

Effects of forest fragmentation on pteridophyte diversity in a tropical rain forest in Brazil*

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Received 30 March 2004; accepted in revised form 28 February 2005

Key words: Atlantic Moist Forest, Brazil, Diversity, Fragmentation, Pteridophyte, South of Bahia

Abstract

The impacts of forest fragmentation on the pteridophyte communities of the Una region of Bahia, Brazil, were investigated by comparing species richness and ensemble diversity among areas of large forest fragments (> 900 ha), small forest fragments (< 100 ha), and landscape matrix. We inventoried the pteridophytes below 1 m in height in interiors of small fragments, interiors of large fragments (control areas), edges of fragments, edges of continuous forest, *capoeiras* (initial stages of forest regeneration) and *cabruças* (cocoa plantations). All ferns were collected following the plot method (plots of 120 × 10 m, each). Sampling units were established in the six main ecotypes of the Una region. These units were allocated within three sampling blocks of 5 per 5 km, which were chosen in order to include the largest forest patches that still remain. Results suggest that fragmentation has a negative impact on species richness at the matrix and the edges of forest remnants. A similar negative matrix end edge effect is reported for diversity of those sites measured by the α Log-series Index. However, small forest fragments have pteridophyte species richness and diversity rates similar to large ones so they should be considered of utmost importance to the conservation of forest-related species in the region.

Introduction

Fragmentation of natural habitats is one of the most important consequences resulting from human activities. It modifies the ecology of forested biomes and several biological processes in many different ways (Laurance et al. 1998a). One of the main aspects previously studied is the alteration of diversity

in the remnants of tropical forests on the local scale (Lovejoy et al. 1984; Turner 1996; Pardini 2004). Such alterations are noticed in the variation of species richness and abundance of individuals in the fragmented landscapes. Differences have frequently been found to be the consequences of (1) the reduction of the forest area used by the species, i.e., reduction of resources (Wilcox and Murphy 1985; Hobbs 1993; Kinzig and Harte 2000), (2) the isolation of the remaining fragments of forest (Metzger and Décamps 1997; Davies et al. 2001), (3) the increased amount of edges and the associated

*This paper is part of the MSc thesis of M.L.B. Paciencia, sponsored by CAPES, Curso de Pós-graduação em Ciências, Área de Botânica, IB, USP.

intensification of the so called “edge effect” (Matalack 1993; Murcia 1995), and (4) the type of matrix that surrounds the fragments (Franklin 1993; Laurance et al. 1997; Lawrence and Ripple 2000).

Although there is a consensus that fragmentation contributes to the local depletion of biological diversity (Lovejoy et al. 1984; Saunders et al. 1991; Tilman et al. 1994; Laurance et al. 1998b), it seems improbable that this process influences every community in the same way. This inference is based on the idea that tropical forests might differ in their resistance and resilience to fragmentation (Beier and Noss 1998; Metzger 1999), in continental or even in regional scale, besides other biological particularities of the affected assemblies (Turner 1996).

Most fragmentation studies of plant groups have focused on modifications of diversity in the tree species communities in different forest types (Williams-Linera 1990; Laurance et al. 1998b). There are few studies reporting the effects on understory communities or herbaceous layer (e.g. Tangney et al. 1990; Benitez-Malvido 1998). The same is true for the pteridophyte group which has been neglected in studies of this nature (e.g. Paciencia 2001; Paciencia and Prado 2004) in spite of being considered an important component of tropical forest biodiversity (Pharo et al. 1999).

Several ecological aspects of this group have already been studied, such as (1) factors determining the local distribution of species (Tuomisto and Ruokolainen 1994; Arens and Baracaldo 1998; Lwanga et al. 1998; Paciencia and Prado 2002; Tuomisto et al. 2003), (2) association of these communities to other vegetal taxonomic groups (van der Werff 1990, 1992; Poulsen and Baslev 1991; Ruokolainen et al. 1997; Tuomisto et al. 2002) and (3) environmental influence on aspects of species growth and morphology (Brade 1961; Rana 1995; Bernabe et al. 1999; Arens and Baracaldo 2000).

As these plants present a relatively stable biology concerning propagule dispersion and establishment, pteridophytes could be a potential indicator of diversity alteration in fragmentation studies. Moreover, the knowledge of how the group behaves in response to habitat loss can be an important tool for the elaboration of conservation strategies for threatened biomes, such as the Atlantic Rain Forest (Fonseca 1985), the object of this study.

Therefore, the purpose of this study is to understand how the pteridophyte community responds to forest fragmentation in the main landscape components of the Una Atlantic Rain Forest mosaic, Bahia, northeastern Brazil, by assessing the influence of forest area reduction and isolation, edge presence and landscape environmental matrix type on the diversity of those plants.

Material and methods

Study area

The study site is located in the lowland ombrophilous forests of the Bahia state, in the Biological Reserve of Una (REBIO Una – 15°10' S and 39°03' W) and surrounding areas of Una municipality, BA (Figure 1). The original vegetation of this region is called Southern-Bahian Wet Forest (Gouvêa et al. 1976; *Mata Higrófila sul-Bahiana*), a formation of the Dense Ombrophilous Forest, which predominates, usually, in sandy soil zones and low altitudes in the entire south and southeast of Bahia. The climate is hot and wet with mean temperatures between 24 and 25 °C, rainfall between 1660 and 2000 mm/year, and a non-existent dry season (Gouvêa 1969).

This forest presents high endemism rates of flowering plants (Mori et al. 1981, 1983; Prance 1982; Carvalho and Thomas 1993), thus 44.1% of the species are endemic to the Atlantic Forest and 28.1% of the southern Bahia and Espirito Santo (Thomas et al. 1998). It also represents a site of endemic insects (Brown 1991), reptiles (Jackson 1978), birds (Haffer 1974) and mammals (Rylands 1982), so Una and surroundings areas are considered one of the hot spots for the world-wide biological conservation (<http://www.conservation.org/Hotspots>, consulted in January, 2002).

Most of the Southern-Bahian Wet Forest is now fragmented, the result of long-standing habitat destruction caused by human activities such as wood removal and implementation of agriculture. Currently, it is estimated that only 10% of the original wet moist forest cover remains, or approximately 30,000 ha. Approximately 40,000 ha of lands in the region are covered by forests in initial stages of regeneration (locally called *capoeiras*) and an additional 200,000 ha is taken by areas of pastures and various cultures, especially

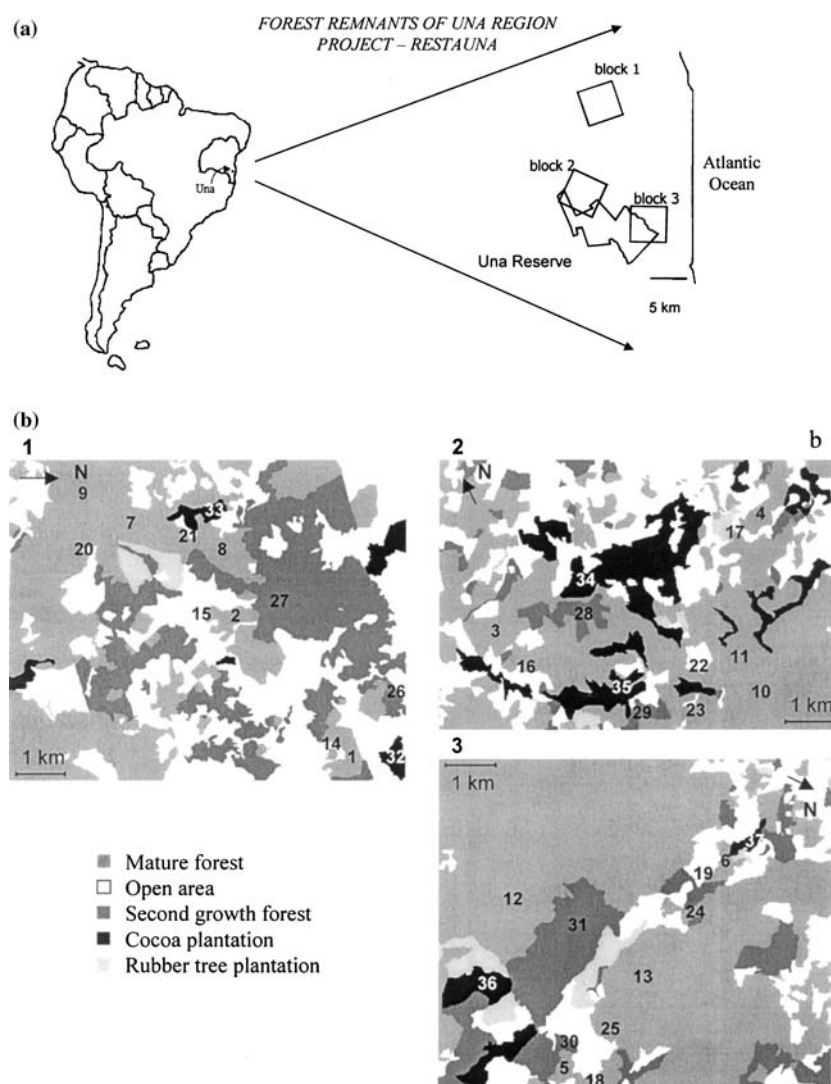


Figure 1. Study area in Una region, south of Bahia State, Brazil. (a) Location of the three demonstration blocks (1, 2, and 3), near and in the Una Biological Reserve. (b) The 37 inventory sites inside the blocks: interiors of small fragments (sites 1–6); interiors of large fragments (7–13); edges of small fragments (14–19); edges of large fragments (20–25); capoeiras (26–31); and cabruças (32–37).

cocoa plantations (*Theobroma cacao* L.), rubber tree plantations (*Hevea brasiliensis* Muell. Arg.), *piçava* (an endemic palm, *Attalea funifera* Mart.) and *dendê* (african oil palm; *Elaeis guineensis* Jacq.) (Alger and Caldas 1996). Specifically in Una, the landscape retains 49% of mature forest within a heterogeneous matrix of open areas (pastures – 27% of the landscape), capoeiras (15%), cocoa plantations (6%), and rubber tree plantations (2%) (Pardini 2004). Therefore, Una landscape exhibits reticular features, forming an environmental mosaic in which a high proportion

of mature forests is in direct contact with open areas.

Despite this fact, Una region is still the last important remainder of south-Bahian Atlantic Forest and is one of the largest continuous forest areas of the entire Brazilian NE region. The maintenance of this great portion of remaining forest was partly due to (1) the presence of the Una Biological Reserve; and (2) the preserved remnants in private lands concentrated around the Reserve. Most of these private lands is made up of cocoa farms, the main local agricultural product,

managed by the system of *cabruca*. In this system, the lower forest layers are replaced by cocoa shrubs, conserving a fraction of the canopy to shade the culture. So the *cabruca* is capable of keeping part of the local floristic composition, supposedly being able to provide resources for forest species. However, these are environments that must be treated as matrix elements of the landscape, as they are the result of human intervention in primary forest.

Experimental design

This study was developed as part as the RestaUna Project – Forest Remnants of Una Region, south of Bahia (NEMA/UESC; <http://www.restauna.org.br>), which aimed to compare the responses of several biological communities to forest fragmentation in Una.

Our study included only the most representative components of Una landscape in proportion of the total area and in which there was tree covering. Thus, research activities were conducted in the six main ecotypes defined as: IL – interior of large remnant (mature forest patches, >900 ha, 100 m from the nearest open area); EL – edge of large fragment (mature forest patches, >900 ha, <20 m from the nearest open area); IS – interior of small fragment (mature forest patches, <100 ha, >100 m from the nearest open area); ES – edge of small fragment (mature forest patches, <100 ha, <20 m from the nearest open area); CP – secondary growth forests in early stage of regeneration (capoeiras); CB – cocoa plantations under native forest (*cabruca*s).

The diversity of pteridophytes was compared in six sampling sites for each of the six ecotypes (except for the IL, which had seven sites), totaling 37 study in Una. The sampling sites were established in three sampling blocks (5 per 5 km) of the landscape, placed according to the spatial distribution of the largest forest areas. Two (three, in case of the IL sites) replicate plots of each of the six ecotypes were placed in these blocks. The experimental design based on these features was a method that allowed the minimization of the influence of the variable that were not considered in our study, such as geographic, geomorphologic or edaphic regional attributes that could cause a difference in the pteridophytes distribution throughout the studied areas (Figure 1).

In each of the 37 sampling sites, one plot of 0.12 ha (120×10 m) was established and all the pteridophytes up to 1 m above the ground were taken into consideration, including the epiphytes found up to this height (Figure 1b). For the survey of some terrestrial species that produce vegetative growth through rhizomes or stipes, the average number of leaves (fronds) constituting a single individual was previously calculated (see Appendix A) and this number was used for the number of leaves found for each species, thereby avoiding an overestimate of the density. For instance, for *Adiantum latifolium* Lam. it was previously obtained 23 individuals at random around sample sites and we thus calculated the average number of leaves. In this case, each individual has retained one to eight leaves resulting in 3.22 leaves per individual ($n = 23$; average = 3.22), and this number was for all inventories concerning that species. Although some other species also had long-creeping rhizomes, we could identify their number of individuals during the field work, and this procedure was not done for them.

Botanical material was collected and stored following the standard recommendations for botanical collections, after pressing in the field to prevent desiccation. Afterwards, the identifications were done in laboratory, with the aid of general keys of identification (Mickel and Beitel 1988; Tryon and Stolze 1993; Moran and Riba 1995), and exclusive keys for some genera [*Cyclodium*, Smith (1986); *Elaphoglossum*, Alston (1958); *Polybotrya*, Moran (1987); *Pteris*, Prado and Windisch (2000); *Selaginella*, Alston et al. (1981) and Hirai and Prado (2000); *Thelypteris*, Smith (1992); *Trichipteris* / *Cyathea*, Barrington (1978) and Fernandes (1997)]. The herbarium samples were deposited in Herbarium SP (Institute of Botany of São Paulo) and duplicates of *Cyathea abbreviata* Fernandes were deposited in the herbarium of the Federal University of Paraíba (UFPB) and, of *Anemia hirta* (L.) Sw, in the herbarium of the New York Botanical Garden (NY).

Data analysis

The sampling effort for each type of environment was determined by the stabilization of the species accumulation curve based on 50 random runs,

calculated by software EstimateS 6.0 (Colwell 2000).

The diversity of pteridophyte assemblies was calculated by the α log-series Index (first attempt conducted by Fisher et al. 1943), using data sets containing information on number of species and on their relative abundances, in each of the 37 sampling units. The index α is an estimate of diversity based on the real number of community species and on the expected number for a determined amount of individuals, since the distribution of species abundances in the community under consideration follows a logarithmic series (Kempton 1979; Hughes 1986). Consequently, it was also examined if the log-series model was a satisfactory fit to the observed species-abundance distribution. The procedure for fitting the model was to run a χ^2 goodness of fit test (Sokal and Rohlf 1995) comparing the expected values and the actually obtained values for the number of species of the different abundance classes, which are pre-assumed in the model. The EstimateS program version 6.0 was used to calculate the model parameters; the distribution curves were elaborated by the program Biodiversity Pro version Beta 2 (McAlecece et al. 1997).

The richness and abundance of pteridophytes obtained for all plots were compared through two-way analysis of variance (Sokal and Rohlf 1995), considering ecotypes and blocks as factors. The ANOVAs were carried out by the program Statistica 5.1 (StatSoft Incorporation 1997) after the existence of homoscedasticity had been tested to the two variables described above. In order to verify in which treatments (ecotypes) the significant differences indicated in the analysis appear (for $p < 0.05$), tests of planned comparisons were applied according to the presence of orthogonality in the comparisons sequence (orthogonal contrast procedure, Montgomery 2001). This method allows the choice of k numbers of comparisons (contrasts) equal to the number of categories minus 1 (as there are six ecotypes, $k = 5$). The five applied comparisons were: (1) IL vs. IS (size area effect); (2) IL + IS vs. EL + ES (edge effect); (3) EL vs. ES (edge intensity); (4) IL + IS + EL + ES vs. CP + CB (matrix effect) and (5) CP vs. CB (type of the matrix). On this procedure total variance is partitioned among the contrasts, which are thus independent and do not increase the probability of type 1 error (Pardini 2004).

Furthermore, the existence of possible relationships between the diversity of pteridophytes and the structure of the studied environments was verified through linear regression analysis between the richness (S) and the factor loadings of the first axis of a PCA analysis (Birkes and Dodge 1993), formulated with non-transformed values of 15 environmental variables, which was obtained from RestaUna Project (unpublished data) for the sites: percentage of canopy cover; percentage of sub-canopy cover; percentage of understorey cover; percentage of ground cover; occurrence of pioneer species; occurrence of grasses; abundance of woody lianas; abundance of herbaceous lianas; abundance of epiphytes; total basal area; number of trees with DBH between 5 and 10 cm, DBH between 25 and 30 cm, and DBH bigger than 50 cm; number of logged trees; and number of dead trees.

The PCA was conducted using the software MVSP 3.1 (Kovach Computing Services 1995), using a matrix of 36 rows and 15 columns, with the values of the environmental variables measured in each plot, except for area 9, where there was not possible to collect structure data.

Results

Diversity of the pteridophyte community

This survey detected 6535 individuals, distributed in 60 species and 17 families, in the 37 plots (Table 1), representing about 85% of the regional pteridophyte flora, sharing 33.6% of species with the Una checklist (www.nybg.org/bsci/res/una, consulted in March, 2003).

The species richness (S) varied considerably among the six studied ecotypes ($F_{5,19} = 3.513$; $p = 0.020$) for the total of the 37 sampled plots, but differences related to the position of these ecotypes in the environmental mosaic were not verified, since the three sampled blocks revealed themselves equally rich ($F_{2,19} = 3.028$; $p = 0.072$). Indeed, differences in the pteridophyte total abundance among ecotypes were not observed ($F_{5,19} = 0.6278$; $p = 0.6807$) nor among blocks ($F_{2,19} = 0.5371$; $p = 0.5930$).

Results indicate that species richness may be affected by the process of forest habitat loss, as

Table 1. Pteridophyte inventory in the Una landscape.

Family	Species	Ecotypes						
		IS	IL	ES	EL	CP	CB	TOTAL
Lomariopsidaceae	<i>Lomagramma guianensis</i> (Aubl.) Ching	201	600	482	528	31	13	1855
Dryopteridaceae	<i>Cyclodium heterodon</i> (Schr.) T. Moore var. <i>abbreviatum</i> (C. Presl.) A. R. Smith	478	149	153	123	11	1	915
Schizaeaceae	<i>Lygodium volubile</i> Sw.	42	28	39	9	411	293	822
Lomariopsidaceae	<i>Lomariopsis marginata</i> (Schr.) Kuhn	86	172	30	87			375
Blechnaceae	<i>Blechnum brasiliense</i> Desv.	1				259	39	299
Tectariaceae	<i>Triplophyllum funestum</i> (Kunze) Holttum var. <i>funestum</i>	130	86	23	6		2	247
Dryopteridaceae	<i>Polybotrya cylindrica</i> Kaulf.	153	16	24	5		36	234
Davalliaceae	<i>Nephrolepis multiflora</i> (Roxb.) F. M. Jarret ex C. V. Morton						220	220
Cyatheaceae	<i>Cyathea corcovadensis</i> (Raddi) Domin	71	85	18	24	10		208
Thelypteridaceae	<i>Thelypteris dentata</i> (Forssk.) E. P. St. John	1					170	171
Dennstaedtiaceae	<i>Lindsaea lancea</i> (L.) Bedd. var. <i>lancea</i>	50	53	12	12	1		128
Davalliaceae	<i>Nephrolepis</i> spp.*	14	3	32	1	6	58	114
Dryopteridaceae	<i>Cyclodium meniscioides</i> (Willd.) C. Presl var. <i>meniscioides</i>	42	66		4	1		113
Cyatheaceae	<i>Cyathea phalerata</i> Mart.	43	4	40				87
Hymenophyllaceae	<i>Trichomanes pinnatum</i> Hedw.	21	43	3	12			79
Dennstaedtiaceae	<i>Pteridium aquilinum</i> (L.) var. <i>arachnoideum</i> (Kaulf.) Brade				1	77		78
Pteridaceae	<i>Adiantum latifolium</i> Lam.						53	53
Pteridaceae	<i>Adiantum diogoanum</i> Glaziou ex Baker						51	51
Aspleniaceae	<i>Asplenium serratum</i> L.	26	18	1	4			49
Schizaeaceae	<i>Anemia phyllitidis</i> (L.) Sw.	3		3		42	1	49
Dennstaedtiaceae	<i>Lindsaea lancea</i> (L.) Bedd. Var. <i>falcata</i> (Dryand) Rosenst	15	19					34
Lomariopsidaceae	<i>Elaphoglossum pteropus</i> C. Chr.	3	26		1			30
Polypodiaceae	<i>Polypodium meniscifolium</i> Langsd. and Fisch.	8	18					27
Selaginellaceae	<i>Selaginella producta</i> Baker	14	3	2	7			26
Hymenophyllaceae	<i>Trichomanes elegans</i> Rich.	4	18		4			26
Thelypteridaceae	<i>Thelypteris</i> sp.						22	22
Cyatheaceae	<i>Cyathea abbreviata</i> Fernandes	2	7			11		20
Marattiaceae	<i>Danaea elliptica</i> Sm.	2	13	1	1			17
Blechnaceae	<i>Blechnum occidentale</i> L.						15	15
Pteridaceae	<i>Adiantum dolosum</i> Kunze	2	6		7			15
Dennstaedtiaceae	<i>Lindsaea macrophylla</i> Kaulf.	11		3				14
Polypodiaceae	<i>Microgramma vacciniifolia</i> (Langsd. and Fisch.) Copel.		1	1	4		7	13
Pteridaceae	<i>Adiantum lucidum</i> (Cav.) Sw.	1	11					12
Thelypteridaceae	<i>Thelypteris macrophylla</i> (Kunze) C. V. Morton				11			11
Thelypteridaceae	<i>Macrothelypteris torresiana</i> (Gaudich.) Ching						10	10
Polypodiaceae	<i>Polypodium triseriale</i> Sw.				1	1	8	10
Hymenophyllaceae	<i>Trichomanes polypodioides</i> Raddi	1	8					9
Lomariopsidaceae	<i>Elaphoglossum</i> sp.		9					9
Schizaeaceae	<i>Schizaea fluminensis</i> Miers ex J. W. Sturm		7					7
Hymenophyllaceae	<i>Trichomanes pedicellatum</i> Desv.	2	2	1	2			7
Cyatheaceae	<i>Cyathea pungens</i> (Willd.) Domin	6						6
Schizaeaceae	<i>Schizaea elegans</i> (Vahl.) Sm.	1	3		1			5
Polypodiaceae	<i>Microgramma geminata</i> (Schr.) R. M. Tryon and A. F. Tryon	2	2				1	5
Polypodiaceae	<i>Microgramma lycopodioides</i> (L.) Copel.	1					3	4
Metaxyaceae	<i>Metaxya rostrata</i> (Kunth) C. Presl.	4						4
Polypodiaceae	<i>Pechuma ptilodon</i> (Kunze) M. G. Price	1					3	4
Vittariaceae	<i>Vittaria lineata</i> (L.) J. Sm.	1					3	4
Schizaeaceae	<i>Anemia hirta</i> (L.) Sw.						3	3
Lomariopsidaceae	<i>Elaphoglossum macrophyllum</i> (Mett. ex Kuhn) Christ	1	1					2
Pteridaceae	<i>Adiantum obliquum</i> Willd.						2	2
Polypodiaceae	<i>Campyloneurum repens</i> (Aubl.) C. Presl.	2						2
Pteridaceae	<i>Hemionitis tomentosa</i> (Lam) Raddi						2	2
Polypodiaceae	<i>Microgramma squamulosa</i> (Kaulf.) de la Sota						2	2
Thelypteridaceae	<i>Thelypteris longifolia</i> (Desv.) R. M. Tryon	2						2
Hymenophyllaceae	<i>Trichomanes crispum</i> L.	2						2

Table 1. Continued.

Pteridaceae	<i>Pteris splendens</i> Kaulf.						1	1
Polypodiaceae	<i>Dicranoglossum desvauxii</i> (Klotzsch) Proctor						1	1
Lomariopsidaceae	<i>Elaphoglossum consobrinum</i> (Kunze) T. Moore					1		1
Dennstaedtiaceae	<i>Lindsaea guianensis</i> (Aubl.) Dryand.					1		1
Polypodiaceae	<i>Polypodium catharinae</i> Langsd. and Fisch.							1
Number of species		41	32	20	22	12	26	60
Abundance		1452	1479	880	844	861	1019	6535

IS = interior of small fragment; IL = interior of large remnant; ES = edge of small fragment; EL = edge of large fragment; CP = initial stage of forest regeneration (capoeiras) and CB = cocoa plantations (cabruças). Ranked in descending order of total abundance.

*Comprising both *Nephrolepis rivularis* (Vahl.) Mett ex Krug. and *N. pectinata* (Willd.) Schott.

evidenced in the planned comparisons among the six ecotypes (Table 2, Figure 2).

The size of the forest areas does not seem to affect pteridophyte species richness (contrast 1). The interiors of small fragments (remnants < 100 ha) did not differ from interiors of large fragments (remnants > 900 ha), although the total number of species and individuals were different between these two ecotypes (41 species in small fragments and 32 in the large ones) (Table 1).

Considering the total area of forest interiors (both small and large fragments) a reduction of richness was noticed in the edge areas (contrast 2), indicating that a loss of forest species might be occurring with the continuing fragmentation

process and the increase of forest edges. When analyzed separately, the edges of small and large fragments do not differ in richness (contrast 3), strengthening the idea that the size of the area is not an important factor for the maintenance of the pteridophyte species in the region.

Beyond the edges, another fragmentation aspect that plays an important role in the regional species loss is the presence of the matrix (matrix acts negatively on the pteridophyte richness – contrast 4). However, such fragmentation effect might be attributed to the matrix type, because it must be noticed that the very matrix presents richness difference between the types that it is made of (contrast 5). Only the early stages of succession

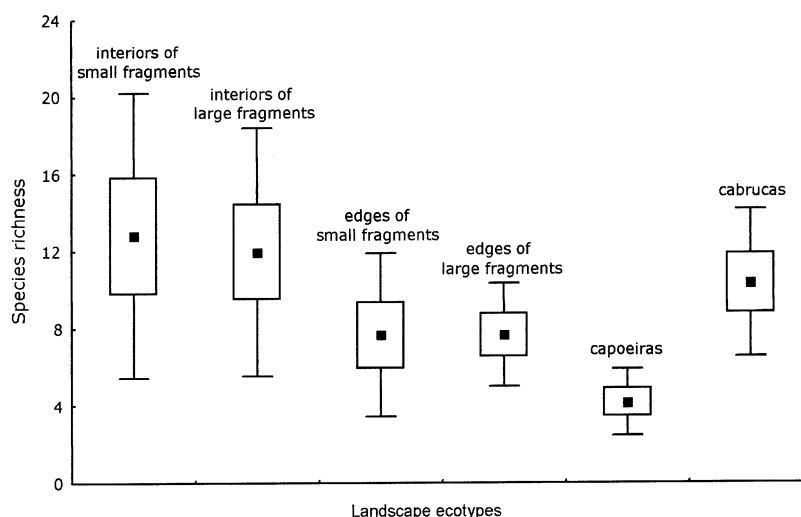


Figure 2. Pteridophyte species richness of study sites ($n = 7$ for the interiors of large fragments; $n = 6$ for other ecotypes) ($\bar{X} \pm SE$; SD).

Table 2. Summary of the planned comparisons for the two way ANOVA (orthogonal contrasts) used to test general effects of fragmentation on the pteridophytes species richness ($F_{5,19} = 3.513$; $p = 0.020$) ($\alpha = 0.05$).

Contrast	Effect	Comparison	Number of species	<i>F</i>	<i>p</i>
1	Size area	Small vs. large	41 vs. 32	0.064	0.804
2	Edge	Interiors vs. edges	40 vs. 27	4.277	0.029
3	Edge type	Small vs. large	20 vs. 22	2.851	0.065
4	Matrix	Mature forest vs. matrix	49 vs. 31	3.106	0.040
5	Matrix	Capoeiras vs. cabrucas	12 vs. 26	3.514	0.020

Small are forest remnants smaller than 100 ha; *Large* are forest remnants larger or equal to 900 ha; *Interiors* are the sites located in mature forest, 100 m from the nearest open area; *Edges* are the sites located in mature forest, 20 m from the nearest open area; *Matrix* are the man-made changed areas.

(capoeiras) show species loss in the system but not the cabrucas, because, while these harbour 26 species, capoeiras have only 12.

In fact, the difference of richness observed for the entire data set, according to an analysis with all the treatments, is caused mainly by the low number of species observed in capoeiras, since these areas are hostile to the establishment of the majority of the forest species. If each of the matrix ecotypes could be compared with the mature forest areas, the results will be distinct (mature forests vs. cabrucas: $F_{4,16} = 2.019$; $p = 0.121$; 49 vs. 26 species; and mature forests vs. capoeiras: $F_{4,16} = 4.423$; $p = 0.007$; 49 vs. 12 species).

Thus, one of the factors responsible for the species richness reduction could be the habitat structure which, in the case of forests, reflects the degree of anthropogenic alteration in them. This idea is corroborated by the regression analysis between richness *S* and the scores of the first axis of a PCA, calculated with abiotic variables verified in the areas (Figure 3). The plots with smaller richness are those located in structurally less complex environments, such as the capoeiras, where the forest is in an initial stage of regeneration. The values of *S* increase gradually, following the structural gradient produced by the first PCA axis, that has 75.15% of the variance explained (eigenvalue 1 = 66.06 and 2 = 9.09) and shows a trend to separate capoeiras, forest edges and forest interiors.

However, it must be considered that the interpretation of the PCA may be relatively faulty, given the high heterogeneity presented by edges. While some show a structure similar to that of the interiors (with distinct canopy cover, great number of trees with DBH between 25 and 30 cm, high basal area and many epiphytes), others more closely resemble the capoeiras (with marked abun-

dance of pioneer species and arboreal individuals with DBH < 10 cm).

Nevertheless, results suggest that the regional deforestation process, which happened in earlier times, contributed primarily to the decrease in pteridophytes species number with regard to the community as a whole (diversity β), because this is the main determining factor of the existing structure in fragments and matrix,

Cabrucas were excluded from this analysis, because, when the ordination included this ecotype (75.77% of total variance; eigenvalues 1 = 46.03 and 2 = 29.74), it was verified that the cabrucas became strongly related only with the second axis, producing the “flattening” of the values in axis 1.

Distribution of the abundance of species

Pteridophyte diversity of the Una region was also analyzed for the species abundance distribution in each environment, both qualitatively and quantitatively. In general, the 6535 pteridophyte records (Table 1) are distributed according to a common shape found in the tropical forests, i.e., in each environment, one or few species are very abundant while the majority of the species are represented by few individuals.

According to the diagrams showing the abundance of species in the six studied ecotypes (Figure 4), a prominent co-dominance of *Lomagramma guianensis* and *Cyclodium heterodon* var. *abbreviatum* can be noticed in forest areas, as much in interiors and as in the edges. These two species are also the most abundant in the total of sampled plots, so that *L. guianensis* accounted for 1855 individuals (28.4% of the total) and *C. heterodon*, 915 (14%).

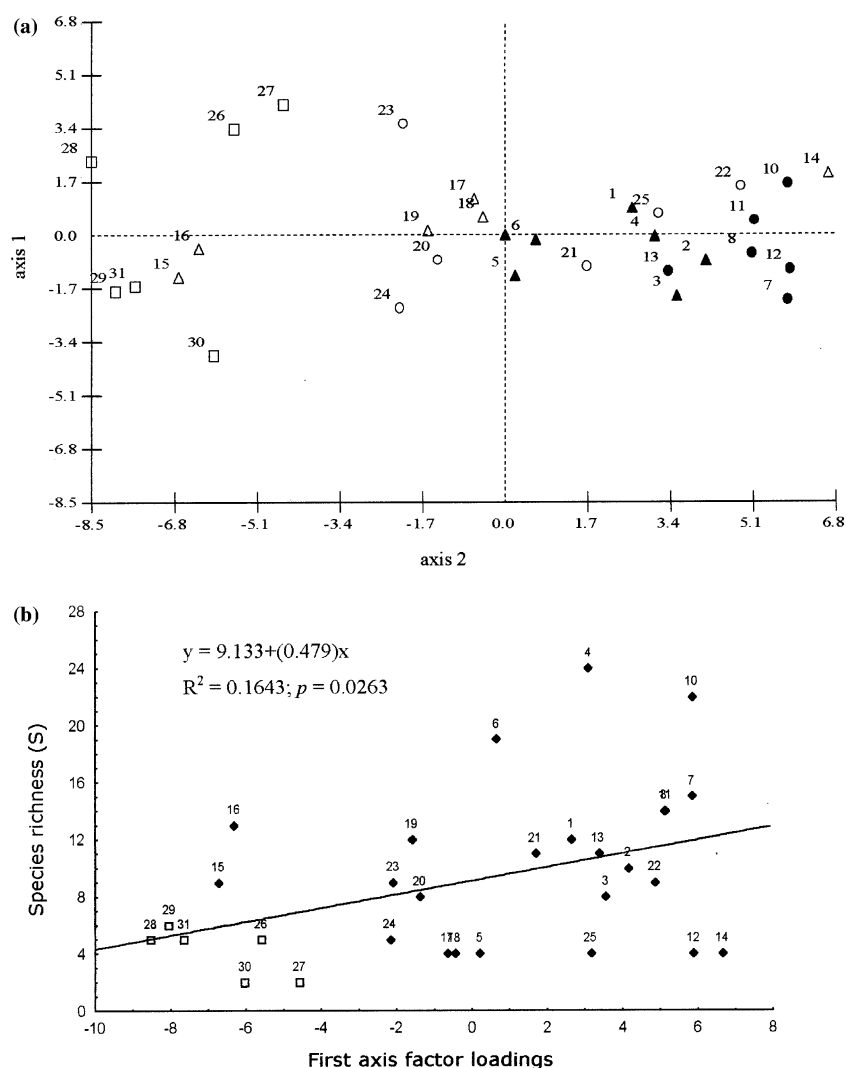


Figure 3. Relationship between habitat structure and pteridophytes species richness in Una region. (a) axis 1 and 2 of a Principal Component Analysis (PCA) applied to the study sites except to cabrucas, based on 15 abiotic variables (cumulated variance is 75.15%; □ = capoeiras; Δ = edges of small fragments; ○ = edges of large fragments; ▲ = interiors of small fragments; ● = interiors of large fragments; numbers refer to the study sites). (b) Linear regression between species richness and the axis 1 factor loadings (eigenvalue 1 = 66.06) calculated for the sites; ◆ = forest sites, □ = matrix sites.

Considering the forest interiors separately (both small fragments and large fragments), it was observed that five of the six most abundant species are the same (*Cyathea corcovadensis*, *Cyclodium heterodon* var. *abbreviatum*, *Lomagramma guianensis*, *Lomariopsis marginata* and *Triplophyllum funestum*). These species can indicate the presence of mature forests, even before the fragmentation.

In the edges, three of the six most abundant species, occur in both small fragments and in large fragments (*C. heterodon*, *L. guianensis* and

Lomariopsis marginata), with populations concentrated in the relatively less disturbed areas. However, what calls attention to these edge environments is the presence of *Lygodium volubile*, at least in the edges of small fragments. This species is the third most abundant among all ecotypes, with 822 sampled individuals (12.6% of the total), being 704 (86%) in the matrix. Thus, *L. volubile* can be described as having a marked preference to disturbed sites. Perhaps the structural alterations reported for some edges (the oldest ones) will

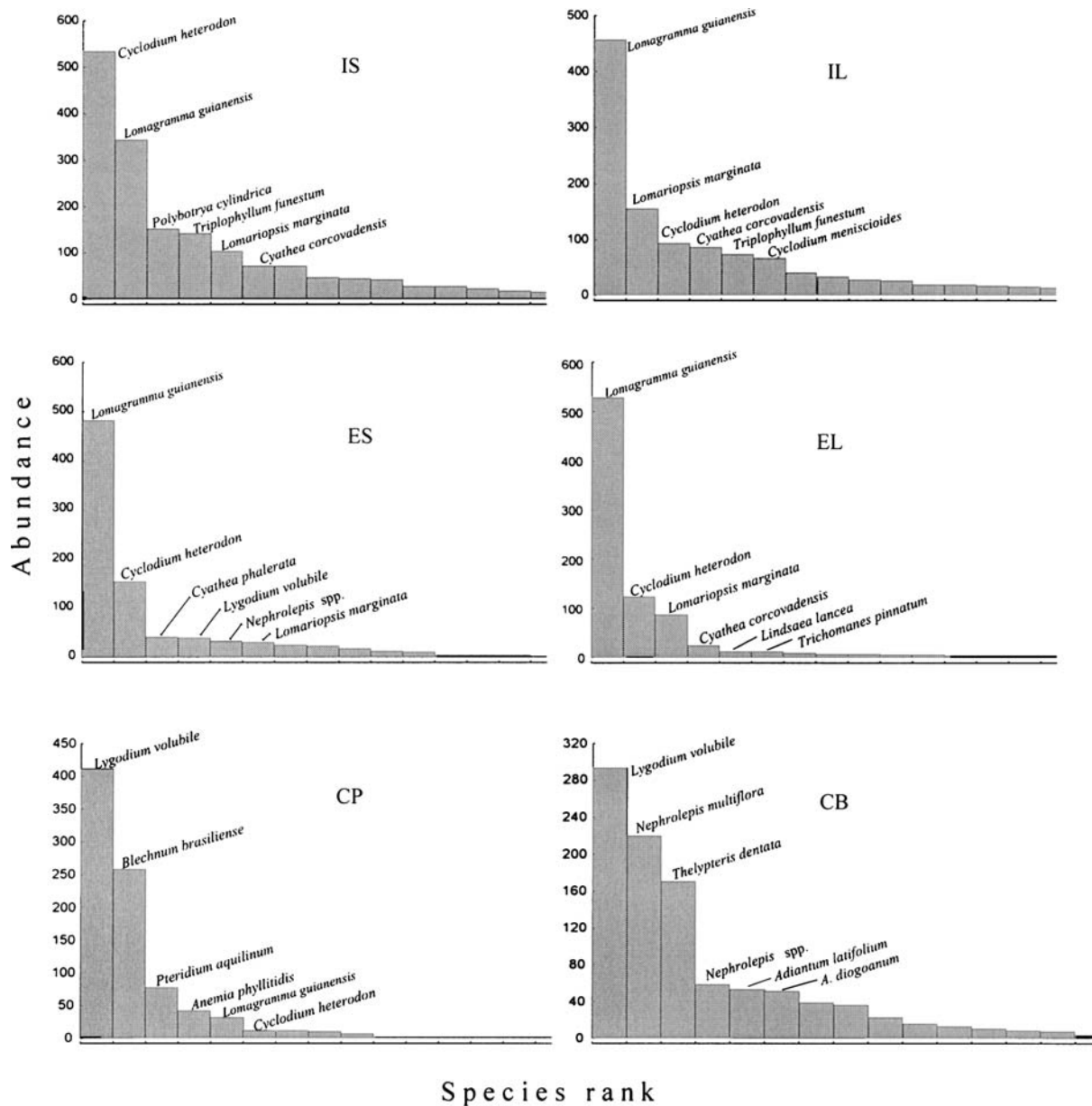


Figure 4. Species abundance of six ecotypes in Una region, with the 15 most abundant species inventoried (the six first are labelled). IS = interiors of small fragments; IL = interiors of large fragments; ES = edges of small fragments; EL = edges of large fragments; CP = capoeiras; CB = cabruças.

promote a gradual alteration of the floristic composition in these areas.

Lygodium volubile is a dominant species in both matrix areas (capoeiras and cabruças). The other very abundant species in these ecotypes are, in general, different from those observed in forested environments. *Cyclodium heterodon* and *Loma-*

gramma guianensis are exceptions, because are also found in the capoeiras, even though with low abundance (11 and 31 individuals, respectively).

These results indicate that the pteridophyte communities differ in the general ratio of individuals by species and in number of species, indirectly suggesting that diversity differs between ecotypes.

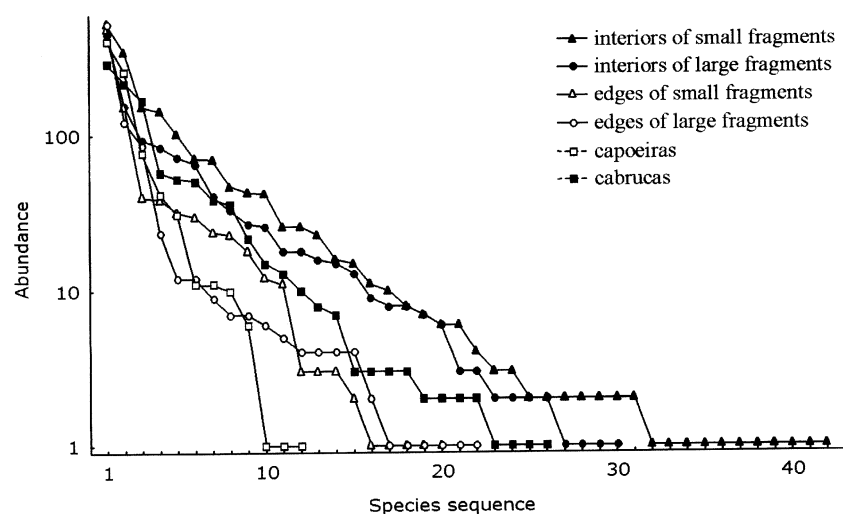


Figure 5. Rank abundance plots of pteridophytes for all study ecotypes in Una landscape.

Patterns of species abundance distribution for all the ecotypes are shown in Figure 5. The log-series model is a rich fit for all Una data (for the goodness of fit test, see Table 3). According to Bazzaz (1975), the bigger the amplitude and the smaller the inclination of curves the more diverse is the community in question. So based on inclination of the species abundance curves as well as the Fisher α Index, the interiors of small fragments are the most diverse areas ($\alpha = 7.88$), followed by the interiors of large ones ($\alpha = 5.77$), cabruças ($\alpha = 4.86$), large and small fragment edges ($\alpha = 4.14$ and $\alpha = 3.65$, respectively) and, finally, the capoeiras ($\alpha = 1.98$) as less diverse areas. Therefore, a gradient in pteridophyte diversity among environments composing the Una landscape is evident, starting from the capoeiras and

culminating in the small fragment interiors. We attribute these variations to the total species richness and to the number of rare species of each landscape component. If the log-series model provides a satisfactory fit to the observed curves, then these curves gradually expand as it approaches the horizontal axis because of a progressive increase in the number of rare species (Hughes 1986), once more species are represented by one individual than by two, and progressively fewer by three, four, and so on.

Discussion

The environmental mosaic of Una landscape region, state of Bahia, Brazil, shelters a relatively

Table 3. Diversity of six main landscapes categories (i.e., ecotypes), estimated by α Log-series Index (Fisher et al. 1943).

Parameters	Ecotypes					
	Forest			Matrix		
	IS	IL	ES	EL	CP	CB
Species richness (S)	41	32	20	22	12	26
Abundance (N_i)	1452	1479	880	844	861	1019
Log-series diversity index (α)	7.88	5.77	3.65	4.14	1.98	4.86
Fit to log-series model (χ^2)	$\chi_7^2 = 9.01$; $p > 0.10$	$\chi_7^2 = 3.20$; $p > 0.75$	$\chi_5^2 = 3.92$; $p > 0.50$	$\chi_6^2 = 3.32$; $p > 0.75$	$\chi_5^2 = 2.61$; $p > 0.75$	$\chi_6^2 = 5.49$; $p > 0.25$

All the communities can be described for a logarithmic series model (based on χ^2 distribution). IS = interior of small fragment; IL = interior of large remnant; ES = edge of small fragment; EL = edge of large fragment; CP = initial stage of forest regeneration (capoeiras) and CB = cocoa plantations (cabruças).

poor pteridophyte flora, in number of species, when compared to other neotropical localities in which quantitative inventories were conducted, even in smaller areas (Whitmore et al. 1985; Poulsen and Nielsen 1995; Young and León 1989). However, the assemblage found in the different components of the Una landscape must be viewed as a valuable study object for conservation biology, because it is threatened by the process of devastation and impoverishment of forest habitats.

The anthropogenic alterations in Una apparently do not have the same impact on all the pteridophytes. While some suffer from the human activities done to the forest (e.g. *Lindsaea lancea*, *Lomagramma guianensis*, *Lomariopsis marginata*, *Triplophyllum funestum*, etc.), others seem to prefer the altered habitats (e.g., *Lygodium volubile*).

Results regarding the effects of forest fragmentation upon Una pteridophytes demonstrate a clear tendency for the loss of forest species in the matrix and a general reduction of richness in the forest edges (Figures 2 and 3). Nevertheless, although there is a strong relationship between environmental structure and species loss, it cannot be determined that this first factor is a good regulator of the phenomenon, given that the regression predictability is low ($R^2 = 0.164$; $p = 0.026$). Perhaps the low value of the obtained regression coefficient (R^2) is due to the accentuated heterogeneity among edge environments. If this heterogeneity is closely related to the age of the edge (see Didhan and Lawton 1999; Metzger 1999), then the structural features are not always reflected in the pteridophyte richness, because, primary edge effects (e.g. microclimatic alterations) seem to influence the pteridophyte communities very quickly, while it is slower for the tree community (Paciencia and Prado 2004). Anyway, even in an imperfect way, qualitative habitat changes in Una landscape have an important role for the establishment of pteridophytes.

Beyond richness depletion, pteridophyte diversity also presents a reduction caused by the fragmentation process and shown mainly in the matrix composed by capoeiras, as evidenced by the diversity index α (Table 3) and the species abundance distribution (Figure 5). Rank abundance curves of smaller inclination and greater amplitude, such as those obtained for the forest interiors, tend to reflect a major diversity, regulated by

many environmental factors that operate together (May 1975). Among these factors are the greater variety of microhabitats and higher complexity of forest structure, typical of these environments (May 1981, 1986); that, in turn, would be the cause of a more equitable number of pteridophyte species, coming closer to the distribution model of a log-normal curve. So, although log-series is an appropriate fit to the both capoeiras and forest interiors data (Table 3) (and so capoeiras diversity could be interpreted as high as the forest interiors), the abundance curve of the capoeiras is the steepest among all six landscape components (Figure 5). This apparently conflicting fact can be related to the great number of dominant species in an assembly that is poor in number of species, as the capoeiras are, resulting in a deceiving high evenness.

Comparisons between pteridophyte diversity curves in Una environments and curves of k -dominance (Figures 5 and 6) (for further explanations see Patil and Taillie 1977; Lambshead et al. 1983; Moreno and Halffter 2001; Willott 2001) indicate that capoeiras really are the least diverse ecotype, followed by edges, cabrucas and interiors. Nevertheless, the α values are concordant with all k -dominance curves only for a total of $k = 12$ species, or the maximum possible comparison, based on the species number of the poorest community (capoeiras). For dominance values of few species (low values of k), the edges reveal themselves as the least diverse ecotypes. This would be expected, because these environments tend to present a very intense biotic and non-biotic dynamic, which works as a species selective factor. Only forest species that are able to stand high luminosity and drought conditions are abundant and well established in the edges (e.g. *Lomagramma guianensis*), along with typical matrix species (e.g. *Lygodium volubile*).

As evidenced in the Una mosaic, small forest remnants (<100 ha) can shelter pteridophyte communities as rich as those of large remnants (>900 ha), if the fragmented forest environment is mature and well preserved (Figure 3). Therefore, the non-biotic habitat conditions as well as its regional availability would be important factors determining the species-apportioning in the communities, ideas already presented by Kohn and Walsh (1994) and Venier and Farig (1996). Actually, Quinn and Harrison (1988), when studying

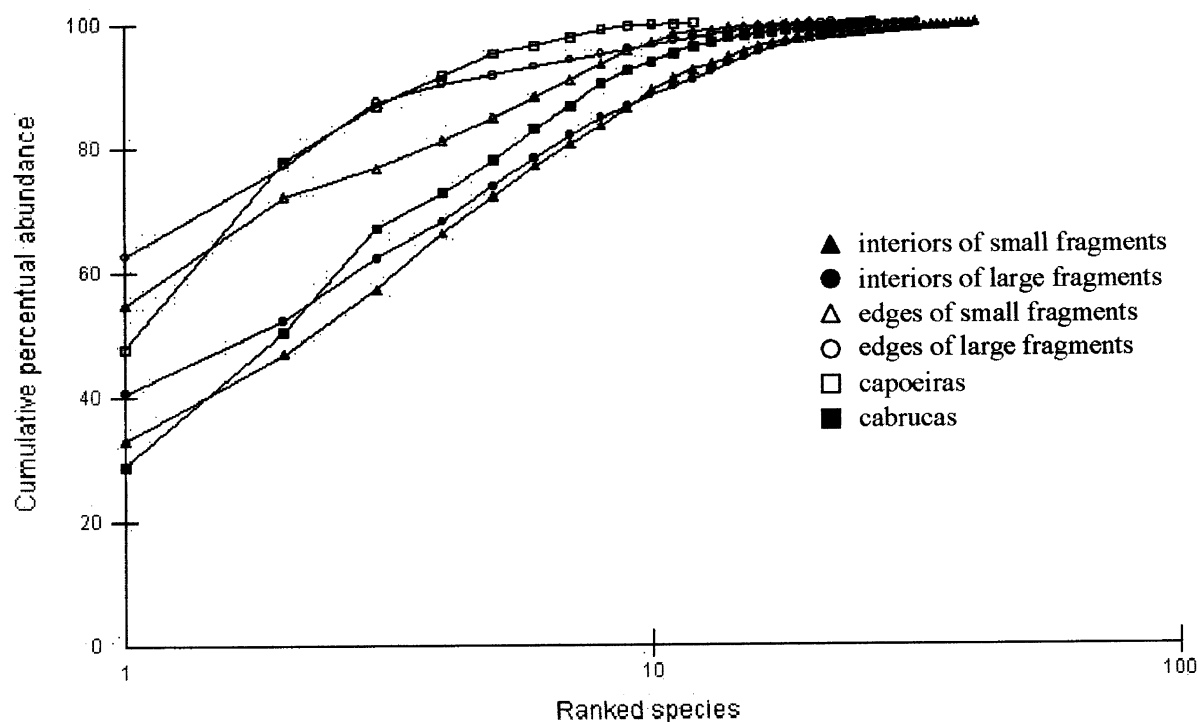


Figure 6. Diversity of pteridophytes showing the k -dominance plots. Comparisons between ecotypes are done using a maximum of 12 species, or the highest value to a species richness of the capoeiras sites.

systems of great and small oceanic islands, placed at different distances, concluded that area size is not so important to detect variations of pteridophyte richness, compared to the distance between habitat units and their quality (vegetation type and/or preservation status). A somewhat similar result was obtained by Lwanga et al. (1998) in their African research which reports no relationship between the relative richness recorded in the sample plots and forest area size. Those results agree with the present study, in that although the matrix is absolutely different in these three cases, the pteridophyte species are apparently capable of easily colonizing adjacent forest areas, crossing the matrix barrier with relative ease. Thus, in the case of the pteridophytes, although the Una landscape shows high level of connectivity (Pardini 2004) this probably is not an important factor to explain patterns of species establishment, as proposed by Taylor et al. (1993) for general landscape models.

The fact that small fragments and large fragments have similar diversity and richness of pteridophyte species disagrees, in part, with the current theory, based on the study of various

biological groups. In accordance with that theory, small forest patches would have to contain fewer species and smaller populations than extensive and more connected areas (Simberloff and Cox 1987; Bierregaard et al. 1992; Dunning et al. 1992; Ouborg 1993; Laurance and Bierregaard 1997). However, it was shown in Una that it was not the degree of isolation degree nor the habitat area reduction that were responsible for diversity and richness depletion in the forest pteridophytes community, but the mature forest loss itself. Hence, the conclusion is that communities of forest pteridophytes do not respond to fragmentation due to size-area effect and, therefore, the small and isolated forest fragments in Una have a high value for the conservation of the local flora. This assumes greater relevance when noting that Una fragments present rare and endemic species of forest pteridophytes, as *Elaphoglossum consobrinuin* and *E. pteropus* (Brade 1961), both found in very low frequency in herbarium collections all around the world.

As briefly discussed above another remarkable factor for the determination of local pteridophyte

diversity in Una is the landscape matrix quality. Depending on the type of element that characterizes the matrix, different processes can be observed. The capoeiras, one of the main matrix components in terms of the soil cover percentage, are responsible for the impoverishment of species number and diversity in the region. The cabruças, although they do not clearly demonstrate decrease of richness and diversity loss, also do not hold large nor, perhaps even viable, populations of forest species. On the other hand, a substitution of these species by others not found in any of the other studied ecotypes is generally verified. This composition alteration may be related to greater soil fertility, since these systems are generally implemented in areas of naturally fertile soil (Leão and Gouvêa 1971). Some of the pteridophytes frequently observed in cabruças are known to be conditioned by the presence of fertile substrates, as, for example, the genera *Adiantum* (Tuomisto et al. 1998) and *Thelypteris* (Tuomisto and Poulsen 1996). In addition to the fertility, the discriminating pH conditions might also determine the establishment of a so particular assembly of species in the cabruças (Petersen 1985), given that these units tend to have a formidable amount of organic matter resulting in supposedly more acid soils. However, these inferences are only speculative, since no soil analysis was done in the cabruças.

Besides promoting a profound alteration in the pteridophytes composition, the cabruças also present high abundances of invading species (e.g. *Lygodium* and *Blechnum*), frequently found with high relative abundances in capoeiras. The connection of these two factors would indicate that cabruças do not work as forest environments for the pteridophytes, because they are highly permeable to the establishment of species typical of disturbed areas and do not allow the effective colonization of forest interior species which, when they occur, are present in very low abundance.

Thus, we conclude that the heterogeneous matrix of Una cannot be considered a connector of forest areas for the pteridophytes but acts as a disaggregating agent for the continuity of the forest species populations, one that favors the establishment of species dissimilar from those found in forest interiors.

The last factor mentioned as a source of alterations for the Una pteridophyte community is the

“edge effect”, usually contributing to the regional reduction of species richness. As it is known, edge effects are a sum of alterations occurring at the edges of forest fragments, resulting from the exposure of *core*-areas to matrix environmental factors (Bernabe et al. 1999), a product of deforestation on the periphery of forest fragments. Among these alterations are the microclimate changes that, in turn, may determine the substitution of forest species by species that are exotic to the forest thus reducing the number of original species.

According to Loope and Mueller-Dombois (1989) areas of continuous forest (and therefore, very large fragments) are, in general, less vulnerable to invasion by exotic species, because environmental conditions do not favor their establishment, and indeed because the vegetal community of slightly disturbed areas seems to possess an inherent resistance to their penetration. However, the transformation of large forest areas to small fragments and the intense frequency of disturbance to adjacent fragments may favor the penetration of invading species, which is verified mainly in fragment edges (Williams-Linera 1990).

In Una, edges of large fragments and of small fragments are likely to present a lower number of pteridophytes species and a lower diversity than the interiors (Paciencia and Prado 2004). This is because some pteridophytes cannot tolerate the supposed greater incidence of winds and increased light intensity at the edges (Grime 1985), reflecting the decrease of richness and diversity in these environments. A possible explanation for this phenomenon is that forest species are apparently more sensitive to fragmentation (Paciencia and Prado 2004). According to Turner (1996), “the man-made fragments are literally created from one day to the other and, therefore, contain a community that during hundreds, perhaps thousands, of years of existence, received very little selection pressure for fragmentation tolerance”. This idea is very appropriate concerning pteridophytes; intensification of the edges or the conversion of forests into capoeiras, cabruças, and pastures can cause the collapse of the forest pteridophytes flora, in one way or another.

Although it was not possible to demonstrate what are the major modification agents in the edges and/or matrixes, it seems extremely likely

that the forest fragmentation in Una causes negative alterations for the group of pteridophytes. Only extensive portions of forest can contain a substantial complement of a region's endogenous biota and, therefore, to assure the integrity of these areas must be a priority to conservationist's studies (Turner 1996). Preventing fragmentation of unbroken forests as much as possible is an obvious first step, even though it is an arduous task to be done, since perennial forests are particularly sensitive to fragmentation, and since a great number of its species are intolerant to open localities.

This does not mean, however, that already fragmented environments should be neglected, because, as found in Una, the maintenance of pteridophyte biodiversity depends, in part, the remaining fragments. Besides, it is known that various small fragments can maintain a high diversity levels years after their formation (Turner et al. 1994; Turner and Corlett 1996), and some species are able to exist indefinitely in those fragments. Even some remaining trees can shelter species of epiphytic orchids, although for a relatively short time (Williams-Linera et al. 1995).

Thus, in the context of preservation of Una region, since the great majority of forest pteridophytes were found in the small forest patches, including endemic and/or rare species, all remaining fragments should be incorporated to the most important conservation unit existent there (Una Biological Reserve), or at least be included in the management plan as part of the adjacent area for environmental protection.

Concerning the matrixes, although being the sources of profound structural and floristic disturbances in the pteridophyte community, they hold also an important conservation value. An illustration of this fact is the recent discovery of species *Adiantum discolor* Prado, in a cabruca of the Una region (Prado 2000). Therefore, these units should be carefully considered for conservation decisions in Una. We believe that if it is possible to maintain the current vegetation structure in Una, there are great possibilities for some naturally rare species of forest pteridophytes to come back, and effectively integrating themselves into the existing forest fragments, increasing their populations, and, therefore, raising the conservation interest in the region.

Acknowledgements

We are grateful to RestaUna Project crew for logistic and scientific helpful (support advice from PROBIO/PRONANABIO/MMA – CNPq/BIRD-GEF for founding); R. Pardini for advice; M. Buchler for reviewing the English version of the manuscript; CAPES for the grant to the first author; Instituto de Pesquisas Ecológicas (IPE) for the use of software Statistica 5.1; and IBAMA for allowing access to the Una Biological Reserve.

Appendix A. Average number of leaves for some species that presented long-creeping rhizomes, in order to avoid an overestimate of the abundance in those species.

Species	Number of individuals	Number of leaves per individual (min–max)	Average number of leaves (per individual)
<i>Adiantum latifolium</i>	23	1–8	3.22
<i>A. diogoanum</i>	7	1–4	2.86
<i>Cyclodium meniscioides</i>	11	2–5	3.45
<i>Lomagramma guianensis</i>	17	3–9	6.59
<i>Lomariopsis marginata</i>	15	2–6	2.73
<i>Polybotrya cylindrica</i>	7	1–5	3.00

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