CHANGES IN SPECIES COMPOSITION AND LITTER DYNAMICS ALONG A FRAGMENT SIZE GRADIENT IN SUBTROPICAL BROADLEAVED FORESTS OF MEGHALAYA, NORTHEAST INDIA

BARBHUYAN, H. S. A.[1] – MIR, A. H.[2] – CHAUDHURY, G.[2] – SARMA, K.[3] – UPADHAYA, K.[4*]

[1]*Department of Botany, School of Life Sciences, North-Eastern Hill University, Shillong 793 022, India*

[2]*Department of Environmental Studies, School of Human and Environmental Sciences, North-Eastern Hill University, Shillong 793 022, India*

[3]*University School of Environment Management, Guru Gobind Singh Indraprastha University, New Delhi 110078, India*

[4]*Department of Basic Sciences and Social Sciences, School of Technology, North-Eastern Hill University, Shillong 793 022, India*

[*]*Corresponding author*
e-mail: upkri@yahoo.com

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Abstract. Habitat fragmentation creates numerous small forest patches separated by human land use that may affect the compositional and structural attributes and ecosysem functions particularly the nutrient dynamics in forest ecosystems. We tested this hypothesis along a fragment size gradient in subtropical broadleaved forests in Cherrapunjee area of Meghalaya, northeast India following standard methods of vegetation sampling and nutrient dynamics. The study revealed that the structure and composition of woody species, shrubs and herbs varied significantly ($p<0.05$) along a fragment size gradient. Similarly, the leaf litter standing crop as well as total litter fall and annual N and P return through litter fall varied significantly ($p<0.05$) across fragments and were higher in the larger fragments as compared to the smaller fragments. Therefore, the results of the study collectively suggest that understanding the overall ecological implications of the effect of fragmentation on the structure and functioning of subtropical broadleaved forest ecosystem of Meghalaya, north east India, is imperative to outline pertinent conservation strategies.
Keywords: *ecosystem function, nutrient dynamics, plant diversity, stand structure, litterfall*

Introduction

Throughout the world, habitat loss and fragmentation have been considered the primary cause for biodiversity loss and ecosystem degradation (Laurance and Bierregaard, 1997; Laurance and Peres, 2006; Wu, 2013; Wilson et al., 2016). The process of fragmentation can be explained as a biphasic event, characterized by the reduction of the total amount of forest area, followed by loss of habitat area, changes in the spatial configuration of the landscape, resulting in the isolation of smaller patches (Wilcove et al., 1986; Saunders et al., 1991; Didham et al., 2012). These processes cause differences not only in species diversity but also in composition between fragments and continuous forests.

The physical and biological changes associated with forest fragmentation include habitat loss and insularization (Lovejoy et al., 1986; Laurance, 1990), reduction in the number of species and changes in plant dynamics owing to difference in the forest

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spatial organization such as the size, shape, and isolation of fragments, edge effects, invasion of foreign species, and other disturbances (Murcia, 1995; Laurance et al., 2002; Hobbs and Yates, 2003). Fragmentation leads to community disassembly following decline of both species abundance and diversity (Turner and Corlett, 1996; Tabarelli et al., 1999; Echeverría et al., 2007) and alters the ability of the remnant forests to maintain their original biodiversity and ecological processes (Echeverría et al., 2007). Fragment size has been reported to be the major determinant of changes in woody plant composition (Tabarelli et al., 1999; Rosati et al., 2010; Fahrig, 2013; Pao and Upadhaya, 2017). Fragmentation has short- and long- term effects on species composition (Harper et al., 2005; Oliveira et al., 2008; Santos et al., 2008; Laurance et al., 2011; Andrade et al., 2015), that often favor the proliferation of generalist and pioneer species (Melo et al., 2007; Laurance and Vasconcelos, 2009; Chabrerie et al., 2013) and hardy exotic species (Laurance and Vasconcelos, 2009; Carmo et al., 2011; Chabrerie et al., 2013; Lambert et al., 2014). Small patches are often exposed to a greater disturbance (Pao and Upadhaya, 2017; Schmidt, 2019) and are prone to a large number of gaps that eventually affect tree regeneration and recruitment (Lovejoy et al., 1986; Laurance et al., 1998). Given the role of biodiversity in the provision of ecosystem services, a reduced resistance (or higher susceptibility) to the increasing frequency and intensity of anthropogenic disturbance is likely to cause widespread degradation of forests and the provision of such ecosystem services (Brockerhoff et al., 2017).

The consequences of habitat fragmentation on biodiversity are well documented (Fahrig, 2003) and there is a general consensus on the strong negative impact that fragmentation has on biodiversity within forests (Sala et al., 2000). Most of the studies that investigated the effects of habitat fragmentation have typically focused on changes in the population or community dynamics of the flora and fauna (Laurance and Bierregaard, 1997), while its effect on ecosystem functioning (*viz.*, nutrient cycling and organic matter decomposition) are limited (Didham, 1998; Vasconcelos and Luizão, 2004; Rubinstein and Vasconcelos, 2005; Vasconcelos and Laurance, 2005; Lindsay and Cunningham, 2009). Fragmentation of habitats is known to cause changes in the community composition as well as the ecosystem functions in fragmented landscapes (Turner and Corlett, 1996; Laurance and Cochrane, 2001; Cochrane and Laurance, 2002) as manifested by alteration of nutrient dynamics following shift in composition of dominant species and microclimatic buffering in the fragments (Saunders et al., 1991; Murcia, 1995; Fahrig, 2003; Haddad et al., 2015).

Among the various ecosystem functions, litter dynamics plays an important role in regulating plant community composition through its effects on recruitment (Facelli and Pickett, 1991; Hastwell and Facelli, 2000) and nutrient cycle (Vitousek, 2004). Litter deposited on the forest floor acts as an input-output system of nutrients and acts as a temporary sink for nutrients and functions as ‘a slow release nutrient source’ (White, 1988), thereby ensuring a permanent input of nutrients to the soil (Cuevas and Medina, 1988). However, it is the rates at which litter falls and decays that are the main regulators of primary productivity, energy flow and nutrient cycling in forest ecosystems (Bray and Gorham, 1964; Swift et al., 1981; Prescott et al., 2004; Prescott, 2010). Feeley (2004) observed that fragmentation can cause significant changes in the quantity of accumulated litter and strongly influence the rate at which nutrients are mineralized and made available to plants.

The state of Meghalaya, situated in the north eastern part of India, lies between 24°58’N to 26°07’N latitude and 89°48’E to 92°51’E longitude and covers an area of

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22,429 km^2, which accounts to 0.68% of the total geographical area of the country (ISFR, 2019). The state is a part of the 'Indo-Burma' global biodiversity hotspots (Mittermeier et al., 2004). The forest cover of the state in the year 2019 was 76.33%. However, during the period 2017-2019, the state has lost a forest area of 23 km^2 (ISFR, 2019) due to a number of human activities such as overexploitation, deforestation, shifting cultivation, mining and urbanization (Pao and Upadhaya, 2017). The current vulnerabilities of the forest systems in Meghalaya arise from forest disturbances and fragmentation. Thus, it is important to address the effects of fragmentation on community structure and ecosystem functioning. It is hypothesized that fragmentation modulates species composition and their abundance in forest patches of different size that would affect nutrient dynamics on the forest floor by influencing resource quality and quantity of above ground litter and nutrient reservoir. This in turn would have an effect on the availability of nutrients on the forest floor. Therefore, the objectives of the present study were to investigate the effect of fragmentation on (i) species diversity and community structure and (ii) nutrient dynamics through the study of accumulation of Nitrogen (N) and Phosphorous (P) by litter in subtropical broadleaved forests.

Methods

Study sites

The present study was undertaken in Cherrapunjee and its adjoining areas in the state of Meghalaya, northeast India (*Figure 1*). The vegetation of the area is classified as subtropical broadleaved forest (Champion and Seth, 1968) and represents the remnants of the climax forest of the area. They are dense evergreen forest with short stature and the tree height rarely exceeds 20 m. The climate of the area is tropical monsoonal and is directly influenced by the southwest monsoon moving from the Bay of Bengal. It has a distinct hot-wet and cold-dry period. The wet period extends from May to October, during which more than 80% of the total rainfall occurs. The dry period prevails from November to March with <22 mm rainfall. The mean annual rainfall varies from 8000-10000 mm and the average temperature ranges from 1.7°C to 24°C. The soils are derived from gneissic complex parent materials; they are dark brown to dark reddish-brown in colour, varying in depth from 50-200 cm. The texture of soils varies from loamy to sandy loam. The reaction of the soils varies from acidic (pH 5.0 to 6.0) to strongly acidic (pH 4.5 to 5.0), rich in organic carbon and nitrogen but deficient in phosphorus and potassium (http://megagriculture.gov.in/PUBLIC/agri_scenario_-soil.aspx).

To assess the impact of fragmentation on species richness, density and population structure of woody species in the subtropical broadleaved forest, a total of fourteen forest fragments ranging in size from 2.01 to >100 ha were selected for the present study. These fragments were grouped into five classes viz. Very small (<3 ha), Small (4-6 ha), Medium (8-10 ha), Large (17-86 ha) and Very Large (>100 ha). For each fragment class three replicate forest patches were selected. However, due to unavailability of continuous forests in the study area, two replicated plots were maintained from a single Very Large fragment. These replicated sites were abbreviated as Very small (VS1, VS2, VS3), Small (S1, S2, S3), Medium (M1, M2, M3), Large (L1, L2, L3) and Very Large (VL1, VL2), respectively (Table 1). All the fragments were once a part of the same forest.

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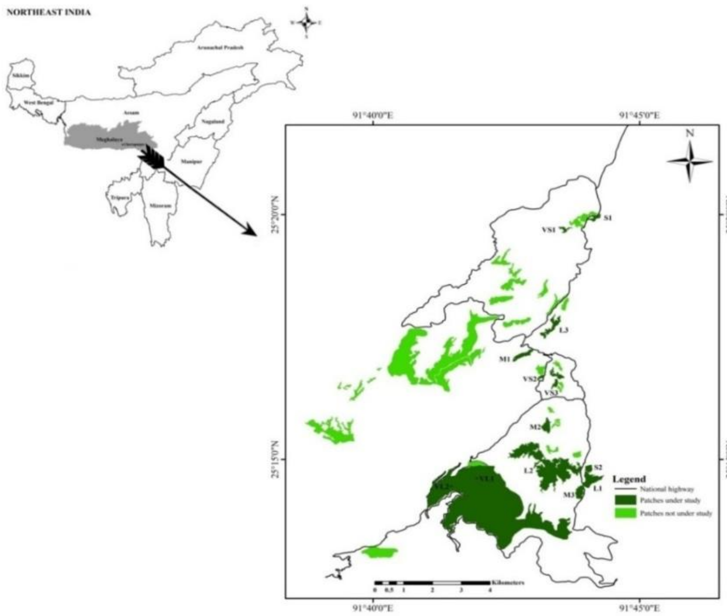

Figure 1. *Map showing the location of the study area at Cherrapunjee in Meghalaya, northeast India*

Plant diversity sampling

The vegetation was assessed by laying a belt transect of 250 m length × 20 m width in each of the selected fragments. The transects were further divided into, quadrats of 10 m × 10 m for inventorizations of all woody species having a minimum diameter at breast height (dbh) of ≥5 cm, quadrats of 5 m × 5 m for shrubs and quadrats of 2 m × 2 m for herbs. Plant samples were collected and identified with the help of regional floras (Kanjilal et al., 1940; Haridasan and Rao, 1987). The Herbaria at Botanical Survey of India (ASSAM), Eastern Regional Circle, Shillong and Department of Botany, North-Eastern Hill University (NEHU), Shillong were also consulted for correct identification of the specimens. The nomenclature of the species follows the regional flora. The field data was analyzed for number of species and quantitative community parameters such as frequency, density, basal area and importance value index (IVI) were computed following Misra (1968) and Mueller-Dombois and Ellenberg (1974). Various diversity indices such as Shannon-Wiener, Simpson and Pielou were calculated following Magurran (1988) as follows:

Shannon-Wiener index of diversity:

$$H' = -\sum pi \ln pi \qquad \text{(Eq.1)}$$

where, H' is the measure of diversity and pi is the proportion of the total sample belonging to the ith species.

Simpson's dominance index:

$$D = \sum pi^2 \qquad \text{(Eq.2)}$$

where, D is the Simpson index of dominance and pi is the proportional individuals of species i in the community.

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Pielou's evenness index:

$$E = \frac{H'}{\ln S} \quad \text{(Eq.3)}$$

where, E is Pielou's evenness index, H' is the Shannon-Wiener index of diversity and S is the number of species in the community

Litter dynamics

Forest floor Litter

Standing crop of litter expressed as the dry mass per unit ground area at a given time (g m^{-2}) was determined at monthly intervals from May 2015-April 2017 by randomly laying ten 1 m × 1 m size quadrats in each studied forest fragment. Litter samples were collected (cleared and swept of any deposited debris) from all the quadrats following the litter sampling procedures by Spain (1984). The litter was then brought to the laboratory and segregated into leaf, woody and miscellaneous (including flowers, fruits and other unidentified plant detritus) fractions. The segregated litter fractions were oven dried at 60°C to a constant weight and expressed as the litter accumulation or standing crop of litter.

Litterfall

Freshly fallen litter was collected from 10 randomly located 1 m × 1 m permanent quadrats at monthly interval to determine aboveground litter production from May 2015-April 2017. The litter present in each quadrat was collected and expressed as the dry mass per unit ground area over a period of one month (g m^{-2} $month^{-1}$). Annual production was expressed as the sum of all positive increments (g m^{-2} yr^{-1}) during each sampling period. The litter samples were brought to the laboratory and segregated into leaf, woody and miscellaneous fractions and oven dried at 60°C to a constant weight. Samples of each fraction of the litter were ground, homogenized and passed through a 0.2 mm mesh for determination of nitrogen (N) and phosphorus (P) contents according to the micro-Kjeldahl method (Allen et al., 1974). All chemical analyses were carried out in triplicate. The nutrient content (kg ha^{-1}) of each litter component was estimated by multiplying the mean concentrations of each mineral-element (g kg^{-1}) in each litter components with the mean mass of the respective litter component (kg ha^{-1}) for each site and expressed as the potential nutrient input.

Data analysis

The data for ecosystem functional attributes such as forest floor litter, total litterfall, and nutrient (N and P) accumulation through litter fall were measured on monthly basis and were pooled seasonally and presented fragment wise. The analysis considered two factors: fragment size (between subjects) and litter fractions (within subject) with four levels (autumn, winter, spring and rainy) spread across two years. Assumptions of ANOVA were met through test for normality of variables (Kolmogorov-Smirnov test), and homogeneity of group variances (Levene's test). The relationships of fragment size with vegetation characteristics and litter dynamics were analyzed using linear regression model. All statistical analysis was performed using the software SPSS, version 20.0.

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Results

Floristic composition, species richness and diversity

A total of 225 woody species belonging to 127 genera and 65 families were enumerated from all the studied fragments (*Table 1*). Species richness, density and basal area of woody (≥ 5 cm dbh) species varied along the fragment size gradient (*Table 1 and Figure 2*). The woody species richness in the fragments ranged from 50 species in VS1 to 78 in VL1 (*Table 1*) of which there were 77 species that did not re-occur in more than one forest fragment, whereas, two species namely *Helicia nilagirica* Bedd. and *Castanopsis tribuloides* (Sm.) DC. occurred in all the studied fragments. The dominant family was Lauraceae (27 species) followed by Rubiaceae (14 species), Rosaceae (13 species), Fagaceae (9 species) and Fabaceae (8 species). There were 29 families that were represented by one species and nine families by two species each.

Shannon-Wiener's diversity index (H') for woody species ranged from 3.09 to 3.72 across the studied forest fragments. Similarly, Simpson dominance index (D) ranged from 0.01 to 0.08. The corresponding Pielou's evenness index ranged from 0.22-0.87 across the studied forest fragments (*Table 1*).

The species richness of shrubs in the fragments showed a reverse trend to that of woody species and ranged from 33 species in VL1 to 52 in S1 (*Table 1 and Figure 2*). A total of 216 shrubs belonging to 92 genera and 65 families were enumerated from all the studied fragments. Among shrubs the dominant family included Rubiaceae, Lamiaceae, Asteraceae, Primulaceae, Ericaceae, Menispermaceae, Rosaceae, Symplocaceae and Urticaceae. Similarly, the species richness of herbs increased from 40 species in S1 to 58 in VL1 thus exhibiting similarity to woody species along the fragment size gradient (*Table 1 and Figure 2*) with a total of 232 herbs belonging to 169 genera and 74 families. The dominant family of herbaceous species in the studied fragments included Poaceae, Asteraceae, Rubiaceae, Polypodiaceae, Araceae, Orchidaceae, Piperaceae, Polygonaceae, Fabaceae and Rosaceae.

Stand density and basal area

The density of woody individuals in the fragments increased along the fragment size gradient and ranged from 560 individuals ha^{-1} in VS1 to 1220 individuals ha^{-1} in VL2 (*Table 1 and Figure 2*) with mean density of 758 individuals ha^{-1} in VS, 949 individuals ha^{-1} in S, 978 individuals ha^{-1} in M, 1107 individuals ha^{-1} in L and 1161 individuals ha^{-1} in VL fragment classes. In terms of density, the dominant species in VS1 was *Quercus kamroopii* whereas *Castanopsis tribuloides* was the dominant species in VS2 and VS3, S, M1, M2, L1 and VL2. The dominant species was *Syzygium cuneatum* in M3, *Castanopsis kurzii*, in L2, *Helicia nilagirica* in L3 and *Syzygium tetragonum* in VL1. The basal area increased along the fragment size gradient from 26.33 m^2 ha^{-1} in S3 to 59.3 m^2 ha^{-1} in VL2 (*Table 1 and Figure 2*). The mean basal area (m^2 ha^{-1}) was 37.92 m^2 ha^{-1} in VS, 28.9 m^2 ha^{-1} in S, 27.37 m^2 ha^{-1} in M, 40.48 m^2 ha^{-1} in L and 49.41 m^2 ha^{-1} in VL classes, respectively.

The shrubs and herbs density are shown in *Table 1*. While, the density of shrubs decreased along the fragment size gradient from 10280 individuals ha^{-1} in VS2 to 6464 individuals ha^{-1} in VL2 (*Table 1, Figure 2*), the density of herbs showed an increase from 226600 individuals ha^{-1} in VS1, to 250600 individuals ha^{-1} in VL2 fragment class (*Table 1 and Figure 2*).

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Table 1. *Vegetation characteristics in different fragment categories*

Habit	Parameters	Fragment category													
		Very Small			Small			Medium			Large			Very Large	
		VS1	VS2	VS3	S1	S2	S3	M1	M2	M3	L1	L2	L3	VL1	VL2
Woody species (≥ 5 cm dbh)	No. of genera	39	52	48	38	43	43	41	49	50	54	53	53	64	53
	No. of species	50	68	60	55	56	55	53	67	65	71	77	72	78	77
	Density (ha^{-1})	560	806	908	974	982	890	902	994	1038	1026	1076	1220	1161	1202
	Basal area (m^2 ha^{-1})	54.54	29.47	29.75	33.11	26.33	27.26	25	29.35	27.76	31.61	38.93	52.06	39.53	59.3
	Shannon-Wiener index	3.29	3.47	3.09	3.25	3.52	2.6	3.063	3.48	3.42	3.52	3.38	3.56	3.56	3.72
	Simpson dominance index	0.06	0.06	0.12	0.08	0.04	0.19	0.11	0.05	0.06	0.04	0.06	0.05	0.08	0.03
	Pielou's evenness index	0.84	0.82	0.75	0.81	0.87	0.64	0.77	0.82	0.83	0.82	0.78	0.83	0.87	0.87
	Disturbance index	55	36	32	31	22	30	41	46	47	18	47	21	13	22
Shrubs	No. of species	51	51	46	52	48	51	48	49	49	36	45	43	33	35
	Density (ha^{-1})	10264	10280	6560	10080	9144	8032	9496	8152	7544	6480	6568	6496	5144	6464
	Shannon Wiener Index	3.83	3.57	3.13	3.68	3.43	3.54	3.32	3.72	3.7	3.27	3.61	3.26	3.19	3.22
	Simpson dominance index	0.03	0.04	0.07	0.03	0.04	0.04	0.05	0.03	0.03	0.05	0.03	0.06	0.05	0.05
	Pielou's evenness index	0.97	0.91	0.82	0.93	0.89	0.9	0.86	0.95	0.95	0.91	0.95	0.87	0.91	0.91
Herbs	No. of species	46	54	47	40	44	47	50	53	57	49	55	44	58	54
	Density (ha^{-1})	226600	299600	199800	201600	252400	225000	200800	202000	254000	246200	211600	217800	203200	250600
	Shannon Wiener Index	3.66	3.44	3.34	3.31	3.42	3.49	3.51	3.72	3.79	3.55	3.77	3.33	3.75	3.45
	Simpson dominance index	0.03	0.05	0.05	0.05	0.04	0.04	0.04	0.03	0.03	0.04	0.03	0.05	0.03	0.05
	Pileou's evenness index	0.95	0.86	0.87	0.89	0.9	0.91	0.89	0.93	0.94	0.91	0.94	0.88	0.92	0.86

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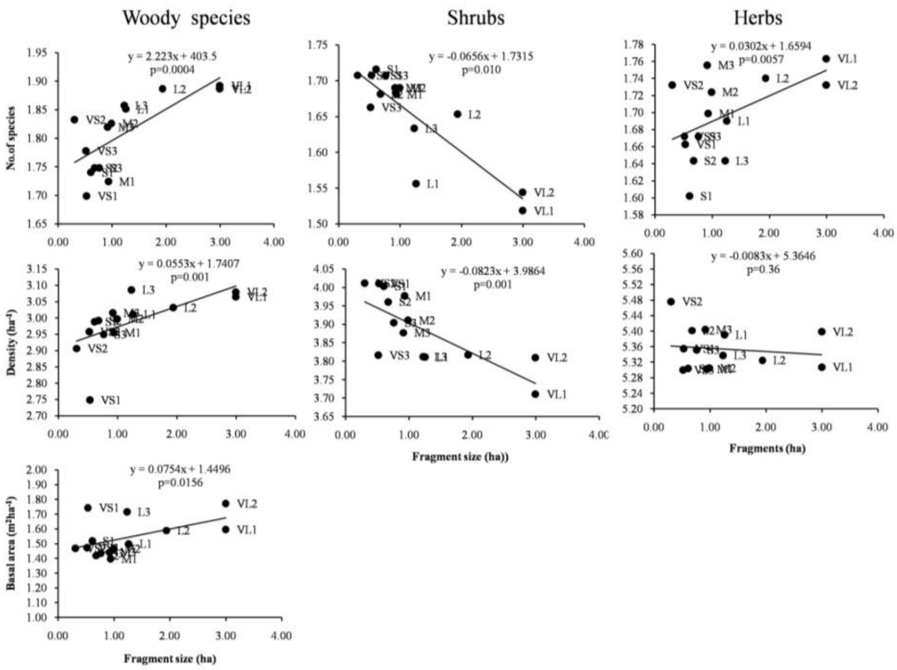

Figure 2. *Vegetation characteristics along a fragment size gradient*

Forest floor litter

The standing crop of litter on the forest floor showed an increasing trend along the fragment size gradient from 229 g m^{-2} in S1 to 371 g m^{-2} in L1 (371 g m^{-2}) (*Table 2*). The proportional fraction of the various litter fractions also varied in the forest fragments and leaf litter mass ranged from 152 to 192 g m^{-2}, while woody and miscellaneous fractions ranged from 61 to 95 g m^{-2} and 31 to 45 g m^{-2}, respectively (*Table 2*). Thus, leaf litter (49-66%) dominated the total litter accumulation across the fragments while the woody and miscellaneous fractions contributed to 21 to 30% and 12 to 16% of the total litter accumulation, respectively (*Table 2*). In terms of seasonality, the various fractions exhibited a more or less similar seasonal pattern with litter accumulation on the forest floor being maximum during winter (274-474 g m^{-2}) followed by spring (233-405 g m^{-2}), and rainy (203-342 g m^{-2}) and minimum during autumn (179-265 g m^{-2}).

Litterfall

The total litterfall varied significantly ($p<0.05$) across the fragments and months and ranged from 266 to 608 g m^{-2} with the highest mean litterfall recorded in VL (451.39 g m^{-2}) and L (418.70 g m^{-2}) fragments and lowest in VS (316.64 g m^{-2}) fragment classes (*Table 3, Figure 3*). Leaf litter constituted about 40 to 57% of total litterfall in all the forest fragments, while woody and miscellaneous fraction, mainly composed of reproductive parts, contributed 26 to 41% and 13 to 23% of the total litterfall, respectively (*Table 3*). A proportional increase of leaf and miscellaneous litter along the increasing fragment size was observed, whereas woody litter decreased proportionally with increasing fragment size (*Table 3, Figure 3*). Litterfall production showed strong seasonal variability with maximum litterfall occurring during the cold and dry period (winter to spring) and minimum during autumn (*Figure 4*). The leaf litter showed similar seasonal patterns to the total litterfall. The woody litterfall occurred mainly from the late dry season

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(March–May) to the beginning of rainy season (May–June) while the miscellaneous fraction peaked between September and November. The highest monthly litterfall contributed 45.2% of the total annual litterfall and the lowest monthly contribution was only 1.3%.

Table 2. *Mean dry weight (g m^{-2}) of different fractions of forest floor litter in the studied forest fragments*

Fragments	First year				Second year			
	Litter Fractions							
	Leaf	Woody	Miscellaneous	Total	Leaf	Woody	Miscellaneous	Total
VS1	187.80 (58.02)	84.37 (26.07)	51.52 (15.92)	323.69	183.81 (58.96)	78.56 (25.20)	49.41 (15.85)	311.78
VS2	149.61 (62.08)	52.49 (21.78)	38.88 (16.13)	240.98	148.52 (63.50)	48.59 (20.77)	36.79 (15.73)	233.90
VS3	180.63 (60.43)	72.26 (24.18)	46.00 (15.39)	298.89	158.95 (58.720	62.97 (23.26)	48.76 (18.01)	270.68
S1	148.27 (64.29)	53.69 (23.28)	28.66 (12.43)	230.62	149.14 (65.25)	51.84 (22.68)	27.57 (12.06)	228.55
S2	164.56 (59.92)	76.97 (28.03)	33.09 (12.05)	274.62	155.26 (60.77)	67.69 (26.50)	32.53 (12.73)	255.48
S3	147.41 (63.35)	55.53 (23.86)	29.75 (12.79)	232.69	145.67 (61.51)	59.23 (25.01)	31.94 (13.49)	236.84
M1	158.17 (63.39)	57.09 (22.88)	34.27 (13.73)	249.53	152.43 (65.67)	51.16 (22.04)	28.54 (12.29)	232.13
M2	187.80 (61.25)	82.53 (26.92)	36.26 (11.83)	306.59	170.84 (60.75)	73.48 (26.13)	36.89 (13.12)	281.21
M3	159.06 (60.76)	67.32 (25.71)	35.42 (13.53)	261.80	153.90 (59.90)	63.02 (24.53)	40.00 (15.57)	256.92
L1	182.97 (49.27)	99.29 (26.74)	89.07 (23.99)	371.33	160.80 (59.94)	75.98 (28.32)	31.48 (11.73)	268.26
L2	168.40 (61.04)	74.41 (26.97)	33.09 (11.99)	275.90	159.23 (62.96)	63.68 (25.18)	30.00 (11.86)	252.91
L3	187.80 (57.74)	99.29 (30.53)	38.15 (11.73)	325.24	179.95 (63.15)	68.75 (24.13)	36.24 (12.72)	284.94
VL1	180.76 (59.27)	85.41 (28.01)	38.79 (12.72)	304.96	186.63 (57.45)	98.19 (30.23)	40.01 (12.32)	324.83
VL2	199.69 (59.87)	91.26 (27.36)	42.58 (12.77)	333.53	202.37 (57.55)	105.38 (29.97)	43.90 (12.48)	351.65

Values in parentheses are percentages of total

Nutrient return through litterfall

Potential nutrient (N and P) return through the different litter fractions varied significantly ($p<0.05$) with the highest input through leaf (17.64 to 29.21 kg ha^{-1} for N and 0.86 to 1.31 kg ha^{-1} for P) followed by woody (7.10 to 16.38 kg ha^{-1} N and 0.39 to 0.77 kg ha^{-1} P) and miscellaneous (3.94 to 8.65 kg ha^{-1} N and 0.18 to 0.32 kg ha^{-1} P) litter (*Table 4*). The highest potential N return occurred through leaf litter (55% for M to 61% of the total for VS) followed by the woody fractions that had higher N returns in M, L and VL. The potential P return from the different fraction of litterfall in the studied fragments followed a pattern similar to N return with maximum input from the leaf (55-59%), followed by the woody (28-32%) and miscellaneous (13-14%) fractions. Although, leaf litter fraction had the highest input of N and P across the forests fragments, however, the comparative contributory nutrient return through leaf litter to the total nutrient return exhibited a declining trend along the fragment size gradient, whereas nutrient return through woody litter showed an upward increase (*Table 4*).

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Table 3. *Annual litter fall (g m^{-2}) in the studied forest fragments*

Fragments	First year				Second year			
	Litter Fractions							
	Leaf	Woody	Miscellaneous	Total	Leaf	Woody	Miscellaneous	Total
VS1	169.00 (56.51)	90.30 (30.19)	39.76 (13.30)	299.06	170.89 (45.45)	155.98 (41.48)	49.16 (13.07)	376.02
VS2	150.80 (56.76)	69.61 (26.20)	45.27 (17.04)	265.68	158.34 (48.06)	124.08 (37.66)	47.02 (14.27)	329.44
VS3	150.34 (46.94)	117.71 (36.76)	52.20 (16.30)	320.25	150.36 (48.60)	111.84 (36.15)	47.19 (15.25)	309.39
S1	170.56 (44.51)	155.19 (40.50)	57.46 (15.00)	383.21	146.08 (39.83)	137.17 (37.40)	83.50 (22.77)	366.76
S2	211.19 (49.91)	150.8 (35.63)	61.19 (14.46)	423.19	204.95 (46.26)	171.51 (38.71)	66.59 (15.03)	443.06
S3	157.3 (47.70)	123.39 (37.42)	49.05 (14.880	329.75	154.21 (40.55)	149.16 (39.22)	76.96 (20.24)	380.32
M1	177.36 (47.06)	139.3 (36.96)	60.19 (15.97)	376.86	148.26 (44.52)	129.50 (38.89)	55.24 (16.59)	332.99
M2	188.07 (53.16)	112.83 (31.89)	52.91 (14.95)	353.81	138.82 (51.54)	94.03 (34.91)	36.50 (13.55)	269.34
M3	190.04 (49.45)	137.60 (35.81)	56.66 (14.74)	384.31	226.72 (47.87)	169.83 (35.86)	77.04 (16.27)	473.59
L1	149.31 (51.75)	93.38 (32.37)	45.82 (15.88)	288.51	170.95 (52.73)	83.60 (25.79)	69.63 (21.48)	324.18
L2	190.04 (49.45)	137.6 (35.81)	56.66 (14.74)	384.31	188.07 (53.16)	112.83 (31.89)	52.91 (14.95)	353.81
L3	274.51 (49.59)	193.51 (34.96)	85.56 (15.46)	553.59	308.18 (50.70)	212.32 (34.93)	87.32 (14.37)	607.82
VL1	202.83 (48.49)	119.73 (28.62)	95.77 (22.89)	418.33	236.65 (49.86)	140.38 (29.58)	97.61 (20.56)	474.65
VL2	224.48 (54.05)	127.73 (30.75)	63.13 (15.20)	415.34	247.78 (49.83)	159.47 (32.07)	89.98 (18.10)	497.23

Values in parentheses are percentages of total

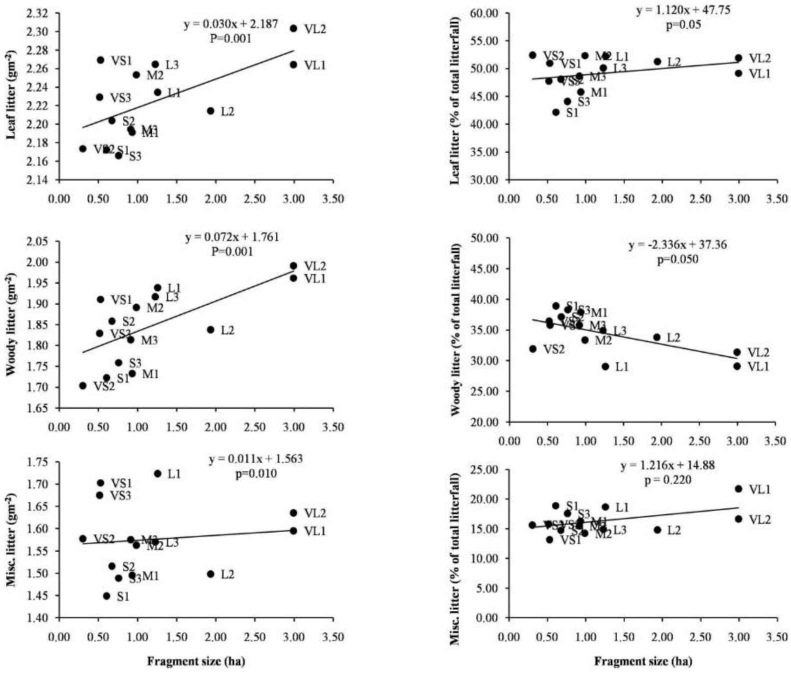

Figure 3. *Effect of fragment size on litterfall and the percentage variation of the litter fractions (% of total litterfall) along a fragment size gradient*

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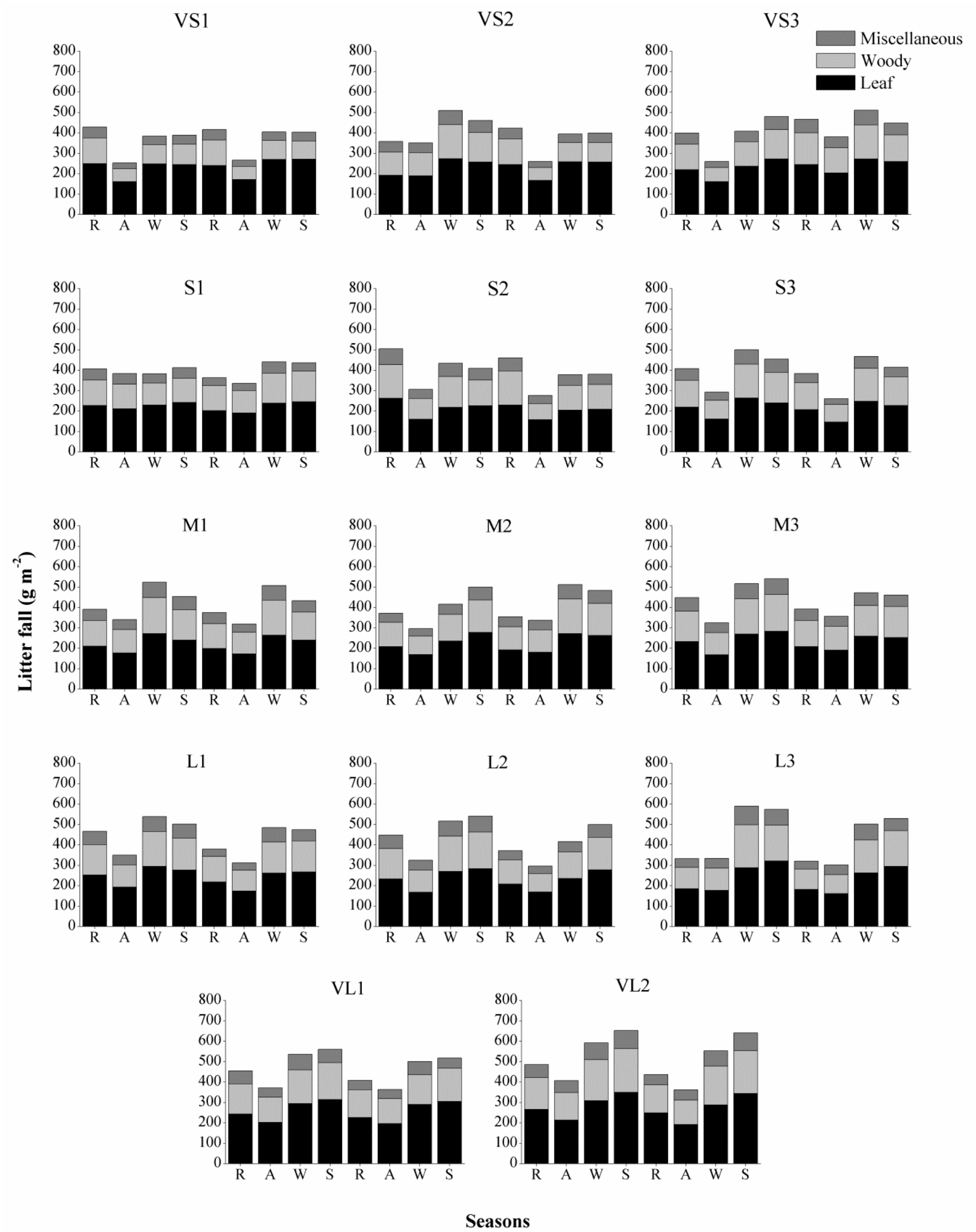

Figure 4. *Seasonal variation in litterfall (g m^{-2}) across the various forest fragments (R: Rainy; A: Autumn; W: Winter; S: Spring)*

Relationship of litter with vegetation characteristics

The relationship of litterfall dynamics with vegetation characteristics showed that leaf and woody litter fractions of litterfall exhibited positive correlation with stand density and basal area of woody species and were proportionally higher in fragments with high density and basal area (*Table 5*) thus explaining the comparable litterfall values of VS3, S1, S2, S3, M1, M2 and L1 (*Table 5*).

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Table 4. *Annual input (kg ha^{-1}) of N and P through different fractions of litter in the studied forest fragments*

Fragments	Nitrogen				Phosphorus			
	Leaf	**Woody**	**Miscellaneous**	**Total**	**Leaf**	**Woody**	**Miscellaneous**	**Total**
VS1	21.55 (65.51)	7.35 (22.34)	4.00 (12.14)	32.90	1.06 (63.94)	0.41 (24.55)	0.19 (11.52)	1.65
VS2	20.54 (59.76)	8.74 (25.43)	5.09 (14.81)	34.37	0.99 (58.46)	0.48 (28.49)	0.22 (13.06)	1.69
VS3	20.87 (56.74)	10.24 (27.84)	5.68 (15.43)	36.79	0.99 (55.34)	0.55 (30.62)	0.25 (14.04)	1.78
S1	20.45 (60.37)	8.65 (25.52)	4.78 (14.11)	33.88	0.98 (56.03)	0.56 (32.18)	0.21 (11.78)	1.74
S2	18.40 (56.99)	8.69 (26.92)	5.20 (16.09)	32.29	0.90 (54.22)	0.52 (31.33)	0.24 (14.46)	1.66
S3	19.23 (57.21)	9.26 (27.54)	5.13 (15.25)	33.61	0.91 (54.49)	0.54 (32.04)	0.23 (13.47)	1.67
M1	20.29 (55.41)	10.16 (27.75)	6.17 (16.84)	36.61	0.99 (55.00)	0.56 (31.11)	0.25 (13.89)	1.80
M2	20.31 (56.45)	10.56 (29.34)	5.11 (14.21)	35.97	1.01 (57.59)	0.52 (29.80)	0.22 (12.61)	1.75
M3	21.02 (53.94)	11.82 (30.34)	6.13 (15.72)	38.96	1.07 (55.76)	0.59 (30.63)	0.26 (13.61)	1.91
L1	22.75 (57.57)	10.77 (27.25)	6.00 (15.19)	39.51	1.06 (56.99)	0.56 (29.84)	0.25 (13.17)	1.86
L2	21.71 (56.53)	11.05 (28.77)	5.65 (14.70)	38.40	1.01 (55.83)	0.56 (30.83)	0.24 (13.33)	1.80
L3	22.79 (55.34)	11.44 (27.77)	6.96 (16.89)	41.18	1.03 (55.38)	0.56 (29.84)	0.28 (14.78)	1.86
VL1	26.13 (58.28)	12.21 (27.23)	6.50 (14.49)	44.84	1.17 (56.66)	0.64 (30.99)	0.26 (12.35)	2.07
VL2	28.17 (56.31)	14.26 (28.51)	7.59 (15.18)	50.02	1.25 (54.59)	0.74 (32.10)	0.31 (13.32)	2.29

Values in parentheses are percentages of total

Table 5. *Relationship of vegetation characteristics and litterfall with fragment size (ha) and the influence of density (individuals ha^{-1}) and basal area (m^2 ha^{-1}) of woody individuals on litterfall dynamics in the studied forest fragments*

Parameters	Regression equation	r	P
Relationship with fragment size			
Woody species richness	y = 2.223x + 403.5	0.726	0.0004
Woody stand density	y = 0.055x + 1.740	0.619	<0.001
Woody basal area	y = 0.075x + 1.449	0.525	0.016
Shrub species richness	y = -0.066x + 1.731	-0.863	0.011
Shrub stand density	y = -0.082x + 3.986	-0.752	<0.001
Herbaceous species richness	y = 0.030x + 1.659	0.528	0.006
Herbaceous stand density	y = -0.008x + 5.365	-0.121	<0.001
Leaf litterfall	y = 0.030x + 2.187	0.607	<0.001
Woody litterfall	y = 0.072x + 1.761	0.669	<0.001
Miscellaneous litterfall	y = 0.011x + 1.563	0.126	0.01084
Relationship with density			
Leaf litterfall	y = 0.605x + 0.456	0.170	0.574
Woody litterfall	y = 0.383x + 0.968	0.322	0.224
Miscellaneous litterfall	y = 0.869x - 0.808	-0.226	0.0161
Relationship with basal area			
Leaf litterfall	y = 0.401x + 1.647	0.784	0.0482
Woody litterfall	y = 0.208x + 1.793	0.656	0.187
Miscellaneous litterfall	y = 0.255x + 1.393	0.386	0.896

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Discussion

The effect of fragmentation on plant diversity was realized by a structural and compositional change in floristic diversity, species richness as well as density of woody species along a fragment size gradient. The high species richness, and density of woody species in larger fragments was attributed to low disturbances, habitat suitability and favorable growth conditions (Mir and Upadhaya, 2017) whereas, low species richness, basal area and tree density in very small and small fragment categories may be attributed to repeated human disturbances such as small timber and NTFPs extraction. Extraction of timber has been known to be a contributing factor to fragment degradation in many tropical and subtropical forest (Ochoa-Gaono et al., 2004; Cayuela et al., 2006; Echeverría et al., 2007; Santos et al., 2007; Lin and Cao, 2009; Majumdar et al., 2014; Pao and Upadhaya, 2017).

Disturbance provides high light accessibility that plays a key factor for the understory plant species to flourish (Tuomisto et al., 2003) in forest gaps (Sonnier et al., 2014). This was proven to be true in the present study as species richness of shrubs in the fragments showed a reverse trend to that of woody species with high species richness and density in the smaller fragments as compared to larger ones due to canopy openness, adequate light and favorable environmental conditions (Laurance and Vasconcelos, 2009). The species richness of herbs however, increased along the fragments size gradient, exhibiting similarity to woody species richness and corroborating the findings that fragments with larger core areas favour herbaceous species in comparison to shrubs, suggesting the importance of maintaining large core areas to conserve herbaceous forest specialist (Hofmeister et al., 2013).

The range (50 to 78) of woody species (≥5 cm dbh) richness recorded in the present study was higher than tropical dry forest of Puerto Rico (30 to 35 species, Murphy and Lugo, 1986), moist deciduous forest of Western Ghats (24–26 species, Valappil and Swarupanandan, 1996) and fragmented moist deciduous forest of West Tripura (31 to 61 species in eleven sites, Majumdar et al., 2014). Shannon-Wiener’s diversity index (H') for woody species in the present study (3.09 to 3.72) was within the range for Indian forests (0.83 to 4.1, Parthasarathy et al., 1992).

The low density of woody species in smaller fragments could be attributed to disturbance. The stand density of woody species (≥5 cm dbh) recorded in the present study (560 to 1220 individuals ha^{-1}) is within the reported estimates from subtropical forests of Khasi Hills (1109 individuals ha^{-1}, Upadhaya, 2015) of Meghalaya, tropical rainforest forests of Congo Basin (144 to 868 individuals ha^{-1}, Ifo et al., 2016), evergreen forests of Thailand (602 to 992 individuals ha^{-1}, Lamotte et al., 1998) as well as fragmented moist deciduous forest ecosystems of northeast India (428 to 884 ha^{-1}, Majumdar et al., 2014).

The high basal area in larger fragments and in VS1 was due to the presence of bigger trees, while the reduction of basal area in smaller fragments was due to the removal of bigger trees. Such an increase in basal area with increasing fragment size has also been observed from other subtropical forest of the region (Tripathi et al., 2010; Pao and Upadhaya, 2017) and tropical rainforest of Western Ghats (Bhat et al., 2000). The stand basal area recorded in the present study (25.00 to 59.3 m^2 ha^1) is close to the reported estimates from other subtropical forests of Jaintia Hills (36.52−77.44 m^2 ha^{-1}, Upadhaya et al., 2003), and Khasi hills (30 to 38 m^2 ha^{-1}, Upadhaya, 2015) in Meghalaya, Ishigaki and Okinawa Island Japan (42 to 43 m^2 ha^{-1}, Feroz et al., 2015) and tropical forests of Myanmar (22.93−47.83 m^2 ha^{-1}, Aye et al., 2014). The differences in the basal area of

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woody species (≥5 cm dbh) among the forest fragments may be attributed to the differences in species composition, the age of trees, the extent of disturbances and successional stages of the stands (Naidu and Kumar, 2016).

The intensity of anthropogenic disturbances through extraction and edge creation greatly influenced species dominance in the studied fragmented forests that may have future repercussions on the structure and composition, succession phases, and species restoration of these forests. Fragmentation may establish several transitional community associations which are mostly dominated by few local adaptable species through direct or indirect competitions as observed in the present study wherein the larger patches were characterized by nemoral species. The smaller patches were dominated by shrubs indicating the susceptibility of smaller fragments to external disturbances (Pao and Upadhaya, 2017). They were also prone to a larger number of gaps that would eventually affect tree regeneration and recruitment (Lovejoy et al., 1986; Turner and Corlett, 1996; Laurance et al., 1998).

The litter accumulation on the forest floor showed an increase along the fragment size gradient (229 g m^{-2} in S1 to 371g m^{-2} in L1) and was within the reported estimates (217 to 2255 g m^{-2}) for tropical-broadleaf semideciduous, -broadleaf deciduous and -broadleaf evergreen forests worldwide (Vogt et al., 1986). The values of forest floor litter were close to the reported estimates of tropical rainforests (550 g m^{-2}, Morellato, 1992) but lower than the litter standing crop in a secondary lowland rain forest in Nigeria (830 to 940 g m^{-2}, Odiwe and Muoghalu, 2003), sub-humid tropical Nigeria (690 – 1170 g m^{-2}, Swift et al., 1981) and three tropical Australian rain forests (250 – 1050 g m^{-2}, Spain, 1984).

Litterfall rates vary to a great extent among different forest fragments. The annual litterfall obtained in the present study (266–608 g $m^{-2}yr^{-1}$) were within the range (300-1100 g $m^{-2}yr^{-1}$) recorded from different forest types (Vogt et al., 1986; Cuevas and Lugo, 1998; Lian and Zhang, 1998; Sundarapandian and Swamy, 1999; Alhamd and Hagihara, 2004; Zhang et al., 2014; Zhou et al., 2016). However, the values were lower than those recorded from tropical forests (550–1200 g $m^{-2}yr^{-1}$; Vitousek and Sanford, 1986), montane rain forests (700–760 g $m^{-2}yr^{-1}$; Edwards, 1982; Vitousek et al., 1995) and tropical lowland forests (750 to 1530g $m^{-2}yr^{-1}$; Bray and Gorham, 1964; Vitousek, 1984; Proctor, 1987). The high litter fall in VS1 and VS3 can be attributed to the comparable stand density and basal area to L3 and medium (M) fragments respectively, thus, suggesting litter production in forest ecosystems as a function of species composition, stand structure, age, quality as well as climatic factors (Haase, 1999; Sundarapandian and Swamy, 1999; Norgrove and Hauser, 2000; Yang et al., 2004). The variation in litter production among stands within the same climate range has been mainly attributed to species composition (Sundarapandian and Swamy, 1999) and an increase in litter production may also be explained by the competitive production principle (Kelty, 2006) according to which an admixture of species that have substantially different characteristics such as foliar phenology, shade tolerance, crown structure and root depth and phenology may use site resources more efficiently in producing materials, resulting in greater biomass than as they would in monocultures of the component species (Binkley et al., 1992). The high spatial heterogeneity in litterfall in fragments of >80ha could be attributed to the variation in the biotic and abiotic conditions within each fragment as smaller fragments were less heterogeneous, likely due to edge effects and microclimatic conditions (such as wind and temperature) when compared with larger fragments (Laurance, 2004).

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The contribution of leaf litter (40 to 57%) to the total litterfall in the present study ranges within the recorded estimates of leaf litter fraction for most subtropical evergreen forests (50 to 80%, Tu et al., 1993; Lian and Zhang, 1998; Lin et al., 1999) as well as tropical forests in China (56 to 61%, Tang et al., 2010) and subtropical broad-leaved forests in Japan (52.6 to 58.4%, Alhamd and Hagihara, 2004). The relatively higher proportion of leaves in the litter fall has been extensively reported from many forest ecosystems (Figueiredo-Filho et al., 2003; Pinto et al., 2008) and is attributed to the fact that, in addition to being the physiologically active organs responsible for photosynthesis (Epstein and Bloom, 2006), leaves are also responsible for the transfer of carbon and nutrients to forest soils, thus causative, to maintain and even enrich their fertility.

The seasonal patterns of leaf, woody and miscellaneous fractions of litterfall showed unanimity to the total litterfall with peak observed during March and minimum values recorded during September that was in conjunction with reports from subtropical evergreen forest of China wherein old leaves of most species were generally replaced by new leaves in spring as well as tropical forests where litter peaks occurred mostly in spring or winter, corresponding to the drought season (Zhang et al., 2014). This seasonal attribute of peaks observed in litterfall in spring, summer and autumn have been measured in tropical climates (Singh et al., 1989; Sundarapandian and Swamy, 1999) and may be associated with physiological leaf senescence (Liang, 1994; Lin et al., 1999; Yang et al., 2004).

Mean annual potential returns of N through litterfall in the studied fragments (32.3-50.02 kg ha^{-1}) were close to the reported estimates from subtropical broadleaved forests (36–128 kg ha^{-1}, Deng et al., 1993; Weng et al., 1993; Zheng et al., 1995; Lin et al., 1999; Yang et al., 2004) as well as pure Chinese fir plantations in Tianlin (39 kg ha^{-1}, Liang, 1994) and Huitong (37 kg ha^{-1}, Tian and Zhao, 1989) in China. The potential returns of P through litterfall (1.65 – 2.29 kg ha^{-1}) were also close to the reported estimates from subtropical rain forest in Hexi (3.8 kg ha^{-1}, Zheng et al., 1995) in China as well as a primary *Lithocarpus xylocarpus* forest in Ailao mountain (1.7 kg ha^{-1}, Deng et al., 1993) and an old-growth evergreen broadleaved forest in Dinghu mountain (5.9 kg ha^{-1}, Weng et al., 1993). However, the values were lower than the range (2.4 – 6.6 kg ha^{-1}, Yang et al., 2004) reported from four plantations compared with a natural subtropical forest in Sanming, Fujian, China. N and P are the major limiting nutrients for tree growth in many subtropical forests because of high soil acidity; hence the relatively high return of N and P through litterfall makes the broadleaved species more advantageous over conifers in nutrient supply, especially in the surface soil horizons (Yang et al., 1993)

Conclusion

Understanding the patterns of species occurrence and ecosystem processes has proven to be challenging because of the idiosyncratic responses of species to habitat fragmentation. Forest fragmentation reduces the ability of the remnant forests to maintain their original biodiversity and ecological processes (Echeverría et al., 2007). In the present study, the variation in species composition in remnant fragments can be attributed to the interaction of fragmentation and human disturbances such as timber and fuel wood extraction as well as NTFP collection (Debinski and Holt, 2000; Cochrane and Laurance, 2002; Santos et al., 2007; Pao and Upadhaya, 2017). The proximity to human settlements has aided the extraction of species for fuel wood and timbers resulting in thinning of forests and fragmentation of the patches (Kumar et al., 2008; Upadhaya et al., 2014) and

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thus impose a serious threat to the biodiversity of the area. The presence of nemoral species in the larger patches and, smaller patches being characterized by shrubs species indicated the susceptibility of smaller fragments to external disturbances (Pao and Upadhaya, 2017). Nutrients are often limiting resources, and so facilitated nutrient cycling of dead organic material is essential for continued forest productivity. However, nutrient cycling studies should also consider other vital aspects such as decomposition rate of litters, microbial mediated processes involved in the conversion of organic nutrients into available forms (Pao and Upadhaya, 2019) and its subsequent uptake through roots in detailed to understand the overall effect of fragmentation on structure and function of subtropical broadleaved forest ecosystems. Nevertheless, the findings of the present study demonstrated that fragmentation of forests mediate an urgent need for conservation and restoration measures to improve landscape connectivity, which will reduce extinction rates and help maintain ecosystem- functions and -services.

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Author contribution. KU conceived the idea, KU and KS designed the experimental layout, HSAB, AHM and GC carried out field and laboratory experiment and all authors contributed equally for the analyses of data and manuscript preparation.

Declaration of competing interests. 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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