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Diversity Patterns of Plants and Phytophagous Beetles in Sub-Saharan Africa¹

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Abstract. Species distribution of flowering plants (Angiospermae) and the phytophagous beetle group *Monolepta* (Chrysomelidae) in Sub-Saharan Africa (south of 17° N) are compared based on species numbers per square degree grid. The beetle data comprise all 89 valid species for Africa (21,000 specimens of Afrotropical *Monolepta* have been currently revised). The plant diversity data are based on 6,269 species with some 330,000 distributional records (10–15 % of all African angiosperm species). Shared centres of species richness of both taxa are geodiverse, montane forests, namely the Albertine Rift, Eastern Arc Mountains, isolated East African volcanoes, montane areas in Cameroon and northeastern parts of the Republic of South Africa. However, the Cape and the Upper Guinea Region show diverging patterns: plant species richness is higher than the richness of Chrysomelidae. Actual diversity patterns versus sampling artefacts are discussed. Certain mechanisms, like allopatric speciation processes, contribute to a diverse flora and fauna in areas of high geodiversity. Thus, if there is a general and taxon-independent positive relationship between geodiversity and species richness, these areas are of explicit value for the conservation of terrestrial biodiversity.

Key words. Angiosperms, Chrysomelidae, biodiversity, biogeography, distribution patterns, conservation

1. Introduction

The understanding of the spatial distribution of biodiversity is a fundamental requirement for its conservation and sustainable use. However, current biogeographic knowledge is restricted to a tiny proportion of terrestrial biodiversity. While there is comparatively detailed information on the global distribution of vertebrate diversity (RODRIGUEZ et al. 2004), there is only little information about the spatial distribution of the remaining 99 % of animal species, particularly for such a megadiverse group like insects. More problematic, the representativeness of patterns of vertebrate diversity, e.g. patterns of insects, might be limited. In contrast, plants in their function as the foundation of food-webs may serve as a surrogate to assess patterns of overall terrestrial biodiversity (BARTHLOTT et al. 1996, 1999).

Flowering plants and beetles, in particular the most speciose phytophagous beetle taxa, Chrysomeloidea and Curculionoidea, represent one of the oldest and largest radiation of plant-animal co-evolution (FARRELL 1998). The diversity of flowering plants (BARTHLOTT et al. 1996, 1999) and the extent to which phytophagous beetles are specialized on their food-plants, were the basis for estimations which dramatically changed our idea of terrestrial biodiversity (ERWIN 1982). Despite the extend of specialisation of phytophagous beetles in tropical biomes and that numbers have been clearly overestimated on the basis of conclusions from temperate

regions (MAY 1990; ØDEGAARD 2000; WAGNER 2000a; NOVOTNY et al. 2002), there is no doubt that the number of existing species is several times higher than the number of yet described species. This is particularly true for the approximately 150,000 species of leaf beetles and weevils (LAWRENCE & BRITTON 1991).

Both beetle groups illustrate the most prominent problem of biodiversity research. The more speciose taxa are and the smaller the mean range size of their species is, the less complete is our knowledge on their large scale biogeographic patterns. While the global distribution patterns; e.g. of the vertebrates, which have on average a large range size, are apparently known on a 0.5° degree resolution (RODRIGUES et al. 2004), the situation for plants (SCHATZ 2002) and particularly arthropods is completely different. While plants are at least relatively well known from a taxonomic perspective, there is a strong need for taxonomic research on arthropods. This includes the phytophagous beetles, which have an key ecological position in the food-web as the most species rich group of first order consumers. Thus, chrysomelids provide a good example for studying speciation processes, including co-evolution of angiosperms and their consumers in tropical systems.

Since a detailed assessment of arthropod diversity patterns at the global scale is impossible, we rely on data for selected groups and selected areas. Based on the most comprehensive databases on the Sub-Saharan distributions of plants and the chrysomelid group of *Monolepta*, we exemplarily compare centres of species richness of plants and phytophagous beetles. We discuss

¹ In commemoration of Clas Michael Naumann zu Königsbrück (26.06.1939 – 15.02.2004)

consequences of the quality of available biogeographic data for our knowledge on the biodiversity of both groups and for potential application of these data for conservation biology.

2. DATA AND METHODS

2.1. Taxonomy and diversity data for *Monolepta* (Chrysomelidae)

Afrotropical species of *Monolepta* Chevrolat, 1837 were recently revised (WAGNER 2003a). These beetles form the largest group of the Galerucinae (Chrysomelidae), having worldwide about 600 nominal species. Many of the 160 species described from Africa were found to be synonyms or needed to be transferred to other genera due to their phylogenetic position. However, 50 valid species remained in *Monolepta*, and there is about the same number of new species, most of them presently described (WAGNER 2000b, 2001b, 2002, 2003b; Wagner this issue) or awaiting description. Unfortunately, food-plants of most *Monolepta* species are still unknown. There are only very few data available from labels of dried specimens, with direct observations in the field and literature (JOLIVET & HAWKESWOOD 1995) indicating that some species feed on *Citrus* sp. and some others on other Rutaceae. The revision of the 89 valid species of Afrotropical *Monolepta* is based on 21,000 specimens. Five hundred specimens are recently collected mainly in eastern Africa, while most are dried specimens from all major collections housing African insects, principally museums in Berlin, Brussels, London, Nairobi, Paris, Pretoria, Tervuren and Windhoek.

After this comprehensive revision of material, detailed data on the distribution of Afrotropical *Monolepta* species are now available. Only four *Monolepta* species are distributed throughout tropical Africa, and known from a variety of biomes such as tropical forests, savannas and even deserts, from coastal regions to montane areas. All other species show more restricted geographical and ecological distributions. Forest-dwelling species are often more restricted and a high degree of endemism is found amongst species from montane areas (WAGNER 2001a). Coordinates are derived from label data on distribution using a gazetteer compiled by Ugo Dall'Asta (Africa-Museum, Tervuren) for locations from Congo (Zaire) and generally using the Alexandria Digital Library Gazetteer Server. Data of all *Monolepta* species is based on 2320 localities in subsaharan Africa.

2.2. Diversity data for Plants

Earlier versions of the plant dataset have been described and analysed in previous publications (LINDER 2001; LOVETT et al. 2000; LINDER et al. 2005; KÜPER et al. 2004; Lovett et al. 2004). Since 2003, an international

group of research institutions has contributed data on the distribution of African plants to the *Biogeographic Information System on African Plant Diversity*, which is hosted and curated by the BIOMAPS Project within the BIOLOG-BIOTA framework (www.biota-africa.org). The spatial precision of the distribution data varies between exact localities mainly from herbarium collections with georeferenced localities, to 1° resolution data from digitised maps. Additional information on the origin of this dataset is documented in BURGESS et al. (in press, see also Acknowledgements).

The current database covers African-wide distribution records for 6,269 species (status as of March 2004), all of which had been taxonomically revised. This comprises between 10 and 15 % of the African angiosperm species (LEBRUN & STORK 1991–1997; BEENTJE et al. 1994). There are currently 330,000 distribution records in the form of confirmed collection localities available.

2.3. Data preprocessing and analysis

Data are organized in MS Access databases and have been plotted and analysed using ArcView 3.2a GIS software. In order to achieve maximum comparability with previous analyses on Sub-Saharan diversity (BALMFORD et al. 2001; BROOKS et al. 2001; BURGESS et al. 2002, in press; DE KLERK et al. 2004), all distribution data were rescaled to a 1° grid resolution within a base map of 1,713 one-degree latitude-longitude grid cells covering mainland Sub-Saharan Africa south of 17° North. By restricting the geographic coverage to Africa south of the Sahara and excluding those species only found on offshore islands, a database with 5,985 plant species and 89 species of *Monolepta* remains for further analyses. For the scatterplot, we only used those 580 grid cells in which at least one species of both groups occurred.

3. RESULTS

3.1. Shared centres of diversity of plants and *Monolepta*

There is an overlap of centres of high plant and *Monolepta* diversity in montane areas, namely the Albertine Rift system including the Virunga Volcanoes, the Ruwenzori, Bwindi Impenetrable Forest and the Kahuzi Biega National Park at the south-western extreme; the Eastern Arc, in particular East Usambara; the isolated East African Mountains such as Mt. Elgon, Mt. Kenya and Mt. Kilimanjaro; southern Katanga (Mitunga and Kundelungu Mountains, major collections in Upemba/ Kundelungu National Park and close to Lubumbashi); and to a lesser extent afromontane regions in Ethiopia, the northeastern parts of the Republic of South Africa, and lower Guinea (Fig. 1a/b).

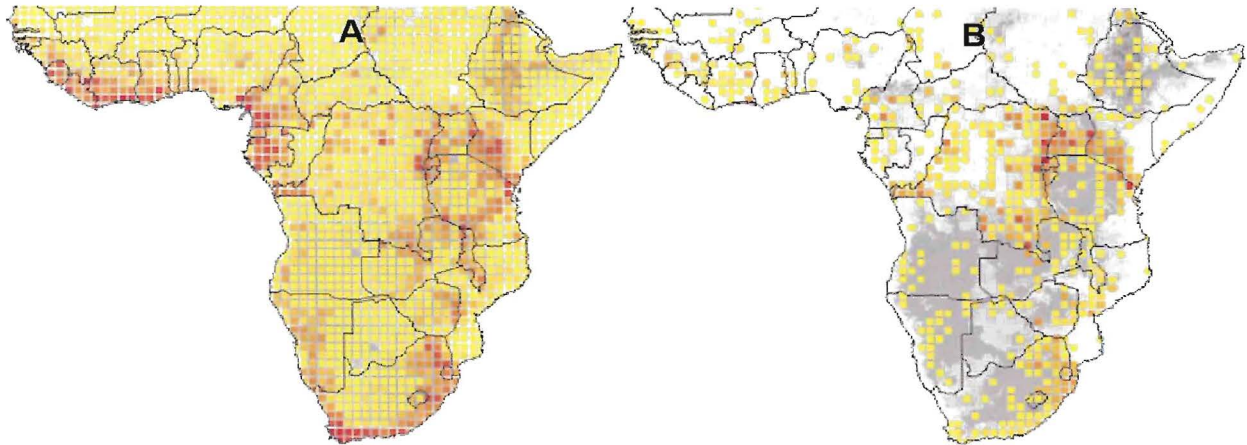


Fig. 1: Species richness per one-degree grid cell in Sub-Saharan Africa south of 18th degree latitude. – A. plants, n (species) = 5985, B. *Monolepta*, n (species) = 89. Richness values are rescaled to percentages of the maximum richness per grid of each taxon (*Monolepta*: max = 20; for plants: max = 682). The scale ranges from high species richness (dark red) to low species richness (bright yellow). In grid cells with no present species, the grey background colour represents elevation above sea level (dark grey: high elevation, bright grey: low elevation). Black foreground lines indicate national boundaries.

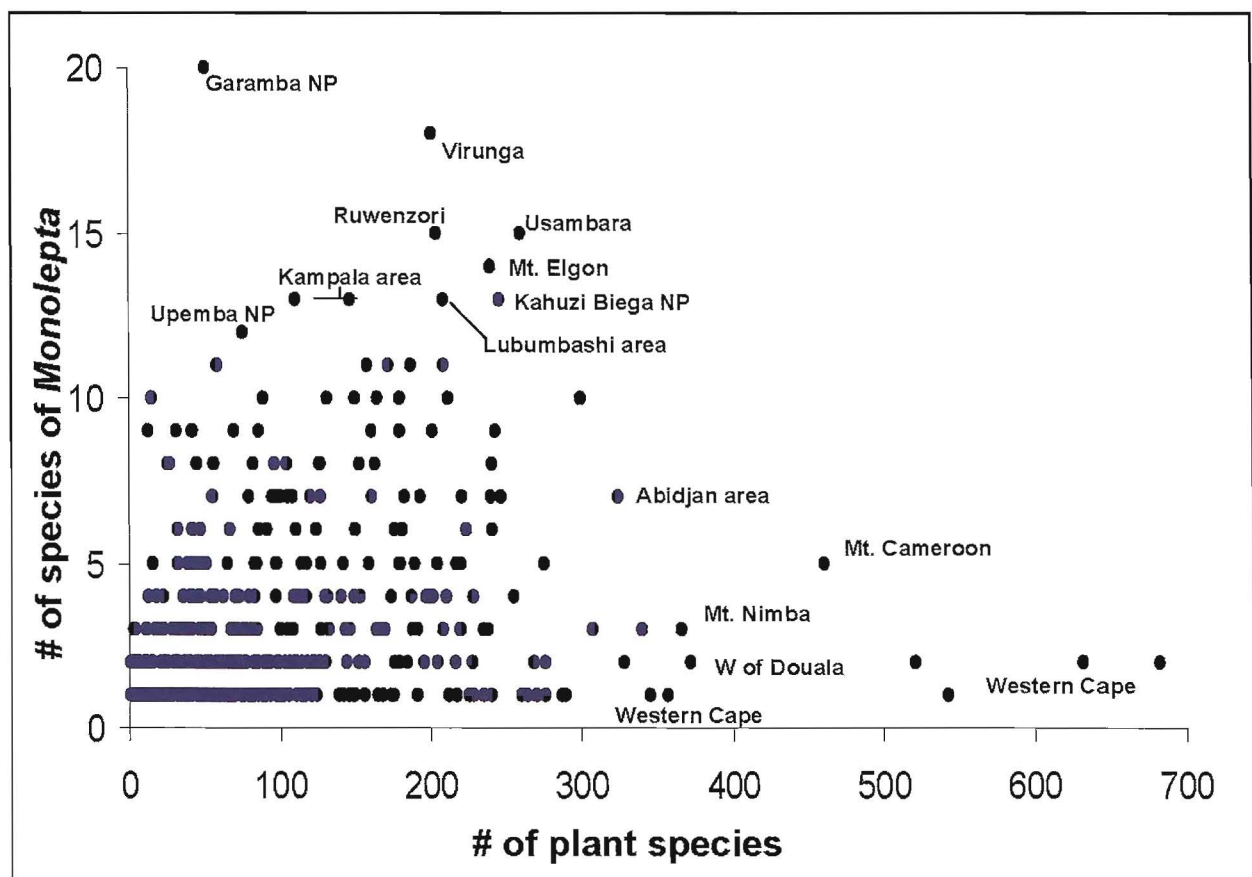


Fig. 2 : Species richness of *Monolepta* and plants in 580 one-degree grid cells in Sub-Saharan Africa. Only grids where both taxa were present with at least one species are considered. Outliers were labelled according to their geographic position (NP: National Park).

3.2. Divergent diversity patterns of plants and *Monolepta*

Even though some centres of species richness of both groups do coincide, the correlation between the patterns of species richness of plants and *Monolepta* are very low (Fig. 2). The correlation can probably be explained merely by the fact that the majority of the *Monolepta* species occur in forest habitats, and that forests are comparatively phytodiverse. The most obvious difference between the diversity patterns of plants and beetles is the outstanding plant diversity of the Cape Floristic Kingdom. This observation is contrary to all animal taxa yet mapped such as vertebrates (BROOKS et al. 2001) but apparently also insects (GILIOME 2003). There is no doubt that this pattern is based on ecological and historical characteristics of this landscape, which seem to favour certain plant taxa more strongly than any animal taxon. The same is true for the Succulent Karoo.

Few grids, all in regions with savannah habitats, have an exceptionally high number of *Monolepta* species, but comparatively low number of plant species. These are Garamba National Park in north-eastern Congo, Upemba National Park in south-eastern Congo (Katanga), the region west of Katanga along the Lulua River and the region around Kampala in Uganda. These areas belong to the best-collected regions for these beetles (and generally for insect groups). Some extended expeditions have been carried out in national parks in the former Belgian Congo over the years, and about 18 % of all known specimens of Afrotropical *Monolepta* are from Garamba National Park alone. Hence, high diversity in these particular grids is biased by high sampling effort. The Upper Guinea region, characterized by high plant diversity, has low beetle diversity. Since West Africa is less well sampled for *Monolepta* than all other African regions, this is most likely also a sampling artefact. However, this region lacks high mountains as typical for the rift systems in Central and East Africa, and *Monolepta* may be generally less diverse in West Africa.

Due to the strong influence of sampling intensity on the *Monolepta* dataset, there are no significant correlations of the derived species richness patterns of these beetles (or the residuals between the species richness of *Monolepta* and plants) with abiotic factors such as hydrothermic parameters (e.g. waterbalance, number of dry months), and topodiversity. Correlations between species richness of *Monolepta* and either plants or abiotic parameters did not improve when tested on the larger spatial scale.

4. DISCUSSION

4.1. Afrotropical Mountains: centres of biodiversity

On a global scale, many centres of plant diversity are located in tropical montane areas such as the South American Andes, the Eastern Arc, Crystal Mountains, Papua New Guinea, Himalaya or the Mesoamerican Cordillera Central (BARTHOLOTT et al. 1999; MUTKE & BARTHOLOTT 2005). In Africa, the montane regions Albertine Rift, the Eastern Arc, the Southern Rift extending into Chimanimani-Nyanga, the northeastern part of South Africa extending from Sekhukhuneland and Soutpansberg into the Maputaland Centre, and the West African Mt. Cameroon are well known centres of richness and endemism for a variety of ecologically very different taxa such as birds, mammals, snakes, amphibians (BROOKS et al. 2001) and plants (MUTKE et al. 2001).

Our study gives evidence that this also is the case for phytophagous beetles. Most *Monolepta* species in Central and East Africa have a restricted distribution. Twelve species are endemic to montane forests along the Albertine Rift, ten are restricted to East African mountains in Kenya and Tanzania, mainly to Mt. Kenya, Mt. Kilimanjaro and to the Eastern Arc Mountain mosaic, and a further nine species are restricted to montane areas in Ethiopia and Eritrea (WAGNER 2001a). To a lesser extent, montane regions in Cameroon also have higher species diversity and some endemic species. The diversification of many *Monolepta* species is obviously strongly effected by geographical speciation in isolated montane forests.

Many of the forest-dwelling *Monolepta* species appear to be young species in evolutionary terms. The Quaternary extension of the forest biome may be crucial in explaining the distribution pattern. In the late Pleistocene, the climate, particularly in central and East Africa was much cooler and drier (HAMILTON 1981). The timberline was about 1000 m lower than at present (e.g. BONNEFILLE et al. 1990; LOVETT 1993) and most lowland areas, including the Congo Basin, were too dry for forest vegetation and were covered by savannahs. The proposed forest refuge core areas coincides well with the highest degree of endemism and diversity of *Monolepta* in montane areas of Cameroon, the Albertine Rift and higher mountains in Kenya and Tanzania, including the Eastern Arc Mountain mosaic. Other *Monolepta* species, which are restricted to dry forest and savannahs, have a wider range. In the early Holocene, the climate became warmer and more humid. Wet tropical forests expanded to a presumed maximum about 6,000 years ago (HAMILTON 1981). During that time the Sudano-Zambesian savannah zone was presumably separated into a north-western and a south-eastern part, leading to a corresponding distribution pattern also found in other

insects like butterflies and paussid beetles (CARCASSON 1964; NAGEL 1987).

Combined analyses on large scale biodiversity, in particular those comparing such different taxa like beetles and plants, have been heavily criticised as paradoxical, since they tend to neglect the diversity of ecological characteristics at the species level (HUSTON 2001). Indeed, the influence of abiotic factors or historical processes depends on the characteristics of each taxon. For example, steep topography or climatic fluctuations can lead to reduced gene flow between populations, but this strongly depends on the mobility of the animals or seed vagility in plants. The high degree of endemism in the Cape flora is partly interpreted as a consequence of the low dispersability of a high proportion of the species; e.g. of about 1000 ant-dispersed species in the Fabaceae, Proteaceae, Restionaceae, Rhamnaceae, and Rutaceae (GOLDBLATT & MANNING 2002). For the most speciose and endemic plant taxon in the South American Andes, the Orchidaceae, it is not dispersal but limited mobility of highly specialized arthropod pollinators that may be a key to understanding the extremely high number of local endemic species (KÜPER et al. 2004).

Nevertheless, if considering biodiversity not exclusively a result of the spatial distribution of abiotic factors (pattern diversity) but as a result of a variety of mechanisms (process diversity), it is clear that geodiverse, montane areas are an ideal place where a high variety of mechanisms in parallel can promote high levels of diversity: the steep orography can promote allopatric speciation processes, whereas orographic rainfall and horizontal mist interception in mountains may facilitate survival of species during long-term climate dynamics (FJELDSA & LOVETT 1997) and opportunistic colonisation by widespread species. Habitat suitability but also habitat diversity as a consequence of geodiversity, provide suitable conditions for a speciose and structurally rich vegetation which in turn promotes consumer diversity due to diverse habitats and a high net primary production.

The afromontane areas, the Cape and parts of the West African upper Guinea Centre of plant diversity, cover more than 80 % of the Sub-Saharan flora on less than 10 % of its total area (KÜPER et al. 2004). Preliminary analyses suggest that the proportion of the Sub-Saharan vertebrate fauna covered by these areas might be even higher than that for plants (BROOKS et al. 2001), and the situation for phytophagous insects may be similar.

Due to the provided habitat diversity, one explanation for species richness of the Afrotropical mountains might be the high number of overlapping ranges contributed by species of taxa which have their actual centre of diversity at different places. However, a significant number of endemic species and species with small distribution ranges of different taxa are restricted to Afro-

tropical mountains. The occurrence of similar diversity stimulating mechanisms in very different taxa highlights the importance of Afrotropical mountains as overall centres of terrestrial biodiversity.

4.2. Consequences of fragmentary biodiversity information

Our plant data are the most comprehensive ever assembled for the study area, but inevitably have limitations. There are certain areas in Ethiopia, the Sudan, the Central African Republic, the Republic of the Congo, the Democratic Republic of the Congo and Angola, whose plant diversity is not adequately documented (KÜPER, unpubl. data), and the scientific exploration of these areas is a most important challenge for the future. Unsurprisingly, the situation is even more problematic for phytophagous beetles. While the low diversity in Upper Guinea may be partly explained by the relative scarcity of montane areas; e.g., the Crystal Mountains in Gabon and Equatorial Guinea, are clearly undersampled. The concentration of the present records to urban areas or such with a comparatively good infrastructure (e.g. Addis Ababa, Mbandaka, and several National Parks) is symptomatic for sampling artefacts. Currently it is not possible to quantify how much of the congruence in richness patterns of beetles and plants in our database is due to the fact that the same areas tend to be better collected for both taxa, resulting in a comparatively high number of species of both groups in these cells.

The more speciose taxa are, and the smaller the mean range size of their species is, the less complete is our knowledge on their large scale biogeographic patterns. At the same time, the restricted knowledge concerning the distribution of any taxon limits its consideration in spatial priority setting approaches for nature conservation.

Current conservation approaches in Africa are mainly based on patterns of vertebrate diversity (BURGESS et al. 2004; FJELDSA et al. 2004; DE KLERK et al. 2004). This may mainly result from their charisma, making them attractive for funding as well as for non-scientific but valuable field survey by lay people, and also from the history of Africa's protected areas (FJELDSA et al. 2004). Whereas about 95 % of the vertebrates in Sub-Saharan Africa are covered by the existing set of IUCN protected areas, the proportion for plants covered by the same set is at 74 % (BURGESS et al. in press). Only in a few cases are large scale patterns of plant diversity more appropriately considered, e.g. for the Republic of South Africa (COWLING et al. 2003). Though an amount of about 140 million plant specimens have been collected globally (BGCI 6/2004), estimations on the basis of the TROPICOS database at the Missouri Botanical Garden revealed that for about 80 % of all taxa which are represented in the form of collections, there are less than ten collection localities worldwide (SCHATZ 2002).

A large attraction of currently available numerical algorithms for selecting conservation areas is that they can go beyond subjective preferences for the cute and the cuddly, but if biogeographic data and phylogenies are available only for "attractive" groups, we are no further forward (MACE et al. 2003). For arthropods, most likely less than 20 % of the existing species have been described so far. The risk of this situation is that we are actually considering only the tip of the iceberg of problems in nature conservation.

The bad message from our study is that even after spending several ten thousand hours of manpower on the collection of the distribution of African plant species and checking label data of about 21,000 beetle specimens, we are far from a satisfying documentation and understanding of the large-scale diversity patterns of these taxa.

The good news might be, if such different taxa like vertebrates, plants and phytophagous beetles do have centres of biodiversity in common, it may be possible to protect a large proportion of species, in relatively well defined and small areas. These areas possibly comprise species that are not yet described. Unfortunately, in many cases exactly these areas are also most attractive for human settling (CINCOTTA et al. 2000; BALMFORD et al. 2001). Hence, more comprehensive evidence showing taxon-crossing relevance of these areas could at least be a solid argument in favour of the sustainable use and protection of its biodiversity.

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