Shrew species diversity and abundance in Ziama Biosphere Reserve, Guinea: comparison among primary forest, degraded forest and restoration plots

Violaine Nicolas · Patrick Barrière · Audrey Tapiero · Marc Colyn

Abstract The aim of our study was to compare the shrew community diversity and structure in gradients of tropical forest degradation and restoration. Four plots within each of six habitats of the Ziama Biosphere Reserve were surveyed, including primary forest, secondary forest, cultivated fields, recently (less than 3 years) abandoned fields, young (10–12 years) forest restoration plots, and old (34 years) restoration plots. From August to November 2003, we pitfall-trapped 2,509 shrews representing 11 species. Shrew species richness and composition was similar in the six habitat surveyed, while shrew species abundance varied between habitats. Canopy height and cover, density of stems and trees and understorey density were shown to constitute important parameters influencing the abundance of several shrew species. After clear-cutting, restoration of key attributes of the forest vegetation structure was possible in 10–34 years, either by natural regeneration or by planting of seedlings. The relative abundance of most shrew species was similar between restoring forest (i.e., young restoration plots or fallows) and primary forest. Considering the advantages and disadvantages of these two methods of forest restoration, one of the most suitable management practices to restore forest while preserving shrew biodiversity could be to perform an alternation of native seedling plantation lines and fallows.

V. Nicolas (✉)
Laboratoire Mammifères et Oiseaux, Département de Systématique et Evolution, USM 601, Muséum National d'Histoire Naturelle, 57 rue Cuvier, CP51, 75005 Paris, France
e-mail: vnicolas@mnhn.fr

P. Barrière
AICA-CREG, Nessadiou BP37, 98870 Bourail, New Caledonia

P. Barrière · A. Tapiero · M. Colyn
Université de Rennes 1, CNRS-UMR 6553, Station Biologique, 35380 Paimpont, France

Introduction

Tropical forests are the richest terrestrial ecosystems on the planet, but they are subject to intensive perturbations, e.g., for timber extraction or for conversion to agricultural lands. These human-induced changes of the forest habitats have many direct and indirect effects on animal communities, such as changes in species richness or species abundance (Bentley et al. 2000; Shanker 2001; Estrada and Coates-Estrada 2002; Mathieu et al. 2005; Pineda et al. 2005). The impact of deforestation on communities depends on the forest type, the size and shape of the deforested patch (Bentley et al. 2000; Goodman and Rakotondravony 2000; Laidlaw 2000; Ramanamanjato and Ganzhorn 2001; Watson et al. 2004a), the intensity of the disturbance (Struhsaker 1997; Lewis 2001) and the landscape context (Saunders et al. 1991; Malcolm and Ray 2000; Putz et al. 2001; Watson et al. 2004b). The impact of deforestation is not uniform across species (Vallan 2002; Watson et al. 2004b). The ability of species to tolerate or exploit modified conditions, or to disperse to alternative sites, will determine their persistence and future survival (Scott et al. 2006).

Recently, an interest in restoring tropical forests increased, and studies were performed on factors influencing the natural recovery process and strategies to restore tropical forests (Holl et al. 2000; Leopold et al. 2001; Parrotta and Knowles 2001; Feyera et al. 2002; Holl 2002a, b; DeWalt et al. 2003). Most of the studies focused on establishment of plant species, while the effect of forest restoration on faunal communities has been poorly investigated. After clear-cutting, forest restoration by natural regeneration allows bird and ant species richness to recover between 20 and 40 years, although recovery of species composition may take longer (Dunn 2004). In Brazil Mathieu et al. (2005), found the community composition and structure of the soil macrofauna (earthworms, ants, termites, beetles, spiders, centipedes and millipedes) to converge with that of the primary forest after only 6 years of natural regeneration.

African tropical forests support a high species richness and abundance of shrews. Shrews are important predators on other small vertebrates and invertebrates and serve as prey for several vertebrate predators (Van Zyll de Jong 1983; Ray 1998; Ray and Hutterer 1996; Churchfield et al. 2004). They are relatively abundant, are ecologically and taxonomically diverse, have a restricted mobility and are not subject to hunting pressure. Finally, because of their short life span and rapid population dynamics, they can respond quickly to habitat changes. Among the species occurring in African rain forest, several species are rare, and considered as vulnerable or near threatened (IUCN 2007). Despite this, information on shrew habitat requirements and response to forest degradation or restoration is scant mainly because they are elusive, because several species and species complexes are difficult to identify and in need of revision, and because the most effective method for trapping shrews, pitfall trapping with drift fences, involves considerable time and effort (Handley and Kalko 1993; Kirkland and Sheppard 1994).

The Ziama forest (eastern Guinea) was designated a Forest Reserve in 1932, made a Biosphere Reserve in 1981, and is now the subject of an internationally funded conservation project. It is accorded importance as one of the remaining relics of the Upper Guinea lowland rain forest, the latter being recognized as an Endemic Bird Area (Stattersfield et al. 1998), Centre of Plant Diversity (WWF and IUCN 1994), and Biodiversity Hotspot (Bakarr et al. 1999; Myers et al. 2000). Moreover, the Ziama forest belongs to the "Guinean Moist Forest" ecoregion, one of the 238 areas identified as the most critical regions for conservation (Olson et al. 2001; Olson and Dinerstein 2002). Despite its recognized importance in terms of species richness, part of this forest was subject to intense degradation, either for timber extraction or for conversion to agricultural lands. In the last

decades a project of forest restoration was undertaken. In this paper we present the results of a study which aims to compare shrew community diversity and structure in a gradient of forest degradation and forest restoration. Six habitat types were surveyed in the Ziama Biosphere Reserve: primary forest, secondary forest, field, 13 years-old fallow, 11–12 years-old forest restoration plots and 34 years-old forest restoration plots. More specifically, we tested the hypotheses that (1) shrew species richness and abundance vary between habitats, (2) that, after clear-cutting, forest restoration allows the shrew community composition and structure to recover and (3) that shrew species abundance is correlated with several specific environmental characteristics such as canopy height and cover, understorey density or leaf litter depth.

Methods

Study sites

This study was conducted from August to November 2003 in south-eastern Guinea, in the Ziama forest (116170 ha) located at the northern boundary of the West African rain forest (Fig. 1). The annual average rainfall at Sérédou is about 2,300 mm (1997–1998). Maximal monthly rainfall usually occurs in August (500–728 mm) and minimal monthly rainfall occurs from January to February (<37 mm).

Six habitat types were surveyed, representing a gradient of forest degradation (primary forest, secondary forest and field); and of forest restoration, (naturally regenerating fallow, young forest restoration plots of 10–12 years-old and old forest restoration plots of 34 years-old).

Shrew sampling

For each of the six habitats types, shrews were collected at four sampling sites (Fig. 1; Table 1). At each site, sampling was done by mean of dry pitfall traps with plastic drift
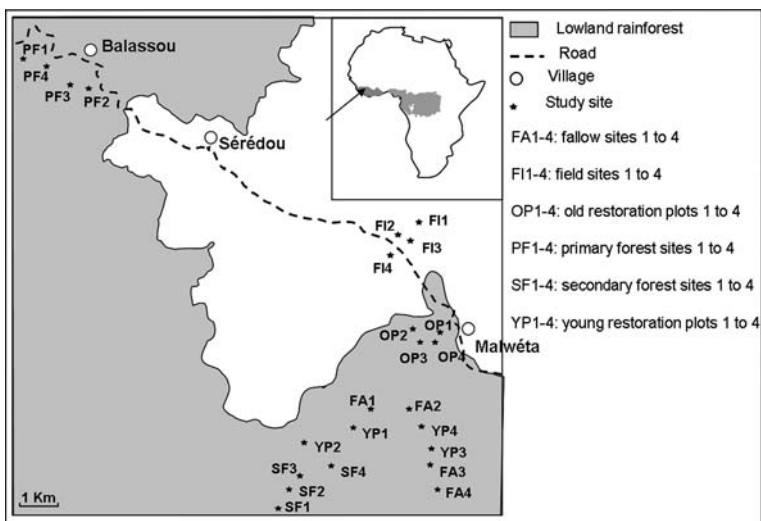

Fig. 1 Localization of the study sites in the Ziama Biosphere Reserve

fences, following the protocol of Nicolas et al. (2003). Buckets (10 l; 26 cm deep, 26 cm top internal diameter, 20 cm bottom internal diameter) were buried in soil, at 5 m intervals. Depending on the site, 40 buckets were set either in two distinct lines of 20 buckets each or in a single one (Table 1). Each pitfall line was set for 21 nights, resulting in a total trapping effort of 840 bucket-nights at each site, 3,360 bucket-nights in each habitat and 20,160 bucket-nights in total. In each habitat type, pitfall lines were always set at a distance of at least 75 m from the adjacent habitat border to avoid possible edge effects.

Habitat surveyed

Primary forest (sites PF1 to PF4)

Four sampling sites were located in undisturbed primary forest. Ziama Biosphere Reserve is a mosaic of evergreen and semi-deciduous forests. Three of our sampling sites were located in evergreen forest, and another one was located in semi-deciduous forest (Table 1). The evergreen forest is characterized by tree species such as *Klainedoxa gabonensis* (Irvingiaceae), *Chrysophyllum perpulchum*, *C. pruniforme*, *Tieghemella heckelii* and *Manilkara multineruis* (Sapotaceae), *Heritiera utilis* (Sterculiaceae), *Drypetes* spp. (Euphorbiaceae), and *Dialium aubrevillei* and *D. dinklagei* (Caesalpiniaceae). The semi-deciduous forest is characterized by the presence of *Guibourtia ehie* and *Amphimas pterocarpoides* (Caesalpiniaceae), *Nauclea diderrichii* (Rubiaceae), *Pycnanthus angolensis* (Myristicaceae), *Parkia bicolor* and *Piptadeniastrum africanum* (Mimosaceae), and *Hannoa klaineana* (Simaroubaceae).

Secondary forest (sites SF1 to SF4)

In secondary forest, selective logging occurred from 1971 to 1975. Several tree species of economical importance were cut: *Entandrophragma* spp. and *Khaya* spp. (Meliaceae), *Antiaris africana*, *Milicia excelsa* and *Morus mesozygia* (Moraceae), *Mitragyna stipulosa* and *Nauclea diderrichii* (Rubiaceae), *Ceiba pentandra* (Malvaceae), *Daniellia thurifera* and *Distemonanthus benthamianus* (Leguminosae), *Erythroxylum mannii* (Erythroxylaceae), *Terminalia ivorensis* and *T. superba* (Combretaceae). During the same period, small areas were cultivated after burning and then abandoned.

Field (sites FI1 to FI4)

Fields were created after clear-cutting of the forest margin and are presently located outside the rain forest zone. They consist of a mosaic of small patches of cornfields, coffee plantations and abandoned plantations for a period of 3 years at the longest. All the abandoned fields were covered by the invasive exotic weed *Chromolanea odorata* (Asteraceae). Four sites with distinct vegetation types were surveyed (Table 1).

Naturally regenerating fallow of 13 years-old (sites FA1 to FA4)

The fallow of 13 years-old is the result of natural forest regeneration after abandon of agricultural activities. The most abundant tree species in this naturally regenerating fallow were *Sterculia tragacantha* (Sterculiaceae), *Millettia stapfiana* (Papilionaceae), *Blighia welwitschii* (Sapindaceae), *Albizia zygia* and *A. sassa* (Mimosaceae).

Table 1 Habitat, pitfall lines and vegetation description for each sampling site

Habitat	Sampling sites (four in each habitat)			
	Abbreviation	No. of shrews captured	No. of pitfall lines/ sampling site	Description
Primary forest	PF1	127	2 lines of 20 buckets	Evergreen forest
	PF2	146	2 lines of 20 buckets	Semi-deciduous forest
	PF3	115	1 line of 40 buckets	Evergreen forest
	PF4	112	1 line of 40 buckets	Evergreen forest
Secondary forest	SF1	135	1 line of 40 buckets	All sites of similar tree composition (see text)
	SF2	138	1 line of 40 buckets	All sites of similar tree composition (see text)
	SF3	146	1 line of 40 buckets	All sites of similar tree composition (see text)
	SF4	90	1 line of 40 buckets	All sites of similar tree composition (see text)
Field	FI1	67	1 line of 20 buckets	1 year-old abandoned field
	FI2	109	1 line of 20 buckets	3 years-old abandoned field
			1 line of 20 buckets	Coffee plantation
			1 line of 20 buckets	1 year-old abandoned field
	FI3	52	1 line of 20 buckets	Cornfield
			1 line of 20 buckets	2 years-old abandoned field
	FI4	44	1 line of 20 buckets	Cornfield
			1 line of 20 buckets	Coffee plantation
Naturally regenerating fallow (13 years-old)	FA1	102	1 line of 40 buckets	All sites of similar tree composition (see text)
	FA2	139	1 line of 40 buckets	All sites of similar tree composition (see text)
	FA3	137	1 line of 40 buckets	All sites of similar tree composition (see text)
	FA4	106	1 line of 40 buckets	All sites of similar tree composition (see text)

Table 1 continued

Habitat	Sampling sites (four in each habitat)			
	Abbreviation	No. of shrews captured	No. pitfall lines/ sampling site	Description
Young restoration plots (10–12 years-old)	YP1	91	1 line of 40 buckets	24.70 ha; 12 years-old; *Terminalia superba* plantation
	YP2	60	1 line of 20 buckets	19.10 ha; 11 years-old; *T. superba* plantation
			1 line of 20 buckets	8.18 ha; 11 years-old; *Cedrela odorata* (Melicaceae) plantation
	YP3	94	1 line of 20 buckets	19.50 ha; 10 years-old; *Khaya ivorensis* (Meliaceae) and *T. superba* plantation (ratio: 1/7)
	YP4	58	1 line of 20 buckets	10.00 ha; 10 years-old; *Cederela odorata* plantation
			1 line of 40 buckets	15.00 ha; 10 years-old; *Terminalia ivorensis* (Combretaceae) and *T. superba* plantation (ratio: 1/1)
Old restoration plots	OP1	127	1 line of 40 buckets	58.42 ha; 34 years-old
	OP2	132	1 line of 40 buckets	58.42 ha; 34 years-old
	OP3	107	1 line of 40 buckets	58.42 ha; 34 years-old
	OP4	75	1 line of 40 buckets	58.42 ha; 34 years-old

Young restoration plots (of 10–12 years-old, sites YP1 to YP4)

Four sampling sites were located is 10–12 years-old forest restoration plots with distinct tree composition (Table 1). All these restoration plots consisted of 625 well-spaced trees ha^{-1}, except those planted with *Cedrela odorata* which consisted of 1,110 trees ha^{-1}.

Old restoration plots (of 34 years-old, sites OP1 to OP4)

Four sampling sites were located in a 34 years-old restoration plot of 58.42 ha. Pitfall lines were set in a patch planted either with *Cedrela odorata* or with both *Terminalia ivorensis* and *T. superba*.

   In both young and old restoration plots only native seedlings were planted in mono-cultures after burning. All naturally regenerating seedlings were cut for the 6 years after planting to allow maintenance of the planted seedlings.

Environmental characteristics

Several environmental characteristics were recorded in 10 × 10 m plots at 50 m intervals along the pitfall lines. These environmental variables were selected because they were previously shown to potentially influence small-mammal species abundance (Ford et al. 1997; Malcolm and Ray 2000; Lehtonen et al. 2001; Schmid-Holmes and Drickamer 2001; Shanker 2001; Lambert et al. 2003; Greenberg et al. 2007).

   Description of vegetation structure included number of stems of more than 2 cm diameter at breast height (dbh), number of trees of more than 10 cm dbh, number of downed coarse-woody debris (boles and branches), number of snags (i.e., standing dead trees), number of lianas, maximal canopy height and percentage of canopy cover. Other habitat characteristics, such as the number of termite mounds and the percentage of rock cover, were also recorded.

   Moreover, we measured density of understorey foliage at four distances from the plot centre (5, 10, 15 and 20 m) using the 'profile board' technique used by Ray (1996).

   Leaf litter depth on the forest floor was measured in four directions and at four distances (5, 10, 15, 20 m) from each plot centre.

   Environmental characteristics recorded at each plot were averaged to represent the general characteristics of each sampling site.

Species identification

Due to the existence of several sibling species, the identification of most of the Afrotropical shrews is not possible by external characteristics only. Moreover, the systematics and taxonomy of numerous African *Crocidura* species groups is still unresolved (Quérouil et al. 2001, 2006). Thus, all shrews captured were euthanized and kept as voucher specimens at the University of Rennes 1. A previous study showed that removal trapping, with similar conditions as those employed in our study, did neither adversely affect shrew species richness nor local population numbers (Nicolas et al. 2003). Species identification was performed by PB by external and crania-dental analysis, and was confirmed, for several specimens, by molecular analysis (16S rRNA). In this paper we will use the notation 'cf.' for species requiring taxonomic revision (*Crocidura* cf. *crossei*, *C.* cf. *buettikoferi*, *C.* cf. *bottegi*, *C.* cf. *theresae* and *C.* cf. *muricauda*): unpublished anatomical and molecular analyses confirmed the existence of several forms, possibly representing distinct sibling

species (already known or new to science), within each of these taxa. Only one form within each complex of sibling species was captured in Ziama forest. Finally, *C. goliath nimba-silvanus* (Hutterer 2003) is under revision and should be renamed (PB, unpublished data). Additional analyses are under study to clarify these taxonomic difficulties.

Data analysis

Rarefaction curves were used to compare species richness between habitats. This statistical method estimates the number of species that can be expected in a sample of *n* individuals drawn from a population of *N* individuals, with 95% confidence intervals (Software Ecosim, version 7; Gotelli and Entsminger 2004). Shannon evenness index was calculated for each site and Mann–Whitney test was used to compare evenness between habitat types. Trap success was defined as the number of shrews caught per 100 bucket-nights.

Species abundance distributions for each habitat type were illustrated as rank-abundance plots, with log-transformed abundance on the vertical axis. Possible differences between habitats were investigated with the Kolmogorov–Smirnov test.

The effect of habitat type on shrew species abundance (i.e., number of individuals captured) was analyzed with a one-way analysis of variance (ANOVA). After data inspection, species abundance was square-root-transformed ($\sqrt{(N+0.5)}$) to reduce heteroscedasticity and to improve normality. When ANOVA resulted in significant F ratios ($P < 0.05$), we used Tukey's multiple comparison test to determine which pairs of habitats were significantly different ($\alpha = 0.05$). The effect of forest degradation on shrew species abundance was investigated by comparing the number of captures between primary forest, secondary forest and field, while the effect of forest restoration was investigated by comparing the number of captures between field, fallow, restoration plots, and primary forest.

To investigate whether distinct habitats were characterized by different shrew communities we used the Renkonen index to generate a matrix of similarity coefficients among the shrew assemblages in the 24 sites (6 habitats, 4 sites per habitat). This similarity coefficient takes into account the relative abundance of species as well as their identities: $P = \Sigma$ minimum (p1i, p2i), where P is percentage similarity between samples 1 and 2, p1i is percentage of species i in community sample 1, p2i is percentage of species i in community sample 2. This similarity coefficient has been shown to be insensitive to variations in species richness among samples (Wolda 1981). We then used a clustering algorithm (unweighted pair-group average) to draw a tree showing the degree of similarity among sites.

We applied both constrained and unconstrained gradient analysis methods on the data to get a reliable picture of the shrew community patterns. To remove any undue effects of rare species on the ordination analyses (Gauch 1982), *C. nimbae* and *C. grandiceps* were removed from the analyses. We used detrended correspondence analysis (DCA) for the unconstrained analysis (Gauch 1982). The arch effect (Gauch 1982) was apparent in the initial correspondence analysis suggesting the need for detrending. Detrending by segments was selected. For the constrained gradient analysis we initially used canonical correspondence analysis (CCA), which, however, gave a marked arch effect. An attempt was made to remove the effect by excluding several strongly intercorrelated geographical variables from the analysis, but the removal did not lead to the hoped-for result, and thus the probable reason for the arch effect was the strength of the first axis in relation to the second. We consequently ran detrended canonical correspondence analysis (DCCA) in which we applied the same options as for DCA to secure the comparability of the results.

DCCA is a non-linear eigenvector ordination technique related to DCA but which, constrains station scores to the predicted values which arise from a multiple regression of

the station scores on the environmental variables (Ter Braak 1986). The method extracts synthetic gradients from the environmental variables that maximize the niche separation among species (Ter Braak and Verdonschot 1995). DCCA is an approximation to Gaussian regression under a set of simplifying assumptions, and is robust to violations of those assumptions (Ter Braak and Prentice 1988). The permutation applying the Monte Carlo method (with 499 permutations) was executed to determine the significance of the eigenvalues. We performed limited variable reduction by examining the Variance Inflation factors for each environmental variable in a DCCA run. Variance inflation factors were used to assess the multicollinearity in sets of environmental variables; a factor >20 indicates that a variable is highly correlated with other variables and does not provide a unique contribution to the ordination (Ter Braak and Prentice 1988). The variable d10 (understory foliage density at 10 m), d15 (understory foliage density at 15 m) and cac (canopy cover) were excluded because they are strongly correlated with the variables d05 (understory foliage density at 5 m) and d15; with the variables d10 and d20 (understory foliage density at 20 m); and with the variable cah (canopy height), respectively.

All the ordinations were performed with the software package CANOCO 4.5 for Windows (Ter Braak and Smilauer 2002). We compared the eigenvalues and the percentage of shrew variation explained by the first four DCA and DCCA axes to find out if the explanatory variables applied in the constrained gradient analysis (DCCA) could adequately explain the main faunal patterns of variation detected by the unconstrained gradient analysis (DCA).

Results

Comparison between habitats: shrew species richness, abundance and evenness

A total of 2,509 shrews representing two genera (*Crocidura* and *Sylvisorex*) and at least 11 species were pitfall-trapped. Species richness varied from 9 in field, fallow and old restoration plots to 11 in primary forest (Fig. 2). Rarefaction curves showed that for a sample of 272 individuals, species richness varied non-significantly from 9 to 10 according to habitat type (95% confidence interval; Fig. 2). For a sample of 440 individuals, species richness varied from 9 to 11 species according to habitat type. It was significantly higher in primary and secondary forest than in fallow and old restoration plots.
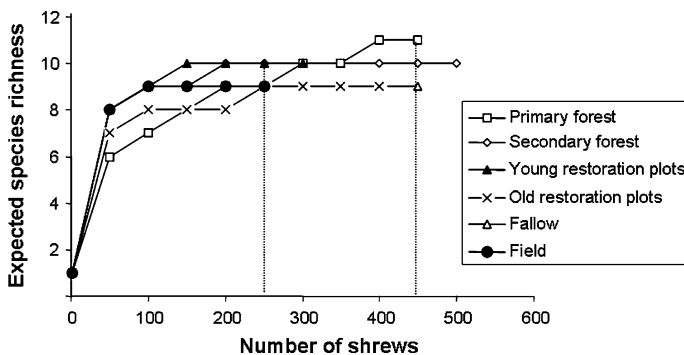

Fig. 2 Rarefaction curves for the six habitats surveyed. Comparison between all habitats were made at $n = 272$. Comparison between old restoration plots, fallow, primary forest and secondary forest were made at $n = 440$

All sites combined, trap success was 12 captures per 100 bucket-nights. It was significantly lower (Tukey's test, $P < 0.05$) in field than in secondary forest and fallow.

The species abundance distribution did not differ significantly among habitats (Fig. 3, Kolmogorov–Smirnov two-sample test $P > 0.10$). The species rank order remained relatively consistent between primary forest, secondary forest and fallow. It was also relatively consistent with those observed in young restoration plots, with the exception of *C.* cf. *muricauda* which was lower-ranking in young restoration plots than the three other habitats. In old restoration plots *C.* cf. *buettikoferi* was higher ranking than in other habitats. The species rank order was very different in field than in all other habitats due to the higher ranking of *S. megalura* and *C.* cf. *theresae*, and the lower ranking of *C.* cf. *muricauda*.

No significant difference in Shannon evenness index was obtained between pairs of habitats except between old and young restoration plots ($P = 0.03$), with a lower evenness in the latter (0.79 and 0.74, respectively), and between secondary forest and young restoration plots ($P = 0.03$), with a lower evenness in the latter (0.79 and 0.74, respectively).

Concerning the effect of forest degradation, shrew species abundance was similar between primary and secondary forest: the only significant difference (Tukey's test, $P < 0.05$) was found for *C. goliath nimbasilvanus* that was more abundant in secondary than in primary forest (Fig. 4). In contrast, numerous significant differences in terms of species abundance were observed between primary forest and field: *C.* cf. *theresae*, *C. olivieri* and *S. megalura* were more abundant in field than in primary forest, while the opposite was true for *C.* cf. *crossei*, *C.* cf. *muricauda* and *C.* cf. *bottegi*.

Concerning the effect of forest regeneration or restoration, abundance of many species varied significantly between field and fallow: *C.* cf. *bottegi*, *C.* cf. *muricauda* and *C. goliath nimbasilvanus* were more abundant in fallow, while *C.* cf *theresae* was more abundant in field. In naturally regenerating fallow, shrew species abundance was close to that of primary forest, even if *C. goliath nimbasilvanus* was significantly more abundant in fallow than in primary forest (Fig. 4). Species abundance varied greatly between young restoration plots
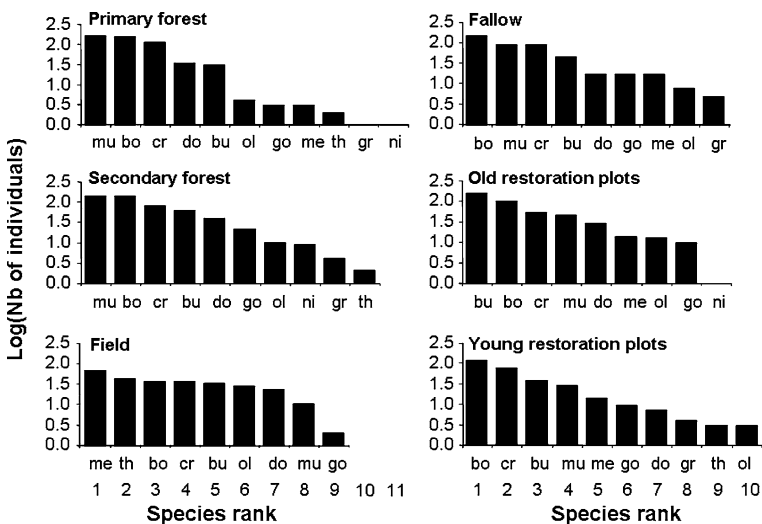

Fig. 3 Species identity per rank for the six habitats surveyed. Species codes: *go Crocidura goliath nimbasilvanus* Thomas, *ol C. olivieri* (Lesson), *ni C. nimbae* Heim de Balsac, *gr C. grandiceps* Hutterer, *bu C.* cf. *buettikoferi* Jentink, *th C.* cf. *theresae* Heim de Balsac, *cr C.* cf. *crossei* Thomas, *me Sylvisorex megalura* Jentink, *mu Crocidura* cf. *muricauda* (Miller), *do C. douceti* Heim de Balsac, *bo C.* cf. *bottegi* Thomas
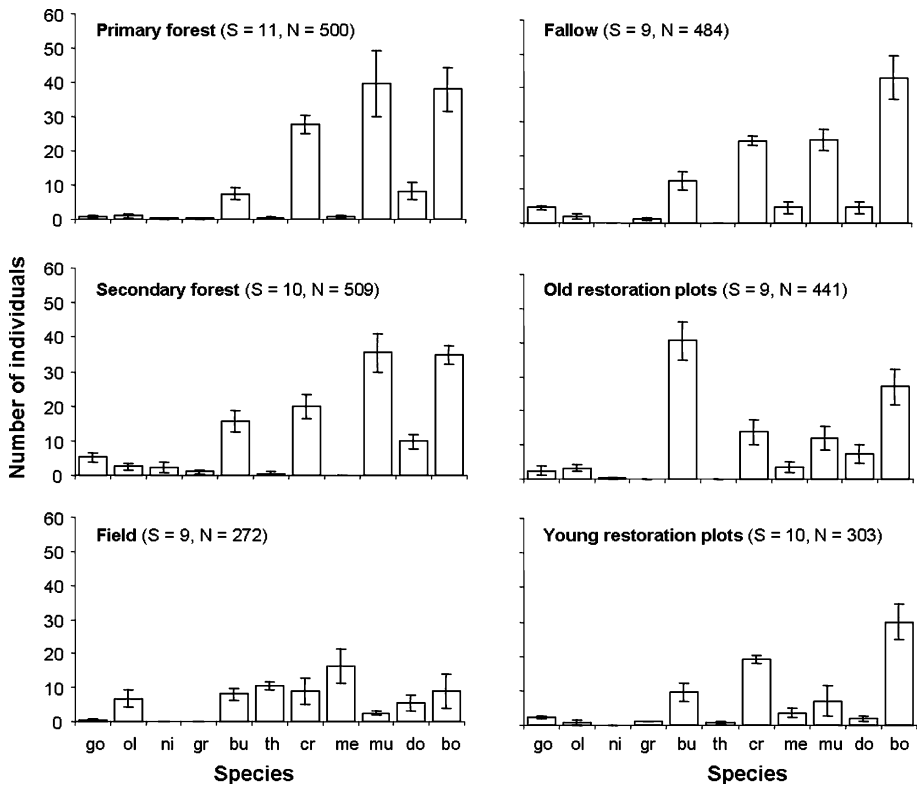
Fig. 4 Mean number (±SE) of shrews captured per species and habitat type (*histograms*). *S* is the species ichness and *N* the total number of shrews captured in each habitat. See Fig. 3 for species codes

and field: *C.* cf. *bottegi* was significantly more abundant in young restoration plots, while *C.* cf. *theresae*, *C. olivieri* and *S. megalura* were more abundant in fields. Shrew species abundance in young restoration plots was close to that of primary forest, even if *C.* cf. *muricauda* was significantly less abundant in young restoration plots. Species abundance also varied greatly between old restoration plots and field: *C.* cf. *bottegi* and *C.* cf. *buettikoferi* were more abundant in old restoration plots, while *C.* cf *theresae* and *S. megalura* were more abundant in field. At last, *C.* cf. *buettikoferi* was more abundant in old restoration plots than in primary forest, while *C.* cf. *muricauda* was more abundant in the latter.

Comparison between sites in terms of shrew species relative abundance

Similarity, measured by the Renkonen index, varied greatly between sites. The four field sites clustered altogether in the UPGMA tree (Fig. 5), indicating that the shrew community structure was more similar among these sites than with other sites. The four old restoration plots also cluster altogether in the UPGMA tree. For the four other habitat types (fallow, young restoration plots, primary forest and secondary forest) the clustering of sites was not congruent with habitat type. The mean Renkonen index of similarity between sites in these three habitat types was 78% (range = 51–91%) indicating a high degree of similarity in terms of shrew species relative abundance.
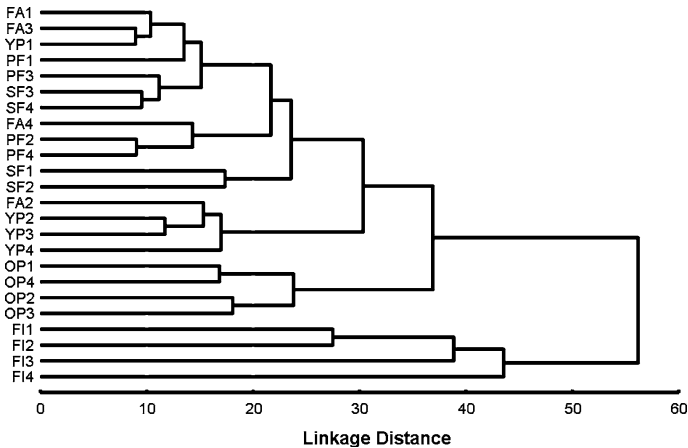
Fig. 5 Degree of similarity among shrew species assemblages in the 24 sampling sites. Tree created using UPGMA clustering of Renkonen similarity values. See Table 1 for sites codes

A matrix with the number of individuals of each shrew species captured per site was constructed. This matrix was subjected to DCA, as implemented in the CANOCO software, to ordinate the sites. The program produced a biplot in which sites and species were ordinated simultaneously (Fig. 6). The first four DCA axes explained 64% of the total variation in faunal data. The first axis had an eigenvalue of 0.318, whereas the second, third and fourth axes had eigenvalues of 0.053, 0.009 and 0.0005, respectively. Only the two-first axes could be satisfactorily interpreted. The first and second axis of the DCA explained, respectively 53 and 9% of the variation within the data set. The mutual position of sample and species points in the ordination diagram allowed us to approximate the relative abundances in the species data table (centroid principle, Leps and Smilauer 2003). In the ordination diagram (Fig. 6) the four field sites are segregated from the remainder of the sites. These sites were characterized by the higher relative abundance of *C.* cf. *theresae*, *S. megalura* and *C. olivieri*, and the lower relative abundance of *C.* cf. *muricauda* and *C. goliath nimbasilvanus*, compared to all other sites. The four old restoration plot sites clustered altogether in the ordination diagram indicating that species relative abundance was similar between these sites. They were characterized by the higher abundance of *C.* cf. *buettikoferi*. Primary forest, secondary forest, young restoration plots and fallow sites tended to cluster together in the ordination diagram, indicating that the shrew species relative abundance was similar between these sites. *Crocidura* cf. *bottegi* tended to be more abundant in these sites than in old restoration plots or field sites. *Crocidura* cf. *crossei* was also more abundant in these sites than in old restoration plots.

We perform another DCA analysis after removing the four field sites (results not shown). The results obtained were similar to those of the first analysis: the four old restoration plot sites clustered altogether in the ordination diagram, and primary forest, secondary forest, young restoration plots and fallow sites tended to cluster together in the ordination diagram.

Shrew species abundance and environmental characteristics

Statistical associations between shrew community patterns and environmental variables were quantified via DCCA. To this aim we used two matrixes: one with the number of
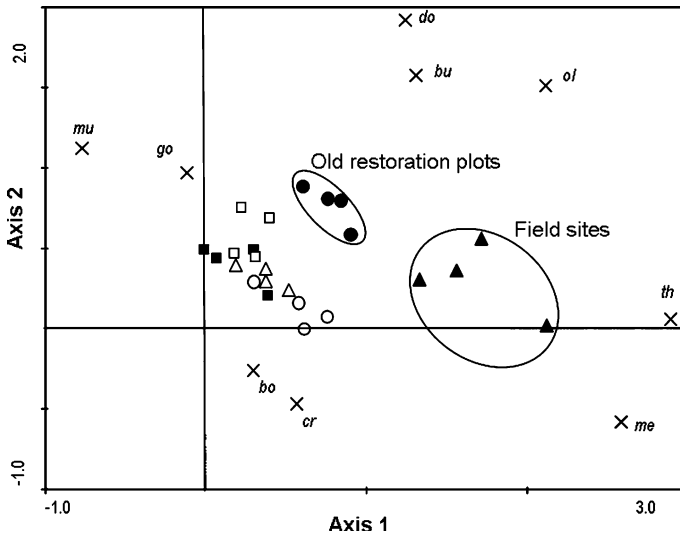
Fig. 6 Ordination diagram obtained by detrended correspondence analysis (DCA) of shrew assemblages in 24 sampling sites. See Fig. 2 for species codes. *Black circles* old restoration plots, *white circles* young restoration plots, *black square* primary forest sites, *white square* secondary forest, *black triangle* field sites, *white triangle* naturally regenerating fallow sites

individuals of each shrew species captured per site, and one with the score of each environmental variable per site. The results of the DCCA are presented as an ordination diagram in Fig. 7. The species and site points jointly represent the dominant patterns in community composition in environmental space. The first DCCA axis was statistically significantly correlated with the full set of external variables ($P = 0.004$, unrestricted Monte Carlo permutation test). The eigenvalues of DCCA axis 1 was 0.274 and this axis explained 46% of the variation in the shrew data. The eigenvalue of DCCA axis 2 (0.024) explained considerably less (4%) and should be used with caution. The external variables used in the constrained gradient analysis can only partly explain the results obtained with the DCA. By reference to the inter-set correlations of environmental variables with axes and the DCCA ordination diagrams, it was evident that the recorded environmental variables most strongly associated with axis 1 were the number of trees, the number of stems, canopy height, and understorey density at 20 m. Field sites were characterized by lower values of these environmental variables, compared to all other sites, where the species of *C. olivieri*, *S. megalura* and *C.* cf. *theresae* were more abundant. The opposite was true for *C. muricauda* and *C. goliath nimbasilvanus*. None of the recorded environmental variables could explain the differentiation observed in the DCA analysis between old restoration plots and the other sites.

Discussion

Importance of Ziama Biosphere Reserve for shrew conservation

Shrew trap success was far higher in Ziama Biosphere Reserve than everywhere else in Afrotropical rain forest (Barrière and Nicolas 2000; Goodman et al. 2001; Churchfield
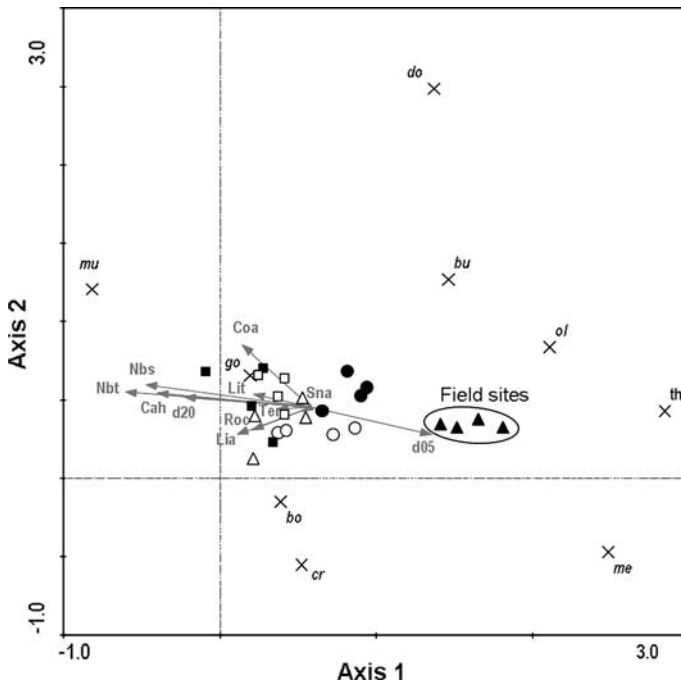
Fig. 7 Detrended canonical correspondence analysis (DCCA) of shrew assemblages in 24 sampling sites. Sites and shrew species ordination (see Fig. 6 for sites codes and Fig. 3 for species codes) with environmental variables gradients overlaid as vectors (*arrows*). Each *arrow points* in the expected direction of the steepest increase of values of environmental variable. The angles between *arrows* indicate correlations between individual environmental variables. Environmental variables codes: *Cah* canopy height, *Coa* number of downed coarse-woody debris, *d05, d20* understory foliage density at 5 and 20 m, respectively, *Lia* number of lianas, *Lit* litter depth, *Nbs* number of stems, *Nbt* number of trees, *Roc* rock cover, *sn* number of snags, *Ter* number of termite mounds

et al. 2004; Nicolas et al. 2005), conferring to this reserve a particular biological interest. Our 4 months longitudinal survey permitted to record several shrew species of major importance in terms of biological knowledge and conservation interest. Two species are endemic to the Upper Guinea rain forest (*C. goliath nimbasilvanus* and *C. nimbae*), four species are relatively rare in collection and especially poorly known (*C. goliath nimba-silvanus, C. grandiceps, C. nimbae* and *C. douceti*) and four are listed in the IUCN Red list (IUCN 2007) as follows: vulnerable (*C. nimbae*), near threatened (*C. grandiceps*) and data deficient (*C. bottegi* and *C. douceti*). The presence and abundance of such shrew species, regarding another significant survey in the Upper Guinea rain forest (Churchfield et al. 2004), confirm the great interest of the Ziama Biophere Reserve in terms of conservation of the Insectivora of the Upper Guinea rain forest.

Habitat characteristics and shrew diversity

According to our results, shrew species richness and community composition were similar in the six habitats types, suggesting that these parameters are little affected by forest degradation and restoration. These relatively moderate effects could be due to the fact that all field, fallow and restoration plot sites were adjacent to primary or secondary forests.

Thus, a system of source and sink populations between these habitats could be possible. This hypothesis is congruent with the fact that shrew species abundance varied greatly between habitats, suggesting that they are not of equal value for shrews. The shrew community structure was indeed very different in field sites compared to all other sites. The abundance of several shrew species seems to be related to environmental characteristics such as understorey density, canopy height and cover, and density of stems and trees. These environmental characteristics were very different between field sites and all other sites (Fig. 7). *Crocidura* cf. *theresae*, *S. megalura* and *C. olivieri* seem to be characteristics of field sites and tend to avoid sites with dense understorey, high canopy height and cover, and high density of stems and trees. *Crocidura* cf. *muricauda* is a typical forest species: it was much more abundant in sites with high understorey density, high canopy height and cover, and high density of stems and trees, than in field sites. The relative abundance of *Crocidura goliath nimbasilvanus* was also higher in these sites (Figs. 6, 7), despite that this species was never abundant (Fig. 4).

Old restoration plots harbor a distinct shrew community structure than all other forest sites (primary and secondary forest, young restoration plots) or fallow (Figs. 5, 6): *C.* cf. *buettikoferi* was much more abundant in old restoration plots. None of the environmental parameters recorded in our study can explain this difference (Fig. 7). However only a small number of environmental parameters were taken into account in our study, and they only partly explain the results obtained with the DCA analysis (only 50% of the variation in the shrew data is represented in the DCCA analysis). Moreover the environmental parameters recorded in our study only concerned vegetation structure. The recovery of floristic composition may also play a key role in the recovery of shrew community, as shown for tropical birds (Shankar Raman and Sukumar 2002). Moreover, habitat characteristics such as moisture in soil or leaf litter, and the invertebrate prey base are often suggested as important determinants of shrew species diversity and abundance in boreal and temperate ecosystems (Getz 1961; Kirkland 1991; Pagels et al. 1994; Shvarts and Demin 1994). These factors should then be taken into account in future studies.

Several significant differences in shrew species abundance were recorded between primary forest, secondary forest, young restoration plots and fallow sites. However, in the UPGMA tree based on the Renkonen index of similarity and in DCA ordination diagram, sites from a given habitat, among the previous four, do not cluster altogether. Shrew species relative abundance was relatively similar in all these habitats. Differences in shrew species relative abundance could be even higher between sites of a given habitat type than between habitats. Differences in shrew community structure between sites in a given habitat type (Figs. 5, 6) may be explained by the fact that sites with different vegetation composition were surveyed in some habitats (e.g., field, young restoration plots and primary forest Table 1). More detailed analyses of environmental characteristics, and a better knowledge of shrew species ecological requirements are necessary to explain the observed pattern of variation between sites for a given habitat type.

Management implications

After clear-cutting, restoration of key attributes of the forest vegetation structure, such as high canopy height and cover, high density of stems and trees and high understorey density, was possible in 10–34 years either by natural regeneration or by planting of seedlings. Moreover, the type of forest restoration (i.e., natural or planting of seedlings) had no effect on the environmental characteristics recorded in our study, suggesting that these two restoration practices are of equal effectiveness. However, this may not be true for

other vegetation characteristics, such as plant species richness which is known to recover more slowly than many structural aspects (DeWalt et al. 2003). These results highlight how difficult it is to predict the fate of a restoring forest, because many parameters are involved, such as the characteristics of the original forest, the origin and history of disturbance and the landscape patterns (Ashton et al. 2001; Holl 2002b; Dunn 2004).

Whatever the restoration practice (natural regeneration or planting of seedlings), shrew community structure was closer between primary and restoring forest than between field and restoring forest, due to the restoration of key attributes of the vegetation structure typical of primary forest. According to DeWalt et al. (2003), 20 years-old restoration forests may provide valuable wildlife habitat for generalist species, in particular birds and mammals with mixed diets of insects and fruits. Our results show that this may also be true for generalist invertebrate eaters like many Afrotropical shrews (Churchfield et al. 2004; Dudu et al. 2005).

The management of restoring forest should be an important component of any large-scale conservation strategy in the tropics. To define suitable management practices to restore forest, it is necessary to take into account both conservation of the biodiversity and cost of the different management options. Forest restoration through planting of seedlings is more costly than natural regeneration and cannot be achieved on large areas. However, by planting tree species that are suitable for timber extraction, planting of seedlings may be useful for the local economy and allows to grow up trees that are homogeneously distributed and of known diameter. Conversely, natural regeneration is less suitable for timber extraction because tree growth is slower and you cannot predict which tree species are going to grow and what will be the distribution and diameter of suitable trees. As an alternative, one of the most suitable management practices to restore forest, while preserving forest shrew diversity, could be to perform an alternation of native seedling plantation lines and fallows. Additional studies are necessary to test if this management practice would also be suitable for the preservation of other animal taxa. Our results should not be taken as general evidence that forest restoration through natural regeneration or planting of seedlings would have little effect on biodiversity as a whole, or that shrews would elsewhere be unaffected by forest restoration type. Individual studies of the effects of forest restoration and degradation on tropical forests will inevitably be prone to the idiosyncrasies of the particular study area and study organisms (Lewis 2001). Generalizations should only be made by looking at a range of studies of different organisms in different forest types and in different parts of the world. Moreover, species abundance alone is not always a good indicator for habitat quality, because some animals stay only temporarily in certain places or in places where they cannot reproduce (Van Horn 1983). Van Horn (1983) proposed the use of an index taking into account density, probability of survival and reproduction rate of inhabitants to measure habitat quality for a species. Additional studies are necessary to test if the probability of survival and the reproduction rate of shrew species are the same in primary forest, restoration plots and fallows.

References

Ashton MS, Gunatilleke CVS, Singhakumara BMP, Gunatilleke IAUN (2001) Restoration pathways for rain forest in southwest Sri Lanka: a review of concepts and models. For Ecol Manage 154:409–430. doi:10.1016/S0378-1127(01)00512-6

Bakarr MI, Bailey B, Omland M, Myers N, Hannah L, Mittermeier CG, Mittermeier RA (1999) Guinean Forests. In: Mittermeier RA, Myers N, Gil PR, Mittermeier CG (eds) Hotspots: earth's biologically richest and most endangered terrestrial ecoregions. Toppan Printing Company, Japan

Barrière P, Nicolas V (2000) Rapport d'expertise sur la biodiversité animale en forêt de Ngotto (République Centrafricaine): écologie et structuration des peuplements de micro-mammifères musaraignes et rongeurs. Programme ECOFAC (Forêt de Ngotto—République Centrafricaine). http://www.ecofac.org/Biblio/TelechargementSommaire.htm

Bentley J, Catterall CP, Smith GC (2000) Effects of fragmentation of Araucarian vine forest on small mammal communities. Conserv Biol 14:1075–1087. doi:10.1046/j.1523-1739.2000.98531.x

Churchfield S, Barrière P, Hutterer R, Colyn M (2004) First results on the feeding ecology of sympatric shrews (Insectivora: Soricidae) in the Taï National Park, Ivory Coast. Acta Theriol (Warsz) 49:1–15

DeWalt SJ, Maliakal SK, Denslow S (2003) Changes in vegetation structure and composition along a tropical forest chronosequence: implications for wildlife. For Ecol Manage 182:139–151. doi:10.1016/S0378-1127(03)00029-X

Dudu A, Churchfield S, Hutterer R (2005) Community structure and food niche relationships of coexisting rain-forest shrews in the Masako Forest, north-eastern Congo. In: Meritt JF, Churchfield S, Hutterer R, Sheftel R (eds) Advances in the biology of shrews II, Special Publication No. 1. International Society of Shrew Biologists, New York

Dunn RR (2004) Recovery of faunal communities during tropical forest regeneration. Conserv Biol 18:302–309. doi:10.1111/j.1523-1739.2004.00151.x

Estrada A, Coates-Estrada R (2002) Bats in continuous forest, forest fragments and in an agricultural mosaic habitat-island at Los Tuxtlas, Mexico. Biol Conserv 103:237–245. doi:10.1016/S0006-3207(01)00135-5

Feyera S, Beck E, Lüttge U (2002) Exotic trees as nurse-trees for the regeneration of natural tropical forests. Trees (Berl) 16:245–249. doi:10.1007/s00468-002-0161-y

Ford WM, Laerm J, Barker KG (1997) Soricid response to forest stand age in southern Appalachian cove hardwood communities. For Ecol Manage 91:175–181. doi:10.1016/S0378-1127(96)03892-3

Gauch HG (1982) Multivariate analysis in community ecology. Cambridge University Press, New York

Getz LL (1961) Factors influencing the local distribution of shrews. Am Midl Nat 65:67–88. doi:10.2307/2423003

Goodman SM, Rakotondravony D (2000) The effects of forest fragmentation and isolation on insectivorous small mammals (Lipotyphla) on the Central High Plateau of Madagascar. J Zool (Lond) 250:193–200. doi:10.1111/j.1469-7998.2000.tb01069.x

Goodman SM, Hutterer R, Ngnegueu PR (2001) A report on the community of shrews (Mammalia: Soricidae) occurring in the Minkébé Forest, north-eastern Gabon. Mamm Biol 66:22–34

Gotelli NJ, Entsminger GL (2004) EcoSim: null models software for ecology, 7th edn. Acquired Intelligence Inc. & Kesey-Bear, Burlington

Greenberg CH, Miller S, Waldrop T (2007) Short-term response of shrews to prescribed fire and mechanical fuel reduction in a Southern Appalachian upland hardwood forest. For Ecol Manage 243:231–236. doi:10.1016/j.foreco.2007.03.003

Handley CO Jr, Kalko EKV (1993) A short history of pitfall trapping in America, with a review of methods currently used for small mammals. Virg J Sci 44:19–26

Holl KD (2002a) Effect of shrubs on tree seedling establishment in an abandoned tropical pasture. J Ecol 90:179–187. doi:10.1046/j.0022-0477.2001.00637.x

Holl KD (2002b) Tropical moist forest restoration. In: Perrow MR, Davy AJ (eds) Handbook of ecological restoration, 2nd edn. Cambridge University Press, Cambridge

Holl KD, Loik ME, Lin EHV, Samuels IA (2000) Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. Restor Ecol 8:339–349. doi:10.1046/j.1526-100x.2000.80049.x

Hutterer R (2003) Two replacement names and a note on the author of the shrew family Soricidae (Mammalia). Bonn Zool Beitr 50:369–370

IUCN 2007 (2007) IUCN red list of threatened species. http://www.iucnredlist.org. Accessed June 14 2008

Kirkland GL Jr (1991) Competition and coexistence in shrews (Insectivora: Soricidae). In: Findley JS, Yates TL (eds) The biology of the soricidae. University of New Mexico Press, Albuquerque

Kirkland GL Jr, Sheppard PK (1994) Proposed standard protocol for sampling small mammal communities. In: Merrit JF, Kirkland GL Jr, Rose RK (eds) Advances in the biology of shrews, Special Publication No. 18, Carnegie Museum of Natural History, Pittsburgh

Laidlaw RK (2000) Effects of habitat disturbance and protected areas on mammals of peninsular Malaysia. Conserv Biol 14:1639–1648. doi:10.1046/j.1523-1739.2000.99073.x

Lambert TD, Adler GH, Riveros CM, Lopez L, Ascanio R, Terborgh J (2003) Rodents on tropical land-bridge islands. J Zool (Lond) 260:179–187. doi:10.1017/S0952836903003637

Lehtonen JT, Mustonen O, Ramiarinjanahary H, Niemela J, Rita H (2001) Habitat use by endemic and introduced rodents along a gradient of forest disturbance in Madagascar. Biodivers Conserv 10:1185–1202. doi:10.1023/A:1016687608020

Leopold AC, Andrus R, Finkeldey A, Knowles D (2001) Attempting restoration of wet tropical forests in Costa Rica. For Ecol Manage 142:243–249. doi:10.1016/S0378-1127(00)00354-6

Leps J, Smilauer P (2003) Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge

Lewis OT (2001) Effect of experimental selective logging on tropical butterflies. Conserv Biol 15:389–400. doi:10.1046/j.1523-1739.2001.015002389.x

Malcolm JR, Ray JC (2000) Influence of timber extraction routes on central African small-mammal communities, forest structure and tree diversity. Conserv Biol 14:1623–1638. doi:10.1046/j.1523-1739.2000.99070.x

Mathieu J, Rossi JP, Mora P, Lavelle P, Martins PFS, Rouland C, Grimaldi M (2005) Recovery of soil macrofauna communities after forest clearance in eastern Amazonia, Brazil. Conserv Biol 19:1598–1605. doi:10.1111/j.1523-1739.2005.00200.x

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858. doi:10.1038/35002501

Nicolas V, Barrière P, Colyn M (2003) Impact of removal pitfall trapping on the community of shrews (Mammalia: Soricidae) in African forests. Mammalia 67:133–138

Nicolas V, Barrière P, Colyn M (2005) Seasonal variation in population and community structure of shrews in a tropical forest of Gabon. J Trop Ecol 21:161–169. doi:10.1017/S0266467404002123

Olson DM, Dinerstein E (2002) The global 200: priority ecoregions for global conservation. Ann Mo Bot Gard 89:199–224. doi:10.2307/3298564

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'Amico JA, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettengel WW, Hedao P, Kassem KR (2001) Terrestrial ecoregions of the world: a new map of life on earth. Bioscience 51:933–938. doi:10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Pagels JF, Uthus KL, Duval HE (1994) The masked shrew, Sorex cinereus, in a relictual habitat in the southern Appalachian Mountains. In: Merritt JF, Kirkland G. L, Rose RK (eds) Advances in the biology of shrews, Special Publication No. 18. Carnegie Museum of Natural History, Pittsburgh

Parrotta JA, Knowles OH (2001) Restoring tropical forests on lands mined for bauxites: examples from the Brazilian Amazon. Ecol Eng 17:219–239. doi:10.1016/S0925-8574(00)00141-5

Pineda E, Moreno C, Escobar F, Halffter G (2005) Frog, bat, and dung beetle diversity in the cloud forest and coffee agroecosystems of Veracruz, Mexico. Conserv Biol 19:400–410. doi:10.1111/j.1523-1739.2005.00531.x

Putz FE, Blate GM, Redford KH, Fimbel R, Robinson J (2001) Tropical forest management and conservation of biodiversity: an overview. Conserv Biol 15:7–20. doi:10.1046/j.1523-1739.2001.00018.x

Quérouil S, Hutterer R, Barrière P, Colyn M, Peterhans JCK, Verheyen E (2001) Phylogeny and evolution of African shrews (Mammalia: Soricidae) inferred from 16s rRNA sequences. Mol Phyl Evol 20:185–195. doi:10.1006/mpev.2001.0974

Quérouil S, Barrière P, Colyn M, Hutterer R, Dudu A, Dillen M, Verheyen E (2006) Phylogenetic relationships between African soricids of the genus Crocidura inferred from mitochondrial DNA sequences. In: Merritt JF, Churchfield S, Hutterer R, Sheftel BI (eds) Advances in the biology of the Soricidae II, Special Publication No. 18, Carnegie Museum of Natural History, Pittsburgh

Ramanamanjato JB, Ganzhorn JU (2001) Effects of forest fragmentation, introduced Rattus rattus and the role of exotic tree plantations and secondary vegetation for the conservation of an endemic rodent and a small lemur in littoral forests of southeastern Madagascar. Anim Conserv 4:175–183. doi:10.1017/S1367943001001202

Ray JC (1996) Resource use patterns among mongooses and other carnivores in a central African rainforest Ph.D. thesis, University of Florida, Gainesville

Ray JC (1998) Temporal variation of predation on rodents and shrews by small African forest carnivores. J Zool (Lond) 244:363–370. doi:10.1111/j.1469-7998.1998.tb00041.x

Ray JC, Hutterer R (1996) Structure of a shrew community in the Central African Republic based on the analysis of carnivore scats, with the description of a new *Sylvisorex* (Mammalia: Soricidae). Ecotropica 1:85–97

Saunders DA, Hobbs R, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. Conserv Biol 5:18–32. doi:10.1111/j.1523-1739.1991.tb00384.x

Schmid-Holmes S, Drickamer LC (2001) Impact of forest patch characteristics on small mammal communities: a multivariate approach. Biol Conserv 99:293–305. doi:10.1016/S0006-3207(00)00195-6

Scott DM, Brown D, Mahood S, Denton B, Silburn A, Rakotondraparany F (2006) The impacts of forest clearance on lizard, small mammal and bird communities in the arid spiny forest, southern Madagascar. Biol Conserv 127:72–87. doi:10.1016/j.biocon.2005.07.014

Shankar Raman TR, Sukumar R (2002) Responses of tropical rainforest birds to abandoned plantations, edges and logged forest in the Western Ghats, India. Anim Conserv 5:201–216. doi:10.1017/S1367943002002251

Shanker K (2001) The role of competition and habitat in structuring small mammal communities in a tropical montane ecosystem in southern India. J Zool (Lond) 253:15–24. doi:10.1017/S0952836901000024

Shvarts EA, Demin DV (1994) Community organization of shrews in temperate zone forest of Northwestern Russia. Carn Mus Nat Hist 18:57–66

Stattersfield AJ, Crosby MJ, Long AJ, Wedge DC (1998) Endemic bird Areas of the world. Priorities for biodiversity conservation. Bird life conservation series, 7th edn. BirdLife International, Cambridge

Struhsaker T (1997) Ecology of an African rain forest: logging in Kibale and the conflict between conservation and exploitation. University Press of Florida, Gainesville

Ter Braak CJF (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167–1179. doi:10.2307/1938672

Ter Braak CJF, Prentice JC (1988) A theory of gradient analysis. Adv Ecol Res 18:271–317. doi:10.1016/S0065-2504(08)60183-X

Ter Braak CJF, Smilauer P (2002) CANOCO Reference manual and CanoDraw for Windows user's guide: Software for canonical community ordination (version 4.5). Microcomputer power, Ithaca, pp 500

Ter Braak CJF, Verdonschot PFM (1995) Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquat Sci 57:255–289. doi:10.1007/BF00877430

Vallan D (2002) Effects of anthropogenic environmental changes on amphibian diversity in the rain forests of eastern Madagascar. J Trop Ecol 18:725–742. doi:10.1017/S026646740200247X

Van Horn B (1983) Density as a misleading indicator of habitat quality. J Wildl Manage 47:893–901. doi:10.2307/3808148

Van Zyll de Jong CG (1983) Handbook of canadian mammals. Marsupials and insectivores, 1st edn. National Museum of Natural Sciences, Ottawa

Watson JEM, Whittaker RJ, Dawson TP (2004a) Avifaunal responses to habitat fragmentation in the threatened littoral forests of south-eastern Madagascar. J Biogeogr 31:1791–1807. doi:10.1111/j.1365-2699.2004.01142.x

Watson JEM, Whittaker RJ, Dawson TP (2004b) Habitat structure and proximity to forest edge affect the abundance and distribution of forest-dependant birds in tropical coastal forests in southeastern Madagascar. Biol Conserv 120:311–327. doi:10.1016/j.biocon.2004.03.004

Wolda H (1981) Similarity indices, sample size and diversity. Oecologia 50:296–302

WWF and IUCN (1994) Centers of plant diversity. A guide and strategy for their conservation. Europe, Africa, South West Asia and the Middle East, 1st edn. IUCN Publications Unit, Cambridge