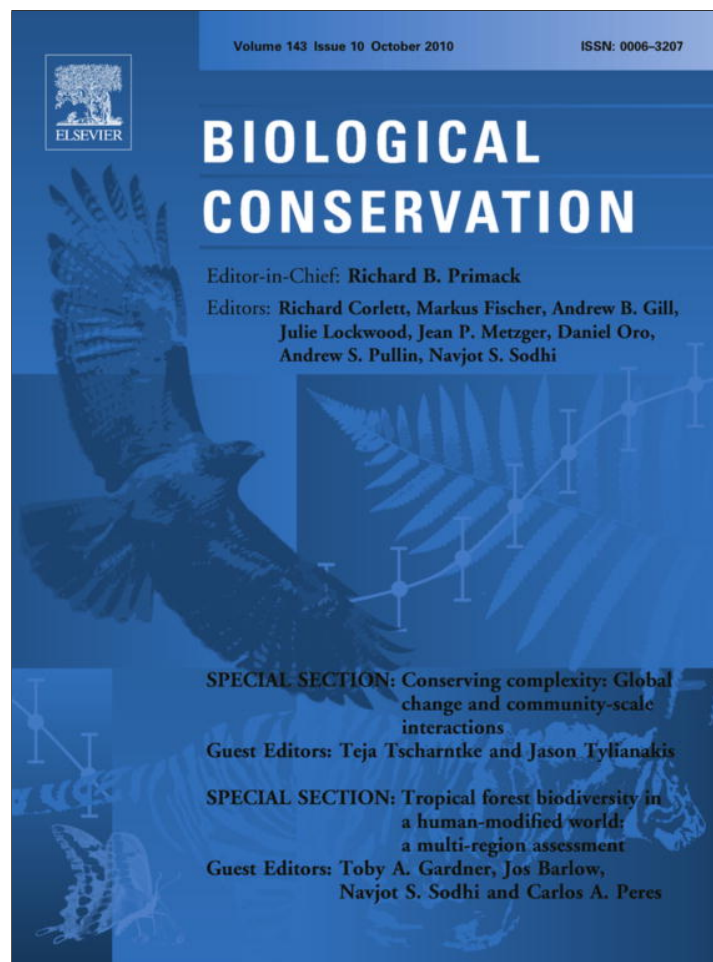


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Biodiversity in a forest-agriculture mosaic – The changing face of West African rainforests

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ABSTRACT

The biodiversity of West African rainforests is globally significant but poorly described, little understood in terms of its functional significance, and under threat from forest loss and degradation. Estimates suggest that about 10 million ha of forest may have been lost in the 20th Century, and around 80% of the original forest area is now an agriculture-forest mosaic. These highly modified forests provide food, fuel, fibre and a range of ecosystem services for over 200 million people. As a consequence, the future of biodiversity in the region is intimately linked with the lives and livelihoods of local people. The available evidence suggests that forest loss and degradation has been caused primarily by agricultural expansion, sometimes facilitated by other human activities such as wood extraction. This expansion is a response to the demand generated by a growing and increasingly urbanised human population, but has been exacerbated by small increases in crop yields over recent decades. We synthesize and review our state of knowledge on the value of human-modified habitats for forest biodiversity in the region. Data on biodiversity are patchy, but we show that across plant, invertebrate and vertebrate groups, there is a significant loss of forest species as tree cover is reduced and vegetation structure simplified. Agricultural expansion clearly causes significant local biodiversity loss. We argue that replicated landscape-scale studies are now needed that describe changes across a range of biodiversity groups (above and below ground) in relation to land-use and landscape context to address knowledge gaps and biases. Such descriptive studies need to be complemented by a deeper understanding of the causes of species turnover patterns, together with work on the consequences of biodiversity loss for ecosystem function and services. Biodiversity conservation in the region is becoming increasingly embedded within a more multi-functional view of agriculture-forest mosaics that attempts to recognise and value the range of services provided by tree cover and other land-uses. This relatively new perspective has the potential, at least in principle, to re-shape the drivers of land-use change because tree cover can generate additional revenue through carbon trading or certification schemes. It will become clearer over the coming decades whether this potential can be realised, but the implications for biodiversity conservation in the region are potentially profound. The socio-economic processes that have driven forest loss and degradation in West Africa are having an increasing impact on the relatively undisturbed rainforest of the Congo Basin. We conclude by pointing out that while West African forest landscapes are a potent reminder of what might happen in Central Africa in the near future, they also provide insights for developing policies and practice that might avoid comparable levels of forest loss and degradation.

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1. Introduction

The forests of West and Central Africa probably originally covered a combined area of about 3 million km². This is just over half

the area of the Amazon. Unlike the Amazon, however, the area of relatively undisturbed, genuinely wild forest is small, and limited largely to Central Africa (Fig. 1) (Ellis and Ramankutty, 2008). The remaining forest is intimately linked with the lives and livelihoods of local people, providing food, fuel, fibre and a range of ecosystem services for a population in excess of 200 million individuals. In every sense of the words, these African forests are

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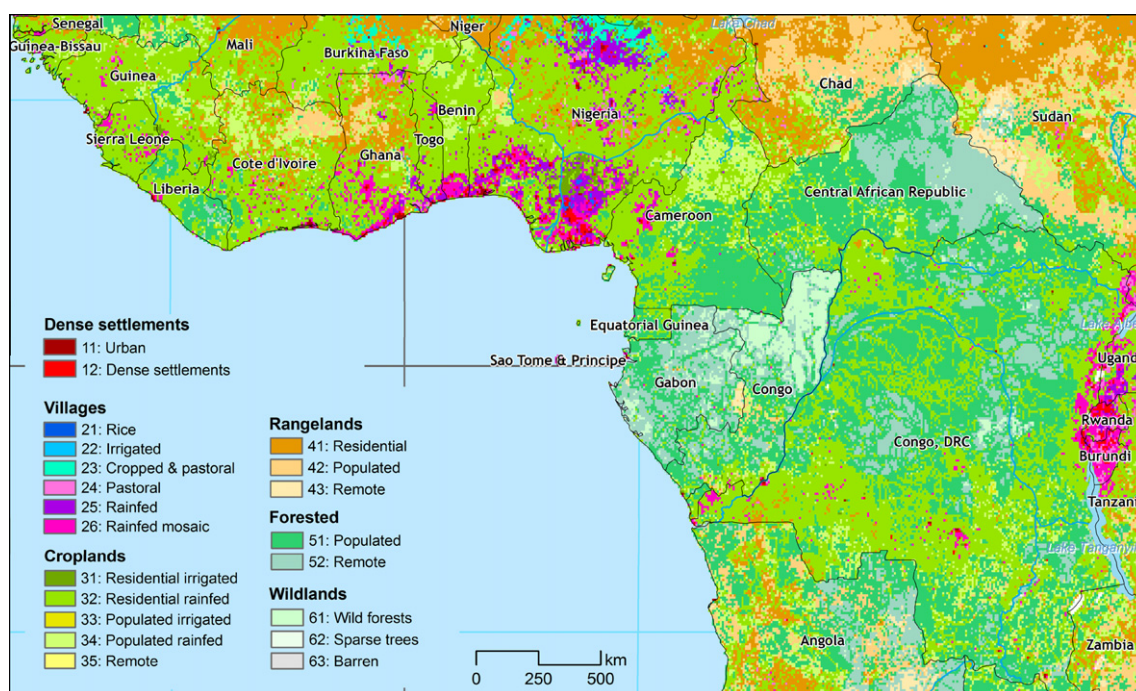


Fig. 1. Anthropogenic biomes in the West and Central African regions. Source: Ellis and Ramankutty (2008).

a tightly coupled socio-ecological system (Tallis and Kareiva, 2006).

Biodiversity in this region of Africa is important, but poorly described and little understood in terms of its functional significance. The Guinean forests of West Africa are recognised as a Biodiversity Hotspot (www.biodiversityhotspots.org/xp/Hotspots/west_africa/), supporting about a quarter of the African mammal fauna, and displaying significant endemism across a range of animal and plant groups. The tight coupling between people and these forest ecosystems inevitably means that biodiversity is threatened by habitat loss, degradation and fragmentation. Estimates of forest loss vary, but even the most conservative estimates suggest that about 10 million ha of forest were lost during the 20th century (Fairhead and Leach, 1998). Numerous endemic species are threatened with extinction and <20% of the area is protected, <5% strictly. Understanding how biodiversity responds to habitat change caused by humans is clearly pivotal for conservation efforts in the region, but our knowledge base is poor. Limited scientific work has been conducted on biodiversity in human-modified forest landscapes in West Africa compared with Amazonia or SE Asia (Gardner et al., 2009).

Against this dynamic background of change, our review has a number of goals. First, we aim to identify the main causes of forest loss and degradation in West Africa. Next, we synthesize and review our state of knowledge on the value of human-modified habitats for forest biodiversity, and the impact of forest fragmentation on biodiversity. Finally, we discuss the implications and limitations of our existing knowledge; assess how biodiversity might fit into an increasingly multi-functional view of human-modified landscapes (Kareiva et al., 2007; Naidoo et al., 2006; Norris, 2008); and speculate on the parallels between West and Central Africa. Our review focuses primarily on the forests of West Africa or the Guinean Forests as they are often termed. These forests stretch from Guinea and Sierra Leone eastwards to the Sanaga River in Cameroon, and include the countries of Liberia, Côte d'Ivoire, Ghana, Togo, Benin, and Nigeria. The Guinean Forests are divided into two distinct sub-regions (*Upper* and *Lower* Guinean Forests) sepa-

rated by the Dahomey Gap ranging from southeastern Ghana across to southern Benin, an area of savannah, dry forests and farmland. In addition to this focus on West Africa, we also include biodiversity studies from Central Africa in order to supplement the limited information available.

2. Causes of deforestation and degradation

In simple terms, forests are lost and degraded because people modify forested landscapes in a range of ways, including agricultural expansion, wood extraction and infrastructure extension. In turn, these changes are driven by an often complex array of socio-economic factors. Although these processes have a number of labels in the literature, we refer to the modification of forested landscapes by humans as *land-use change*, and the factors causing land-use change as *drivers of land-use change* (Mattison and Norris, 2005). Understanding both is important if biodiversity conservation is to be addressed by policy and practice in the region that affects forest landscapes.

2.1. Land-use change

We outline the most significant land-use changes affecting the West African Guinean Forests in Table 1. Remote sensing shows that agricultural expansion is the most significant cause of deforestation (Fig. 1, Table 2). Under the assumption that the forest-agricultural mosaic was once dense forest, it is estimated that 83% of these forests had been converted by 2000. This is probably an over-estimate because not all forest-agricultural mosaic was derived from forest, and fallow-cropping cycles are a typical part of the farming system. Nevertheless, it is clear that forested landscapes in West Africa are now dominated by forest-agriculture mosaics (Fig. 1, Table 2). Agricultural expansion has been equivalent across commercial commodities and food staples with an increase of 7.3 million ha in the area harvested of cassava *Manihot esculenta*, plantain *Musa x paradisiaca*, cocoyam *Colocasia* spp., oil

Table 1
Principal land-use changes in the Upper and Lower Guinea rainforest of West Africa.

Agricultural expansion	Staple food expansion (smallholder)	
	Commercial agriculture (large-scale and smallholder)	
Wood extraction	Timber extraction	Private company selective logging Undeclared logging
	Fuelwood/charcoal	Domestic uses rural urban Industrial uses
Infrastructure extension	Roads (public, logging)	
	Private enterprise infrastructure	Hydropower Mining Human settlements

Table 2
Area in dense forest (DF) versus forest-agricultural mosaic (FAM) land-use in the year 2000. Source: Mayaux et al. (2003).

Country/region	Area in production (000 ha)		
	Dense forest	Forest-ag. mosaic	Ratio of FAM to DF
Cote d'Ivoire	1124	13,792	12.27
Ghana	1193	6525	5.47
Guinea	665	6108	9.18
Liberia	2488	6211	2.50
Nigeria	3411	8736	2.56
Sierra Leone	603	5156	8.55
Togo	53	206	3.89
West Africa	9537	46,734	4.90
Central Africa	203,367	54,140	0.27

Table 3
Annual growth rates^b in area harvested, yield per ha, and production for five major commodities produced in the humid lowland agro-ecosystems of Guinea, Sierra Leone, Liberia, Côte d'Ivoire, Ghana, Togo, and Nigeria from 1988 to 2007. Source: FAOSTAT.

Commodity	Area (%)	Yield (%)	Production (%)
Cassava	3.89	0.617	4.51
Oil palm	2.20	-0.173	2.03
Cocoa	3.17	0.789	3.96
Cocoyams ^a	5.87	-0.293	5.58
Plantain	3.29	0.806	4.10

^a Data are from 1998 to 2007 for cocoyams.

^b Annual growth rates are calculated using the least-squares regression method, which takes into account all observations in a period.

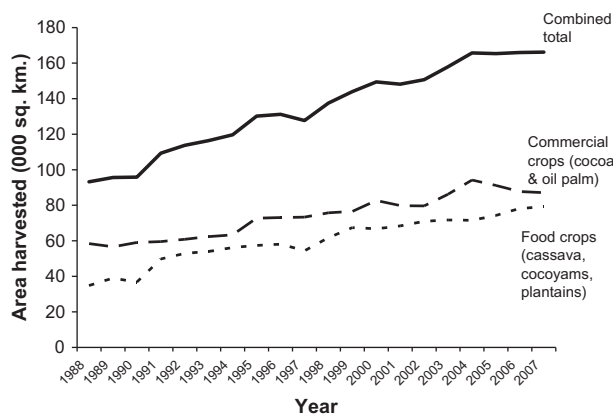


Fig. 2. Trends in aggregate area harvested in the humid lowlands of Guinea, Sierra Leone, Liberia, Côte d'Ivoire, Ghana, Togo, and Nigeria for the principal food and commercial commodities from 1988 to 2007. Source: FAOSTAT, April 28, 2009.

palm *Elaeis guineensis* and cocoa *Theobroma cacao* from 1988 to 2007 (Fig. 2).

Agricultural expansion has also interacted with other land-use changes (Table 1). Although direct deforestation in West Africa due to selective logging is relatively low, because of the low density of trees actually cut, the road infrastructure associated with logging activities can increase agricultural expansion. For example, in Côte d'Ivoire, the road infrastructure left by the timber concessionaires facilitated, at least in part, the influx of agricultural migrants from the savannah regions of Côte d'Ivoire, Burkina Faso, and Mali which led to agricultural expansion, particularly of cocoa and coffee *Coffea robusta*, causing rapid deforestation (Ruf, 2001). A similar process has been reported from other forested regions (Michalski et al., 2008).

Studies on fuelwood and charcoal production for domestic urban and rural use have shown that this is generally not a primary driver of deforestation, but that it can be an important cause of forest degradation (Deméno, 1997). Private infrastructure associated with hydro-electric dams and mining plays a role in forest loss, although on a much smaller scale to agriculture. Lake Volta in Ghana and Lakes Kossou and Buyo in Côte d'Ivoire with a combined area of 10,550 km² (roughly 10% of the remaining area of dense forest) were constructed in the 1960s and 1970s to provide electricity. In Ghana over 58,000 km² are currently licensed to gold mining concessions, much of it in the forest zone. Although more environmentally responsible policies have been adopted by some companies, most large industrial and artisanal mining operations in West Africa use surface mining techniques that result in significant deforestation.

2.2. Drivers of land-use change

While agricultural expansion is clearly the primary cause of deforestation in West Africa, a range of factors have contributed to this expansion, including human population growth and movements, limited investment in agricultural research and poor rural support services, and the management of commodity markets. One of the fundamental factors has been demographic growth and the growth in urban food demands. Population growth in the countries comprising the Guinea Forest has averaged 2.8% over the last five decades and the 236 million West Africans today are nearly four times the population at independence (Source: FAOSTAT). Urbanization rates in excess of 4–5% per annum have provoked similar growth in aggregate urban food demand, resulting in higher food prices. Higher food prices in turn have promoted an expansion of output destined for urban markets. Production of the four major food crops of the humid lowlands all increased from 1988 to 2007 at rates of growth that were roughly parallel with urbanization rates (Table 3). The countries of the dense forest in

West Africa also expanded output in the cocoa sector over this period, mainly the result of increased cocoa planting by smallholder farmers operating along the forest margins (as defined by Chomitz et al. (2006)). This latest expansion has come at a high environmental cost as cocoa farmers have encroached on the most important remaining protected areas of the Upper and Lower Guinea Forest including Tai National Park, Bia National Park, Cross River National Park and Korup National Park. Agricultural expansion has also been fuelled by human migration into the forest zone in a number of countries, including Côte d'Ivoire, Ghana, Cameroon and Nigeria. This not only promotes deforestation, but studies elsewhere suggest that migrant populations may employ different, and sometimes more intensive, land management strategies than indigenous people (Steffan-Dewenter et al., 2007).

While population growth coupled with migration has contributed to agricultural expansion on the demand side, the failure to develop land saving innovations and continued reliance on low input traditional technology on the supply side has greatly contributed to the area harvested. The share in the growth in production due to improved yields was in no case greater than 20% for any commodity, with oil palm and cocoyam yields actually declining over the last 20 years (Table 3). Several factors underlie the yield stagnation which has led to the 7.3 million ha expansion in area harvested over the last 20 years, including limited access to and uptake of new technologies by farmers; poor investment in agricultural research; a lack of extension services; and poorly developed rural financial services.

Lastly, Ghana and Côte d'Ivoire cocoa producers' ability to intensify their production has been hampered by high rates of export taxation over recent years. For example, in Ghana, the policy of a single pan-territorial price set annually by the price review committee of COCOBOD, the cocoa marketing board, results in the subsidization of producers in the more remote enclaves where marketing costs are higher. These enclaves are also usually where the last remnants of forest are still to be found (Chomitz et al., 2006).

3. Biodiversity in human-modified landscapes

3.1. Forest baselines

In order to measure the effects of changing land-uses, their biodiversity value must be compared with some baseline. The timeframes of most studies are too small to assess changes before and after forest conversion, so instead, change is frequently estimated by comparing modified land-uses with forest baselines. However, those forest baselines can themselves be highly modified, such that all studies are prone to unquantified shifting baselines (Gardner et al., 2009). The result is that many studies are likely to underestimate the impacts of human activities on forest species. All West African forests are affected by human activities to some extent, even those apparently not yet affected by direct land-use change. Understorey plants are affected by livestock grazing, and other plants and lichens are subject to uncontrolled collection for local use or commercial sale (Chapman et al., 2004; Porembski and Biedinger, 2001). Non-native species, such as the little fire ant *Wasmannia auropunctata*, can damage populations of native species, often in synergy with habitat disturbance (Ndoutoume-Ndong and Mikissa, 2007; Walker, 2006). Populations of many larger vertebrates have been greatly reduced by hunting (Chapman et al., 2004; Fa et al., 2003; Oates et al., 2000).

Over past centuries and millennia, most West African forests have been affected by climatic fluctuations and human activities (Fairhead and Leach, 1998; White and Oates, 1999). Vascular plants endemic to West Africa appear to be more tolerant of habi-

tat disturbance than species in other tropical forest regions, and it could be that West Africa has already experienced an extinction filter and has lost its most disturbance-sensitive species (Holmgren and Poorter, 2007). Larsen concluded that probably no species of forest butterfly has gone extinct in West Africa in recent decades, despite high recent rates of deforestation (Larsen, 2008). Again, this could suggest resilience, but species extinction is a very extreme measure of change, and equally, this conclusion might need to be re-examined in the face of evidence that the rates of 20th century deforestation have been overestimated (Fairhead and Leach, 1998).

3.2. Land-use change impacts

We used keyword searches in ISI Web of Knowledge to locate studies that assessed the biodiversity value of modified land-uses compared to natural forest in West and Central Africa (details available from the authors on request; Table 4). The paucity of well-designed studies assessing the change in biodiversity value of modified land-uses compared to natural forest is noteworthy. We used species richness and the proportion of species shared with baseline forest as common metrics across studies. While these metrics provide only a crude assessment of biodiversity change, more informative metrics such as community similarity indices (Holbech, 2009) were not consistently available. Many of the studies we found acknowledged the modified nature of their baseline forests, which included "near-primary" forests, old secondary forests, small forest fragments, previously logged forests and forests subject to agricultural encroachment. Not all land within the "forest zone" would necessarily have been forest even in the absence of human impact (Fairhead and Leach, 1998; Karr, 1976), and even unmodified forests show differences in species richness and composition because of geographical, topographical and climatic variation (Ojo and OlaAdams, 1996; Poorter et al., 2008).

We found 35 studies that met our search criteria, and between them they provided quantitative species richness information on 25 plants, 44 invertebrates and 18 vertebrates comparisons between forest and other land-uses. For studies that sampled multiple replicates of a single land-use type, we included an average value, while for studies that reported the results of different sampling methods we took the results of each sampling method as a separate comparison. For each comparison, we extracted the best estimate of species richness of the modified land-use relative to forest, and, where available, the number of species shared between that land-use and forest. The methods, design, scope and scale of the studies varied enormously, and for that reason, appropriate caution should be used in the interpretation of Fig. 3, which aims to summarise changes in species richness across different land-uses.

3.2.1. Logged forests

Most of the remaining forests in West Africa have been logged to some degree, and 30% of the forests of Central Africa are under logging concessions (Laporte et al., 2007). Understanding the value of logged forests to biodiversity is thus of considerable importance. For plants, invertebrates and vertebrates, logged forests were consistently comparable to unlogged forests in terms of overall species richness (Fig. 3). They supported a greater proportion of forest species than any other modified land-use (Fig. 3). There was some variation between studies: the most extreme outlier (2.8 times the species richness of unlogged forest) is a result of reporting estimates of mean richness per 40 m² plot, rather than estimates of the species richness in each land-use (Swaine and Agyeman, 2008).

Logging can enhance the recruitment of pioneer tree species, including commercial timber species, and had relatively minor ef-

Table 4

Data sources used in Fig. 3.

Study	Location	Taxon
<i>Plants</i>		
Bobo et al. (2006b)	Cameroon	Trees ≥ 10 cm, understorey plants
Van Gernerden et al. (2003)	Cameroon	Trees
Zapfack et al. (2002)	Cameroon	Vascular plants
Hall et al. (2003)	Central African Republic	Trees ≥ 10 cm
Malcolm and Ray (2000)	Central African Republic	Overstorey trees
Makana and Thomas (2006)	Democratic Republic of Congo	Trees ≥ 10 cm, trees ≥ 1 cm
Attua (2003)	Ghana	Trees ≥ 20 cm, plants < 20 cm
Swaine and Agyeman (2008)	Ghana	Trees > 5 cm dbh
Oke and Odebiyi (2007)	Nigeria	Trees
Onyekwelu et al. (2008)	Nigeria	Trees ≥ 10 cm, saplings < 10 cm
Loumeto and Huttel (1997)	Republic of the Congo	Understorey woody plants
<i>Invertebrates</i>		
Lachat et al. (2006b)	Benin	Saproxyllic beetles
Lachat et al. (2007)	Benin	Saproxyllic beetles
Lachat et al. (2006a)	Benin	Multiple arthropod taxa
Bobo et al. (2006a)	Cameroon	Butterflies
Deblauwe and Dekoninck (2007)	Cameroon	Ants
Bloemers et al. (1997)	Cameroon	Nematodes
Lawton et al. (1998)	Cameroon	Flying beetles, canopy beetles, leaf-litter ants ^a
Stork et al. (2003)	Cameroon	Butterflies
Eggleton et al. (2002)	Cameroon and Congo	Termites
Bourdanne (1997)	Côte d'Ivoire	Millipedes
Fermon et al. (2000)	Côte d'Ivoire	Fruit feeding nymphalid butterflies
Yanoviak et al. (2008)	Gabon	Arboreal ants
Basset et al. (2008a,b)	Gabon	Multiple arthropod taxa
Belshaw and Bolton (1993)	Ghana	Leaf-litter ants
Davis and Philips (2005)	Ghana	Dung beetles
<i>Vertebrates</i>		
Lawton et al. (1998)	Cameroon	Birds
Waltert et al. (2005)	Cameroon	Birds
Malcolm and Ray (2000)	Central African Republic	Small mammals
Ernst and Rodel (2008)	Côte d'Ivoire	Arboreal frogs
Holbech (2005)	Ghana	Birds
Holbech (2009)	Ghana	Understorey birds
Ernst and Rodel (2005)	Ivory Coast	Leaf-litter frogs
Blankespoor (1991)	Liberia	Birds
Karr (1976)	Liberia	Birds

^a For other taxa included in this paper, more detailed information was extracted from other papers.

fects on climbing plants and on dung beetles (Davis and Philips, 2005; Hawthorne, 1993; Kouame et al., 2004; Swaine and Agyeman, 2008). The abundance and diversity of rodents on trap transects increased along skid trails and access roads relative to that in unlogged forests (Malcolm and Ray, 2000). Bird species richness increases with logging activity up to removal rates of about 3 trees per ha, but this increase is attributable to an influx of generalist species and masks a decline in species richness of forest obligates (Holbech, 2005). A similar pattern was found in Nigeria (Abalaka and Manu, 2007). Together with the other logging studies, we included a study that looked at the effects of liberation thinning, which involved the cutting of lianas and climbers, and girdling (but not felling) of non-commercial trees (Fermon et al., 2000). Liberation thinning increased the richness and diversity of butterflies, but the species that benefited most were widespread, while those that declined were mainly Upper Guinea endemics or restricted to the Guineo-Congolian biome.

Many of the logging studies were carried out decades after logging and examined areas with low rates of selective logging: < 1 – 4 trees per ha (Hall et al., 2003; Holbech, 2005; Swaine and Agyeman, 2008; van Gernerden et al., 2003). One study that reported that their logged forest sites had suffered “heavy and repeated timber exploitation” recorded the greatest drop in species richness of the logging studies, to 75% of tree species richness, and less than 40% of sapling species shared with unlogged forest (Onyekwelu et al., 2008). Intensive logging activities have greater impacts on biodiversity, especially those that cause considerable canopy dam-

age, or that allow the invasion of the invasive non-native shrub *Chromolaena odorata* which increases the risk of fire (Holbech, 2005; Malcolm and Ray, 2000; Swaine and Agyeman, 2008).

3.2.2. Secondary forests

There are different definitions of secondary forests: some define them as any forest that has been disturbed, including logged forests, while others restrict use of the term to forests that have regrown on land that was previously completely cleared. Not all of the studies we reviewed were clear about their choice of definition. Overall species richness of various taxa in secondary forests was again mostly similar to that in baseline forests, in some cases exceeding it, while in others it was similar or slightly reduced (Fig. 3). There was a slight, but non-significant, reduction in nematode species richness (Bloemers et al., 1997). Ant species richness was similar (Belshaw and Bolton, 1993; Deblauwe and Dekoninck, 2007; Yanoviak et al., 2008) or higher (Lawton et al., 1998) in secondary forests compared to baseline forests. Species richness and composition of termites were similar in near-primary and secondary forests with good canopy cover, and turnover was as high within these land-uses as between them (Deblauwe and Dekoninck, 2007; Eggleton et al., 2002). Species richness and guild composition across multiple arthropod taxa were similar between secondary and baseline forests (Basset et al., 2008b; Lachat et al., 2006a).

Species composition of many taxa was altered in secondary forests. Plant species assemblages in secondary forests contained more light-demanding pioneer species such as *Musanga cecropio-*

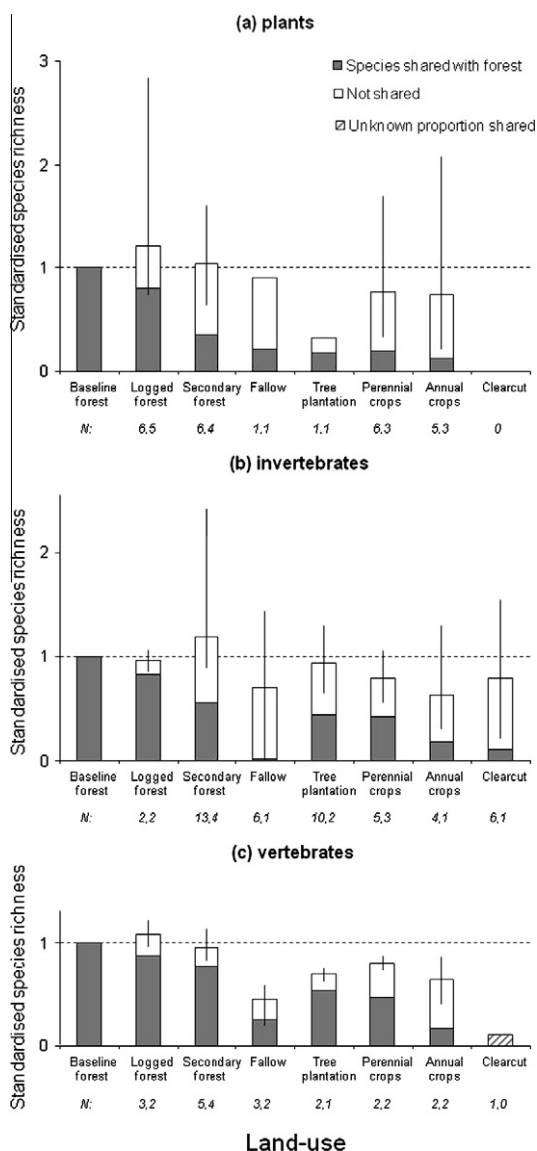


Fig. 3. Mean species richness (\pm range) of (a) plants, (b) invertebrates and (c) vertebrates in a range of land-uses, standardised relative to that in baseline (primary, near-primary or old-growth) forest (dashed line). Height of bars indicates total species richness relative to forest baseline, grey indicates the proportion of species shared with baseline forest, hatching is used when the latter proportion is unknown. The numbers below each bar refer to the number of comparisons used for total species and for shared species richness.

ides, and fewer understorey specialists typical of old-growth forests (Bobo et al., 2006b; Makana and Thomas, 2006; Zapfack et al., 2002). Young secondary forest had higher alpha diversity but lower beta diversity of ants than older forest (Deblauwe and Dekoninck, 2007). Ant community composition differed in some studies (Deblauwe and Dekoninck, 2007) but not others (Belshaw and Bolton, 1993; Yanoviak et al., 2008). Butterflies reached higher abundance in secondary forest, but species with the smallest ranges showed a preference for near-primary forest (Bobo et al., 2006a). The species richness of frogs was reduced in secondary forest, with the loss of some forest species and an influx of farm-bush species such as *Afrixalus dorsalis* (Ernst and Rodel, 2005, 2008). Most bird guilds had similar species richness in secondary forest and near-primary forest, but terrestrial insectivores and large foliage-gleaners declined (Waltert et al., 2005).

The age of secondary forests, and their proximity to mature forests that can act as colonisation sources influence the extent and

rate of recovery of their biodiversity value (Deblauwe and Dekoninck, 2007; Makana and Thomas, 2006). Where ages were given, we included secondary growth of less than 10 years as fallow (see below), but some studies pooled data from forests of 5–50 years, or gave no information on age.

3.2.3. Fallow

Fallow land is essentially young secondary growth, but it will only develop into secondary forest if it is released from the cycle of cultivation and temporary abandonment (Carriere et al., 2002). Across all taxa, fallows generally had lower species richness, and shared fewer species with baseline forest, than secondary forest (Fig. 3), although more species of flying beetles were caught in traps in fallow than in near-primary forest (Lawton et al., 1998). Fallow is typically dominated by herbaceous pioneer plant species, and remnant non-native species such as papaya *Carica papaya* and cocoa can be abundant (Hall and Okali, 1979; Zapfack et al., 2002). Nematode species richness was significantly higher in a fallow plot than in an annual crop plot, suggesting some recovery of soil microfauna after abandonment (Bloemers et al., 1997). Bird species richness was greatly reduced in fallows, and most of the species that did occur were generalists, with secondary forest species becoming more common in older fallows (Blankespoor, 1991; Karr, 1976; Lawton et al., 1998).

3.2.4. Tree plantations

While natural forest has declined across West Africa, plantations, often but not always of non-native species, have been established to help meet increased demand for timber, fuelwood and pulp. Clearly, such plantations are of limited value for native tree species, and species richness in other taxa was also typically lower relative to baseline forests (Fig. 3). If established near to mature forests, tree plantations can provide more suitable habitat than savannah for some forest plant species, especially if protected from fire, undergrowth weeding and herbicides (Loumeto and Huttel, 1997). Species richness of many invertebrates was similar in tree plantations to that in baseline forests (Bloemers et al., 1997; Eggleton et al., 2002; Lachat et al., 2006a, 2007; Lawton et al., 1998; Stork et al., 2003) but reduced in others (Fermon et al., 2000; Lachat et al., 2006b). The method of land preparation makes a large difference: plantations established by partial manual clearance rather than complete mechanical clearance held greater diversity of a range of taxa (Eggleton et al., 2002; Lawton et al., 1998; Watt et al., 2002). Reduced species richness of saproxylic beetles in non-native tree plantations was associated with a paucity of dead wood in plantations, as a result of firewood collecting by local people (Lachat et al., 2006b).

3.2.5. Perennial crops

Perennial crops are a mainstay of West African agriculture, and there is a worrying possibility that some might start to replace Central African forests on a large scale (Fitzherbert et al., 2008). The studies we reviewed included assessments of biodiversity in cocoa, oil palm, coffee, coconut *Cocos nucifera*, plantain and avocado *Persea americana* farms. Management practices, such as the extent to which native trees are retained, probably affect biodiversity more than the crop *per se* (Holbech, 2009), but we found insufficient studies to examine this issue in detail. Some studies failed even to state whether crops were grown under shade or not. Assessments of the effects of changing management practices are important, because there are economic incentives for farmers to switch to unshaded systems, or systems where shade is provided by a small number of useful tree species (Sonwa et al., 2007).

Diverse agroforestry systems, where crops are grown in the shade of forest trees, are recognised as supporting relatively high species richness relative to unshaded systems (Bisseleua et al.,

2009; Herve and Vidal, 2008). Cocoa farms supported more plant species overall, but fewer tree species, than open-canopy forest (Attua, 2003). Other studies found that while cocoa and coffee agroforests supported a greater species richness and abundance of trees than unshaded cocoa, they still had many fewer species and individual trees than baseline forests (Bobo et al., 2006b; Oke and Odebiyi, 2007). Cocoa agroforests supported about 70% of the tree densities and basal area as near-primary forests, but very few small-sized trees, suggesting limited recruitment (Waltert et al., 2005).

Cocoa agroforests supported as many butterfly species as did forests, but had few butterflies with narrow geographical ranges (Bobo et al., 2006a). Cocoa agroforests supported fewer than half as many termite species as primary forest (Eggleton et al., 2002). One-quarter of the millipede species recorded in baseline forests were not found at all in any of three different perennial crops nearby, but other species increased in abundance by as much as two orders of magnitude in perennial crops (Bourdanne, 1997). Dung beetle species richness was lower in perennial crops, and forest species were largely replaced by species typical of savannas (Davis and Philips, 2005). In contrast, a high proportion of forest bird species were found in semi-shaded coconut and cocoa farms located in or near forests (Holbech, 2009). In cocoa agroforests, groups of birds such as ant-followers, insectivores and biome-restricted species declined, while flower-visitors (sunbirds) increased (Waltert et al., 2005).

3.2.6. Annual crops

A variety of more-or-less annual crops are grown in West and Central Africa, often in small mixed farms for domestic consumption. The studies we reviewed included farms containing a wide diversity of crop species, including cassava, maize *Zea mays*, groundnuts *Arachis hypogaea*, taro/cocoyam and vegetables as well as scattered forest and fruit trees (Basset et al., 2008b; Bobo et al., 2006b). In a farm-fallow mosaic in Cameroon, species richness of trees was only one-fifth of that in nearby closed canopy forest, but there were more than twice as many understorey plant species (Bobo et al., 2006b). Other studies found much lower diversity of vascular plants in mixed food crops relative to that in forests (Attua, 2003; Zapfack et al., 2002). Very few plant species were shared between forests and annual crop farms.

Invertebrate species richness in annual crops ranged from less than half that in forests (Bloemers et al., 1997; Bobo et al., 2006a; Eggleton et al., 2002) to 1.3 times that in old forest (Basset et al., 2008b). Bird species richness was lower in annual crop farms relative to that in forest, and some groups of species, such as ant-followers, insectivores, bulbuls and medium and large foliage-gleaners were largely replaced by others, including granivores, sunbirds and non-breeding visitors (Blankespoor, 1991; Waltert et al., 2005). The retention of isolated forest trees in farms helped to maintain higher species richness of some ants and beetles relative to farms without trees (Dunn, 2000).

3.2.7. Clearcut

Assessments of the biodiversity value of completely cleared land came from multiple studies of the same two 1 ha plots in southern Cameroon, and give an indication of the capacity of a range of species to recolonise from adjacent forests. The plots were bulldozed to remove all vegetation and dead wood, removing topsoil and causing compaction (Lawton et al., 1998). After 1–5 years, they had less than half as many soil nematode species as near-primary forest: a similar level of species richness to that in an annual crop field (Bloemers et al., 1997). The plots were planted with *Terminalia ivorensis*, and sampled for termites when the trees were 1–2 m high: one-fifth as many species were found as in near-primary forests (Eggleton et al., 2002). More species of flying beetles, fewer

canopy beetle species and slightly fewer leaf-litter ant species were collected from the clearcut plots than from near-primary forest (Lawton et al., 1998). Sampling of butterflies about a year later found reduced abundance but similar species richness relative to near-primary forest (Stork et al., 2003).

3.3. Forest fragmentation

Although West African forests are among the most highly fragmented in the world, there have been surprisingly few studies of the impacts of fragmentation on forest species. Large fragments held more species of trees, and also a higher proportion of rare species, than smaller fragments (Hill and Curran, 2003). Butterfly communities in forest fragments were affected by edges to a distance of at least 100 m; large fragments supported more forest species, but small fragments also held considerable species richness and facilitated dispersal (Bossart and Opuni-Frimpong, 2009; Bossart et al., 2006). One study of birds found fewer species in smaller fragments, but no effect of isolation, while another found no effect of fragment area, but significant losses in more isolated fragments (Beier et al., 2002; Manu et al., 2007): the discrepancy probably results from the different ranges of fragment sizes and isolation distances included in each study. A study of leaf-litter frogs found reduced species richness and altered community composition in fragments, which were attributed to habitat degradation consistent with edge effects, rather than area or isolation effects *per se* (Hillers et al., 2008).

4. Discussion

4.1. Biodiversity and forest loss

The picture in West Africa is one of highly modified tropical forest landscapes, with the remaining dense forest often degraded and fragmented. Much of the tree cover in these landscapes is part of a forest-agriculture mosaic (Fig. 1; Table 2), which is changing from shifting cultivation systems to short-fallow and permanent crops. Tree cover, in both dense forest and the agricultural mosaics, is lost as a result. This is a complex socio-ecological system in which the fate of biodiversity is intimately linked to the way people use land, particularly for agriculture.

Data on biodiversity in these human-modified landscapes from the region are patchy, and prone to a number of generic problems that affect many biodiversity datasets from tropical forests. Nevertheless, our synthesis does reveal some clear patterns (Fig. 3). Across plant, invertebrate and vertebrate groups, there is a significant loss of forest species as tree cover is reduced and vegetation structure simplified (moving from left to right in Fig. 3). Although in some instances overall species richness increases in modified habitats (Fig. 3, logged and secondary forest), richness of endemic species tends to decline. There is considerable species turnover between modified habitats and baseline forests: non-forest species and habitat generalists replace many of the original forest species (grey shaded portions of bars in Fig. 3). The loss of forest species seems most pronounced for plants, in which species turnover occurs in logged and secondary forests to a greater extent than is apparent for certain animal groups (i.e. vertebrates). While caution is required in interpreting this pattern due to data limitations, this is perhaps not surprising as plant biodiversity is actively managed in all the land-use systems we reviewed.

While some broad statements about biodiversity patterns can be made, there are significant gaps in both our knowledge and understanding. The biodiversity data we do have often consist of species inventories collected over limited spatial and temporal scales, and without information on species' abundances or their

ecological attributes. The detectability of most taxa varies between habitat types, and is typically lower in densely vegetated forests with tall inaccessible canopies than in more open modified habitats with broken, lower canopies (Gardner et al., 2009). Some of the studies we reviewed used species richness estimators to correct for this problem, which can help but cannot correct for inadequate sampling design, e.g., failure to sample insects from the canopy. Landscape context is frequently neglected in study design: biodiversity in small plots of modified habitat surrounded by forest are likely to contain many “tourist” species unable to persist in them (Basset et al., 2008a). Extinction lags are also likely in modified landscapes: some species, such as shade tolerant trees, can persist as remnants for decades or centuries in farmed landscapes, but cannot complete a reproductive lifecycle there. Estimates of beta diversity, which is often high in tropical forests, require considerable sampling effort and are often neglected (Baselga, 2010). Most biases, therefore, are likely to be in the direction of overestimating the biodiversity value of modified habitats, a point that should be borne in mind when interpreting Fig. 3.

Basic species inventory data from key habitats are limited, particularly from the forest canopy and below ground. The latter in particular is an important issue given the role of soil biodiversity in key ecosystem processes such as decomposition and nutrient cycling; our limited understanding of how soil biodiversity and ecosystem functioning respond to land-use change; and the implications this might have for soil health and the sustainability of farming systems in the medium to long-term. This functional perspective is important because with the exception of the traditional uses of forest plants, we have a very rudimentary understanding of the functional role of biodiversity in modified tropical forest landscapes. While some basic patterns are beginning to emerge from studies elsewhere (Klein et al., 2006; Ricketts, 2004), this issue is virtually unexplored in a West African context. Taken together, these limitations mean we increasingly need to collect biodiversity data from replicated landscape-scale studies in which we explore the interaction between land-use and landscape context simultaneously across a range of biodiversity groups (Gardner et al., 2008, 2009; Norris, 2008). Such descriptive studies need to include a deeper understanding of the causes of species turnover patterns, together with work on the functional importance of biodiversity in these landscapes.

4.2. Multi-functional landscapes

The fact that all biodiversity groups show species loss and turnover as intact forest is converted to other land-uses implies that the protection of intact, dense forest has to be part of any biodiversity conservation strategy in the region designed to protect forest biodiversity. Improved management of forests that are already used for logging and hunting could additionally benefit many species (Clark et al., 2009; Malcolm and Ray, 2000). In areas that have been largely deforested, forest fragments can have considerable biodiversity value, and cultural institutions that protect these fragments (e.g., as sacred groves) (Decher, 1997) potentially have a role to play. In farmed lands, efforts to quantify the trade-offs and synergies between the strategies of intensification to spare forests and agroforestry interventions to boost on-farm biodiversity are still at an early stage (Green et al., 2005; Norris, 2008). What is clear is that opportunities to increase yields with minimal impact on biodiversity, and those to improve forest protection with minimal impact on livelihoods, need to be identified and developed. The complex interplay between conservation efforts and issues such as land tenure, rural livelihoods, farming, governance, commodity markets and the local environment is beyond the scope of our review, but will have implications for biodiversity and its protection in the future.

There is an increasing trend towards considering human-modified landscapes as multi-functional ecosystems that deliver a range of services that in turn affect human well-being (Fisher et al., 2006; Kareiva et al., 2007; Naidoo et al., 2006; Norris, 2008). In the context of forest landscapes, this ecosystems-approach is potentially important because it attempts to recognise and value the range of services provided by tree cover and other land-uses, and hence has the potential, at least in principle, to re-shape the drivers of land-use change. For example, forest and agro-forestry systems producing crops like cocoa store significant amounts of carbon (Albrecht and Kandji, 2003; Lewis et al., 2009). If this carbon could be brought to market for sale as carbon credits then this could provide farmers with a financial incentive to replant or retain tree cover in the landscape, thereby protecting other ecosystem services and biodiversity, at least to some extent. Whether such a mechanism would work in practice, the scale at which it should be considered, and the extent, to which it is capable of delivering wider benefits for the environment and biodiversity, remains to be seen. We have a limited understanding of carbon stocks in different land-use types above and below ground, and how these change through time; the potential socio-economic impact of carbon payments; the mechanisms required for successfully linking rural communities to carbon markets; and the policy instruments needed at national level. Nevertheless, it seems likely that pilot projects within the region will be established within the next few years to explore these issues in more detail, and their outcome could have profound implications for biodiversity conservation in the future.

Multi-functionality is also being promoted by a range of certification schemes (e.g. Rainforest Alliance Certification; www.rainforest-alliance.org/). These schemes represent land management standards that are intended to protect or enhance biodiversity and other environment values. Certification benefits the land owner/manager through premium price payments for produce or access to markets in which consumers demand products with a relatively low environmental impact. Although such schemes clearly have the potential to benefit biodiversity and the wider environment, further research is required to quantify the benefits and risks, assess the scales over which benefits are being and are likely to be delivered, and to assess the socio-economic implications for livelihoods and land-use (Perfecto et al., 2005).

4.3. Wider implications

The tropical forest zone in West Africa has experienced centuries of human modification, leading to a substantial decline in forest cover and loss of forest biodiversity. In contrast, large areas of undisturbed, wild forest remain in Central Africa (see Fig. 1), implying that in this region significant opportunities to protect forest biodiversity exist in the absence of extensive human modification. The extent to which this opportunity remains depends on how humans are likely to modify Central African forests in the near future. Are there parallels between the future of this region and West Africa? Logging activities in Central Africa are increasing (Laporte et al., 2007), bringing with them infrastructure (e.g. roads), which makes the forest interior more accessible. In West Africa, the opening up of the forest interior through logging concessions effectively facilitated agricultural expansion to service increasing food demands from a growing and increasingly urban human population, as well as making forest areas more accessible to bushmeat hunters. There is growing concern and accumulating evidence to suggest that comparable processes are likely to drive deforestation, forest fragmentation and biodiversity loss in the Congo basin in the near future (Laurance et al., 2006a,b; Wilkie et al., 2000; Zhang et al., 2006). Industrial-scale agricultural may also play an important role (Butler and Laurance, 2008). West Afri-

can forest landscapes are a potent reminder of what might happen in Central Africa in the near future, but could also provide insights to inform conservation and development decisions in Central Africa that may avoid comparable levels of forest loss and degradation.

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