Can forest plantations harbour biodiversity similar to natural forest ecosystems over time?

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ABSTRACT
This study assessed and compared tree species diversity in a 26-year-old Gmelina arborea plantation with tree diversities in primary and degraded natural forests in southwestern Nigeria. In each forest type, a one-hectare block was divided into 400 m² sample plots from which 4 were randomly selected, which was repeated on another one-hectare block, yielding eight 400 m² plots per forest type. A 25 m² quadrat was laid at the centre of each 400 m² plot while a 4 m² sub-quadrat was laid at the centre of each quadrat. Overstory, sapling and seedling species were inventoried in all 400 m² plots, 25 m² quadrats, and 4 m² sub-quadrats, respectively. Family and species richness were significantly lower in G. arborea plantation overstory (7 families, 8 species) than in primary (8, 28) and degraded (18, 30) forest overstories. Diversity indices were also significantly lower for G. arborea plantation overstory than for primary and degraded forests. However, in the sapling layer, family and species richness in the G. arborea plantation (10, 13) were similar to those of primary (9, 15) and degraded (9, 16) forests. The species richness of G. arborea plantation seedling layer (24) was similar with that of degraded forest (25) but significantly higher than that of primary forest (18). Primary (18 species), and degraded forests (25 species). Species diversity of the G. arborea sapling layer/ct 2 (2.07) was significantly higher than that of its overstory (0.26) but significantly lower than those of primary (2.26) and degraded (2.44) forests. Of the species found in the G. arborea plantation seedling layer, 25% were absent in natural forests. Thus, this plantation understory harbours high biodiversity and can conserve biodiversity over time. Understory species diversity should be considered in biodiversity comparisons between plantations and natural forest.

Introduction
Globally, the area of natural and semi-natural forests is decreasing by about 13 million ha annually (FAO 2006). Contrary to this, the average annual rate of forest plantation establishment is 5 million ha (FAO 2014). The area of global forest plantations has witnessed a phenomenal growth since the middle of the twentieth century. Global forest plantation area increased from 17.8 million ha in 1980 to 187 million ha in 2000, an increase of about 950% (Onyekwelu et al. 2006). By 2014, global forest plantation area had risen to 264 million ha and accounts for 7% of total global forest estates (FAO 2014). There are indications that the area of forest plantations will continue to increase, making it necessary to assess its potentials to fulfill ecological purposes (e.g., biodiversity conservation) in addition to wood production. While plantations are known for high timber productivity, little is known about their potential to conserve and harbour biodiversity. The question remains whether plantations of economic tree species can harbour biodiversity similar to that in naturally regenerated forests over time.

Thus, a critical issue for future plantation forests is how to create a synergy between management of plantations for production of high-value timber and biodiversity conservation at various spatial scales (i.e., stand, forest, landscape). Managing forest plantations to produce high-quality timber while also enhancing ecological services, such as biodiversity conservation involves trade-offs, which can be made only with a clear understanding of the ecological context of plantations in the broader landscape and agreement among stakeholders on the desired balance of goods and ecological services from plantations (Carnus et al. 2003).

This issue of biodiversity conservation in forest plantations is highly debated (Carnus et al. 2006; Brockerhoff et al. 2008). Although plantation forest managers increasingly recognize the need to conserve biodiversity and many adhere to sustainable management guidelines, criticism of biodiversity conservation potentials of plantation forests remains strong (Cossalter & Pye-Smith 2003). The industrial scale of many forest plantations, their typical structure as monocultures, and the fact that they are sometimes established on land previously covered by natural forests all raise the concern of environmental lobbyists (Brockerhoff et al. 2008). A common perception of plantation forests is that they are...
ecological deserts that do not provide habitat for valued organisms (Brockerhoff et al. 2008).

There is ample evidence that natural forests may harbour higher biodiversity than forest plantations. For example, while many forest plantations have one or two tree species at planting, natural tropical forests could have between 70 and 300 or more tree species per hectare (Sollins 1998; Onyekwelu et al. 2008). However, the comparison of biodiversity conservation status of natural and plantation forests is usually undertaken at the overstory levels (i.e., trees with diameter at breast height (dbh) of 10 cm and above) of the forests (Kessler et al. 2005), while understory species are usually not considered in the comparison. In fact, the understories of tropical forests may be as species rich as their overstories (Tchouto et al. 2006). The understory is an integral component of the forest ecosystems, generally supporting a large fraction of total community floristic diversity (Gentry & Dodson 1987; Tchouto et al. 2006) and providing habitats and foods for many animal species (Gentry & Emmons 1987). Forest plantations often support a great diversity of native species, particularly in understory communities and thus can play important role in conserving or even restoring native species biodiversity (Carnus et al. 2003). Onyekwelu and Fuwape (2008) reported 18 and 19 understory tree species in Gmelina arborea plantations and a degraded forest in Nigeria, respectively and concluded that understory vegetation could be as tree species diverse in forest plantations as in degraded natural forest. However, it remains to be established whether this comparatively rich understory tree species diversity in forest plantations and natural forests can be generalized and whether it is influenced by tree species and plantation age. This study investigates whether monoculture forest plantations can harbour biodiversity similar to naturally regenerated tropical rainforest ecosystems over time.

**Methods**

**Study area**

This study was conducted in two purposefully selected forest reserves: Akure and Oluwa forest reserves in Ondo State in the humid tropical rainforest zone of south-western Nigeria (Figure 1). Tree species diversity assessment was undertaken in primary forest, degraded forest, and a 26-year-old G. arborea monoculture plantation forest. The plots in primary forest were selected from Strict Nature Reserve (SNR) located in Akure Forest Reserve, while the plots in the G. arborea plantation and degraded forest were located in Oluwa Forest Reserve. Akure Forest Reserve is located between latitude 5° 45’ and 8° 15’ N and longitude 4° 30’ and 6° E (Adekunle et al. 2013) and covers an area of 69.93 km², with an average elevation of 279 m above sea level. Oluwa Forest Reserve lies between latitude 6° 55’ and 7° 20’ N and longitude 4° 30’ and 4° 45’ E and covers an area of 87,816 ha, with an average elevation of 100 m above sea level. Both reserves have humid tropical climates. The rainy season in Oluwa and Akure Forest Reserves lasts from March to November, while the months of December–February constitute the dry season. In both reserves, annual rainfall ranges from 1,700 to 2,500 mm (Onyekwelu et al. 2006; Adekunle et al. 2013), average daily relative humidity is 80%, and daily mean

![Figure 1. Map of Nigeria showing the location of Ondo State](image)
temperature ranges from 20.6°C to 33.5°C, while mean annual temperature is 27°C.

The soils of Akure and Oluwa Forest Reserves are predominantly ferruginous tropical soils. They are typical of the variety found in the intensively weathered areas of basement complex formations in the rainforest zone of south-western Nigeria. Smyth and Montgomery (1962) classified the soils of the two reserves among the representative soils in Ondo association. The soil of Oluwa is alfisols (SSS 2003), while that of Akure Forest Reserve is ferric luvisol soil (FAO/UNESCO 1988). The soils are well drained. Onyekwelu et al. (2006) showed that soil nutrients of old growth *G. arborea* plantations and those of degraded and primary forests in Oluwa Reserve are similar.

Akure and Oluwa Forest Reserves are dominated by broadleaved hardwood trees that form dense, layered forest canopy. They contain many indigenous tree species found in Nigeria’s rainforest, which include: *Khaya* spp., *Terminalia* spp., *Milicia excelsa*, *Sterculia* spp., *Lophira alata*, and *Triplochiton scleroxylon*. However, due to extensive exploitation and forest degradation, some parts of both reserves are being replanted with exotic and indigenous tree species. *G. arborea* accounts for about 60% of total forest plantations in Nigeria.

**Brief history of the forest reserves and plantation development in Oluwa Forest Reserve**

Most of Akure Forest Reserve has been highly degraded. However, 600 ha of the reserve was constituted as SNR in 1954 by Forestry Research Institute of Nigeria. The SNR has no record of timber exploitation within living memory and there is little or no record of human disturbance or activities. Thus, the SNR is an undisturbed primary forest. The SNR is bounded on one side by a river, which makes accessibility to it very difficult. There is adequate protection of the SNR by forest guards.

Most parts of Oluwa Forest Reserve were already seriously degraded by the early 1970s. Degradation within the reserve was mainly caused by illegal encroachment by farmers, uncontrolled timber logging (legal and illegal), felling damage to residual forests and unregulated collection of non-timber forest products. Though Oluwa was designated for forest plantation establishment, only about 19,000 ha of its land have been converted to forest plantations (Onyekwelu et al. 2006). The remaining parts of the reserve consist of degraded forests (27,000 ha) and illegal farmland (31,000 ha) while primary forest, rock outcrops and water bodies account for 11,000 ha.

Large-scale plantation establishment at Oluwa Forest Reserve started during the early 1960s. Usually, the degraded forests were completely cleared through mechanized land preparation and the plantations established on the cleared land. The plantations were spot weeded during the first two years of establishment and protected against fire. Currently, *G. arborea* accounts for about 89% of total plantations in Oluwa (Onyekwelu et al. 2006). The plantations were established to provide pulpwood at rotation age of 8–10 years. Consequently, thinning and pruning operations were not intended, thus, the plantations have not been thinned, though the management objective has changed to timber provision because of the inability of the paper mills to utilize the resources (Onyekwelu et al. 2006). Thus, the plantations were left to grow without any deliberate management treatment. The *G. arborea* plantations are adjacent to the degraded forests.

**Data collection**

Data for understory tree species assessment were obtained from three forest types: primary, degraded, and *G. arborea* plantation forests. The SNR in Akure Forest Reserve served as the primary forest. The degraded portion of Oluwa Forest Reserve served as the degraded forest, while old-growth *G. arborea* plantation (26 years old) in Oluwa constituted the monoculture plantation. *G. arborea* plantation was chosen for this study because it is the dominant (89%) plantation species in Oluwa Forest Reserve. An old-growth plantation forest (26 years) was used for this study because it has been shown that the soil nutrient status of old growth *G. arborea* plantations is similar to that of adjacent natural forest sites (Onyekwelu et al. 2006).

Within each forest type, one 1-hectare plot was divided into 20 m × 20 m (400 m²) temporary sample plots from which four plots were randomly selected. This was repeated on another 1-hectare plot within the same forest type, resulting in 8 sample plots per forest type and 24 for the study. Within the 400 m² sample plot, all tree species in the forest overstory (i.e., trees with dbh ≥ 10 cm) were identified and their dbh measured. For the purpose of this study, understory species were stratified into sapling layer (trees with diameter >1 cm but <10 cm) and seedling layer (individuals with diameter <1 cm). For assessment of the sapling layer, a 5 m × 5 m (25 m²) quadrat was laid at the centre of each 400 m² plot and all sapling tree species within the quadrat were identified and their dbh measured. For seedling layer assessment, a 2 m × 2 m (4 m²) sub-quadrat was laid within the centre of each 25 m² quadrat and the seedling species
within the sub-quadrat identified and their frequency taken. Nomenclature of species followed Keay (1989).

Data computations and analysis
The basal area of each overstory tree was calculated using Equation (1). The basal area values were then extrapolated to per hectare basis.

\[ BA = \frac{\pi D^2}{4} \]  
(1)

Where \( BA \) = basal area (m\(^2\)); \( D \) = diameter at breast height (cm); and \( \pi \approx 3.142 \).

All understory and overstory tree species were classified into families according to Keay (1989). Their frequencies of occurrence were obtained to ascertain species abundance and species evenness. The following biodiversity indices were computed.

(A) **Species relative dominance (RDo)**: This was obtained using Equation (2):

\[ RDo = \frac{\sum B_{ai} \times 100}{\sum B_{an}} \]  
(2)

Where \( RDo \) = relative dominance; \( B_{ai} \) = basal area of trees belonging to the \( i \)th tree species; \( B_{an} \) = stand basal area

(B) **Species relative density (RD)**: This refers to the number of individuals of a given species divided by the total number of individuals of all species. This was obtained using Equation (3):

\[ RD = \frac{n_i}{N} \times 100 \]  
(3)

Where \( RD \) = relative density; \( n_i \) = number of individuals of species; \( N \) = total number of individuals in the entire population.

(C) **Importance value index (IVI)**: This was obtained by summing RD and RDo, and then dividing it by 2 as given by Equation (4).

\[ IVI = \frac{RD + RDo}{2} \]  
(4)

(D) **The Shannon–Wiener diversity index (\( H' \))**: This was used to calculate forest diversity index because it takes into account the number of species and the abundance of each species in the different forests. It was obtained using Equation (5):

\[ H' = \sum_{i=1}^{s} p_i \ln (p_i) \]  
(5)

Where: \( H' \) = Shannon diversity index; \( S \) = number of species in the habitat; \( p_i \) = proportion \( S \) (species in the family) made up of the \( i \)th species; \( \ln \) = natural logarithm.

(E) **Species evenness (E)**: This was calculated using Shannon’s equitability index (\( E_{ij} \)) (Equation 6):

\[ E_{ij} = \frac{\sum p_i \ln (p_i)}{\ln (S)} \]  
(6)

(F) **Shannon’s maximum diversity index**: This was calculated using Equation (7):

\[ H_{max} = \ln (S) \]  
(7)

Statistical analysis
The tests of significance for each diversity index (species diversity index, evenness, richness, etc.) in the three sites were conducted using one-way analysis of variance (ANOVA). The analysis was performed using SPSS 17.0 for windows. Treatment means that differed significantly were separated using Fishers least square difference (LSD).

Results
There was a distinct difference in species compositions and diversities in the overstories of the three forest types. Tree species richness in the overstory of the *G. arborea* plantation (8) was significantly lower than in the overstories of primary (50) and degraded (45) forests (Table 1). Shannon–Wiener diversity indices of overstory species in primary and degraded forests were similar; however, both sites had significantly higher diversity than *G. arborea* plantation (Table 1). The numbers of species in primary and degraded forests were not significantly different. The number of families in both primary (23) and degraded (21) forests were statistically similar but significantly higher than that of *G. arborea* plantation (7) (Table 1). Common families in the overstories of all three forest types

| Tree growth/ biodiversity indices | Primary forest | Degraded forest | *Gmelina arborea* plantation |
|----------------------------------|----------------|----------------|-----------------------------|
| Mean dbh                         | 50.1*          | 24.3*          | 24.5*                       |
| Basal area                       | 65.0*          | 31.3*          | 26.19*                      |
| H'                               | 3.30*          | 3.41*          | 0.26*                       |
| E                                | 0.59*          | 0.65*          | 0.13*                       |
| Hmax                             | 3.47*          | 3.55*          | 2.08*                       |
| No. of families                  | 23*            | 21*            | 7*                          |
| No. of species                   | 51*            | 45*            | 8*                          |
| No. of endangered spp            | 14 (27.5%)     | 13 (28.9%)     | 2 (25.0%)                   |

Values in parentheses are percentages of the number of endangered species among the total number of species in the particular land-use type; values followed by the same letter within the same row are not significantly different (\( p < 0.05 \)). \( H' \) = Shannon–Wiener diversity index; \( E \) = species evenness; \( H_{max} \) = Shannon’s maximum diversity index.
include Sterculiaceae, Euphorbiaceae, Ulmaceae, Moraceae, and Combretaceae.

Tree species with high IVI in each forest type were: *Mansonia altissima*, *Celtis zenkeri*, and *Sterculia* spp. (primary forest); *Bosquia angolensis*, *Ficus exasperata*, and *C. zenkeri* (degraded forest); and *G. arborea*, *C. zenkeri*, and *Myrianthus arbores* (G. *arborea* plantation). Species evenness in the overstories of both primary and degraded forests was similar but statistically higher than that of *G. arborea* plantation. The number of tree species classified as endangered in Nigerian forests by FORMECU (1999) found in the overstories of the three forest types varied from 2 (25% of total species) in *G. arborea* plantation to 13 (28.9%) and 14 (27.5%) in degraded and primary forests, respectively (Table 1). The five most important overstory tree species in the three forest types are presented in Table 2. *Celtis zenkeri* was found in both primary and plantation forests while *Cleistopholis patens* was common to degraded and plantation forests. Other species were only important in their respective forest types (Table 2). The growth characteristics of the five most important sapling layer tree species in the three forest types are presented in Table 3. *Strombosia pustulata* was found to be important in the three forest types while *Funtumia elastica* was important in both primary and the *G. arborea* forests (Table 3). Other species were important in only one forest type.

Trees in the overstory of the primary forest were significantly bigger than those found in the overstories of degraded and *G. arborea* plantation forests, both of which did not differ significantly from each other (Table 1). The same trend was observed in the basal area of the three forest types. The mean dbh of sapling species in *G. arborea* plantation was equal to that of the saplings in degraded forest and significantly higher than that of saplings in primary forests (Table 4).

The trend of biodiversity indices in the understories of the three forest types was different from those of the overstories. There were no significant

**Table 2.** Population characteristics of the five most important overstory tree species in the three forest types.

| Tree species             | Frequency | Dbh (cm) | Basal area (m²) | Rdo (%) | RD (%) | IVI (%) |
|--------------------------|-----------|----------|-----------------|---------|--------|---------|
|                          |           | Max      | Min         | Mean    |        |         |
| Primary forest           |           |          |              |         |        |         |
| 1. *Mansonia altissima*  | 35        | 43.2     | 10.3        | 22.0    | 1.334  | 9.49    | 22.44   | 15.96   |
| 2. *Sterculia oblonga*   | 14        | 230.0    | 13.2        | 65.3    | 4.692  | 19.41   | 8.97    | 14.19   |
| 3. *Celtis zenkeri*      | 31        | 62.0     | 10.1        | 23.6    | 1.335  | 8.38    | 19.87   | 14.13   |
| 4. *Sterculia rhinopetala* | 9       | 178.0    | 13.1        | 80.4    | 4.565  | 15.70   | 5.77    | 10.74   |
| 5. *Triplochiton scleroxylon* | 9     | 192.0    | 25.0        | 72.9    | 3.753  | 10.01   | 5.77    | 7.89    |
| Degraded forest          |           |          |              |         |        |         |
| 1. *Ficus exasperata*    | 13        | 50.0     | 10.5        | 25.0    | 0.638  | 22.76   | 11.30   | 17.03   |
| 2. *Musanga cecropioides* | 10       | 50.1     | 11.8        | 22.7    | 0.405  | 13.23   | 8.70    | 10.96   |
| 3. *Cleistopholis patens* | 7        | 68.6     | 25.3        | 36.1    | 0.717  | 11.83   | 6.09    | 8.96    |
| 4. *Myrianthus arbores*  | 8         | 33.4     | 12.6        | 21.1    | 0.280  | 9.12    | 6.96    | 8.04    |
| 5. *Macaranga barteri*   | 9         | 20.5     | 10.1        | 15.8    | 0.176  | 5.51    | 7.83    | 6.67    |
| *Gmelina arborea* planta* | 259      | 10.5     | 54.5        | 27.7    | 15.655 | 99.88   | 95.57   | 97.72   |
| 2. *Celtis zenkeri*      | 4         | 13.8     | 33.0        | 19.9    | 0.123  | 0.03    | 1.48    | 0.76    |
| 3. *Myrianthus arbores*  | 2         | 19.2     | 37.6        | 28.4    | 0.126  | 0.03    | 0.74    | 0.38    |
| 4. *Cleistopholis patens* | 2        | 15.0     | 20.5        | 17.8    | 0.0495 | 0.02    | 0.74    | 0.38    |
| *Terminalia superba*     | 1         | 18.5     | 18.5        | 18.5    | 0.0269 | 0.01    | 0.37    | 0.19    |

Rdo = species relative dominance; RD = species relative density; IVI = species importance value index.

**Table 3.** Population characteristics of the five most important sapling layer tree species in the three forest types.

| Tree species             | Frequency | Dbh (cm) | Basal area (m²) | Rdo (%) | RD (%) | IVI (%) |
|--------------------------|-----------|----------|-----------------|---------|--------|---------|
|                          |           | Max      | Min           | Mean    |        |         |
| Primary forest           |           |          |                |         |        |         |
| 1. *Strombosia pustulata* | 13        | 4.5      | 1.2           | 2.8     | 0.008  | 17.74   | 28.26   | 23.00   |
| 2. *Funtumia elastica*   | 8         | 6.0      | 1.6           | 3.5     | 0.007  | 19.35   | 17.39   | 18.37   |
| 3. *Sterculia rhinopetala* | 4        | 9.5      | 3.0           | 6.1     | 0.012  | 21.77   | 8.70    | 15.23   |
| 4. *Drypetes papu*       | 6         | 5.7      | 2.5           | 3.9     | 0.007  | 12.10   | 13.04   | 12.57   |
| 5. *Mansonia altissima*  | 3         | 7.5      | 1.3           | 4.3     | 0.004  | 8.87    | 6.52    | 7.70    |
| Degraded forest          |           |          |                |         |        |         |
| 1. *Ravonolia vomitoria* | 8         | 9.7      | 3.1           | 5.8     | 0.021  | 26.26   | 17.02   | 21.64   |
| 2. *Strombosia pustulata* | 10        | 7.4      | 2.4           | 4.9     | 0.019  | 21.23   | 21.28   | 21.25   |
| 3. *Musanga cecropioides* | 6        | 7.8      | 3.2           | 5.7     | 0.015  | 25.42   | 12.77   | 19.09   |
| 4. *Ficus exasperata*    | 4         | 9.2      | 5.3           | 7.3     | 0.017  | 6.98    | 8.51    | 7.75    |
| 5. *Diospyros monbuttensis* | 3       | 7.5      | 2.4           | 5.5     | 0.007  | 4.19    | 6.38    | 5.29    |
| *Gmelina arborea* planta* | 13       | 9.2      | 1.9           | 4.8     | 0.023  | 35.11   | 34.21   | 34.66   |
| 2. *Strombosia pustulata* | 8         | 8.2      | 2.4           | 5.4     | 0.019  | 20.21   | 21.05   | 20.63   |
| 3. *Funtumia elastica*   | 4         | 8.1      | 3.4           | 5.6     | 0.010  | 11.17   | 10.53   | 10.85   |
| 4. *Macaranga barteri*   | 2         | 8.5      | 7.0           | 7.8     | 0.009  | 10.11   | 5.26    | 7.68    |
| 5. *Bridelia ferruginea* | 2         | 7.2      | 5.6           | 6.4     | 0.006  | 6.91    | 5.26    | 6.09    |

Rdo = species relative dominance; RD = species relative density; IVI = species importance value index.
Table 4. Community characteristics of the sapling and seedling (understory) layers in the three forest types.

| Tree growth/biodiversity indices | Primary forest | Degraded forest | Gmelina arborea plantation |
|----------------------------------|----------------|-----------------|---------------------------|
| Mean dbh                         | 4.9<sup>b</sup> | 6.2<sup>a</sup> | 6.2<sup>a</sup>           |
| H<sup>′</sup>                    | 2.26<sup>a</sup> | 2.44<sup>a</sup> | 2.07<sup>b</sup>         |
| E                               | 0.83<sup>a</sup> | 0.88<sup>b</sup> | 0.81<sup>b</sup>         |
| H<sub>max</sub>                  | 2.71<sup>a</sup> | 2.77<sup>a</sup> | 2.5<sup>b</sup>          |
| No. of families                 | 9<sup>a</sup>   | 9<sup>a</sup>    | 10<sup>a</sup>           |
| No. of species                  | 15<sup>a</sup>  | 16<sup>a</sup>   | 13<sup>a</sup>           |

Table 5. The five tree species with the highest frequency of occurrence in the seedling layers of the three forest types.

| Tree species                      | Primary forest | Gmelina arborea plantation | Degraded forest |
|-----------------------------------|----------------|---------------------------|-----------------|
| Aframomom melegueta               | 27             | –                         | 10              |
| Bridelia ferruginea               | –              | 14                        | –               |
| Cleistopholis patens              | –              | –                         | 7               |
| Diospyros monbuttersis            | –              | –                         | 9               |
| Dracaena mannii                   | 25             | –                         | –               |
| Drypetes pasii                    | 8              | –                         | –               |
| Elaeis guineensis                 | –              | 11                        | –               |
| Funtumia elastica                 | 6              | –                         | 10              |
| Gmelina arborea                   | –              | 19                        | –               |
| Lecaniodiscus puberuloides        | –              | 9                         | –               |
| Strombosia pustulata              | 29             | 15                        | 8               |

H<sup>′</sup> = Shannon–Wiener diversity index; E = species evenness; H<sub>max</sub> = Shannon’s maximum diversity index.

Discussion

The results of this study indicate that to adequately capture the biodiversity conservation status of forest plantations, understory species must be included. The forest understory plays a central role in the dynamics and functioning of forest ecosystems by influencing long-term successional patterns (Royo & Carson 2005). In addition, the understory of tropical forest can be as species rich as, or richer than, the overstory (Tchouto et al. 2006). Thus, the understory deserves as much attention as the overstory in biodiversity assessments.

One common perception of a forest plantation is that it as an ‘ecological desert’ (Dyck 1997), which was based on the conclusion that plantation forests have lower species diversity and richness compared with natural forests (Brockerhoff et al. 2008). However, most of the studies that made such conclusions compared only the overstory components of forest plantations and natural forests, without considering the understory species diversities of the forests. When only the overstories of the three forest types in this study were considered, our results support the view noted above. It is expected that the overstory of a forest plantation would have lower species diversity and richness than those of natural forests, since most plantations are monocultures or mixed plantings of a few tree species. Also, at the early stage of development, understory plants in plantations are usually removed during weeding operations. Thus, the trees planted in plantations grow with little or no recruitment in the understory, resulting in low species diversity in the overstory at later stages of development. Active recruitment in forest plantation starts after canopy closure, when weeding is no longer necessary, which could produce richer understory vegetation at a later stage.

Plantation forests can contribute to biodiversity conservation by providing habitat for plant and animal species (Oberhauser 1997; Svenning 2000; Carnus et al. 2006). Gentry and Dodson (1987) reported 176 and 32 species in the understories and overstories, respectively, of an Ecuadorian Rainforest. Onyekwelu and Fuwape (2008) and Onyekwelu et al. (2010) reported 18 and 26 tree species in the understories of G. arborea monoculture plantations and mixed species plantations in Nigeria, respectively. In these plantations, high species diversity and richness were found in the understory and not the overstory, which is corroborated by our results. At the sapling layer in our study, the G. arborea plantation had species richness comparable with both primary and degraded forests. More differences in species richness, species evenness, or number of families among the sapling layers of the three forest types (Table 4). In the sapling layer, Shannon–Wiener diversity index was the only biodiversity index that was lower in the G. arborea plantation than in the primary and degraded forests (Table 4). In the seedling layer, the G. arborea plantation had statistically comparable species richness with the degraded forest and statistically higher species richness than the primary forest (Table 4). The understory of the G. arborea plantation had statistically comparable number of families with primary and degraded forests.

The five most frequent tree species in the seedling layer of each forest type are presented in Table 5. Among the five species, Strombosia pustulata was the only species that occurred in all three forest types, while Funtumia elastica and Aframomom melegueta were important in both primary and degraded forests (Table 5). Other species were frequent in only one forest type. The understory of the G. arborea plantation contained seedlings of some economically important indigenous tree species usually found in natural forests, such as: Cola gigantea, Celtis zenkeri, Bridelia ferruginea, Pterygota macrocarpa, Cleistopholis patens Sterculia rhinopetala, and Strombosia pustulata.
remarkably, the species richness of the seedling layer of the G. arborea plantation was significantly higher than the richness of the seedling layer of primary forest and similar to that of the degraded forest (Table 5). Thus, when viewed holistically, plantations are not 'biological deserts', a view also supported by Allen et al. (1995) and Dyck (1997).

Tree species diversity and richness in the G. arborea plantation increased from the overstory (0.26; 8 species) to sapling (H’ = 2.07; 13 species) and seedling (24 species) layers (Tables 1 & 3), such that higher tree species diversity and richness were found in the understory. Also, tree species diversity and richness of the plantation became increasingly comparable to, and/or higher than, those of the two natural forests as one moves from the overstory to sapling and seedling layers (Tables 1 & 3). The comparable understory tree species diversity and richness in the 26-year-old G. arborea plantation with those in natural forests in this study strengthens the views that the effects of plantations on species diversity may be negligible after several years (Scheller & Mladenoff 2002). This process is a function of stand age, that is, enough time had elapsed (26 years) since plantation establishment that the plantation understory had been colonized by different plant species. In some cases, the process may also be related to management intensity and site history (i.e., whether the stand was established on a site previously occupied by natural forest, as was the case with G. arborea plantations in this study). Another indication of biodiversity conservation in the understory of the G. arborea plantation is the fact that 25% of tree species found in its seedling layer were absent in the two natural forests.

The implication of high tree species richness under the G. arborea plantation is that after the current plantation is harvested, the site has the potential of returning to a multi-species ecosystem akin to natural forests, if plantation is not re-established on the site. Moreover, this re-established ecosystem would likely include economically important indigenous and endangered tree species in Nigeria, whose seedlings were found in the plantation understory. Other researchers have also shown that plantations may have an understory of indigenous plants and fauna that resemble those of natural forests (Brockerhoff et al. 2002). Allen et al. (1995) found that the proportion of indigenous species present in the understory of a Pinus radiata plantation increased with time from planting to 82% in a 29-year-old stand.

Conclusion

The overstory of the G. arborea plantation was poorer in tree species diversity and richness compared to the overstories of the primary and degraded forests. However, the understory of the G. arborea plantation had comparable and/or significantly higher species diversity and richness than understories of the primary and degraded forests. Tree species diversity and richness in the G. arborea plantation increased progressively from the overstory to sapling and seedling layers. The high number of understory tree species in the old growth G. arborea plantation (26 years) indicates that forest plantations can harbour high species richness. In addition, the increasing number of species from overstory to understory suggests that forest plantations have the ability to conserve biodiversity at later stages, as different species colonize the forest understory, and the potential to return to a multi-species ecosystem similar to natural tropical forests.

Much of the biodiversity conservation benefit obtained in the G. arborea plantation in this study was gained by chance rather than design, since biodiversity conservation was not among the initial management objective(s). Thus, forest plantations will conserve higher biodiversity if biodiversity conservation is included in their initial management objectives. Further enhancement of biodiversity is possible through greater attention to structural diversity across landscapes and within stands, applying site-specific stand management, using indigenous species, and increasing rotation length. Management of plantations of economic tree species must seek to strike a balance (synergy) between timber production and biodiversity conservation.

Disclosure statement

No potential conflict of interest was reported by the authors.

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