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ORIGINAL PAPER

Effects of *Broussonetia papyrifera* invasion and land use on vegetation characteristics in a tropical forest of Ghana

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Abstract The purpose of this study was to evaluate the effects of *Broussonetia papyrifera* (paper mulberry) invasion and land use on the floristic composition of a dry semi-deciduous forest in Ghana. Forty-five plots (25 m × 25 m each), distributed among three land uses—selectively logged (SL); abandoned farmlands (AF); and an undisturbed reference (RF)—were surveyed. Results showed lower tree species richness (*S*), diversity (*H′*), evenness (*S*) and basal area (*BA*) in the SL (46, 0.78, 0.32 and 269.12 m^2 ha^{-1}, respectively) and AF (40, 0.53, 0.45, and 131.16 m^2 ha^{-1}) sites compared to the RF site (79, 2.66, 0.87, 963.72 m^2 ha^{-1}). Similar patterns were found at the shrub layer, but no differences were observed at the herb layer. Non-metric multidimensional scaling ordination revealed distinct species composition among the land uses. The two disturbed habitats, SL and AF, were associated with increased *B. papyrifera* invasion particularly in the overstory, with importance value index and mean relative density of 45 and 65.03%, and 42 and 53.29%, correspondingly. However, the species was only sparsely represented in the RF site. Tree density of *B. papyrifera* correlated negatively with *H′*, *S*, *E*, *BA*, and native tree density and richness. These findings highlight the strong link between human land use (i.e., logging and slash-and-burn farming), invasion, and vegetation characteristics, and suggest the need to limit these disturbances to conserve biodiversity within tropical forest ecosystems.

Keywords Afram Headwaters Forest Reserve · *Broussonetia papyrifera* · Forest community characteristics · Human-caused disturbances · Plant invasion

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Introduction

Alien plant species invasion is increasing globally, creating severe economic and ecological problems (Davis et al. 2000; Pimentel et al. 2000). Invasive alien plant species (IAPS) affect virtually all ecosystems, and constitute a pervasive agent of global environmental change (Mack et al. 2000; Sala et al. 2000; Simberloff et al. 2013; Franklin et al. 2016). Recognition of this effect has stimulated numerous studies to elucidate the ecology, impacts and mechanisms of spread of invasive species in native ecosystems. Understanding the spread and impacts of invasive plants species on native ecosystems is of particular interest to ecologists worldwide as they play a key role in community dynamics and function (Barney et al. 2013). However, empirical quantitative studies on these factors, particularly in tropical ecosystems, have been limited due to lack of understanding of the many confounding factors, including the influence of human land use.

Land use by humans represents a novel, broad-scale disturbance that strongly influences forest composition and structure (Brent et al. 2010; Caño et al. 2007; Foster et al. 1998; Perrings et al. 2002; Uriarte et al. 2009). Human land-use disturbances such as logging and agriculture often elicit new biotic responses and disrupt existing biotic-environmental relationships (Foster et al. 1998). Through these, and other mechanisms such as destruction of species interactions, increase in colonizing opportunity, reduction in competitive ability of native species and alteration of resource availability, land-use disturbances can tremendously increase the susceptibility of natural ecosystems to invasion (Davis et al. 2000; Hobbs and Huenneke 1992; Mack et al. 2000). Canopy disturbances, for example, create gaps that directly support exotic species invasion through the creation of "empty niches", and indirectly through their effects on light availability, water availability and forest fires, among other factors (Brent et al. 2010; Caño et al. 2007).

In many tropical forest ecosystems, intensive human land-use disturbances, including farming and logging, have become widespread because of increasing population size and heavy dependence on natural resources (Addo-Fordjour et al. 2009; Anning and Yeboah-Gyan 2007). These disturbances vary both in nature and effects, and constitute perhaps the most pressing environmental issue in these areas (Uriarte et al. 2009). As a consequence, human-mediated disturbances have become a key determinant of ecosystem invasibility and their associated impacts (Catford et al. 2012a).

Invasive plant species alter ecosystem properties, including species composition, nutrient cycling, and productivity, and ultimately threaten biodiversity conservation in complex ways (Catford et al. 2012a; Mack et al. 2000; Pimentel et al. 2000; Vila et al. 2011). The proliferation of invasive species can also derail efforts to maintain productive agrosystems, sustain functioning ecosystems, and protect human health (Mack et al. 2000). However, as noted by Chisholm (2009), the spread and impact of these species could merely be a secondary outcome of disturbance. Turner et al. (2003) further argued that the spread of IAPS can be considered a distinct type of disturbance that could become a continuous stress on the environment. Understanding the ecological impacts of plant invasion in relation to human-caused disturbance is vital for forest managers and ecologists interested in preventing, controlling, and eradicating this problem, and in conserving biodiversity (Catford et al. 2012a).

In this study, we evaluate the effects of *Broussonetia papyrifera* (L.) L'Hér. ex Vent. (paper mulberry; family Moraceae) invasion as a legacy of two common land uses (selective logging and farming) on the floristic composition of a dry semi-deciduous tropical rainforest in Ghana. This plant invader, native to Taiwan and Japan, was deliberately introduced into Ghana in 1969 by the Forestry Research Institute of Ghana (FORIG) to evaluate its potential for industrial cellulose, pulp, and paper. Indigenous people have also cultivated the plant for firewood, fodder, charcoal, and soil stabilization (Bosu et al. 2009).

However, after almost 25-year lag period, *B. papyrifera* is reported to be rapidly invading many forest ecosystems in the country (Addo-Fordjour et al. 2009; Apetorgbor and Bosu 2011; Bosu et al. 2013). Some researchers have attributed this fast expansion to increasing forest disturbances by humans (Bosu et al. 2013) and the ability of the species to tolerate different environments and climates (Whistler and Elevich 2006). Notwithstanding this spread, the impact of paper mulberry on vegetation characteristics in Ghana is scarcely studied. Bosu et al. (2013) found comparable species composition between invaded and uninvaded forest stands, although this study did not consider the confounding effect of the local land-use disturbance regime. We hypothesized that: (1) plant composition would vary among land uses, with greater species diversity at the reference site compared to the selectively logged site and abandoned farmlands; and (2) increased level of *B. papyrifera* invasion would adversely affect the diversity of species in the forest reserve.

Materials and methods

Site description

The study was conducted in the Afram Headwaters Forest Reserve (AHFR) (Fig. 1), located within the dry semi-deciduous forest zone (DSFZ) of Ghana in the Offinso District of Ashanti Region (Latitude: 6°45′ and 7°25′N, and Longitude: 1°32′ and 1°48′W). The reserve covers an area of 201.2 km^2 (Hall and Swaine 1981). Altitude ranges from 300 to 410 m above sea level. Rainfall is bimodal with the major season between April and July, and the minor season from September to November. Mean annual rainfall is 1250–1500 mm, annual average relative humidity is 80% and average daily minimum and maximum temperatures are 22 and 30 °C, respectively (Dwomoh 2009). The AHFR was established in 1928 (Hall and Swaine 1981) purposely for conservation and forest farming, and to provide timber for export as well as to protect some river bodies. However, the forest reserve has been under heavy encroachment with most of the landscape severely degraded (Bosu et al. 2013). The present vegetation cover is

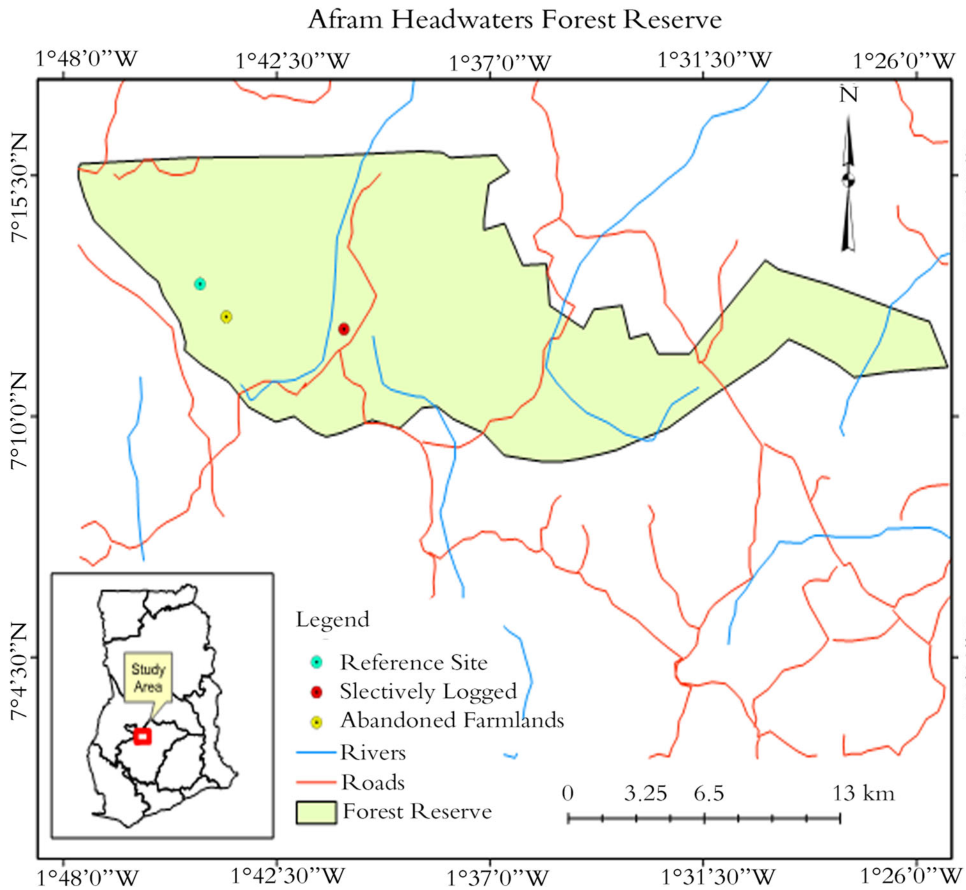

Fig. 1 Location of the study sites (reference, selectively logged and abandoned farmland) within the Afram Headwaters Forest Reserve

made of fragments of the original forest, degraded areas, plantation farms, and agro-forests (Dwomoh 2009).

Vegetation sampling

Vegetation analyses were carried out in three stands representing three different land uses in the AHFR: selectively logged (SL), abandoned farmlands (AF), and a relatively undisturbed stand (reference, RF). The SL forest included areas that had been disturbed through selective logging by illegal chainsaw operators as well as licensed contractors. The AF comprised abandoned farmlands where farming activities had taken place in the past (between 5 and 30 years), but these lands have since been allowed to regenerate naturally. The reference stand had at least not been disturbed in the last 50 years and had previously been used as reference stand by researchers from the Forestry Research Institute of Ghana (FORIG) of the Council for Scientific and Industrial Research (CSIR).

Fifteen plots, each measuring 25 m × 25 m, were randomly demarcated within each of the three land uses for vegetation sampling. The plots were demarcated using a 100-m tape measure and the edges marked with pegs and flags. The coordinates of these plots were recorded using a Global Positioning System (GPS) and transferred onto a map in a Geographic Information System (GIS) environment. The plots were systematically surveyed to identify all trees and to determine their densities. The diameters of all trees (diameter at breast height, DBH $\geq$ 10 cm) were measured, using a diameter tape. Similarly, densities of shrubs (DBH $<$ 10 cm; height $\geq$ 1.5 m) were determined in two 5 m × 5 m plots whilst herbs, shrubs, and seedlings (height $<$ 1.5 m) were enumerated in two 1 m × 1 m nested plots. Species identification was done with the help of a plant taxonomist, and the nomenclature followed The Plant List (Version 1.1 2013). Sampling was done between November 2015 and April 2016.

Data analysis

The relative density and frequency values were computed for all species. In addition, the relative basal areas of all trees were determined from their respective diameter measurements (Avery and Burkhart 2002). The Cottam and Curtis Importance Value Index (IVI), which measures the relative importance of species (van Andel 2003), was computed for all trees as the sum of three vegetation attributes: relative density, relative frequency, and relative

Table 1 Summary of floristic characteristics of the studied forests in the Afram Headwaters Forest Reserve

Attribute	Reference site	Selectively logged	Abandoned farmland	*p* value
Combined	–	–	–	–
Number of individuals	1683	1041	1180	–
Number of species	137	100	93	–
Number of families	37	26	30	–
Tree layer	–	–	–	–
Number of individuals	713	408	234	–
Number of species	79	46	40	–
Number of families	28	18	16	–
Mean Shannon diversity	2.66[a]	0.78[b]	0.53[b]	< 0.001
Mean evenness	0.87[a]	0.32[b]	0.45[b]	0.009
Mean basal area (m^2 ha_{-1})	64.25[a]	17.94[b]	8.74[b]	< 0.001
Shrub layer	–	–	–	–
Number of individuals	584	383	478	–
Number of species	84	61	50	–
Number of families	25	20	15	–
Mean Shannon diversity	2.21[a]	2.31[a]	1.73[b]	< 0.001
Mean evenness	0.81[a]	0.90[b]	0.78[a]	< 0.001
Herb layer	–	–	–	–
Number of individuals	386	250	468	–
Number of species	43	46	51	–
Number of families	16	20	23	–
Mean Shannon diversity	1.85[a]	1.87[a]	1.83[a]	0.920
Mean evenness	0.86[a]	0.87[a]	0.85[a]	0.568

Different letter superscripts indicate significant differences among means at 5% significant level. Measures of dispersion are standard errors of the means

dominance. The IVI for each species was divided by the sum of IVIs for all species to obtain the relative IVI. The Shannon diversity index (H') and evenness (E) (Begon et al. 2006) were also calculated for the tree species in each plot.

Analysis of variance (ANOVA) was used to evaluate differences in the means of the diversity measures (Shannon diversity index and evenness), and basal area of trees among the three land uses. Post-hoc multiple comparison tests (Tukey's honestly significant difference—HSD) were performed to tease out the differences among studied forest stands. The non-metric multidimensional scaling (NMDS) ordination technique was used to explore and visualize the ecological distances among these forests based on species occurrences (i.e., presence or absence). The NMDS analysis was implemented using the metaMDS function in the R-package "vegan" (Oksanen et al. 2015). The stressplot was used to check the degree of fit between the ordination distance and the observed dissimilarity. In addition, the Pearson's product-moment correlation analysis was used to explore the relationship between the level of *B. papyrifera* invasion (i.e., the proportion of *B. papyrifera* stems in each plot) and the diversity indices (i.e., richness, Shannon diversity index, evenness, basal area, native species density, and richness). All analyses were done using the R software (R Core Team 2016) and at 5% significance level.

Results

Effects of land-use type on floristic composition of the AHFR

Overall, 216 plant species from 159 genera and 52 families were identified within the Afram Headwaters Forest Reserve (AHFR, Appendix S1). Leguminosae, Malvaceae, Apocynaceae, Meliaceae, and Rubiaceae with 32, 16, 15, 15, and 13 species, correspondingly, emerged as the most dominant plant families across the AHFR. Other important families encountered in the forest reserve included Euphorbiaceae (10 species), Sapindaceae (9), Sapotaceae (8), Moraceae (8) and Ebenaceae (7). Nineteen families had between two and five species, whereas the remaining 23 families recorded one species each. Trees were the dominant growth form encountered in the study area, accounting for 71% of species sampled, followed by herbs (12%), climbers/lianas (9%) and shrubs or saplings (6%).

Land use had a strong negative effect on the species composition in the reserve as indicated by the considerable differences among the RF, SL, and AF stands in many of the floristic attributes measured (Table 1). The list comprised a total of 1683 individuals belonging to 137 species and 37 families from the RF site, with corresponding numbers of 1041, 100, and 26 for the SL and 1180, 93, and 30 for the AF sites. Analysis of the data by growth form further revealed much lower tree species richness (*S*), mean diversity (H') and mean evenness (*E*) at the AF (40, 0.53, 0.45, respectively) and SL (46, 0.78, 0.32) stands compared to the RF site (79, 2.66 and 0.87).

Fewer individual trees and tree families were also recorded at the disturbed sites than the undisturbed RF site. Similarly, mean basal area was markedly lower ($p < 0.05$) for the AF (8.74 m^2 ha^{-1}) and SL (17.94 m^2 ha^{-1}) sites than the RF (64.25 m^2 ha^{-1}). With respect to shrubs, considerably lower number of individuals, species, families and Shannon diversity were recorded in the AF plots relative to the other land uses. Mean species evenness was greatest at the SL site but did not differ ($p > 0.05$) between the RF and the AF stands. No consistent variations in species diversity and evenness were found among the land uses with respect to the herb stratum. However, the number of individuals, species, and families appeared to be greater at the AF than at the RF and SL sites.

Family dominance reflected differences in land use: Meliaceae, Malvaceae, and Sapotaceae dominated (in terms of both species richness and IVI) the reference site that had seen very little anthropogenic disturbances (Fig. 2). On the contrary, Moraceae, despite recording only a few species (including the invasive *B. papyrifera*), accounted for almost 50% of the total IVI in both the SL and AF sites.

Comparison of the relative importance value indices of species among the three land uses and vegetation strata showed noticeable variation in the composition and relative abundance of tree species (Table 2). Although the three stands shared some of the most abundant species, the overwhelming dominance of *B. papyrifera* in the SL and AF sites (44.83 and 41.71% of IVI, respectively) was clearly evident. None of the remaining species encountered in the study recorded IVI that exceeded 12%.

Consequently, the 10 most abundant species in the disturbed sites accounted for a substantial proportion of the IVI (> 74%) than those of the reference site (54%). Like the trees, the most dominant species in the shrub and herb layers varied somewhat. However, there was very little difference in terms of the total IVI accounted for by these species among the three land uses as *B. papyrifera* decreased in importance particularly in the herb layer.

Non-metric multidimensional scaling (NMDS) ordination analysis, based on the presence or absence of species in a plot, provided further evidence of the distinct floristic composition of the three land uses (Fig. 3). Plots from the RF stands were clearly separated from those of the disturbed habitats. However, there was considerable overlap between the SL and AF plots, indicating a higher degree of compositional similarity of these two land uses compared to the RF. This ordination technique summarized the observed distances among the measured parameters quite well, with a stress value of 0.17 (non-metric fit $r^2 = 0.97$; linear fit $r^2 = 0.87$). Moreover, the plots in the AF stand were apparently more variable in their species composition compared to the other two stands.

B. papyrifera invasion in relation to land use and its effects on vegetation characteristics in the AHFR

The level of *B. papyrifera* invasion in the AHFR, as determined from its relative density, was generally high and differed substantially ($p < 0.05$) among the three land uses, and also with respect to the vegetation strata (Fig. 4). Among the trees, mean relative density of *B. papyrifera* was significantly higher ($p < 0.05$) at the SL (65.03%) and AF (53.29%) sites compared to the RF site (6.71%), although no statistical differences existed between the two disturbed sites.

On the other hand, *B. papyrifera* formed a comparatively greater ($p < 0.05$) proportion of shrubs or saplings in the AF (averaged 37.03%) than in the SL (9.70%) and RF (0.47%) stands, which did not differ statistically. The relative abundance of the species within the herbaceous layer was the lowest among the different vegetation strata, with mean range of 0.33% in the RF to 4.42% in the AF. In general, *B. papyrifera* exhibited a pattern of decreasing dominance from tree to shrub to herb strata.

Strong negative correlations were found between the proportion of *B. papyrifera* trees and several vegetation attributes (Fig. 5). Of the vegetation attributes examined, the strongest relationship was found for the Shannon diversity, H' ($r = -0.59$; $t = -4.78$; $p < 0.01$) and native species density ($r = -0.58$; $t = -4.66$; $p < 0.01$), followed by evenness, *E* ($r = -0.53$; $t = -4.06$; $p < 0.01$) and native species richness ($r = -0.51$; $t = -3.86$; $p < 0.01$).

The proportion of *B. papyrifera* trees also correlated strongly with tree species richness ($r = -0.48$; $t = -3.54$; $p = 0.03$) and total basal area ($r = -0.48$; $t = -3.54$; $p = 0.03$) of the plants within the studied forests. These results provided further evidence of the low level of *B. papyrifera* in the RF site relative to the disturbed sites.

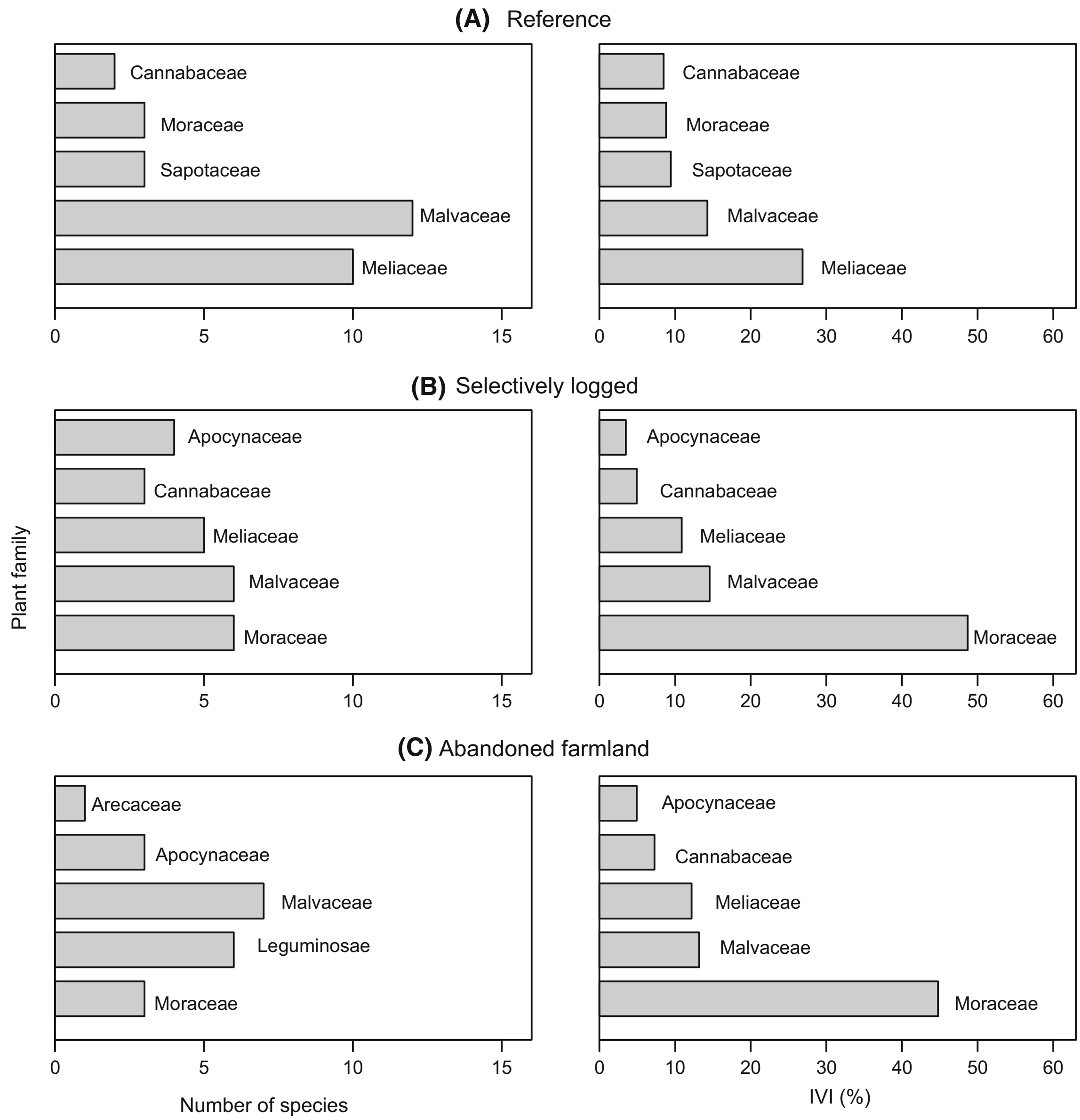

Fig. 2 Family dominance based on number of species (left column) and the relative importance value index (right column) compared for the three land uses studied

Discussion

Land-use effects on floristic composition and *B. papyrifera* invasion

Plant species diversity in the AHFR was generally low (a total of 216 species in ca. 2.8 ha) compared to other tropical forests, some of which have over 300 plant species per hectare (Anning et al. 2008; Hawthorne et al. 1999; Hawthorne and Gyakari 2006; Hawthorne and Jongkind 2006). This, coupled with the generally low abundance of trees in the logged and abandoned farmland plots relative to the reference plots in this forest ecosystem shows a legacy of past human disturbances (Biswas and Mallik 2010). Established in 1928, principally to meet the timber production needs of the country (Hall and Swaine 1981), the AHFR has seen dramatic increases in logging, farming and other anthropogenic disturbances over the past few decades (Dwomoh 2009; Bosu et al. 2013). This history of human disturbances has negatively affected the floristic composition of the forest and created opportunities for the extensive invasion by several exotic plant species, including *B. papyrifera*, in this forest ecosystem. This finding supports the view that human-caused disturbances could have profound and lasting impacts on vegetation characteristics (Turner et al. 2003).

Table 2 Relative abundance of the most important species compared for the three land uses and vegetation strata in the Afram Headwaters Forest Reserve, Ghana

Reference Site		Selectively Logged		Abandoned Farmland	
Species	IVI (%)	Species	IVI (%)	Species	IVI (%)
Tree layer					
Cedrela odorata	11.61	*Broussonetia papyrifera*	44.83	*Broussonetia papyrifera*	41.71
Celtis mildbraedii	6.43	*Trichilia prieuriana*	7.71	*Albizia zygia*	6.43
Trichilia prieuriana	6.37	*Cola gigantea*	5.94	*Alstonia boonei*	5.71
Chrysophyllum perpulchrum	6.09	*Celtis zenkeri*	3.25	*Elaeis guineensis*	4.91
Broussonetia papyrifera	5.04	*Sterculia oblonga*	2.50	*Ceiba pentandra*	3.19
Triplochiton scleroxylon	4.82	*Nesogordonia papaverifera*	2.49	*Erythrina vogelii*	3.17
Sterculia rhinopetala	3.80	*Elaeis guineensis*	2.41	*Bombax buonopozense*	2.81
Nesogordonia papaverifera	3.66	*Alstonia boonei*	1.98	*Antiaris toxicaria*	2.38
Entandrophragma angolense	3.23	*Sterculia tragacantha*	1.93	*Cola gigantea*	2.25
Guarea cedrata	3.19	*Manilkara obovata*	1.70	*Blighia sapida*	2.05
Total	54.24		74.75		74.61
Shrub layer					
Baphia nitida	14.29	*Trichilia prieuriana*	11.40	*Broussonetia papyrifera*	19.08
Trichilia prieuriana	6.12	*Broussonetia papyrifera*	8.17	*Baphia nitida*	5.53
Celtis mildbraedii	5.77	*Baphia nitida*	7.54	*Manihot esculenta*	3.83
Nesogordonia papaverifera	4.66	*Microdesmis puberula*	4.71	*Leucaena leucocephala*	3.35
Rinorea oblongifolia	3.85	*Lecaniodiscus cupanioides*	4.07	*Trichilia prieuriana*	3.26
Microdesmis keayana	3.33	*Millettia zechiana*	3.76	*Antiaris toxicaria*	3.22
Aningeria robusta	3.28	*Blighia sapida*	3.55	*Griffonia simplicifolia*	3.14
Guarea cedrata	3.28	*Blighia unijugata*	3.21	*Blighia unijugata*	2.81
Microdesmis puberula	2.30	*Cola gigantea*	3.10	*Ficus exasperata*	2.59
Antiaris toxicaria	2.24	*Celtis zenkeri*	2.90	*Cola gigantea*	2.00
Total	49.12		52.41		48.82
Herb layer					
Calycobolus africanus	9.47	*Oplismenus burmanni*	12.13	*Chromolaena odorata*	13.17
Griffonia simplicifolia	8.96	*Landolphia dulcis*	8.31	*Centrosema pubescens*	6.83
Nesogordonia papaverifera	4.65	*Paullinia pinnata*	7.94	*Griffonia simplicifolia*	6.72
Khaya anthotheca	3.50	*Griffonia simplicifolia*	7.52	*Commelina erecta*	6.56
Alafia barteri	2.49	*Olyra latifolia*	6.54	*Broussonetia papyrifera*	5.74
Guarea cedrata	1.78	*Baphia nitida*	4.54	*Motandra guineensis*	5.09
Celosia sp.	1.71	*Aframomum cordifolium*	3.58	*Paullinia pinnata*	4.93
Antiaris toxicaria	1.70	*Cnestis ferruginea*	3.54	*Oplismenus burmanni*	3.90
Aningeria robusta	1.53	*Broussonetia papyrifera*	3.15	*Aspilia africana*	2.76
Agelaea pentagyna	1.46	*Turraea heterophylla*	2.19	*Secamone afzelii*	2.65
Total	37.26		59.44		58.35

The distinct composition of species observed among the three stands reflects the varying nature and effects of the land uses on vegetation characteristics. Plant communities tend to exhibit higher species diversity given moderate human interference (Connell 1978). Conversely, intensive land use leads to loss of species and create variable habitats (McIntyre and Lavorel 1994). This presumably explains the diverse and distinct assemblage of species in the reference site compared to the disturbed sites.

Logging activities in the study forest had largely been selective (i.e., no clear-cutting), thus maintaining a considerable number of "less desirable species" and the seed bank to drive regeneration. Selective harvesting of timber can be useful because it creates openings that mimic

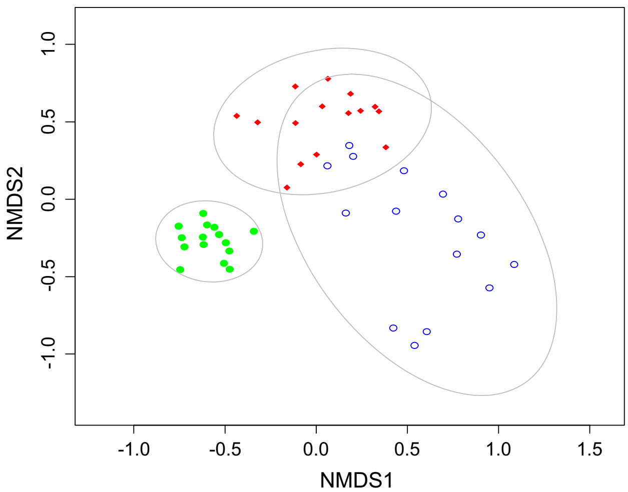

Fig. 3 Non-metric multidimensional scaling ordination of sampling units in the three land uses (solid circles represent reference plots; open circles represent abandoned farmland plots; squares represent selectively logged plots) based on species occurrences, with 95% confidence ellipses. A multivariate analysis of variance based on Bray–Curtis distance showed significant differences in the composition of the land uses ($p = 0.001$)

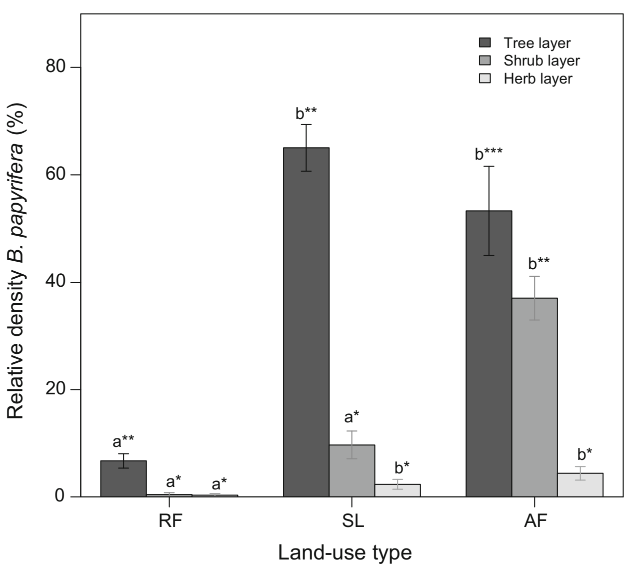

Fig. 4 Relative density of *B. papyrifera* compared for the three land uses (RF is reference site, SL is selectively logged, AF is abandoned farmland) studied in the Afram Headwaters Forest Reserve, Ghana. For each land use, different number of asterisk indicates statistical differences, whereas different letters on bars denote statistical differences for each vegetation stratum at an alpha level of 0.05

natural gaps thereby enhancing recruitment of new species and growth of residual species. On the other hand, the abandoned farmland had been frequently cultivated through slash-and-burn, a farming method that involves clear-cutting. Frequent use of this farming technique typically removes most of the aboveground plant species (except for few shelter trees), modifies the soil conditions, and ultimately alters forest characteristics (Isaac et al. 2005).

Prolonged slash-and-burn farming may also erode the seed bank and subsequently reduce the natural regeneration capacity of the vegetation. Further, deliberate introduction of cultivated species by farmers may lead to changes in vegetation composition. Moreover, the greater abundance of herbs and shrubs in the abandoned farmlands suggests this forest stand might be early in its successional trajectory (had been disturbed within the last 5–10 years). These effects might have contributed to the greater variability within the abandoned farmlands compared to the other two land uses. Nonetheless, the higher degree of similarity between the disturbed stands compared to the reference is largely attributable to the greater dominance of *B. papyrifera*.

The disproportionately large importance value of Moraceae compared to the other families reflects the greater relative abundance of the invasive *B. papyrifera* in the disturbed sites. This overwhelming abundance and importance of *B. papyrifera* demonstrates the severity of the species' invasion in the reserve and the presence of "empty niches" which are vulnerable to further invasion (Catford et al. 2012b). This result agrees with the notion that plant invasion increases with disturbance intensity or in human-modified environments (Catford et al. 2012a; Duggin and Gentle 1988).

Despite its wide ecological tolerance (Whistler and Elevitch 2006), *B. papyrifera* was poorly represented in the shrub- and herb-layers especially in the selectively logged and reference stands compared to the abandoned farmlands, suggesting the species does not grow well under shade. Whereas the abandoned farmland area had not yet recovered from recent farming activities, canopy cover in the selectively logged and the reference forests had obviously increased following the initial disturbances, reducing the amount of light reaching the forest floor and the competitive ability of *B. papyrifera*.

Nonetheless, the greater relative density of *B. papyrifera* trees in the disturbed areas suggests a higher initial colonization rate post-disturbance, which might be expected given the ability of most invasive species to tolerate conditions at high disturbance sites (Catford et al. 2012a). This result has two important management implications. First, it supports the view that *B. papyrifera* is indeed a highly tolerant and persistent plant invader that requires effective management to mitigate its potential impact on ecosystem structure and function. Second, reducing canopy disturbance by limiting logging and other anthropogenic activities may greatly impede the growth and invasion of *B. papyrifera*. On the contrary, frequent human-caused disturbances are likely to facilitate *B. papyrifera* invasion as

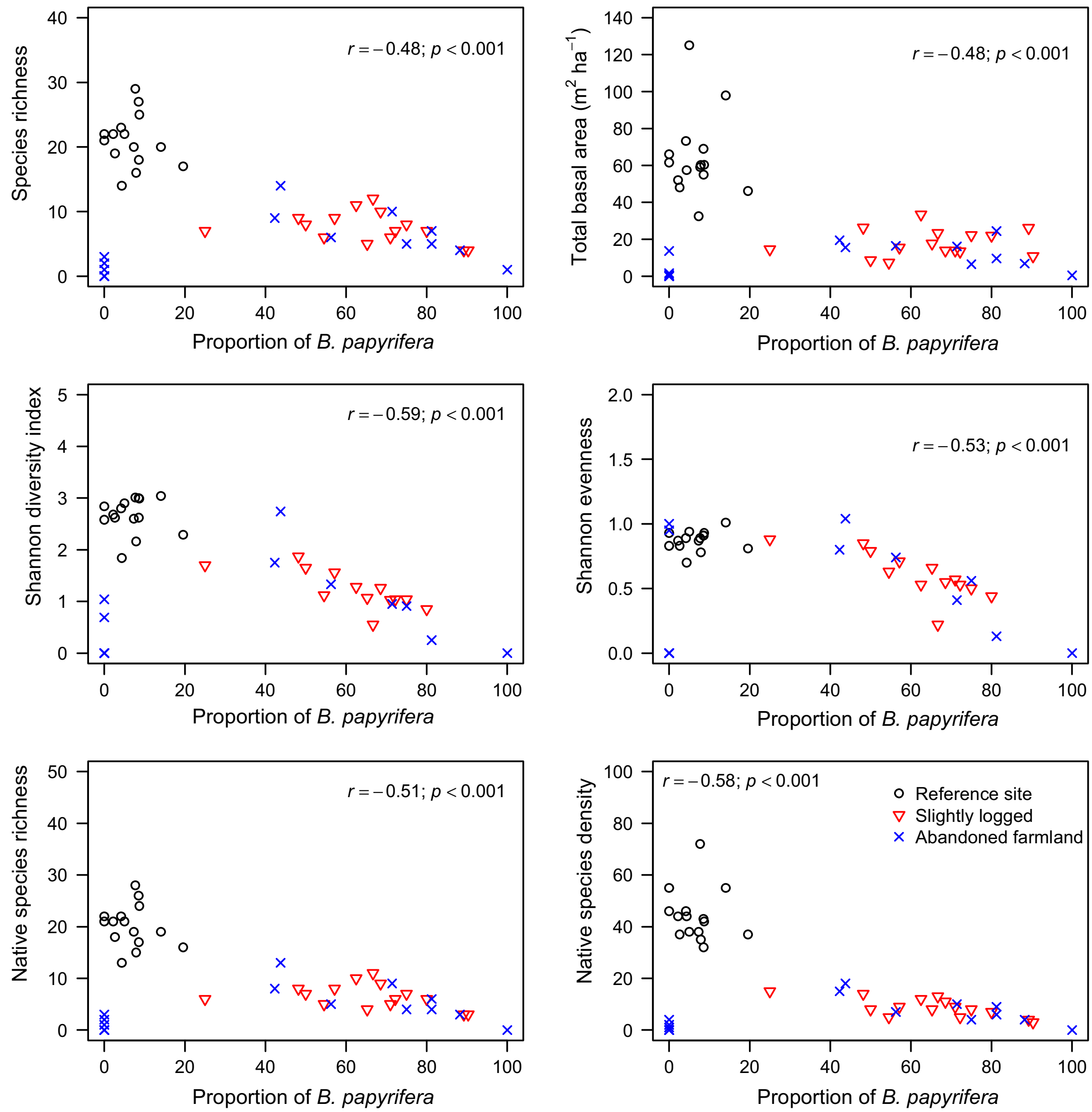

Fig. 5 Correlation of proportion of *B. papyrifera* trees with some vegetation attributes (i.e., Shannon (H'), evenness (E), species richness, basal area, native species richness and density) in the Afram Headwaters Forest Reserve

they increase resource availability and propagule pressure. This observation probably explains why attempts by local farmers to control *B. papyrifera* invasion using the slash-and-burn method have so far been unsuccessful (Bosu et al. 2009). The practice rather creates more canopy openings allowing this shade-intolerant but fire-resistant plant (Whistler and Elevitch 2006) to thrive.

Effects of *B. papyrifera* invasion on forest characteristics

The strong negative correlations of *B. papyrifera* density with the species diversity metrics suggest substantial impact on the floristic composition of the AHFR. This finding is consistent with the widely recognized negative consequences of non-native plant invasions on forest structure and functions, mediated by mechanisms such as niche pre-emption, competition, and transformation of the environment (Catford et al. 2012a; Mack et al. 2000; Pimentel et al. 2000; Vila et al. 2011). While these effects were predictable, the strong association of *B. papyrifera* with the species evenness suggests that disruption of species' distribution pattern (i.e., through biotic homogenization) may be an important mechanism by which this invader transforms local vegetation.

However, how the relationship between *B. papyrifera* density and diversity measures varies with the disturbance type is unclear as data from all three land uses were combined in analysis. Moreover, the presence (albeit at much lower densities) of other invasive species such as *Cedrela odorata, Chromolaena odorata*, *T. grandis* and *L. leucocephala* could obfuscate the relationship between *B. papyrifera* and the species diversity.

Conclusion

Human land-use disturbances such as logging and clear cutting or slash-and-burn agriculture negatively impacted the floristic composition of the studied reserve. These disturbances displaced some native plant species, altered the general floristic composition, and facilitated the invasion of *B. papyrifera* and other alien plants in the reserve. The level of invasion of *B. papyrifera* was evidently high in the disturbed area and also varied somewhat with the land use. Besides the negative effect on native species density, *B. papyrifera* invasion also correlated negatively with species diversity and evenness. In general, the results highlight the link between anthropogenic disturbances (i.e., selective logging and slash-and-burn-farming), plant invasion, and vegetation characteristics within the tropical forest environment. Management programs that promote recovery of forest canopy cover or prevent their further destructions will be critical in stemming *B. papyrifera* invasion, and thereby limit its impacts on community structure and function, and conserve biodiversity in the forest.

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