The result showed that the response of species composition to environmental factors varied with plant growth forms. Altitude accounted for the significant variation in species composition for trees and shrubs, but not for herbs (Supplementary Material Table 4). Figures 3 and

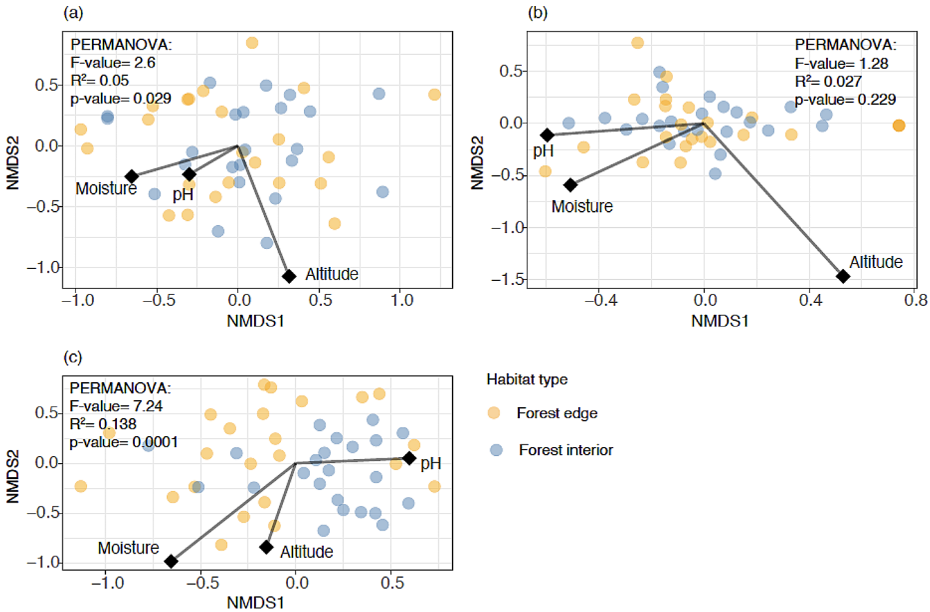

Fig. 4 Differences in community composition between the edge and interior habitat types of (**a**) trees, (**b**) shrubs, and (**c**) herbs. The graph also shows the influence of environmental factors on the community composition of different plant growth forms

Table 2 Result of the ANOVA of generalized linear model showing the effects of forest patch size, habitat type, patch age and their interactions on environmental factors

Environmental factors	Predictors	df	F value	*P* value
pH	Patch size	1	0.92	0.3435
	Habitat type	1	0.05	0.8219
	Age	1	0.026	0.8716
	Patch size × Habitat type	1	0.075	0.7853
	Patch size × Age	1	0.055	0.8157
	Habitat type ×Age	1	0.21	0.652
	Patch size × Habitat type × Age	1	0.02	0.9006
Soil moisture	Patch size	1	0.075	0.78521
	Habitat type	1	3.35	0.07514.
	Age	1	0.26	0.6159
	Patch size × Habitat type	1	1.04	0.31352
	Patch size × Age	1	1.73	0.19612
	Habitat type ×Age	1	1.88	0.17742
	Patch size × Habitat type × Age	1	0.60	0.44226

****P*<0.001; ***P*<0.01; **P*<0.05

Table 3 Wald type III tests of fixed effects in linear mixed-effect models showing the effects of environmental variables, growth forms, and their interactions on plant abundance and diversity

Community metrices	Predictors	df	χ^2	*P* value
Abundance	pH	1	0.009	0.9232592
	Moisture	1	1.22	0.2687241
	Altitude	1	7.26	0.0070207**
	Growth forms	2	17.86	0.0001319**
	pH × Growth forms	2	1.18	0.5541648
	Moisture × Growth forms	2	1.97	0.372371
	Altitude × Growth forms	2	9.41	0.0090387**
Diversity	pH	1	0.29	0.589001
	Moisture	1	0.57	0.448318
	Altitude	1	6.65	0.009906**
	Growth forms	2	7.50	0.023509*
	pH × Growth forms	2	1.57	0.454966
	Moisture × Growth forms	2	3.48	0.175151
	Altitude × Growth forms	2	3.70	0.157225

***$P<0.001$; **$P<0.01$; *$P<0.05$

4 showed the strong correlation of altitude with the community composition of trees and shrubs while soil pH and moisture did not have a significant correlation with species composition in the study area.

Discussion

Effect of forest fragmentation on plant abundance, diversity, and composition

While our results showed that forest fragmentation has a considerable effect on plant biodiversity, the strength and direction of the effect was found to vary depending on plant growth forms. The abundance of woody species (Trees and shrubs) increased with the size of the forest patch, whereas forest patch size has a negative relationship with the abundance of non-woody herb species. The diversity of trees, shrubs, and herbs did not respond in a similar way, showing the different effects of fragmentation on plant biodiversity. Consistently, previous studies reported that forest fragmentation does not affect all plant growth forms in the same way (Rodríguez-Loinaz et al. 2012; Pasion et al. 2018) highlighting that one type of plant growth form may not represent the fragmentation response of other plant growth forms. The different life history characteristics of species may cause forest fragmentation to have different effects on plant growth forms. Non-woody herbaceous species have fast growth strategies by growing and dying more rapidly and investing their energy in reproduction (Ewers and Didham 2006). On the contrary, wood species have slow life histories with slow growth and reproduction strategies and invest their energy more in the structural materials for long-term survival (Chapin 1991). These life-history differences among growth forms may, therefore, result in different growth forms to respond differently to fragmentation.

Habitat fragmentation has been found to have a negative impact on plant biodiversity in small forest fragments (Haddad et al. 2015). However, there is increasing evidence that forest fragmentation does not always negatively affect biodiversity (Fahrig 2017; Rybicki et al. 2020; Riva and Fahrig 2022). Consistent with this evidence, our results showed that several small habitat patches contain more species than a few large habitat patches showing that our results do not support the Habitat amount hypothesis, at least for trees. It was also widely reported that small habitat patches were found to support a disproportionately higher number of species than a few large habitat patches (Fahrig 2020) suggesting that small fragmented forests should be considered to conserve the remaining biodiversity. We also tested whether habitat patch sizes interact with their ages to influence plant diversity and abundance, and found no interaction suggesting that the effect of patch size is age-independent. However, the effect of patch age on diversity found to depend on plant growth forms. It negatively affects shrub and tree diversity, but enhance herb diversity, indicating that old forests may not necessarily support higher woody diversity. Similarly, Tullus et al. (2022) reported that the effect of stand age depends on the group of plants under study. It negatively influences the number of vascular plant species while positively affecting lichen and bryophyte communities. Our result, therefore, underlines that, regardless of age, the conservation value of many small habitat patches needed to be acknowledged despite the current strong promotion of area-based conservation approach. If the aim is to promote biodiversity conservation in a human-dominated landscape, our result together with other previous findings collectively suggested that there is no ecological reason to favor a few large forest fragments over several small forest patches (Deane and He 2018; Wintle et al. 2019; Riva and Fahrig 2022). Small forest patches, hence, needed to be the focus of biodiversity conservation despite preventing large forest patches from further fragmentation. Due to the high extinction risk in small habitat patches, historically, small forest patches have been ignored in biodiversity conservation (Riva and Fahrig 2022). It has been indicated that small habitat supports small populations and they are susceptible to extinction risk due to genetic, environmental, and demographic stochasticity (Laurance 2002). However, a high extinction risk in each small habitat may not necessarily lead to a higher risk of population extinction across the entire small forest patches than few large habitats (Fox et al. 2017). Due to the presence of many small habitat patches, the probability of extinction to occur decreases over the entire set of several small patches (Tulloch et al. 2016). Furthermore, a recent experimental study has shown that several small habitat patches may have an overall lower extinction risk as compared to a few large habitat patches of the same area (Hammill and Clements 2020) as the negative relationships between the small population in small habitat and extinction risk may not always occur in each of numerous habitat patches. The finding of this study together with previous similar findings, therefore, suggests a paradigm shift for biodiversity conservation to focus not only on big forest patches but also equally on small fragmented forests.

Forest fragmentation is also known to create different habitats (forest edges vs. forest interiors) where biotic and abiotic conditions change (Lin and Cao 2009). We found that habitat type has a significant and consistent effect on species abundance and diversity. In contrast to Ruwanza (2019) who reported mixed results on the response of different growth forms to different habitats, compared to edge habitats, interior habitats were found to support a greater species abundance for all plant growth forms. This could be related to adequate resource availability in the forest interior, high soil moisture availability for instance. In contrast to our prediction, however, habitat type did not interact with plant growth forms to determine species diversity. We expected that the response pattern of plant diversity along the gradient from the forest edge to the forest interior forest gradient would vary with plant growth forms due to the change in microhabitat conditions. Greater availability of light at the habitat edge was expected to promote higher diversity for herbaceous species (Dormann et al. 2020) but not for trees and shrubs. However, we found no effects of the different habitat types on the diversity of all plant growth forms. Similarly, Phillips et al. (2006) reported that tree richness was not significantly influenced by the habitat edges. While Normann et al. (2016) and Valadi et al. (2022) reported a greater diversity of herbs at the habitat edge compared to the interior habitat, higher tree richness was observed at the interior habitat than at the edge habitats (Ruwanza 2019; Mendes and Prevedello 2020).

Species composition is also found to be affected by forest fragmentation. This study showed that small and large forest patches were found to differ with their community composition. Except for shrubs, we found significant differences in composition of trees and herbs between the edge and interior habitats. Likewise, McDonald and Urban (2006) also reported significant differences in species composition between edge and interior habitats. We associated differences in species composition with environmental factors and found that environmental factors did not have the same effect on all growth forms. Altitude was responsible for the variation in species composition for trees and shrubs, but not for herbs. Soil pH and soil moisture did not greatly influence the species composition of all growth forms. Difference in plant community composition has not been strongly correlated with the moisture contents of the soil suggesting that other unmeasured multiple environmental drivers (for instance, soil nutrients) might be responsible for the variation. It has been indicated that the effect of habitat edges on the biotic process of the environment can have complex interactions thereby affecting community composition and population dynamics (Weiher and Keddy 1995). We, thus, showed that fragmentation-induced edge effects can change the biotic composition by altering resource availability and microhabitat conditions.

Effect of forest fragmentation on environmental factors

Forest fragmentation alters the physical component of the environment thereby changes the biotic assemblage. Our result showed that forest patch size did not interact with patch age to influence soil moisture and soil pH. We also found no significant interaction effect of forest patch size and habitat type on soil moisture and soil pH. Soil moisture declined with the increase of forest patch size in which interior habitats have relatively larger amount of soil moisture than edge habitats. Consistently, Valadi et al. (2022) found that soil moisture was higher in small forest fragments than in large forest fragments. In addition to high soil moisture content, forest interior habitats were also found to support more soil nutrients than forest edge habitats in Ethiopian church forests (Cardelús et al. 2020). This could be because forest edges are mostly exposed to higher solar radiation and daily maximum temperature than forest interiors and consequently moisture content of the soil could be reduced through evaporation (Chen et al. 1999). Also, the presence of high species abundance and diversity in forest interior habitats may contribute to the relatively higher content of soil moisture through canopy shading. The absence of a significant effect of fragmentation size on soil properties in pine forests of central Finland (Rantalainen et al. 2008), and the absence of edge effects on soil characteristics in small fragment sizes were also reported (Bunyan et al. 2012). Especially at larger scale, including more vegetation types, disturbance levels, and fragment sizes could help to find the general patterns of forest fragmentation effect on environmental conditions (Santana et al. 2021).

Effects of environmental factors on plant diversity and abundance

Forest fragmentation greatly influences plant community structure by altering the microclimatic conditions and resource availability. We investigated the effect of fragmentation-induced environmental change on plant diversity and abundance across plant growth forms. Despite their effects, environmental factors did not similarly affect all plant growth forms. Altitude, but not soil moisture and soil pH, has a significant effect on the abundance and diversity of species. As expected, tree and shrub diversity and abundance declined with the rise of altitude as Gebrehiwot et al. (2019) also found the negative effect of elevation on the diversity and abundance of plant communities. Harsh environmental conditions in higher altitudes coupled with the less adaptive capacity of plants are mostly accounted for the less species richness and abundance in mountain ecosystems. Although our result is consistent with most previous studies (Rahbek 2005; Sharma et al. 2009; Trigas et al. 2013), it is also important to highlight that the elevational gradient of plant diversity does not globally follow rigid patterns as there are findings that show a decrease, increase (Baruch 1984) and no pattern of diversity with elevation (Lovett 2010). Despite the key role of soil moisture and soil pH in previous studies, our result, however, shows the limited role of these factors in our study area suggesting that the response of plants to fragmentation should also be looked through the lens of other important biotic and abiotic factors, such as plant interactions and soil nutrients.

Conclusion

We investigated the effect of forest fragmentation and associated changes in environmental conditions on plant biodiversity with the following outcomes: (i) Forest fragmentation was found to greatly influence species abundance, diversity, and composition with the effect varying with plant growth forms showing that a single plant growth form cannot represent the response of other plant growth forms to forest disturbance. Our results showed that small fragments can support more species richness compared to large forest fragments. This implies that a shift in conservation priorities may be needed to recognize the value of small fragmented forest patches. Here, we are not suggesting the replacement of large forest patches with sets of small forest patches, instead, we are showing the importance of small forest patches to maintain the remaining biodiversity, as a lack of protection of small forest patches can lead to high cumulative impacts on plant biodiversity loss. (ii) Environmental factors were not found to explain adequately the observed pattern of species diversity, abundance, and composition in fragmented forests, suggesting that more environmental factors needed to be included. We only considered few fragmented forest patches in this study, and to ensure the generality of the patterns being observed here many forest patches with different sizes should be considered in the future. Despite the little effort we put to find and explain the patterns, the underlying ecological mechanisms for the observed patterns in the fragmented forests are not yet well understood. Therefore, by measuring as many environmental factors as possible, such as soil nutrients, more studies are required to better understand the drivers of plant response to habitat fragmentation.

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Author contributions AA and MA designed the study; AA collected the data; MA analyzed the data; AA, MA and EK wrote the manuscript. All authors greatly contributed to the manuscript and provided final approval for the publication.

Data availability The dataset will be available from the corresponding author upon request.

Declarations

Competing interests The authors declare no competing interests.

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