



Priority sites for conservation of land snails in Gabon: testing the umbrella species concept

Benoît Fontaine*, Olivier Gargominy and Eike Neubert

Muséum National d'Histoire Naturelle, Paris (France), Département Systématique et Evolution, USM 602, Case Postale No. 51, 57 rue Cuvier, 75231 Paris Cedex 05, France

ABSTRACT

In order to assess the potential for molluscan conservation of a protected area considered representative of regional megafauna, we sampled molluscs inside and outside Lopé National Park in Gabon. In the northern part of Lopé National Park, 116 stations were surveyed and 71 species collected. Outside the park, 37 stations yielded 96 species, including 71 in Lastoursville, a small limestone area where molluscs are significantly more abundant than in other collecting sites. Lastoursville is among the richest sites known for molluscs in Africa. Overlap between sampling areas was limited, with 20.0% of the species found only in Lopé National Park, and 40.8% of the species found only outside. This suggests that Lopé National Park does not protect the whole molluscan diversity of central Gabon. Given the high levels of allopatric diversity of tropical land snails, conservation strategies cannot be the same for snails and for wide-ranging vertebrates. Protecting small areas with a high abundance and diversity of molluscs would be less expensive and as efficient for molluscan conservation as protecting large tracts of rainforest. Despite limited general knowledge of central African molluscs, robust estimates of site-specific diversity can be produced. Limestone areas harbour a remarkable biodiversity: sites such as Lastoursville would be ideal candidates for small protected areas dedicated to the conservation of land snails, and would complement the role of large protected areas.

Keywords

Mollusca, Gabon, umbrella species, rarity, limestone, allopatric diversity.

*Correspondence: Benoît Fontaine, Muséum National d'Histoire Naturelle, Paris (France), Département Systématique et Evolution, USM 602, Case Postale No. 51, 57 rue Cuvier, 75231 Paris Cedex 05, France. Tel.: 00 33 1 40 79 31 02; Fax: 00 33 1 40 79 57 71; E-mail: fontaine@mnhn.fr

INTRODUCTION

Most species have a restricted range (Gaston, 1994): in this context, the clearing of tropical forests, which harbour a large proportion of the world's species (WCMC, 2000), could lead to the extinction of many species. As most are still undescribed invertebrates (Hammond, 1995), their extinction would go unnoticed. It is therefore important to find strategies to protect this unknown biodiversity. One of these strategies relies on the umbrella species concept: protecting large animals implies protecting their habitat, and so protecting all the species, known or unknown, that live in this habitat, provided that they have less extensive spatial requirements than the umbrella species (Hunter, 1996). This strategy has been proven useful for species that rely on the same resources as the umbrella species (Martikainen *et al.*, 1998; Suter *et al.*, 2002), but its value in other cases is questionable. Considering mammals only, a study in Tanzania (Caro, 2003) showed that this concept is not always effective, as in certain circumstances background species are more abundant outside protected areas set up for umbrella species (background species

are defined as species that live in the same geographical area as species that have been used to identify an area of conservation concern — Caro, 2003). A critical review of the literature to assess the usefulness of the umbrella species concept listed 18 studies that investigated the protection conferred by various umbrella taxa on various background taxa (Roberge & Angelstam, 2004). Most of these studies were performed in temperate regions, and none in tropical rainforests. Only six investigated the usefulness of this concept for the conservation of invertebrates, generally butterflies. The protection conferred was ineffective in three of the 18 studies, limited in six and effective in one, and a mixture of these in the other cases, depending on the taxa, the scale or the context. At a large scale, there is generally low congruence of species richness across taxa (Prendergast *et al.*, 1993; Lombard, 1995; Kerr, 1997; Howard *et al.*, 1998). The use of surrogate species to select areas for the conservation of poorly known taxa is thus not necessarily useful, and should be tested whenever possible (Caro & O'doherty, 1999; Simberloff, 1999; Fleishman *et al.*, 2001). Moreover, most studies of the umbrella species concept are based on hypothetical reserves

derived from the distribution of the umbrella species, and do not provide an *in situ* evaluation of their usefulness based on data from existing protected areas and their surroundings (Roberge & Angelstam, 2004).

Located in central Gabon, Lopé National Park (Lopé NP) was first gazetted as a protected area in 1946 for its megafauna (Christy & Wilmé, 2003). It is still renowned for these animals, harbouring 45 species of large and medium-sized mammals (Tutin *et al.*, 1997), with a fauna considered typical of central Africa, including primates, antelopes, buffaloes, and elephants (Ecofac, 2006), and 'its mammal populations give to Lopé NP a nationwide reputation' (Christy & Clarke, 1994). Lopé NP qualifies for Birdlife criteria A1, A2, and A3, i.e. (A1) it harbours populations of bird species listed in the IUCN Red List; (A2) has a global importance for all restricted-range bird species of Endemic Bird Area 'Cameroon and Gabon lowlands'; and (A3) ensures adequate representation of species restricted to the Guinea-Congo forests biome (Birdlife International, 2003).

In this context, we test here the relevance of a large protected area famous mainly for its megafauna to safeguarding the invertebrate fauna in a tropical rainforest environment. For this purpose, we sampled land snails inside and outside Lopé NP in order to assess whether this park is representative of the diversity of Gabonese rainforest molluscs.

METHODS

Study area

Central Gabon is covered with lowland tropical rainforest, with pockets of savannas in the northern and eastern side of Lopé NP (Reitsma, 1988). Most of the forest has been logged selectively or is planned for exploitation (Collomb *et al.*, 2002). In the Lopé NP area, the forest was selectively logged at low intensity (1–2 trees ha⁻¹) more than 30 years ago (White, 1995). We sampled in the north-eastern part of Lopé NP, mostly in the study area of the Station d'Etude des Gorilles et des Chimanzés (SEGC), but also along the Offoué river and in the Mikongo ecotourism area. Outside Lopé NP, the main sampling regions were: (1) Langoué, an area of lowland primary forest 100 km east of Lopé NP (seven stations); (2) Forêt des Abeilles, a selectively logged lowland rainforest east of Lopé NP (seven stations); (3) around Lastoursville on limestone in secondary forest (nine stations), and (4) along the Lastoursville-Mouila road in old secondary forests (15 stations) (Fig. 1). Altogether, this represents 116 stations inside Lopé NP and 38 stations outside. Inside Lopé NP, 87 stations were in various forest types and 29 in gallery forests or patches of forest in the forest-savanna mosaic. Stations sampled in savanna-like habitats (savannas and colonized savannas, only found in Lopé NP) are not included in this paper. For a precise description of habitats sampled in Lopé NP, see Fontaine *et al.* (2007). Outside Lopé NP, 16 stations were in mixed/mature forest and 22 in secondary forest or patches of forest in savannas. Altitudinal ranges of stations were 100–600 m a.s.l., 250–600 m a.s.l., and 100–700 m a.s.l. for Lopé NP, Lastoursville, and other areas outside Lopé NP, respectively.

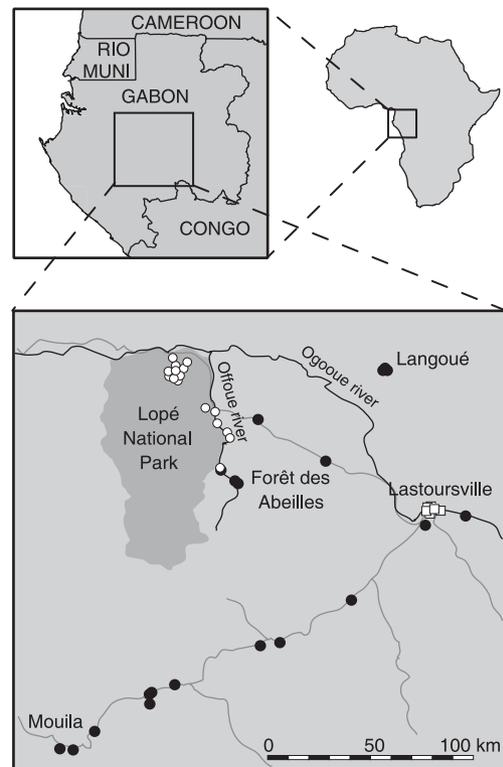


Figure 1 Location of the mollusc sampling stations in Gabon, inside and outside Lopé National Park. Circles and squares represent sampling stations: open circles: inside Lopé NP; open squares: Lastoursville limestones; solid circles: outside Lopé NP except Lastoursville. Grey lines represent main roads.

Climate is characterized by a well-defined dry season of about 3 months between June and September. There is usually a less pronounced and short dry season in January–February (Reitsma, 1988). The mean annual rainfall in Lopé NP is 1548 mm, and temperatures vary little but are lowest in the dry season; mean monthly maxima vary from 26.8 to 30.8 °C and minima from 20.5 to 22.3 °C (Tutin & Fernandez, 1993).

The geology of central Gabon is dominated by deeply weathered Precambrian metamorphic and granitic bedrocks (Nicklès, 1952). The Lastoursville area is characterized by limestone outcrops spread over c. 80 km², but covering only a small proportion of this surface (Delorme, 1979).

For the purpose of this paper, three sets of sampling stations (hereafter named sampling areas) are distinguished: inside Lopé NP, limestone area around Lastoursville, and all other sites outside Lopé NP.

Collecting effort

Sampling took place during the periods 30 August to 7 October 1999 (transition between dry and rainy seasons), 19 June to 11 August 2000 (dry season), and 21 April to 7 June 2001 (rainy season).

A station was defined as a collecting locality, spread over 5–10 m² at most, in a single habitat. At each station, two people (BF and OG) spent 30 min searching at ground level for live snails, then leaf litter and a few millimeters of topsoil were collected and subsequently sieved. Altogether, 492 L of leaf litter were collected and sorted. This combination of visual searching and litter sieving is considered the best for inventory (Cameron & Pokryszko, 2005) and is the standard procedure in mollusc sampling (Tattersfield, 1996; De Winter & Gittenberger, 1998; Cowie, 2001). We processed this sample initially at the collecting location with a Winkler sieve (1 cm mesh), the coarse material being checked by eye for snails and discarded. The remaining material was bagged and sun-dried as soon as possible. The molluscs collected alive were drowned overnight and fixed in 70% ethanol.

Once dried, the volume of leaf litter was measured. We passed the leaf litter through 5 mm, 2 mm, and 0.6 mm sieves. The two larger fractions were thoroughly searched with the naked eye, the third one sorted under a dissecting microscope. We searched the material passing through the 0.6 mm sieve for the first three stations, but as it contained no molluscs, as was the case in earlier studies (e.g. Tattersfield, 1996; De Winter & Gittenberger, 1998), it was subsequently discarded.

Taxonomic processing and data analysis

All specimens were sorted to morphospecies, or recognizable taxonomic units (RTU — New, 1999), by an experienced taxonomist (EN) according to shell characters, assigned to a family and, when possible, to a described genus or species. As we did not dissect animals, closely related species with similar shells may not have been distinguished (in particular, urocyclid semislugs), so our diversity results could be underestimates. However, most of our RTUs are equivalent to species as generally understood by mollusc taxonomists, and in the Results and Discussion sections, 'RTUs' and 'species' refer to the same concept. The rationale for this approach is that naming all species in such poorly known areas would take several years. Indeed, recent papers on tropical malacofaunas, written by experienced malacologists, have not

named all the species collected: only 20.6% of the morphospecies in De Winter & Gittenberger (1998) (Cameroon) are attributed to known species; 21.9% in De Winter (1995) (Gabon), and 34.4% in Schilthuizen & Rutjes (2001) (Borneo). The genus and, to some extent, family allocations we have used are tentative. Thus, our results are comparable to those of other studies at the species level, but not at the genus or family levels.

In our analyses, we have combined animals collected alive and those collected dead, for two reasons: (1) we collected more dead shells than live animals, and did not want to exclude the bulk of our data from the analyses, and (2) because litter and shells were sun-dried and sometimes sorted out long after their collection, it is difficult to know, especially for minute species, whether they were alive when collected.

When possible, we assigned juvenile specimens to a RTU for which we had adult specimens. In cases of ambiguity (specimen matching more than one RTU) these juveniles were excluded from the following analyses. If a juvenile did not match any of the adult shells, we treated it as a separate RTU, and included it in the analyses.

We used the Jaccard Index to examine similarity between sampling areas. It is calculated by dividing the number of species found in both of two samples by the total number of species in both samples. It ranges from zero (no species in common) to one (identical faunas).

Voucher material is deposited in the Muséum National d'Histoire Naturelle, Paris (France).

RESULTS

Species richness

Altogether, we collected 120 species belonging to 17 families, including 96 species found in Lastoursville and in other stations outside Lopé NP. The most speciose families were Streptaxidae (38 species), Subulinidae (33 species), Urocyclidae (19 species), and Achatinidae (10 species). A list of the RTUs collected is given in Appendix S1 in Supplementary Material. Table 1 summarizes the overall data for the three sampling areas.

Table 1 Summarized results of land snail sampling in the three sampling areas in central Gabon.

	Number of species	Number of families	Number of specimens	Volume of sieved leaf litter (L)	Most speciose families (number of species)	Average number of species L ⁻¹ (range; median)	Average number of specimens L ⁻¹ (range; median)
Lopé NP	71	13	3334	367	Subulinidae (25) Streptaxidae (18) Urocyclidae (12)	1.4 ± 1.0 (0–6.5; 1.3)	7.7 ± 15.1 (0–141.8; 3.7)
Lastoursville	71	13	1535	24	Subulinidae (24) Streptaxidae (19) Urocyclidae (9) Achatinidae (8)	5.6 ± 3.1 (3.0–10.0; 4.3)	58.0 ± 28.4 (36.7–107.6; 46.7)
Outside	58	10	937	101	Subulinidae (18) Streptaxidae (17) Urocyclidae (8)	1.9 ± 1.8 (0.2–6.7; 1.1)	8.8 ± 12.2 (0.2–56.7; 4.2)

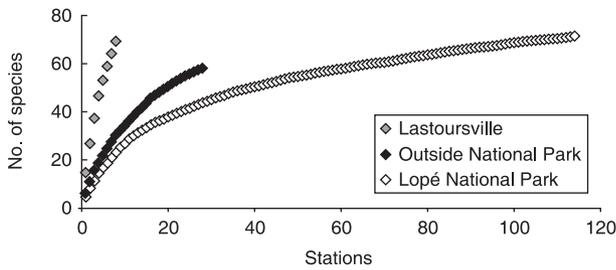


Figure 2 Species accumulation curve for Lopé National Park, Lastoursville and outside Lopé National Park except Lastoursville (Colwell, 2005). Despite a limited number of sampling stations in Lastoursville, this area appears as the richest, and the inventory here is far from complete.

The mean number of specimens per litre of leaf litter is not significantly different between Lopé NP and outside Lopé NP (*t*-test, $t = 0.32$, d.f. = 126, ns). It is significantly higher in Lastoursville than both in Lopé NP (*t*-test, $t = -6.91$, d.f. = 105, $P < 0.001$) and outside Lopé NP (*t*-test, $t = -6.51$, d.f. = 29, $P < 0.001$).

For the area sampled in Lopé NP, richness estimators (Colwell, 2005) give a total species richness between 78 (Michaelis–Menton equation) and 131 species (Chao2). The species accumulation curves calculated using ESTIMATES 7.5 (Colwell, 2005) (Fig. 2) show that despite a limited number of sampling stations in Lastoursville, this area is the richest, and its inventory is far from complete. No species richness estimates were calculated for Lastoursville and outside Lopé NP, because the species accumulation curves show no sign of leveling off, i.e. the sampling there was not exhaustive enough.

Rarity

Biological rarity

Biological rarity (*sensu* Bouchet *et al.*, 2002) is based on the number of specimens found of a given species. In our sampling, the dominant feature is the long tail of the rank–abundance relationship, for all areas together as well as when they were considered separately (Fig. 3). Most species are rare: 23.3% of all species are represented by one specimen only, i.e. they together represent 0.5% of the specimens collected, and 19.1% of the species are represented by two to five specimens. Species represented by one specimen only represent approximately one fifth (19.7–24.1%) of the fauna in each area (Fig. 4a). In Lastoursville, where the number of specimens collected per litre of leaf litter was high, the pattern of biological rarity is similar to the other areas.

Ecological rarity

Ecological rarity (*sensu* Bouchet *et al.*, 2002) is based on the number of stations at which a species occurred. Again, rarity is a major feature of the fauna: 44 species (36.6%) were found in one

station only when all areas are taken together. The percentage of species found in one station only in each area ranges from 31.0% (Lopé NP) to 47.9% (Lastoursville) (Fig. 4b). Among the 30 species found in more than six stations, all areas taken together, all but six (only found in natural forests) were found in natural and degraded habitats. Among the 44 species found in one station only (6 Subulinidae, 20 Streptaxidae, 8 Urocyclidae, and 10 species belonging to other families), 17 were found in Lopé NP, 18 in Lastoursville and 10 elsewhere outside Lopé NP, and 24 were found in degraded habitat. No taxonomic or ecological characteristics shared among rare species were found.

Fauna overlap

Among the 120 species collected, only 23 (19.2%) were found in all three sampling areas. A similar proportion (24 species, 20.0%) was found only in Lopé NP; 25 (20.8%) only in Lastoursville, and 14 (11.7%) only in the other sites outside Lopé NP. Forty-nine species (40.8%) were only found outside the protected area (Fig. 5). The Jaccard Index was 0.34, 0.35, and 0.31 for Lopé NP/Lastoursville, Lopé NP/outside, and Lastoursville/outside, respectively.

In order to control for habitat differences in the three sampling areas, we compared the malacofauna in the same habitat (old-growth forest with open understorey) inside (33 stations), and outside Lopé NP (13 stations), excluding limestone areas. This represents a total of 61 species. Of these, only 23 (37.7%) were found both inside and outside Lopé NP. Nineteen (31.1%) were found only inside the protected area, and 19 others were found only outside, despite the fact that there were more old-growth forest stations inside Lopé NP than outside. For these stations only, the Jaccard Index was 0.38 between inside and outside Lopé NP.

To account for the influence of rare species on fauna overlap, these were excluded from the analysis. Rare species were defined following the quartile definition of rarity (Gaston, 1994), which corresponded in our sample to species represented by one or two specimen(s) in each sampling area. Fauna overlap was also assessed using only the most common species in each sampling area (first quartile of species in each sampling area, according to abundance). Table 2 compares the percentages of species found in the various sampling areas with all species, without rare species and with most common species only. It shows that removing rare species made little difference to faunal overlap percentages. When the most common species only are considered, overlap is slightly greater, but still 37.9% of the fauna is not represented in Lopé NP.

DISCUSSION

Sampling bias or allopatric diversity?

Until recently, sympatric molluscan diversity in tropical forests on acidic substrate was supposed to be low, because of lack of available nutrients, low amount of litter, and numerous predators (e.g. Solem, 1984). However, field studies throughout

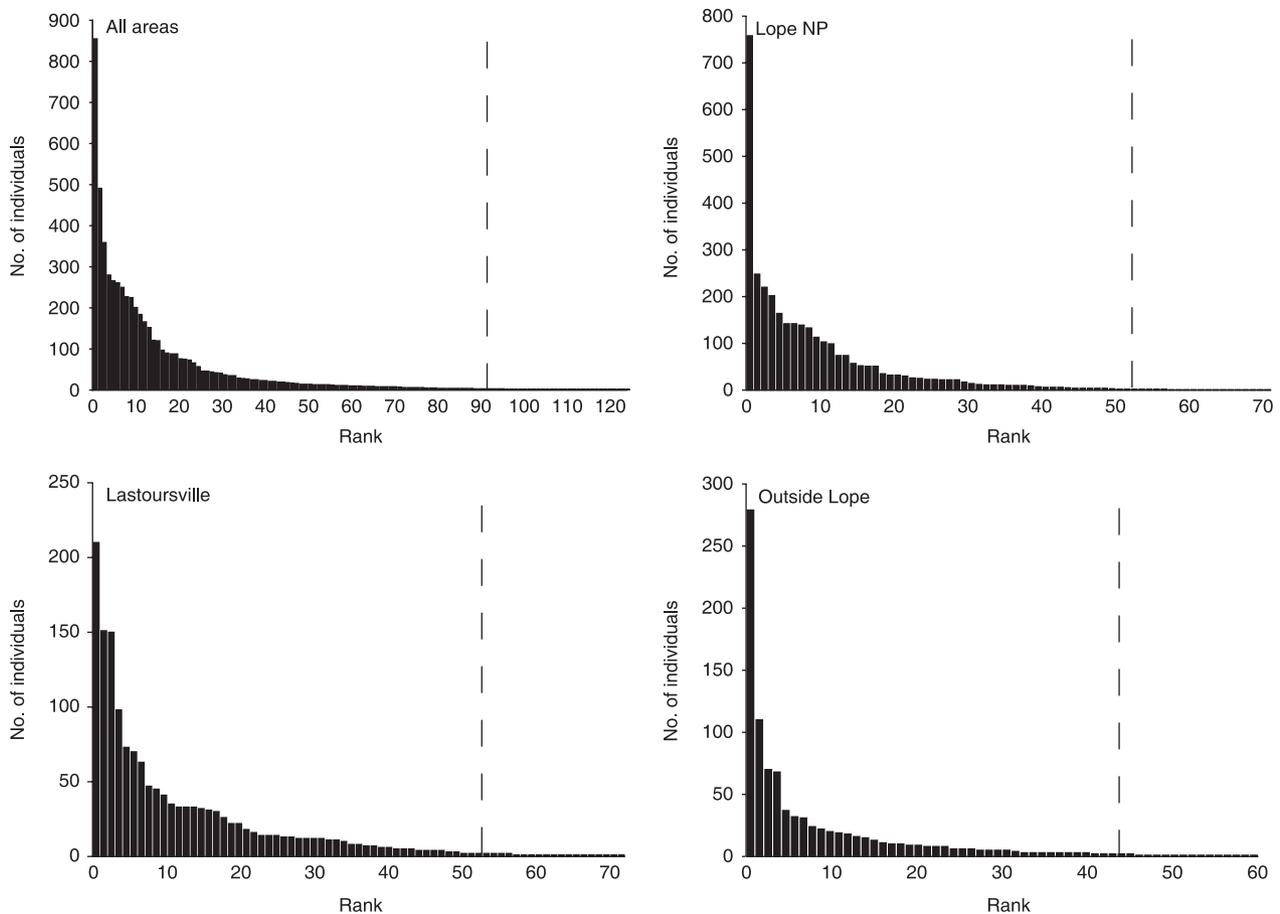


Figure 3 Rank–abundance (number of individuals) relationship for the whole sampling and for the three sampling areas. Dashed line delineates species categorized as rare under the quartile definition (Gaston, 1994).

Africa (Emberton *et al.*, 1996; Tattersfield, 1996; De Winter & Gittenberger, 1998; Seddon *et al.*, 2005; Fontaine *et al.*, 2007), South-East Asia (Schilthuizen & Rutjes, 2001), and tropical America (Gargominy & Ripken, 1998) have shown that previous assumptions on low sympatric diversity were wrong, and a result of biological and ecological rarity of molluscs in tropical rainforests.

Solem (1984) suggested that ‘evidence is now accumulating that allopatric diversity is exceptionally high among land snails’, and predicted a median range of less than 100 km, and probably less than 50 km for land snail species. Indeed, more and more examples of high allopatric diversity (i.e. increase of species number associated with an increase in the number of stations in a given area) have been documented in molluscs, and this pattern is more pronounced in the tropics, range size declining towards the equator (Cameron, 1998). For instance, 28 species of camaenid snails in the Kimberley Range (Western Australia) have a median range of 0.825 km² (Solem, 1988); 115 species occur on the 2000 km² Usambara Mountains in Tanzania, yet fewer than 25 can be found at a single site (Verdcourt in Solem, 1984). Islands also show a high level of allopatric diversity: the Hawaiian

archipelago has more than 750 mollusc species, 70–80% of which are single island endemics (Cowie, 1996). Other examples of high land snail allopatric diversity can be found in Van Bruggen (1978), Seddon *et al.* (2005), and Tattersfield (1998). For the Congo Basin, data on molluscan diversity, let alone allopatric diversity, are rare. De Winter (2001) compared three sites 30 km apart in Cameroon and found that 40% of the species occurred in one site only, the figure being 13% when the most common species only were considered. In Lopé NP, the composition of the fauna in similar forest habitats was different at two sites 15 km apart (Fontaine *et al.*, 2007). Similarly, comparison of the fauna in similar habitat (old-growth forest with open understorey) inside and outside Lopé NP showed a low level of overlap between sampling sites.

Moreover, allopatry is not an artefact of some species that are present being too rare to be found (undersampling): when the most common species only are considered in our sample, the level of overlap is still low (Table 2). This implies that allopatric diversity is a shared characteristic of species, regardless of their abundance: locally abundant mollusc species are not necessarily large-range species.

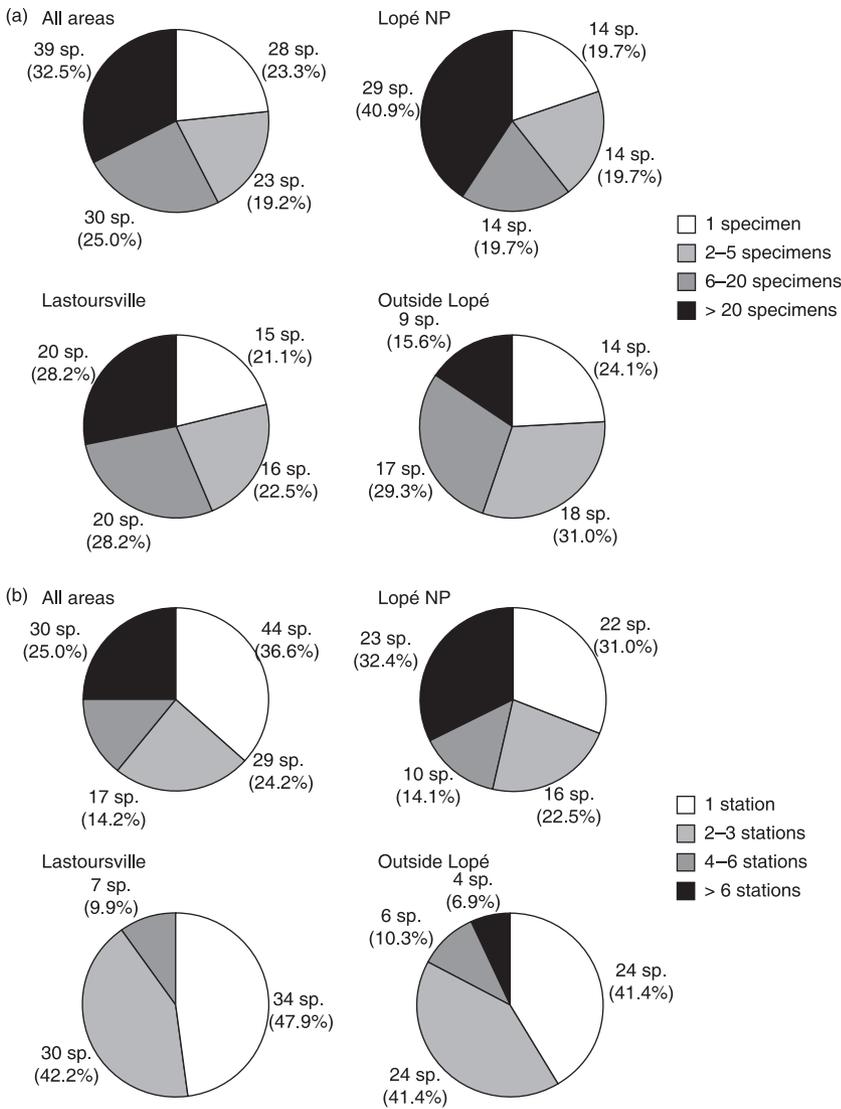


Figure 4 Rarity of the terrestrial molluscs for the whole sampling and for the three sampling areas. (a) Biological rarity. (b) Ecological rarity. Proportions of species in four arbitrary abundance (number of specimens or number of stations of occurrence) categories.

Sampling discrepancies

For logistical reasons and time constraints, we were not able to inventory the entire Lopé NP nor to have a rigorous design of sampling locations that would allow a robust comparison of the malacofauna inside and outside the Park. Strictly speaking, our test of the validity of the umbrella species concept is valid only for the 5000 ha around the SEG. Lopé NP was the only area that was well covered (Fig. 2). Moreover, sampling in Lopé NP was done during both dry and rainy seasons, whereas other areas were surveyed in only one season (Lastoursville during the dry season, Langoué during the rainy season for instance), which could account for the faunal differences among the three areas: in Cameroon, the abundances of certain species vary greatly in different seasons (De Winter & Gittenberger, 1998).

These sampling discrepancies preclude a robust comparison among the three sampling areas. However, they do not undermine the conclusion that the northern part of Lopé NP is not

representative of the whole region: though it was the most extensively sampled area, during dry and rainy seasons, 40.8% of the species were not found there. Sampling in the southern part of the Park would certainly increase the number of species found, but Lastoursville was also not completely inventoried and is undoubtedly a hotspot. The Gabonese rainforest probably shows the same pattern of high molluscan allopatric diversity as other parts of the Tropics (Solem, 1984, 1988; Cowie, 1996; Tattersfield, 1998; Seddon *et al.*, 2005), making the design of an efficient conservation strategy for molluscs difficult.

Limestone as mollusc diversity hotspots

Limestone outcrops are known to harbour a specific fauna (bats, certain birds, molluscs, and subterranean arthropods) and flora, with obligate calcicolous species and a high level of narrow-range endemism (WWF & IUCN, 1994; Vermeulen & Whitten, 1999). In tropical Asia, these have been the subject of considerable

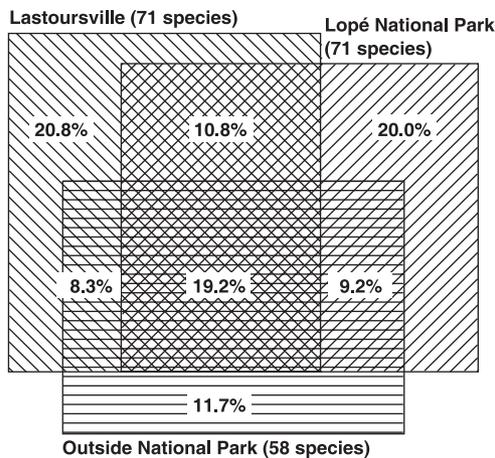


Figure 5 Fauna overlap for terrestrial molluscs between Lopé National Park, Lastoursville area and sites outside Lopé National Park (Lastoursville excluded). Less than one fifth of the species are ubiquitous, only 20.0% were only found in the protected area, and 40.8% were not found in the protected area.

research (e.g. references in Vermeulen & Whitten, 1999), whereas limestone biodiversity in tropical Africa has hardly been studied.

Molluscs constitute a significant and vulnerable component of biodiversity on limestone substrates in both temperate areas (Solem, 1984; Graveland *et al.*, 1994; Waldén, 1995) and tropical areas, mostly in South-East Asia (Vermeulen & Whitten, 1999; Schilthuizen *et al.*, 2005), but also in the West Indies (Rosenberg & Muratov, 2005). In Borneo, molluscan abundance is much higher on limestone hills than on non-limestone substrates, though diversity is not much higher, only a few species only being obligate calcicoles in this area (Schilthuizen *et al.*, 2003). However, despite increasing survey work, several species are still considered obligate calcicoles, and even small outcrops can harbour true endemic species (Schilthuizen *et al.*, 2005). In East Africa, among coastal forest localities, the sites having the highest single-station diversity are on calcium-rich soils (Seddon *et al.*, 2005).

The other main characteristic of the malacofauna on limestone is an outstanding abundance, in contrast to the surrounding acidic substrate: molluscs species found on limestone might not be so different from those found in the surrounding areas, but

they occur here in very abundant populations. For these reasons, the protection of even small limestone outcrops could be an efficient way to preserve a large component of the molluscan diversity, and these areas might act as reservoirs from which degraded surrounding areas could potentially be restocked (Schilthuizen, 2004).

Lastoursville, one of the richest sites in Africa for molluscs

Although not directly comparable with the results of Seddon *et al.* (2005) on molluscan diversity in East African forest sites, because of methodology discrepancies, our results show that Lastoursville is among the richest sites known in Africa, at least in number of species. In East African sites, there are between 13 and 61 species per site (average 36.8 species). Compared to other central African sites, Lastoursville has a similar number of species to Lopé NP (this study) and 73% of the species richness of a primary forest site in Cameroon (De Winter & Gittenberger, 1998), despite a low sampling intensity (24 L of litter collected in Lastoursville vs. 144 L in Cameroon and 367 L in Lopé NP). The mean number of species per station in Lastoursville (21.4) was close to the highest figures for East Africa (Seddon *et al.*, 2005) (mean: 16.22 species per station, range: 5.5–26.5), although the total number of species in East African forest sites was always lower than in Lastoursville, these sites being much more intensively searched than Lastoursville (over 15 person hours spent in several stations at each site) (Seddon *et al.*, 2005). As shown by Fig. 2, more sampling would increase significantly the species richness in Lastoursville. For comparison, the mean number of species per station in Lopé NP, intensively sampled, was 4.69, which is similar to the figures given by van Bruggen for South Africa (in Solem, 1984).

Which conservation strategy for poorly known invertebrates?

Gabon has one endemic mammal, the sun-tailed guenon *Cercopithecus solatus*, restricted to c. 10,000 km² centred in the Forêt des Abeilles and occurring in Lopé NP (Brugière *et al.*, 1998). Part of Gabon (including Lopé NP) is in the Endemic Bird Area 'Cameroon and Gabon lowlands', with six restricted-range bird species that occur in several protected areas in the region (Birdlife International, 2003). Compared to molluscs, these

Table 2 Proportion of the total fauna for the various sampling areas, with all species, without rare species (defined as the fourth quartile according to species abundance in each area), and with most common species only (first quartile).

Sampling area	All species	Without rare species	Most common species
All three areas	19.2%	19.0%	24.1%
Lopé NP only	20.0%	22.6%	17.2%
Lastoursville only	20.8%	20.2%	17.2%
Other sites outside Lopé NP only	11.7%	11.9%	13.8%
Lastoursville + other sites outside Lopé NP only	40.8%	40.5%	37.9%

'restricted-range' birds occur over large areas: for instance, the extent of occurrence of *Hirundo fuliginosa* is 150,000 km², and the range of *Picathartes oreas* is 314,000 km² (Birdlife International, 2003). The comparatively wide distribution of large charismatic vertebrates makes the chance that their distribution encompasses protected areas much higher than for invertebrates. Indeed, 84% of the large mammal species and 91% of the bird species of Central Gabon are present in the northern part of Lopé NP (SEGC, unpublished data), but only 59% of land snail species. The conservation strategies cannot be the same for large vertebrates and for invertebrates with virtually unknown distributions, but suspected to be several orders of magnitude smaller. Moreover, regions of high species diversity are not necessarily regions of high endemism, especially when more than one major taxonomic group is considered (Prendergast *et al.*, 1993), so the use of mammals or birds as umbrella species for invertebrate conservation is unreliable (Kerr, 1997; Andelman & Fagan, 2000). Despite limited sampling, 59% of the snail fauna was found in Lastoursville: to protect the molluscan diversity of Central Gabon, focusing on the limestone of Lastoursville (c. 10 km²) would be as effective, in terms of the number of species concerned, and less expensive than protecting the whole Lopé NP (c. 5000 km²), although the species covered would not be the same.

In practice, because of the lack of a sound molluscan taxonomy for central Africa and the paucity of records, comprehensive distributional databases are not presently feasible and it is impossible to avoid using RTUs. This has a major drawback, because endemism cannot be evaluated without naming species. So it is impossible, with current knowledge, to assess the value of sites such as Lastoursville as endemism hotspots, or their importance in conserving unique taxa. However, we cannot wait for taxonomic impediments to be solved. We should use the data that are available (i.e. RTUs) to select priority areas for conservation. Species-rich areas with a high abundance, be they centres of endemism or not, are certainly targets for conservation action.

CONCLUSION

To the general public and megafauna-orientated managers, Lopé NP is representative of the Gabonese rainforest environment. Indeed, most of the large mammal and bird fauna of central Gabon are present in the northern part of Lopé NP. We have shown that this is not the case for land snails, so mammals or birds could not act as umbrella species for molluscs in Gabon. Moreover, the Lastoursville area, a centre of molluscan diversity, has a high human density, with roads, railway station, and villages, and the large mammalian fauna has been wiped out by hunting (Barnes *et al.*, 1991; Lahm *et al.*, 1998; Laurance *et al.*, in press). In this case an area without large animals is valuable for invertebrate conservation.

Given the high allopatric diversity in land snails and the lack of knowledge of species ranges, it is impossible to design an optimal protected areas network based on sound data. The use of a large number of small reserves widely distributed for the conservation of molluscs has been suggested (Cameron, 1998), but this is

probably not feasible, given the scarce funding and lack in interest for the conservation of invertebrates. In this context, large protected areas set up for umbrella or flagship species are certainly useful for the conservation of molluscs, as they will inevitably encompass part or all of the range of numerous species, but they will not necessarily cover the main centres of diversity.

This given, limestone areas are biodiversity hotspots and should be targets for the conservation of land snails, as well as other animal and plant taxa favouring limestone. The sound selection of a few small protected areas on limestone would greatly improve the existing network of large protected areas for the conservation of molluscs, for their uniqueness (obligate calcicolous species and endemic taxa) and as viable reservoirs of more widespread species. Convincing authorities to protect an area for non-charismatic species such as molluscs would not be easy in a context of limited resources. However, these protected areas would be useful for the conservation of other taxa such as limestone flora or bats, which could be used as flagship species.

ACKNOWLEDGEMENTS

This study was funded by the Research Fellowship Program of the Wildlife Conservation Society. We thank the Direction de la Faune for permission to work in Lopé NP, and K. Abernethy and L. White for allowing us to stay at the SEGC and for support in Lopé. P.T. Telfer provided logistical support outside Lopé. E. Dimoto and J.-T. Dikangadissi helped in the field. A. de Winter helped with taxonomic processing. R. Cowie, M. Schilthuizen, and an anonymous referee made constructive comments on the manuscript.

REFERENCES

- Andelman, S.J. & Fagan, W.F. (2000) Umbrellas and flagships: Efficient conservation surrogates or expensive mistakes? *Proceedings of the National Academy of Sciences*, **97**, 5954–5959.
- Barnes, R.F.W., Barnes, K.L., Alers, M.P.T. & Blom, A. (1991) Man determines the distribution of elephants in the rain forests of northeastern Gabon. *African Journal of Ecology*, **29**, 54–63.
- Birdlife International (2003) *Birdlife's online world bird database: the site for bird conservation*, Version 2.0. <http://www.birdlife.org>. Accessed 24 April 2006.
- Bouchet, P., Lozouet, P., Maestrati, P. & Héros, V. (2002) Assessing the magnitude of species richness in tropical marine environments: exceptionally high numbers of molluscs at a New Caledonia site. *Biological Journal of the Linnean Society*, **75**, 421–436.
- Brugière, D., Gautier, J. & Lahm, S. (1998) Additional data on the distribution of *Cercopithecus (lhoesti) solatus*. *Folia Primatologica*, **69**, 331–336.
- Cameron, R.A.D. (1998) Dilemmas of rarity: biogeographical insights and conservation priorities for land Mollusca. *Journal of Conchology. Special Publication*, **2**, 51–60.
- Cameron, R.A.D. & Pokryszko, B.M. (2005) Estimating the species richness and composition of land molluscs communities: problems, consequences and practical advice. *Journal of Conchology*, **38**, 529–547.

- Caro, T.M. (2003) Umbrella species: critique and lessons from East Africa. *Animal Conservation*, **6**, 171–181.
- Caro, T.M. & O'doherty, G. (1999) On the use of surrogate species in conservation biology. *Conservation Biology*, **13**, 805–814.
- Christy, P. & Clarke, W. (1994) *Guide des oiseaux de la réserve de la Lopé*. ECOFAC, Libreville, Gabon.
- Christy, P. & Wilmé, L. (2003) *Lopé, un almanach équatorial*. ECOFAC, Libreville, Gabon.
- Collomb, J.-G., Mikissa, J.-B., Minnemeyer, S., Mundunga, S., Nzaio Nzaio, H., Madouma, J., Mapage, J.D.D., Mikolo, C., Rabenkogo, N., Akagah, S., Bayani-Ngoya, F. & Mofouma, A. (2002) *A first look at logging in Gabon*. http://pdf.wri.org/gfw_gabon.pdf. Accessed 17 March 2006.
- Colwell, R.K. (2005) *EstimateS: statistical estimation of species richness and shared species from samples*, Version 7.5. <http://purl.oclc.org/estimates>. Accessed 12 April 2006.
- Cowie, R.H. (1996) Variation in species diversity and shell shape in Hawaiian land snails: in situ speciation and ecological relationships. *Evolution*, **49**, 1191–1202.
- Cowie, R.H. (2001) Decline and homogenization of Pacific faunas: the land snails of American Samoa. *Biological Conservation*, **99**, 207–222.
- De Winter, A.J. (1995) Gastropods diversity in a rain forest in Gabon, western Africa. *Biodiversity and conservation of the Mollusca* (ed. by A.C. Van Bruggen, S.M. Wells and T.C.M. Kemperman), pp. 223–228. Backhuys Publishers Oegstgeest, Leiden, the Netherlands.
- De Winter, A.J. (2001) Land snail species diversity among three rainforest sites in southern Cameroon. *World Congress of Malacology 2001* (ed. by L. Salvini-Plawen, J. Voltzow, H. Sattmann and G. Steiner), p. 77. Unitas Malacologica, Vienna, Austria.
- De Winter, A.J. & Gittenberger, E. (1998) The land-snail fauna of a square kilometer patch of rainforest in southwestern Cameroon: high species richness, low abundance and seasonal fluctuations. *Malacologia*, **40**, 231–250.
- Delorme, G. (1979) Recherches spéléologiques dans l'est du Gabon. *Spelunca*, **4**, 151–160.
- Ecofac (2006) *Lopé National Park — General presentation*. http://www.ecofac.org/ECotourisme/_EN/Lope/Presentation.htm. Accessed 2 June 2006.
- Emberton, K.C., Pearce, T.A. & Randalana, R. (1996) Quantitatively sampling land-snail species richness in Madagascan rainforests. *Malacologia*, **38**, 203–212.
- Fleishman, E., Blair, R.B. & Murphy, D.D. (2001) Empirical validation of a method for umbrella species selection. *Ecological Applications*, **11**, 1489–1501.
- Fontaine, B., Gargominy, O. & Neubert, E. (2007) Land snail diversity of the savanna/forest mosaic in Lopé National Park, Gabon. *Malacologia*, in press.
- Gargominy, O. & Ripken, T. (1998) Micro-pulmonates in tropical rainforest litter: a new bio-jewel? *Abstracts of the World Congress of Malacology, Washington, D.C. 1998* (ed. by R. Bieler and P.M. Nikkelsen), p. 116. Unitas Malacologica, Chicago.
- Gaston, K.J. (1994) *Rarity*. Chapman and Hall, London.
- Graveland, J., Van Der Wal, R., Van Balen, J.H. & Van Noordwijk, A.J. (1994) Poor reproduction in forest passerines from decline of snail abundance on acidified soils. *Nature*, **368**, 446–448.
- Hammond, P.M. (1995) The current magnitude of biodiversity. *Global biodiversity assessment* (ed. by V.H. Heywood), pp. 113–138. Cambridge University Press, Cambridge.
- Howard, P.C., Viskanac, P., Davenport, T.R.B., Kigenyi, F.W., Baltzer, M., Dickinson, C.J., Lwanga, J.S., Matthews, R.A. & Balmford, A. (1998) Complementarity and the use of indicator groups for reserve selection in Uganda. *Nature*, **394**, 472–475.
- Hunter, M.L. (1996) *Fundamentals of conservation biology*. Blackwell Science, Cambridge.
- Kerr, J.T. (1997) Species richness, endemism, and the choice of areas for conservation. *Conservation Biology*, **11**, 1094–1100.
- Lahm, S.A., Barnes, R.F.W., Beardsley, K. & Cervinka, P. (1998) A method for censusing the greater white-nosed monkey in northeastern Gabon using the population density gradient in relation to roads. *Journal of Tropical Ecology*, **14**, 629–643.
- Laurance, W.F., Croes, B.M., Tchignoumba, L., Lahm, S.A., Alonso, A., Lee, M.E., Campbell, P. & Ondzeano, C. (2006) Impacts of roads and hunting on Central African rainforest mammals. *Conservation Biology*, **20**, 1251–1261.
- Lombard, A.T. (1995) The problems with multi-species conservation: do hotspots, ideal reserves and existing reserves coincide? *South African Journal of Zoology*, **30**, 145–163.
- Martikainen, P., Kaila, L. & Haila, Y. (1998) Threatened beetles in white-backed woodpecker habitat. *Conservation Biology*, **12**, 293–301.
- New, T.R. (1999) Descriptive taxonomy as a facilitating discipline in invertebrate conservation. *The other 99%. The conservation and biodiversity of invertebrates* (ed. by W. Ponder and D. Lunney), pp. 154–158. Royal Zoological Society of New South Wales, Mosman, New South Wales.
- Nicklès, M. (1952) *Carte géologique de l'A.E.F. et du Cameroun au 1/2,000,000*. Direction des Mines et de la Géologie de l'A.E.F., Paris.
- Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C. & Gibbons, D.W. (1993) Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature*, **365**, 335–337.
- Reitsma, J.M. (1988) Forest vegetation of Gabon. *Tropenbos Technical Series*, **1**, 1–142.
- Roberge, J.-M. & Angelstam, P. (2004) Usefulness of the umbrella species concept as a conservation tool. *Conservation Biology*, **18**, 76–85.
- Rosenberg, G. & Muratov, I.V. (2005) Status report on the terrestrial Mollusca of Jamaica. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **155**, 117–161.
- Schilthuizen, M. (2004) Land snail conservation in Borneo: limestone outcrops act as arks. *Journal of Conchology Special Publication*, **3**, 149–154.
- Schilthuizen, M., Chai, H.-N. & Kimsin, T.E. (2003) Abundance and diversity of land-snails (Mollusca: Gastropoda) on limestone hills in Borneo. *The Raffles Bulletin of Zoology*, **51**, 35–42.
- Schilthuizen, M., Liew, T.-S., Bin Elahan, B. & Lackman-Ancrenaz, I. (2005) Effects of Karst forest degradation on pulmonate and

- prosobranch land snail communities in Sabah, Malaysian Borneo. *Conservation Biology*, **19**, 949–954.
- Schilthuizen, M. & Rutjes, H.A. (2001) Land snail diversity in a square kilometre of tropical rainforest in Sabah, Malaysian Borneo. *Journal of Molluscan Studies*, **67**, 417–423.
- Seddon, M.B., Tattersfield, P., Herbert, D.G., Rowson, B., Lange, C.N., Ngereza, C., Warui, C.M. & Allen, J.A. (2005) Diversity of African forest mollusc faunas: what we have learned since Solem (1984). *Records of the Western Australian Museum Supplement*, **68**, 103–113.
- Simberloff, D. (1999) The role of science in the preservation of forest biodiversity. *Forest Ecology and Management*, **115**, 101–111.
- Solem, A. (1984) A world model of land snail diversity. *World-wide snails. Biogeographical studies on non-marine Mollusca* (ed. by A. Solem and A.C.V. Bruggen), pp. 6–22. Backhuys Publisher, Leiden, the Netherlands.
- Solem, A. (1988) Maximum in the minimum: Biogeography of land snails from the Ningbing Ranges and Jeremiah Hills, northeast Kimberley, Western Australia. *Journal of the Malacological Society of Australia*, **9**, 59–113.
- Suter, W., Graf, R.F. & Hess, R. (2002) Capercaillie (*Tetrao urogallus*) and avian biodiversity: testing the umbrella-species concept. *Conservation Biology*, **16**, 778–788.
- Tattersfield, P. (1996) Local patterns of land snail diversity in a Kenyan rain forest. *Malacologia*, **38**, 161–180.
- Tattersfield, P. (1998) Patterns of diversity and endemism in East African land snails, and the implications for conservation. *Journal of Conchology Special Publication*, **2**, 77–86.
- Tutin, C.E.G. & Fernandez, M. (1993) Relationships between minimum temperature and fruit production in some tropical forest trees in Gabon. *Journal of Tropical Ecology*, **9**, 241–248.
- Tutin, C.E.G., White, L.J.T. & Mackanga-Missandzou, A. (1997) The use by rain forest mammals of natural forest fragments in an equatorial African savanna. *Conservation Biology*, **11**, 1190–1203.
- Van Bruggen, A.C. (1978) The biogeography and ecology of southern Africa. 28. Land molluscs. *Monographiae Biologicae*, **31**, 877–923.
- Vermeulen, J. & Whitten, T. (1999) *Biodiversity and cultural property in the management of limestone resources. Lessons from east Asia*. The International Bank for Reconstruction and Development/ The World Bank, Washington D.C.
- Waldén, H.W. (1995) Norway as an environment for terrestrial molluscs, with viewpoints on threats against species and diversity. *Biodiversity and conservation of the Mollusca* (ed. by A.C. Van Bruggen, S.M. Wells and T.C.M. Kemperman), pp. 111–132. Backhuys Publishers, Leiden, the Netherlands.
- WCMC (2000) *Global biodiversity: earth's living resources in the 21st century*. World Conservation Press, Cambridge.
- White, L.J.T. (1995) Factors affecting the duration of elephant dung piles in rain forest in the Lopé Reserve, Gabon. *African Journal of Ecology*, **33**, 142–150.
- WWF & IUCN. (1994) *Centres of plant diversity. A guide and strategy for their conservation. 3 volumes*. IUCN Publications Unit, Cambridge.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 List of the RTUs collected in the three sampling areas.

This material is available as part of the online article from:

[http://www.blackwell-synergy.com/doi/abs/](http://www.blackwell-synergy.com/doi/abs/10.1111/j.1472-4642.2007.00376.x)

10.1111/j.1472-4642.2007.00376.x

(This link will take you to the article abstract).

Please note: Blackwell Publishing are not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.