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Authors: Cronin, Drew T., Libalah, Moses B., Bergl, Richard A., and Hearn, Gail W.

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Biodiversity and conservation of tropical montane ecosystems in the Gulf of Guinea, West Africa

Drew T. Cronin*†‡

Moses B. Libalah‡

Richard A. Bergl§ and

Gail W. Hearn*†

*Department of Biology, Drexel University, 3245 Chestnut Street, PISB 503, Philadelphia, Pennsylvania 19104, U.S.A.

†Bioko Biodiversity Protection Program, Calle Botuku Luba s/n, Barrio Presidencia, Malabo, Bioko Norte, Equatorial Guinea

‡Laboratory of Plant Systematics and Ecology, Higher Teachers' Training College, University of Yaoundé I, Yaoundé, Cameroon

§North Carolina Zoological Park, 4401 Zoo Parkway, Asheboro, North Carolina 27205, U.S.A.

#Corresponding author: dtc33@drexel.edu

Abstract

Mount Cameroon (4095 m), the highest peak and only active volcano in West Africa, is located in the center of the Gulf of Guinea Pleistocene refugium. The associated forests and highlands along the southern Nigerian-Cameroon border and on the island of Bioko, known as the Biafran forests and highlands, are important formations of the Cameroon Volcanic Line owing to their wide elevational range, and on Mount Cameroon, a continuous gradient of unbroken vegetation from sea level to over 4000 m. The montane zones in the region begin 800 m above sea level forming the critically endangered Mount Cameroon and Bioko Montane Forests ecoregion.

The broad elevational gradient of the region has resulted in high habitat diversity, leading the region to be a center for species endemism and richness across many taxa. Some of the densest human populations in Africa also occur in this region, putting intense pressure on the forests and highlands mostly due to overexploitation and habitat loss. The governments of Nigeria, Cameroon, and Equatorial Guinea have designated protected areas in the region, but coverage is inadequate, especially for the rare montane ecosystems and endemic taxa. More importantly, protected areas are often not accompanied by effective management and regulatory enforcement. We recommend improved law enforcement and an expansion of the protected area network, as well as stronger commitments of institutional, financial, and technical support from governments and non-governmental organizations, in order to move conservation in the region in a positive direction. Without significant and immediate conservation progress, increasing anthropogenic pressure and systemic ineffectiveness of protected area management represent major concerns for the future of this important area.

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Introduction

The West-African rainforest zone centered between the Cross and Sanaga Rivers, including Bioko Island, Equatorial Guinea, and the Cameroon Highlands, has long been recognized for its unique ecological and biological diversity (Eisentraut, 1973; Barthlott et al., 1996; Myers et al., 2000; Olson et al., 2001; Oates et al., 2004). One of the driving factors behind the region's diversity patterns is the wide variety of habitats resulting from its extensive highland areas (Fig. 1). The region includes broad interconnected plateaus, like the Bamenda Highlands, as well as isolated peaks, such as Mount Cameroon (4095 m) in southwest Cameroon, and Pico Basilé (3011 m) on Bioko Island, the largest insular portion of Equatorial Guinea (Cable and Cheek, 1998; Oates et al., 2004). Referred to collectively by Bergl et al. (2007) as the Biafran forests and highlands (BFH), the region has been identified as a center of biodiversity at both continental (Brooks et al., 2001; Oates et al., 2004) and global scales (Myers et al., 2000; Olson et al., 2001). The BFH form part of the West African Forests biodiversity hotspot, and encompass three ecoregions: the Mount Cameroon-Bioko montane forests, the Cameroon Highlands, and the Cross-Sanaga-Bioko coastal forests (Olson et al., 2001). High levels of species richness and endemism are represented in the BFH across many taxa, such as primates (Oates, 2011), amphibians (Lawson, 1993; Schiotz, 1999), birds (Stattersfield et al., 1998), and vascular plants (Onana and Cheek, 2011). Geographically, the diversity of the BFH is not distributed evenly; patterns of endemism appear to follow an elevational gradient, with highland areas harboring the greatest species concentrations (Barthlott et al., 1996; Oates et al., 2004).

The biological richness of the BFH is currently under increasing threat from human activities. Although there are no permanent human settlements within the highest elevation areas of the BFH, much of the highland zone, which supports the many montane endemic species in the BFH, has no formal protection (Bergl et al., 2007). Additionally, highland areas are encircled by some of the highest human population densities in tropical Africa, some of which exceed 100 inhabitants km⁻² (Albrechtsen et al., 2006; CIA, 2013). These people rely on the forested regions for their health and livelihoods, either directly for their subsistence, or indirectly through the services provided by those ecosystems (SWPDFW et al., 2005). High population densities, coupled with a strong rate of population growth, has led to increased exploitation of remaining forests and an ever-expanding "human footprint" (Sanderson et al., 2002). This encroachment has led to the loss of much of the original lowland forest cover and the degradation and fragmentation of many remaining tracts of forest (Achard et al., 1998; Bergl et al., 2007). Existing protected areas have done reasonably well at protecting habitats more effectively than alternative land uses (Bruner et al., 2001; Oates et al., 2004; Struhsaker et al., 2005) thanks, in part, to their relative isolation and inaccessibility, but habitat loss at the fringes (Achard et al., 1998; Wittemyer et al., 2008) and hunting within protected areas are widespread (Fa et al., 2006; Abernethy et al., 2013). Truly adequate protection will require an expansion of the protected area network (Table 1) in the BFH and, more importantly, increased efficiency in the enforcement of existing legislation and the management of protected areas within the region.

In this paper, we review the physical history and patterns of biodiversity and endemism in an effort to assess the current status

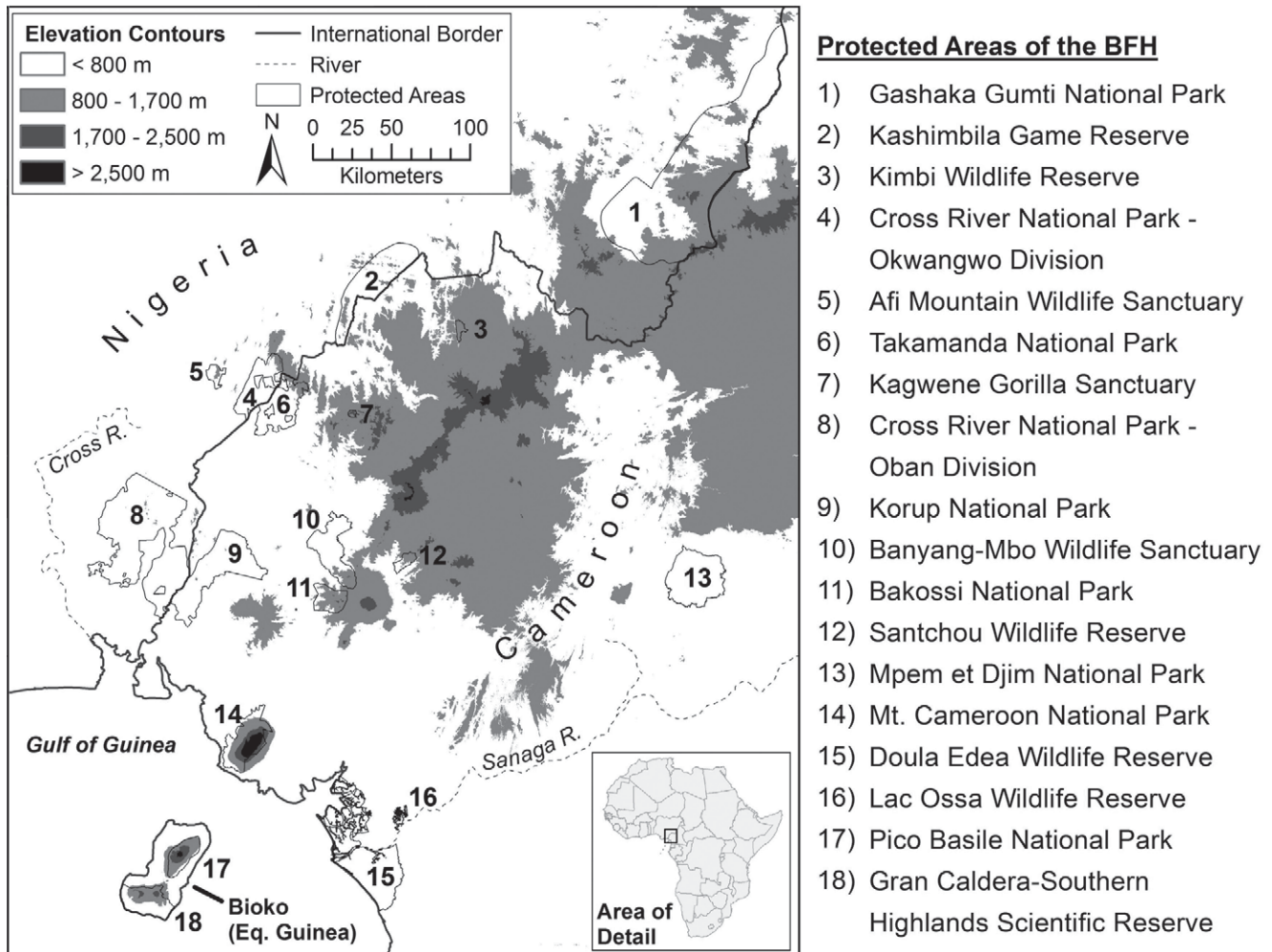


FIGURE 1. Protected areas in the Biafran forests and highlands (BFH). Topography information from the Shuttle-Radar Topography Mission (SRTM; available from U.S. Geological Survey). Protected area boundaries from IUCN and UNEP (2010).

of threats and conservation progress in the BFH, with an emphasis on the unique montane ecosystems of the region. We focus particular attention on the “twin peaks” of Bioko Island and Mount Cameroon, due to the authors’ expertise, as well as the peaks’ high elevations, recent shared biogeographic history, and relative isolation from other highland areas in the BFH (Onana and Cheek, 2011). We assess the coverage of existing protected areas, as well as major policies that have been established to combat increasing threats and conserve biodiversity. Finally, we suggest ways in which the conservation of biodiversity in the region could be improved for the future.

Geologic and Biogeographic History

The BFH are situated on the margin of the West African and Congo cratons, where volcanic activity in the Lower Cretaceous (100 Ma) led to the formation of the extensive chain of highlands called the Cameroon Volcanic Line (CVL) (Tye, 1984). The CVL stretches approximately 1000 km from Lake Chad along a SE-NW axis of continental volcanoes to the volcanic islands of Bioko, Príncipe, São Tomé, and Annobón, in the Gulf of Guinea (Marzoli et al., 2000; Burke,

2001; Tsafack et al., 2009). Its highest formation, Mount Cameroon, remains the only active volcano in West Africa with seven eruptions recorded since 1900 (1909, 1922, 1954, 1959, 1982, 1999, and 2000) (Suh et al., 2003; Tsafack et al., 2009). All other major areas of volcanic activity on the continent are associated with the East African Rift Valley, over 1800 km away (Cable and Cheek, 1998). The CVL is unique for being nearly equally divided between the oceanic and continental lithosphere (Burke, 2001; Tsafack et al., 2009). Mount Cameroon, on the mainland, and Pico Basilé, on Bioko Island, are situated on the continental side of the lithospheric boundary, while the outer Gulf of Guinea islands are oceanic in origin (Jones, 1994; Burke, 2001; Tsafack et al., 2009). The oceanic islands, though not reaching elevations in excess of 2024 m above sea level (São Tomé), are surrounded by waters approximately 3000 m in depth (Deruelle et al., 1991). Bioko Island is separated from Cameroon by a 37-km-wide ocean shelf, which is less than 100 m deep, forming a land bridge with the African mainland until sea levels rose approximately 10,000 years ago (Jones, 1994; Oates et al., 2004). Patterns of biodiversity and endemism on Bioko are therefore more similar to those of Mount Cameroon and mainland Africa than to the outer islands of the Gulf of Guinea, due to parallels in their recent biogeographic history (Jones, 1994).

TABLE 1
Protected areas of the Biafran forests and highlands.

Protected area	Country	Classification	IUCN PA Category	Total area (km ²)	Area (km ²) at:			
					0–800 m	800–1700 m	1700–2500 m	>2500 m
Gashaka Gumti NP	Nigeria	National Park	II	5876	3717	2077	82	0
Oban Division Cross River NP	Nigeria	National Park	II	2687	2661	26	0	0
Douala-Edéa WR	Cameroon	Wildlife Reserve	IV	1681	1681	0	0	0
Korup NP	Cameroon	National Park	II	1295	1288	7	0	0
Kashimbila GR	Nigeria	Game Reserve	IV	1065	972	93	0	0
Mpem et Djim NP	Cameroon	National Park	IV	976	976	0	0	0
Banyang Mbo WS	Cameroon	Wildlife Sanctuary	IV	690	573	116	1	0
Takamanda NP	Cameroon	National Park	II	628	539	89	0	0
Okwangwo Division Cross River NP	Nigeria	National Park	II	607	557	48	2	0
Mt. Cameroon NP	Cameroon	National Park	II	582	88	254	120	120
Gran Caldera-Southern Highlands SR	Equatorial Guinea (Bioko)	Scientific Reserve	Ib	510	289	197	24	0
Pico Basilé NP	Equatorial Guinea (Bioko)	National Park	II	322	10	224	78	10
Bakossi NP	Cameroon	National Park	II	293	81	207	5	0
Afi Mountain WS	Nigeria	Wildlife Sanctuary	IV	104	84	20	0	0
Santchou WR	Cameroon	Wildlife Reserve	IV	95	44	51	0	0
Kimbi WR	Cameroon	Wildlife Reserve	IV	52	1	51	0	0
Lac Ossa WR	Cameroon	Wildlife Reserve	IV	46	46	0	0	0
Kagwene GS	Cameroon	Gorilla Sanctuary	IV	19	0	10	9	0
				17,528	13,607	3470	321	130

Notes: Adapted from Bergl et al. (2007); zonal delineation follows Cable and Cheek (1998). IUCN categories follow Dudley (2008): (Ib) wilderness area—large unmodified or slightly modified areas, retaining their natural character and influence, without permanent or significant human habitation; (II) national park—large natural or near-natural areas protecting large-scale ecological processes with characteristic species and ecosystems; (IV) habitat/species management area—areas protecting particular species or habitats, and management reflects this priority.

Climate

In general, the BFH have a distinctly seasonal climate (tropical equatorial) and rainfall pattern driven by the north-south movement of the Intertropical Convergence Zone (ITCZ) (Oates et al., 2004). The northward movement of the ITCZ brings heavy rains from April through October, with a peak between July and September. When the ITCZ is to the south, there is a distinct dry period from November to March that brings dry Harmattan winds sweeping down from the Sahara (Nosti, 1947; Tchouto et al., 1999; Oates et al., 2004). The BFH have some of the regions with the highest mean annual rainfall in Africa, but there is high variation in local annual rainfall dependent upon topography and proximity to the coast (Oates et al., 2004). Annual rainfall exceeds 10,000 mm on the southern coast of Bioko and the southwestern foot of Mount Cameroon, while in the rain shadows, to the north, annual rainfall is approximately 2000 mm (Nosti, 1947; Tchouto et al., 1999; Bergl et al., 2007). At least 100 mm of precipitation occurs each month on the southern coasts of Bioko and Mount Cameroon,

but to the north, in areas like the Obudu Plateau, rainfall may not exceed 50 mm over a 5 month span (Oates et al., 2004). Due to the proximity to the equator, the mean annual temperature is about 25 °C with little seasonal variation (Oates et al., 2004). However, elevational gradients can create strong temperature extremes, ranging from 35 °C at sea level to 4 °C at the summit of Mount Cameroon (SWPDFW et al., 2005). Persistent high humidity levels (75%–80%) throughout the year maintain dense cloud cover on the upper elevations of the southern extent of the region (i.e., Bioko and Mount Cameroon) (Payton, 1993).

Biodiversity and Endemism

PLEISTOCENE REFUGE

Due to its unique geologic and biogeographic history, the BFH have been identified as an important Pleistocene refuge area, which has contributed to its high biodiversity and endemism (Haffer, 1969; Hart et al., 1989; Maley et al., 1990; Oates et al., 2004;

Anthony et al., 2007). During Pleistocene glaciations, the African tropics were considerably cooler and drier. Much of the current lowland closed canopy was open savannah, and the montane zone extended 1000–1500 m lower than today, occupying significantly larger areas (Flenley, 1979; Bonnefille et al., 1990; deMenocal, 1995; Gottelli et al., 2004; Assefa et al., 2007). During this period, the area of montane habitat increased and the distance between montane habitat patches decreased, which is likely to have facilitated the existence of larger and less isolated populations of species currently restricted to mountains (Moreau, 1963; Assefa et al., 2007). Roy (1997) suggested that refugia were more impactful on montane species, leading to rapid divergence of non-continuous populations, and that montane regions have also acted as centers of speciation.

FLORA

The Mount Cameroon massif is the only remaining area in Africa where natural vegetation rises uninterrupted from lowland forest at sea level to subalpine grassland at the summit (Forboseh et al., 2011). The southwestern region of the BFH also encompasses an area of approximately 26,000 km² of forest that is considered one of the largest relatively intact contiguous forest blocks in West Africa (Oates et al., 2004). On a finer scale, however, the structure of the vegetative community of the BFH is highly dependent on elevation and can differ between sites based on local climate variation related to features such as latitude, aspect, or proximity to ocean (Oates et al., 2004). The overall phytogeography of the region includes formations dominated by Guineo-Congolian and Lower Guinea rain forest species, with Afromontane elements at higher elevations, and can be broadly categorized into strata according to elevation (Table 2) (Fa, 2000).

Plant species diversity in the BFH is the highest in tropical Africa (Barthlott et al., 1996), owing largely to its varied habitat mosaic. Mount Cameroon, for example, is an especially speciose center of plant diversity, with a total of 2435 species of vascular plants, relative to 1693 species in nearby lowland Korup National Park, and 1105 species (angiosperms only; Figueiredo, 1994) on Bioko Island (Cable and Cheek, 1998; Onana and Cheek, 2011). There is high affinity between the plant species of Bioko and western Cameroon, which suggests that Bioko is floristically part of the mainland (Exell, 1973). There are no strict endemic plants at the upper extent of Mount Cameroon (3500–4095 m); however, Cable and Cheek (1998) listed a total of 49 total endemics for the massif, of which 20 are montane species (11: 800–1800 m; 5: 1800–2100 m; 4: 2100–3500 m). There are four montane grassland endemics, of which two (*Silene biafrae* [Caryophyllaceae], *Hypseochloa cameroonensis* [Gramineae]) are listed as vulnerable and two (*Bulbostylis densa* var. *cameroonensis* [Cyperaceae], and *Habenaria obovata* [Orchidaceae]) are recognized as endangered (Onana and Cheek, 2011; IUCN, 2013). Relative to Mount Cameroon, whose 49 endemics constitute 2.01% of its overall species number, Bioko Island has at least 40 endemic species, giving it a higher relative level of endemism (3.62%) (Figueiredo, 1994).

FAUNA

The BFH are a hotspot for faunal species richness and endemism across taxonomic groups (Myers et al., 2000; Brooks et al., 2001). As a result, the Cameroon Highlands are considered one of the top five conservation priorities in Africa for terrestrial vertebrates (Brooks et al., 2001), the Mount Cameroon and Bioko montane forests ecoregion is among the most important for the conservation of forest-dependent bird species (Buchanan et al.,

TABLE 2

Generalized forest type strata of the Biafran forests and highlands (BFH) with corresponding altitudinal range, coverage extent, and proportion occurring within protected area boundaries, and characteristic species.

Forest type ¹	Altitudinal range (m) ¹	Extent covered (m) ¹	Proportion protected (%)	Common species ¹
Lowland forest	0-800	123,731	11.00	<i>Ficus</i> spp. are dominant; <i>Chlorophora excelsa</i> ; <i>Chrysophyllum africanum</i> ; <i>Strombosia scheffleri</i> ; <i>Symphonia globulifera</i> ; Caesalpinioideae (Leguminosae) ^{1,2,3}
Submontane forest	800-1700	53,407	6.50	<i>Alangium chinense</i> ; <i>Cyathea camerooniana</i> ; <i>Cyathea manniana</i> ; <i>Polyscias fulva</i> ; <i>Psydrax dunlapii</i> ; <i>Oncoba lophocarpa</i> ; <i>Oncoba ovalis</i> ; <i>Xylopiya africana</i> ; large tracts of monocarpic Acanthaceae (e.g. <i>Mimulopsis solmsii</i>); <i>Afromomum</i> spp. and <i>Maranthaceae</i> prominent in understory ¹
Upper montane forest	1700-2500	4,034	7.96	<i>Schefflera abyssinica</i> ; <i>Schefflera mannii</i> ; <i>Prunus africana</i> ; <i>Xymalos monospora</i> ; <i>Hypericum revolutum</i> ; <i>Clausena anisata</i> ; <i>Nuxia congesta</i> ; <i>Afromomum</i> spp. and <i>Maranthaceae</i> prominent in understory ^{1,4}
Montane scrub	2500-2800	99	48.72	<i>Erica mannii</i> , <i>Erica tenuicaulis</i> , <i>Agarista salicifolia</i> ; <i>Hypericum roeperianum</i> , <i>Hypericum lanceolatum</i> ; <i>Gnidia glauca</i> , <i>Maesa lanceolata</i> , and <i>Myrica arborea</i> ^{1,3,5}
Subalpine grassland	>2800	89	92.25	<i>Veronica mannii</i> ; <i>Pentaschistis mannii</i> ; absence of <i>Loudetia simplex</i> ; presence of temperate plant genera including <i>Helichrysum</i> spp., <i>Geranium</i> spp., <i>Clematis</i> spp., <i>Senecio</i> spp., and <i>Solanum</i> spp. ^{1,3}

Forest types, altitudinal ranges, and common species are approximated from Cable and Cheek (1998). Information on the extent of coverage approximated from the Shuttle-Radar Topography Mission (SRTM; available from U.S. Geological Survey). Protected area boundaries from IUCN and UNEP (2010).

¹Cable and Cheek (1998); ²Richards (1963); ³Fa (2000); ⁴Richards (1996); ⁵Leuschner (1996).

2011), and Bioko Island has been ranked as the single most important place in Africa for the conservation of primate diversity (Oates, 1996). Biodiversity and endemism patterns within the BFH vary widely between taxa but seem linked to terrain and dispersal ability. For example, primate endemism is highest in the lowlands, where rivers appear to be a major dispersal barrier. Birds, on the other hand, are not restricted by rivers, but do exhibit high levels of montane endemism, largely due to the relative isolation between montane areas in the BFH (e.g., ~50 km between Mount Cameroon and Pico Basilé) and from any similar region in Africa (Oates et al., 2004). A number of endemic taxa are present in current protected areas, although the variety of endemism patterns across taxa has led to a disconnect between faunal distributions and protected areas. The majority of taxa endemic to the BFH are montane, yet insufficient highland area is formally protected (Bergl et al., 2007). The following faunal overview follows Bergl et al. (2007), focusing primarily on primates, birds, and amphibians, as these taxa are better studied and adequate data were available.

Mammalian species, and especially primates, are particularly well represented in the region (see Oates et al. [2004] for a descriptive list). A total of 32 primate taxa are distributed across the BFH,

including 13 endemics, of which 8 are endangered and 2 are critically endangered (Oates, 2011; IUCN, 2013). Numerous primate species inhabit highland areas throughout the BFH, but although Preuss's monkey (*Allochrocebus preussi*) is primarily associated with montane forest, there are no strict montane endemics (Oates, 2011). Patterns of montane endemism in mammals in the region are perhaps best represented in the distribution and elevational range of endemic rodents across highland areas in the BFH (Table 3). For example, seven species across three genera, *Crocidura*, *Myosorex*, and *Sylvisorex*, comprise the endemic Soricidae taxa. Each of these species exhibits a distribution confined to montane habitats in either a single highland area, or small series of highlands (Fig. 2) (IUCN, 2013).

The BFH have the highest bird species richness in west and central Africa due to the overlap of Upper and Lower Guinea species and the spectrum of habitats afforded by the elevational range and topography of the highlands (Smith et al., 2000; Oates et al., 2004). Furthermore, localized estimates of species richness (Bioko and western Cameroon: Eisentraut [1973]; Korup: Green and Rodewald [1996]) are believed to be an underestimate of the total number of bird species in the region (514 species; Myers et al., 2000; Oates et al., 2004). Avian endemism is high, but there

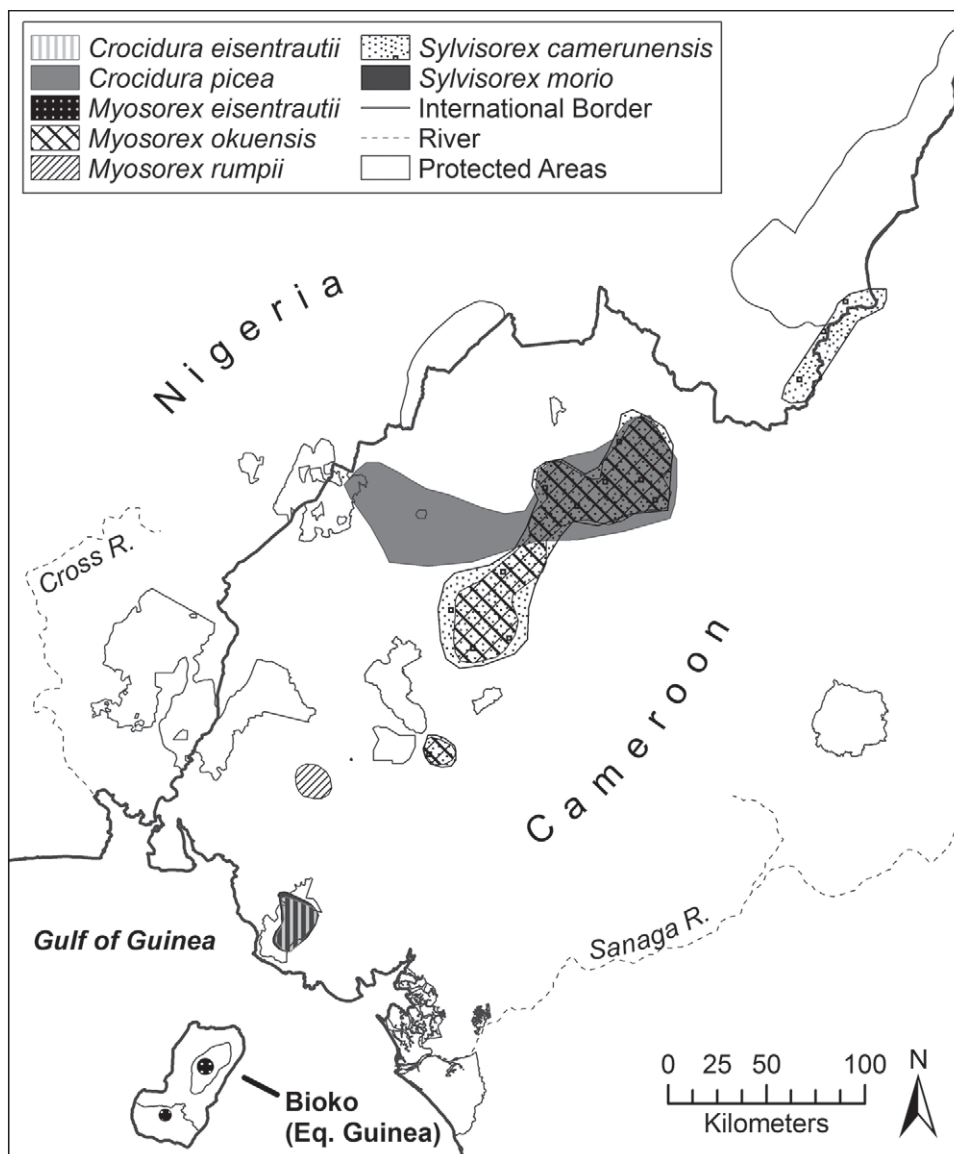


FIGURE 2. Distribution of montane endemic rodents (Soricidae) in the BFH. Distribution data from IUCN (2013). Protected area boundaries from IUCN and UNEP (2010).

TABLE 3
Endemic montane rodents of the Biafran forests and highlands, their altitudinal range, and IUCN Red List category.

Binomial	Common name	Altitudinal Range (m)	IUCN Category
Muridae			
<i>Hybomys badius</i>	Eisentraut's Striped Mouse	> 800	EN
<i>Hybomys basili</i>	Father Basilio's Striped Mouse	450–2000	EN
<i>Hylomyscus grandis</i>	Mt. Oku Hylomyscus	2100	CR
<i>Lamottemys okouensis</i>	Mt. Oku Rat	2100–2900	EN
<i>Lemniscomys mittendorfi</i>	Mittendorff's Striped Grass Mouse	2100–2300	VU
<i>Lophuromys dieterleni</i>	Dieterlen's Brush-furred Mouse	2100	EN
<i>Lophuromys eisentrauti</i>	Eisentraut's Brush-furred Mouse	2550	EN
<i>Lophuromys roseveari</i>	Roseveari's Brush-furred Mouse	1000–3100	LC
<i>Otomys burtoni</i>	Burton's Vlei Rat	2000–4000	EN
<i>Otomys occidentalis</i>	Western Vlei Rat	1900–3000	VU
<i>Praomys hartwigi</i>	Hartwig's Soft-furred Mouse	2700–2900	EN
<i>Praomys morio</i>	Cameroon Soft-furred Mouse	1100–2135	EN
<i>Praomys obscurus</i>	Gotel Mountain Soft-furred Mouse	1600–2400	EN
Sciuridae			
<i>Paraxerus cooperi</i>	Cooper's Mountain Squirrel	~800–2500	DD
Soricidae			
<i>Crocidura eisentrauti</i>	Eisentraut's Shrew	2000–3000	VU
<i>Crocidura picea</i>	Cameroonian Shrew	1200–1800	EN
<i>Myosorex eisentrauti</i>	Eisentraut's Mouse Shrew	>2000	CR
<i>Myosorex okuensis</i>	Oku Mouse Shrew	1800–2300	EN
<i>Myosorex rumpii</i>	Rumpi Mouse Shrew	1100	EN
<i>Sylvisorex camerunensis</i>	Cameroonian Forest Shrew	2000–2300	VU
<i>Sylvisorex morio</i>	Mt. Cameroon Forest Shrew	>1200	EN

Notes: Species occurrence from Kingdon, 1997; Maisels et al., 2001; Oates et al., 2004; Amori et al., 2008. Approximate altitudinal range from IUCN, 2012. Species recorded from a single elevation are listed as single values. IUCN Red List categories: critically endangered (CR), endangered (EN), vulnerable (VU), least concern (LC), data deficient (DD).

is little consistency in distribution patterns among endemic taxa, apart from exhibiting a preference for montane forests and grasslands (Bergl et al., 2007). Only three species are recorded from a single montane site: the Mount Cameroon francolin (*Francolinus camerunensis*) and the Mount Cameroon speirops (*Speirops melanocephalus*) from Mount Cameroon, and the Fernando Po speirops (*Speirops brunneus*) from Pico Basilé (Pérez del Val et al., 1994; Oates et al., 2004; IUCN, 2013). Of the 26 regional endemics, 58% are currently threatened (6: endangered; 4: vulnerable; 5: near threatened) (IUCN, 2013).

Myers et al. (2000) estimated 139 reptile species and 116 amphibian species occur in the West African forests hot spot. Eisentraut (1973) listed 52 reptile and 32 amphibian species from Bioko, while Lawson (1993) listed 83 reptile and 90 amphibian species in Korup National Park. Similar to the total number of bird species in the region, it is suggested that the overall species richness of herpetofauna in the region is currently underestimated and may actually be considerably higher (Oates et al., 2004). Amphibians are relatively better studied in

the region and exhibit higher estimates of endemism (77%) than reptiles (33%) (Myers et al., 2000). In contrast to the respective lowland- and montane-centered distribution of the primates and birds, Gartshore (1984) and Bergl et al. (2007) described a vertically stratified distribution of endemic amphibians, with distinct lowland, lower montane, and upper montane species. Of the 53 species endemic to the region, 39 (73.6%) species are recorded only above 800 m. Twelve (30.1%) of these species are restricted to an altitudinal range of 800–1600 m, 16 (41.0%) are found only over 1200 m, and among these, 10 (25.6%) are found only at altitudes greater than 1600 m (Bergl et al., 2007; Zimkus, 2009; Blackburn, 2010).

Protected Areas

The BFH contains 18 strict protected areas, comprising three International Union for Conservation of Nature (IUCN) categories (Ib, Scientific Reserve; II, National Park; IV, Wild-

life Sanctuary), and encompassing a total area of over 17,500 km² (Table 1). Based on the breakdown of vegetation strata in Cable and Cheek (1998) (Table 2), approximately 3921 km² (22%) are at an elevation above 800 m, 451 km² (2.6%) are above 1700 m, and 446 km² (0.74%) are above 2500 m. It is also noteworthy that all land above 1600 m on Bioko Island is in protected areas. Gashaka Gumti National Park in Nigeria encompasses a majority (55%) of the total protected highland area; however, the park lies outside the Guineo-Congolian moist forest zone, with only small patches of montane forest and limited habitat for endemic montane species (Bergl et al., 2007). Overall, it is estimated that only 6.0% of approximately 65,000 km² of highland ecosystems above 800 m in the region have any formal protection (Bergl et al., 2007).

Effective conservation within established protected areas is uncommon. Existing protected areas, often by nature of their terrain, have been relatively successful in protecting large tracts of habitat (Bruner et al., 2001; Oates et al., 2004; Struhsaker et al., 2005); however, they are under intense threat from burning, agriculture, livestock grazing, and, most especially, the hunting of larger vertebrates, such as anthropoid primates and ungulates (Maisels et al., 2001; Chapman et al., 2004; Oates et al., 2004; Fa et al., 2006; Linder and Oates, 2011; Abernethy et al., 2013; Cronin, 2013; Cronin et al., 2013). Moreover, many of the region's protected areas lack both clarity in their legal boundaries and any effective management plan (Oates et al., 2004). Indeed, many exist solely as "paper parks," where conservation and management activities are limited or nonexistent (Blom et al., 2004; Oates et al., 2004; Bergl et al., 2007; Cronin et al., 2010). On Bioko, for example, there is no management plan in place for the Gran Caldera–Southern Highlands Scientific Reserve (GCSH), the protected area with the highest IUCN designation (Ib; Table 1) in the BFH. The GCSH boundary remains unmarked, and, in addition to the absence of park rangers or management staff, the few military personnel responsible for law enforcement within the reserve regularly hunt primates within its boundaries (Cronin, 2013). On Mount Cameroon, despite the creation of a national park in 2010 (Forboseh et al., 2011), a management plan has yet to be implemented, much of the boundary remains unmarked, and regular exploitation from surrounding populations remains common. Ultimately, active noncompliance and the absence of effective management occur throughout the BFH, essentially nullifying much of the value of gazetted a protected area (Bergl et al., 2007).

Human Population

The BFH support some of the most densely populated areas on the continent. Nigeria is the second most densely populated country in Africa (184 people km⁻²), with densities upward of 500 people km⁻² in some southeastern areas along the Cameroon-Nigeria border (Oates et al., 2004; CIA, 2013). Cameroon is less densely populated (42 people km⁻²), but the Bamenda Highlands, which lie entirely within the study region, are one of the most densely populated areas in the country (Oates et al., 2004; CIA, 2013). For instance, Mount Cameroon, the most unique formation in the CVL, is estimated to support 300,000 individuals (SWPDFW et al., 2005). Human settlements consisting of high-density urban areas and smaller villages form a ring with little remaining forest cover around its base up to 1500 m in places (Fotso et al., 2001; SWPDFW et al., 2005). The population of Bioko Island is estimated at roughly 180,000 people, with approximately 137,000 people living in and around the northern capital city of Malabo (CIA, 2013;

Cronin, 2013). The remainder of the island's population lives in villages and towns encircling Pico Basilé at low elevations and on the northern flanks of the GCSH, with population densities less than 10 people km⁻² in the south (Albrechtsen et al., 2006).

Threats

The threat to biological diversity is high in West Africa, relative to other places in sub-Saharan Africa, as a result of high human population density and growth rate, as well as a high rate of habitat loss (Brashares et al., 2001; Wittemyer et al., 2008). Wittemyer et al. (2008) suggested human settlements around protected areas are strong predictors of illegal timber and mineral extraction, bushmeat hunting, fire frequency, and species extinctions. Exacerbating the situation is that protected areas seem to attract human settlement, as rates of population growth surrounding protected areas are nearly double that of average rural growth rates (Wittemyer et al., 2008). The associated increase in anthropogenic activities, especially deforestation and bushmeat hunting, in the BFH has had progressively more deleterious effects on the biodiversity and fragile ecosystems of the region (Achard et al., 1998; Oates et al., 2004).

DEFORESTATION

Although there has been considerable deforestation and forest degradation in the BFH associated with development and the expansion of subsistence activities, such as agriculture, energy (e.g., fuelwood), and timber (Charlotte, 2010; de Wasseige et al., 2012; Megevand et al., 2013), Africa has contributed considerably less overall (5.4%) to the global loss of humid tropical forests relative to Asia and the Neotropics (Hansen et al., 2008). The annual net deforestation rate in the Congo Basin has accelerated recently, however, with losses corresponding to about 0.17%, or approximately 300,000 km², each year (de Wasseige et al., 2012). Deforestation estimates for Cameroon suggest the loss of approximately 800–1000 km² per year (Alpert, 1993; Wolfe et al., 2005), with the coastal region suffering the most intensive exploitation (Laporte et al., 2007; de Wasseige et al., 2012). Remote sensing has also indicated that Cameroon and Equatorial Guinea had the greatest densities of logging roads (0.09 km km⁻²) and the greatest amount of forest disturbance (15%) in Central Africa, while the Mount Cameroon and Bioko montane forests had the highest percentage of mean forest loss from 2000–2005 (2.40%), out of the 20 ecoregions most important for the conservation of forest-dependent bird species (Buchanan et al., 2011). High human densities and continued human immigration to the area have driven this trend and led to the clearance of much of the natural vegetation for both subsistence and commercial agricultural use, while the majority of lowland forests have been cleared for industrial plantations, such as oil palm (*Elaeis guineensis*) (Forboseh et al., 2011; Linder, 2013). Deforestation was once widespread on Bioko, as nearly 60% of its lowland forests were cleared for cocoa and other tropical crops; however, nearly half of the converted land has since been abandoned for agricultural use and has been reclaimed by scrub and secondary forest (Butynski and Koster, 1994).

The higher elevations of both Mount Cameroon and Bioko remain largely intact due to their low potential value for exploitation and their relatively inaccessible rugged terrain (Butynski and Koster, 1994; Fotso et al., 2001; Oates et al., 2004). As a result, no major human activities or settlements occur above 2000 m. On Mount Cameroon, paved roads reach Buea (870 m), but go no

further. On Bioko, Moeri (720 m) is the highest permanent settlement on Pico Basilé, however, a guarded road provides access to a meteorological and telecommunications facility and its associated military installation at the summit. The village of Moka (1400 m) is the highest overall on Bioko, situated at the northern border of the GCSH.

BUSHMEAT HUNTING

Bushmeat hunting is extensive and unsustainable throughout the BFH (Fa et al., 2000, 2006; Albrechtsen et al., 2007; Morra et al., 2009; Linder and Oates, 2011; Cronin, 2013; Cronin et al., 2013), threatening many large vertebrates with extinction, especially primates (IUCN, 2013). It is a highly commercialized activity, fueled by human population growth and increased per capita wealth in urban centers, modernized hunting techniques, and increased accessibility to remote areas of forest (Robinson and Bennett, 2000; Albrechtsen et al., 2007). The magnitude of faunal exploitation is great; over 197,000 carcasses were counted from Bioko from 1997–2010 (Cronin, 2013), while Fa et al. (2006) recorded over 42,000 kg of bushmeat in Cross-Sanaga region of the mainland in a six-month study period alone. Hunting has a negative impact on the diversity and densities of large-bodied vertebrates and can lead to adverse and cascading effects on ecosystem functioning (Redford, 1992; Chapman and Onderdonk, 1998; Wang et al., 2007; Vanthomme et al., 2010; Abernethy et al., 2013). Although much of the region is classified as protected (e.g., ~42% of Bioko Island), legislation aimed at restricting hunting has failed, due to a lack of management and to ineffective or absent enforcement regimes (Oates et al., 2004; Struhsaker et al., 2005; Bergl et al., 2007).

CLIMATE CHANGE

It is projected that climate change will most severely affect the African continent (IPCC, 2014b), particularly in the central African region of the BFH (Penlap et al., 2004; James et al., 2013). Warming projections suggest the rise in mean annual temperature is likely to exceed 2 °C across large swaths of the continent under medium scenarios, and its entirety under high-emission scenarios (IPCC, 2014b). Highland areas, such as the BFH, will be especially affected, as warming is expected to be more intense relative to lowlands (Pounds et al., 1999), and rainfall patterns are predicted to change dramatically (IPCC, 2014b). Indeed, montane ecosystems throughout Africa are already responding to climate change (Chen et al., 2009; Allen et al., 2010; Eggermont et al., 2010; Chen et al., 2011; Laurance et al., 2011; Willis et al., 2013; IPCC, 2014b).

Global modeling studies have predicted that over 30% of plant and animal species will be threatened with extinction given a rise in mean annual temperature in excess of 1.5 °C (Thomas et al., 2004). These extinctions will be disproportionately attributed to tropical areas (Thomas et al., 2004; Colwell et al., 2008), due to a number of factors including species richness and high endemism (Colwell et al., 2008; Raxworthy et al., 2008). Because the effects of climate change are predicted to be amplified in highland areas (Pounds et al., 1999; IPCC, 2014b), tropical montane zones will likely be particularly affected (Colwell et al., 2008; Ohlemüller et al., 2008; Raxworthy et al., 2008). Climate models for the tropics suggest that the coolest climatic zones at the upper elevations will be lost (IPCC, 2014a), and that there will be a shift of remaining vegetation strata upslope threatening corresponding species and montane endemics with extinction (Still et al., 1999; Beniston, 2000; Thomas et al., 2004; Raxworthy et al., 2008; Sekercioglu

et al., 2008; Chen et al., 2009). Montane endemics will be faced with substantial range contractions, increasing prevalence of climate-driven infectious disease (Pounds et al., 2006), and even “mountain top” extinctions (Pounds et al., 1999; Colwell et al., 2008), resulting from limited dispersal capabilities (Laurance et al., 2011), narrow ranges (Ohlemüller et al., 2008), and restricted physiological tolerances (Beniston, 2000; Schloss et al., 2012). For example, species like Hartwig’s soft-furred mouse (*Praomys hartwigi*), currently known from a highly restricted elevational range (2700–2900 m) just below the summit of Mount Oku (3011 m), may have difficulty adapting to rapid environmental change.

Anthropogenic impacts are expected to exacerbate the effects of climatic change (Bush, 2002; Colwell et al., 2008), as bushmeat hunting is interfering with forest regeneration and seed dispersal (Wilkie et al., 2011; Abernethy et al., 2013), and rapid habitat loss and fragmentation are disrupting dispersal capabilities (Achard et al., 1998; Bergl et al., 2007; Laporte et al., 2007; Bergl et al., 2008; Laurance et al., 2009). Given current levels of habitat loss and anthropogenic pressure, the higher elevations of the BFH are increasingly becoming “sky islands,” acting as refuge (Pounds et al., 1999; Chen et al., 2009) from increasing encroachment from the lowlands, but isolated from other highland areas (Butynski et al., 1997; Newmark, 2008).

OTHER THREATS

Additional threats to BFH include fires and volcanic eruptions, as well as the unregulated collection of non-timber forest products, including honey, wild vegetables, and medicinal plants. The high-elevation vegetation communities of the BFH are prone to damage by fire and exhibit slower growth rates and natural regeneration than other regions, making the effects of even short-lived fire events long-lasting (Charlotte, 2010; Forboseh et al., 2011). Fires in the montane zone can be of natural (e.g., lightning, volcanic eruption) or anthropogenic origin (e.g., hunters flushing out game, honey collectors flushing out bees) (Forboseh et al., 2011). Anthropogenic fire events are readily observable and often grow swiftly out of control (Cronin; Libalah, personal observation). The collection of non-timber forest products, such as African jointfir (*Gnetum africanum*), the fruits of *Afromomum* spp., bush mango (*Irvingia gabonensis*), and African whitewood (*Enantia chlorantha*), is also common throughout the BFH (Charlotte, 2010). Even so, the exploitation of the montane scrub and subalpine grasslands in the region has been primarily restricted to hunting of game. Recent findings by Zofou et al. (2011), however, justified the use of stem bark from *Hypericum laceolatum* (Hypericaceae), found in the upper montane zone of the BFH (Table 2), for the treatment of malaria, and suggest that it will likely yield new anti-malarial drug candidates. Given the gravity of malaria infection worldwide, further positive results may lead to local overexploitation similar to that of another montane species, the red stinkwood (*Prunus africana*), whose bark is used to treat prostate hyperplasia (Ingram and Nsawir, 2007; Charlotte, 2010).

Environmental Legislation

Ineffective protected area management is rampant in the BFH. Widespread illegal exploitation of the resources within protected areas results from a myriad of factors, such as unclear borders, lack of enforcement, limited institutional capacity, and inadequate financial resources (Oates et al., 2004; Njuh Fuo and Memuna Semi, 2011). Additionally, those tasked with legislation and enforcement

are often either underpaid or involved in the exploitation—by consuming the resource in question, turning a blind eye, accepting bribes, actively hunting, or falsifying official documents regulating resource use (Nguiffo and Talla, 2010; Peh and Drori, 2010; Cronin, 2013). Unfortunately, the inability to effectively impose legislation appears common in Africa, despite well-intentioned efforts from numerous individuals, non-governmental organizations (NGOs), conservation departments, and governments (Peh and Drori 2010).

The environmental legislation of Equatorial Guinea provides clear insight into the underlying systemic mismanagement of the region. Equatorial Guinea has passed four major laws on the environment (Republic of Equatorial Guinea, 1988, 2000, 2003, 2007). Laws No. 8/1988 (Hunting, Wildlife, and Protected Areas) and No. 4/2000 (Protected Areas) were both superseded by No. 7/2003 (Environmental Regulation), which tasked a new government agency, INCOMA/FONAMA, with the responsibility of managing protected areas. To date, INCOMA/FONAMA does not exist and there is no enforcement of the law's provisions. Articles (34, 36, 37, and 46) of Law No. 7/2003 also cover the same tenets as Decree No. 72/2007, which bans the hunting, sale, and consumption of primates. Furthermore, both Pico Basilé National Park and the GCSH lack management plans, an urgent conservation concern (Cronin et al., 2010). Given the unclear nature of environmental law, jurisdiction, and protected area management in Equatorial Guinea, it is not surprising that there has been little conservation progress via legislation.

The main legal framework for environmental management in Cameroon is Law No. 96-12 of 5 August 1996 (Republic of Cameroon, 1996); however, there are a number of policies that regulate specific environmental sectors. The “wildlife code” was established through Law 94-01 of 19 January 1994 (Republic of Cameroon, 1994), which provides a legal code for the use of forests, wildlife, and fisheries, and Decree 95-466-PM of 20 July 1995 (Republic of Cameroon, 1995), which specifies the conditions for the implementation of Law 94-01 (Nguiffo and Talla, 2010; Njuh Fuo and Memuna Semi, 2011). Similar to the example given above for Equatorial Guinea, the wildlife code also suffers from a number of shortcomings. For instance, effective implementation of the wildlife code is dependent on “enabling decrees” (Republic of Cameroon, 1994), a number of which have not been enacted, and can sometimes take years to be put into effect (Njuh Fuo and Memuna Semi, 2011). The wildlife code also mandates that logging companies must develop forest management plans for each of their forest parcels and submit it to the Ministry of Forests and Fauna (MINFOF) for approval within three years of allocation (Republic of Cameroon, 1994), but many of the approved management plans do not comply with minimum legal prescriptions (Cerutti et al., 2008), and critics argue that the delegation of forest surveys to logging companies has sacrificed the environment for economic considerations (Njuh Fuo and Memuna Semi, 2011). Another central tenet of the wildlife code obliges the government to classify animal species into three classes, according to their level of protection (Republic of Cameroon, 1994), and requires that the classification is updated every five years (Republic of Cameroon, 1995). Despite the requirement, the government has not regularly updated the classification, which diminishes the currency and reliability of data available to policy-makers and management professionals (Nguiffo and Talla, 2010). Furthermore, despite legislative classification as ‘Class A’ species, that may on no occasion be killed, illegal hunting of wildlife, such as the endangered chimpanzee (*Pan troglodytes*)

and critically endangered gorilla (*Gorilla gorilla*), is extensive (Fa et al., 2006; Bergl et al., 2011; Djeukam et al., 2012).

Recommendations

The threats facing the BFH are multifaceted and may require localized strategies to best manage resources. Hunting mitigation strategies, for example, should vary given the primarily commercial nature of the trade on Bioko relative to Cameroon, where a greater proportion is subsistence based. However, across the BFH there is a commonality of requirement for improved law enforcement, and strong commitments to environmental protection from governments and NGOs, by way of institutional, financial, and technical support (Struhsaker et al., 2005; Njuh Fuo and Memuna Semi, 2011; Cronin, 2013).

Increased effectiveness of law enforcement is of paramount importance to the conservation of the BFH (Oates et al., 2004; Struhsaker et al., 2005; Bergl et al., 2007; Bennett, 2011; Wilkie et al., 2011; Tranquilli et al., 2012), to which the most practical short-term solution is the implementation of forest guards (Bennett, 2011). Forest guards have been a successful strategy that has been linked to reductions in hunting and improved effectiveness of protected areas (Bruner et al., 2001; Rowcliffe et al., 2004; de Merode and Cowlshaw, 2006; Hilborn et al., 2006; Bennett, 2011; Campbell et al., 2011; Tranquilli et al., 2012). An expansion of the protected area network, as well as increasing the size of existing reserves, will also be essential to the conservation of the BFH. Many protected areas in the region are too small and are suffering from levels of exploitation that are too high to sustain populations of many species (Brashares et al., 2001; Struhsaker et al., 2005). Increasing the size of protected areas will reduce the area to edge ratio, as well as hunter accessibility to the core of the reserve. Furthermore, an expansion of the protected area network to provide coverage for the inadequately protected highland ecosystems and endemic taxa in the BFH would greatly improve conservation overall in the region (Bergl et al., 2007). New protected areas, or an expansion of existing protected areas, like the proposed corridor linking montane areas of GCSH and PNB on Bioko (UNDP-GEF, 2010), will be important, but effective management and law enforcement in existing protected areas is the most critical factor for the conservation of biodiversity in the BFH (Struhsaker et al., 2005; Bergl et al., 2007; Cronin et al., 2010). The primate hunting ban on Bioko, for instance, includes prohibitive fines that, if enforced, would threaten the entire estimated annual hunting income for hunters and make it uneconomical for both suppliers and consumers alike to persist (Fa et al., 2000).

The cost of biodiversity conservation is minimal relative to the value of the ecosystems being protected (James et al., 1999), with estimates suggesting that conservation in protected areas could be effectively achieved for just 1% of the annual value of natural ecosystems (Pimentel et al., 1997). This is particularly true in the BFH, where the total costs of biodiversity conservation are minuscule in comparison to estimates of profits from environmental exploitation (e.g., industrial logging accounts for 11% [~\$3 billion] of the GDP of Cameroon) (Huarez et al., 2013; World Bank, 2014a). A 2005 assessment (Struhsaker et al., 2005) identified that most African rain forest protected areas were underfunded, and at least 75% lacked a secure long-term funding source despite significant involvement from international donors. This represents a long-term concern, but also identifies a glaring problem with protected area funding in the BFH, lending further support to the lack of a credible commitment from regional governments to en-

vironmental protection. The cost of operating a protected area in African rain forest was between \$23 and \$208 km⁻² in 2005, and even doubling those estimates to \$400 km⁻² would still have left the costs significantly lower than protected areas in developed nations (James et al., 1999; Struhsaker et al., 2005). Adjusted for inflation, \$400 km⁻² would be approximately \$490 km⁻² in 2014, which results in a projected operating cost of just over \$8.5 million for all identified protected areas in the BFH (Table 1), less than 1% of the gross profits from timber in Cameroon. On Bioko, the estimated annual cost of operating its two protected areas would be just \$408,000, only 0.003% of the overall GDP of Equatorial Guinea (World Bank, 2014b). There are, of course, myriad factors that govern protected area funding, and the values presented here are simply an estimate. However, despite Cameroon's leading role in Congo Basin forestry legislation (Cerutti et al., 2008) and the designation of environmental conservation as one of Equatorial Guinea's 'Five Pillars' of reform (Qorvis, 2010), these estimates are illustrative of the lack of funding allocated to protected areas in the BFH and the relatively low cost at which environmental protection in the region could operate efficiently. True commitment to conservation in the BFH will ultimately require greater financial investment from regional governments. Moreover, future funding structures need to be both secure and long-term, such as trust funds or endowments, where the annual return on investment will continue to supply funding for the protected area over time.

Many of the flaws of environmental conservation and management in the BFH ultimately stem from governments that are lacking in political will (Smith et al., 2003; Cerutti et al., 2008; Njuh Fuo and Memuna Semi, 2011; de Wasseige et al., 2012), and conservation departments that have little political clout. The empowerment of conservation departments will be critical in order for them to more effectively combat environmental offenses by citizens and other sectors (Smith et al., 2003). Situations, such as false CITES (Convention on the International Trade in Endangered Species) certificates for the export of 1200 parrots from Cameroon (Nguiffo and Talla, 2010), or illegal permits signed by senior military officials for the poaching of marine turtles on Bioko (Cronin, personal observation), can only truly be combated if the perpetrators cannot act with impunity, and can be prosecuted by conservation departments to the fullest extent of the law. Moreover, institutional corruption, a problem throughout the BFH, can detract from the conservation progress and lower the effective funding available for conservation initiatives (Smith et al., 2003; Struhsaker et al., 2005). Efforts have been made to address corruption in the BFH by organizations, such as the Last Great Ape Organization (LAGA), which have had success in lobbying for the enforcement of environmental laws in Cameroon; however, fixing the institutionalized corruption common in the BFH will require a governmental overhaul, as well as the political will and leadership to see such a divisive undertaking through (Peh and Drori, 2010).

NGOs also play an essential role in environmental conservation and law enforcement in the BFH, and going forward, their role will only be greater. Organizations, such as LAGA, Wildlife Conservation Society (WCS), and the World-Wide Fund for Nature (WWF), have been instrumental in helping to bring environmental offenders to justice (Njuh Fuo and Memuna Semi, 2011), and technical and/or financial NGO support has been strongly linked to the creation and some degree of success of protected areas (Struhsaker et al., 2005). Meanwhile, many smaller NGO's, like the Central African Biodiversity Alliance (CABA) in Cameroon and the Bioko Biodiversity Protection Program (BBPP) on Bioko, have been successful by partnering with local institutions and promoting conservation through education and research. Expanding long-term NGO

involvement and partnerships through further proliferation of research initiatives in the BFH appears to be one viable path toward immediate on-the-ground conservation success. Studies suggest that effective conservation can be achieved through the establishment of a research presence (Campbell et al., 2011; N'Goran et al., 2012). Successful projects, like San Diego Zoo Global's Ebo Forest Research Project and WCS's gorilla monitoring work at Kagwene Gorilla Sanctuary, demonstrate the value of research for conservation in the BFH. Expanded research initiatives in the BFH could also generate data critical for improving conservation management and future planning (e.g., N'Goran et al., 2012), which are lacking for many protected areas (Struhsaker et al., 2005).

While an expansion of NGO-led research could have significant conservation impacts, it is clear that the extent of threat in the BFH will also require considerable law enforcement intervention in order to secure the region's biodiversity. Increasingly, evidence suggests that effective conservation in tropical Africa must be tied to effective protection programs (e.g., Holmern et al., 2007; Fischer, 2008; Jachmann, 2008; Tranquilli et al., 2012). Lack of capacity and political will on the part of governments in the region has provided opportunities for NGOs to play significant roles in the support and management of protected areas in the BFH. Both WCS and WWF are engaged at various levels with conservation law enforcement in Cameroon, and in Nigeria, WCS directly manages ranger programs, in partnership with government agencies and community groups, at two sites. Public-private partnerships such as these will likely be the best way to control threats to biodiversity and prevent local extinctions in the immediate term.

More broadly focused institutions, such as the Central African Forests Commission (COMIFAC) and Congo Basin Forest Partnership (CBFP), have also leveraged the collective expertise of their numerous stakeholders in order to promote regional scientific exchange and collaboration on conservation action. Moving forward, multi-stakeholder, regional planning of unified and comprehensive conservation strategies will be critical to the future of the BFH, as mitigation of transboundary issues, such as wildlife trade, biodiversity loss, and climate change, will need to be agreed upon by all parties and enforced collaboratively.

Finally, it is imperative that local people are actively involved and/or employed in ongoing research, conservation, and education projects, as it allows communities to attach a necessary personal value to the conservation of their wildlife, but Oates (1999) and Bergl et al. (2007) argued that community-based conservation projects increase pressure on protected areas and detract from overall conservation goals. Rather, Oates (1999) suggested that government-sponsored conservation of nature for its intrinsic value alone, supported by strict regulations and enforcement, can be successful. Given the current state of the BFH, the management of natural resources must seek to bridge the gap between conservation, economic development, and human interests to ensure that the environment and the services it provides are not lost or overexploited to the point of ecological collapse.

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