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Assessing fern diversity: relative species richness and its environmental correlates in Uganda

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Techniques for the rapid quantification of tropical biodiversity are of critical importance in deciding where to invest scarce conservation resources. Here we describe a simple survey method for assessing species-level richness of a poorly known plant group, the pteridophytes. We then illustrate the use of a powerful, rarefaction-based technique of controlling for inevitable differences in sampling effort to calculate the relative species richness of our study sites. Lastly, we explore how closely observed patterns of relative species richness of Ugandan forests are correlated with a suite of simple environmental variables. We find that fully 75% of the variance in our estimate of fern diversity can be predicted from just two measures: soil fertility (scored as C/N ratio, itself related to rainfall); and distance from the nearest putative Pleistocene refugium.

Keywords: ferns; relative species richness; environmental predictors; biodiversity surrogates; Uganda.

Introduction

In recent years, assessing and understanding the distribution of biological diversity have shifted from being topics of largely theoretical interest to occupying centre-stage in conservation biology (Rosenzweig, 1995). Conservation resources are limited, and so should in part be focused on those vulnerable areas of highest biological value (Mittermeier, 1988; Myers, 1988, 1990; Pressey *et al*., 1993; Balmford and Long, 1994). However, we know depressingly little about the fine-scale distribution of the great majority of species, especially in the tropics, where most diversity occurs. There is therefore an urgent need to explore ways in which the diversity of little-known groups can either be rapidly assessed in the field or else reliably predicted using readily obtainable information on other taxa, or on climatic or edaphic variables.

We have attempted to examine both of these issues using data from the first ever survey of the diversity of ferns across Ugandan forests. Field and herbarium work spanned 6 months, covered 12 forests (Fig. 1), and was conducted under tight financial and logistic constraints. Although we tried to distribute sampling effort evenly, adverse weather

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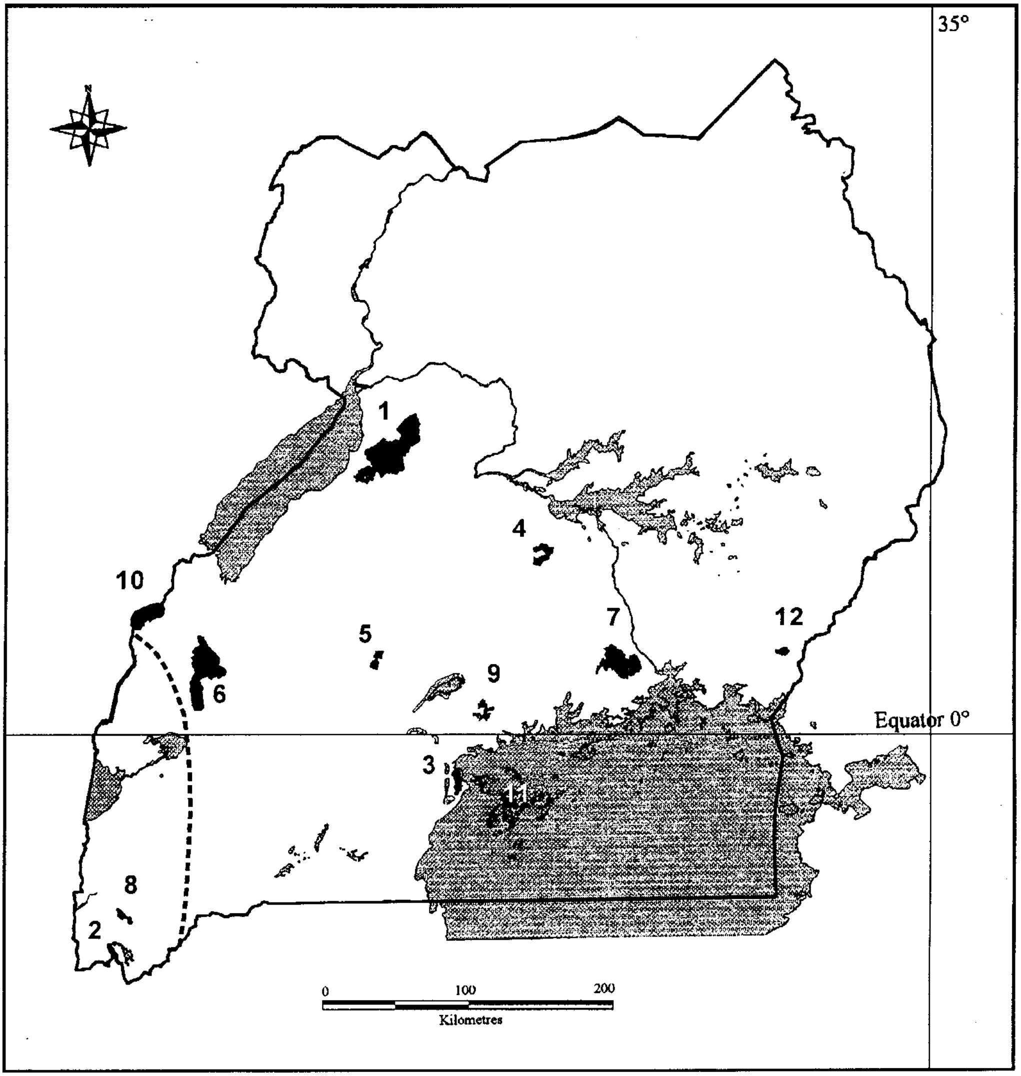

Figure 1. Map of Uganda showing location of 12 forests studied: 1, Budongo; 2, Echuya; 3, Jubiya; 4, Kasagala; 5, Kasana-Kasambya; 6, Kibale; 7, Mabira; 8, Mafuga; 9, Mpanga; 10, Semliki; 11, Sesse Islands; 12, West Bugwe. Dashed line depicts approximate eastern limit of the nearest putative Pleistocene refugium, the East Zaïre core area (Hamilton, 1982).

conditions, vehicle breakdowns and difficulties in hiring local labour meant that in practice, some forests were sampled more intensively than others. Despite yielding imperfect results, we believe that all of these circumstances are probably typical of those under which most contemporary surveys of tropical biodiversity take place. In a companion paper, we use the fern data to quantify the likely consequences for reserve selection of adopting a variety of proposed short-cut methods for biodiversity assessment, and suggest guidelines for future surveys (Balmford and Lwanga, in prep.). In the present paper we first illustrate the use of a new and powerful technique for quantifying the relative species richness of unequally sampled sites (Prendergast *et al.*, 1993), and then examine how closely the patterns of fern richness which we observe correlate with local environmental conditions.

Pteridophytes are an ideal group of plants for such a study. Compared with angiosperms, their distribution is poorly documented (Kramer, 1993): robust techniques for predicting areas of high fern diversity would thus be of considerable use. Moreover, their general lack of co-evolved relationships with pollen or seed vectors suggests that fern biogeography may be rather more straightforwardly linked to abiotic factors than is the case for many other plants (Barrington, 1993).

Africa is remarkably depauperate in ferns (Parris, 1985; Kornas, 1993). While there are some 3000 species of pteridophytes in South and Central America and 4500 in south-east Asia, Africa has fewer than 600 species. One likely reason for this is that while most ferns require a continuous supply of moisture, much of Africa is characterized by strongly seasonal or irregular rainfall (Parris, 1985; Tryon, 1985). A second potential explanation is that shifting vegetation zones during the early Tertiary and climatic oscillations during the Pleistocene drastically reduced the extent of Africa's moist forests and so led to widespread extinctions of moisture-dependent species (Parris, 1985; Kornas, 1993).

These two non-exclusive hypotheses in turn suggest a suite of environmental variables to consider as potential predictors of Ugandan fern diversity. Rainfall (and in particular its impact on soil moisture) is an obvious candidate which has been shown to be positively correlated with local species richness in several studies of ferns (Dwzonko and Kornas, 1978, 1994; Kornas, 1993) as well as other plants (e.g. Hall and Swaine, 1976; Gentry, 1982; Linder, 1991; Clinebell *et al.*, 1995). Similarly, it is possible that fern species richness (like that of angiosperms and primates) (Hamilton, 1974, 1981; Struhsaker, 1981) is in part predicted by proximity to the nearest putative a Pleistocene forest refugium (in this case the East Zaïre core area) (Hamilton, 1982) (Fig. 1). Lastly, given that across much of Africa, rainfall is strongly coupled with other abiotic variables such as altitude and soil fertility (Hall and Swaine, 1976; Dwzonko and Kornas, 1994; Clinebell *et al.*, 1995), we consider whether any of these (rather than rainfall itself) may be the underlying determinants of pteridophyte diversity and hence the best predictors of fern species richness (Tuomisto *et al.*, 1995; Tuomisto and Poulsen, 1996).

Methods and results

Measuring species richness

The fern species richness of each of our 12 study forests was estimated from a series of adjacent 2 m × 100 m plots arrayed along gradient-oriented transect lines ('gradsects'; Gillison and Brewer, 1985; Austin and Heyligers, 1989, 1991). For every forest, we aimed to run one 1 km transect line in each of five 5 km × 5 km gridsquares picked at random from the 1:50 000 Forest Department map. One transect was run on each day of fieldwork. The starting points of transects were picked so that between them they sampled all habitat types (other than open grassland) found in the forest (as defined by Langdale-Brown *et al.*, 1964). The transects were then oriented so that they crossed the maximum number of contour lines. Thus in principle this design meant that in every forest, ferns were sampled in 10 adjacent 2 m × 100 m plots along each of five transect lines. In practice, the number of plots sampled per forest ranged from 33 to 50, with plots missed out either because of logistical difficulties or (as often happened in smaller forests) because they extended beyond the forest edge.

In each 100 m-long plot we recorded all ferns within 1 m of the transect line and 12 m of the ground; epiphytic species growing high in the canopy were thus not covered by the survey (and we do not know how closely patterns of epiphyte species richness match variation in numbers of terrestrial species). We collected voucher specimens of every species encountered on each day. These were then lodged at the Uganda Forest Department's own herbarium, where difficult specimens were identified down to species (with reference where necessary to collections at Makerere University, Kampala, and the National Museums of Kenya, Nairobi).

In total we recorded 147 fern species across our 12 forests. The cumulative number of fern species recorded in each forest is plotted as a function of sampling effort in Fig. 2a. These simple accumulation functions illustrate three points. First, the number of fern species recorded varied very considerably between forests (mean recorded species richness: 29.5 species; range: 2–54 species). This variation both demands explanation, and suggests that the forests differ widely in their value for fern conservation. Second, although for most forests the rate of addition of new species was decreasing by the end of the sampling period, there was no evidence for any forest that the cumulative total had reached a clear asymptotic value. Third, the fact that no forest was surveyed exhaustively, combined with differences in sampling effort between forests (see above), suggests that species richness scores should be standardized for number of plots examined before the relative richness of the forests can be interpreted.

One straightforward way of standardizing for differences in sampling effort is to compare the number of species recorded in each forest at the lowest level of sampling for any forest (in this case, after just 33 plots). A more sophisticated version of this approach, which takes account of the inevitably irregular way in which new species are added with increasing effort, involves first smoothing accumulation functions using rarefaction procedures (modified from Sanders, 1968), so that for each forest the curves describe the average species total expected after a given level of sampling (see Fig. 3). The richness of the sites can then once again be compared at a constant level of sampling, equal to the lowest for any site (i.e. at point x in Fig. 3). Both of these techniques suffer from the obvious disadvantage that they throw information away. In particular, changes in the relative richness of forests that become apparent only after the lowest level of sampling has been exceeded will not be incorporated into the relative richness scores. As a hypothetical example, in Fig. 3 the use of all available information suggests that forest A, with a steep accumulation function, contains fewer total species than forest B. However, this point would not be captured by a relative richness index based on comparing species totals at only the lowest level of sampling for any forest (point x).

An elegantly simple solution to this problem has been proposed by Prendergast and colleagues (Prendergast *et al.*, 1993). This again involves initial rarefaction of accumulation curves, but this time compares the richness of any pair of forests at the highest level of sampling common to both of them. Thus in Fig. 3, the relative richness of forest A compared with forest B is calculated as the number of species expected in A divided by that expected in B for sampling effort y. Likewise, the richness of A relative to C is to derived from the elevations of the two curves at point x, and that of A relative to D calculated after sampling effort z. The overall index of relative species richness for forest A is

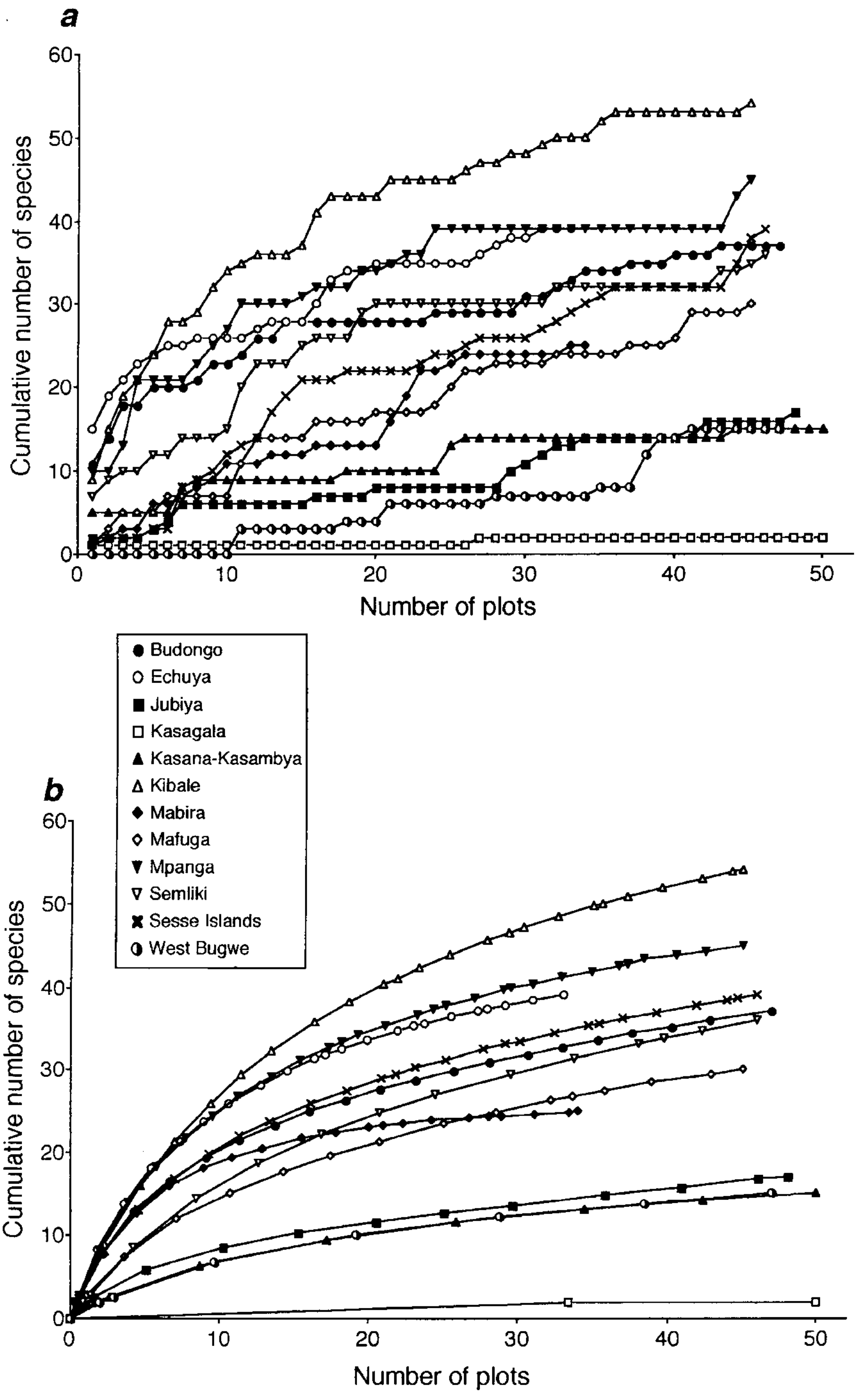

Figure 2. Cumulative a fern species richness as a function of sampling effort in the 12 forests. (a) Recorded species richness; (b) smoothed species richness, after rarefaction.

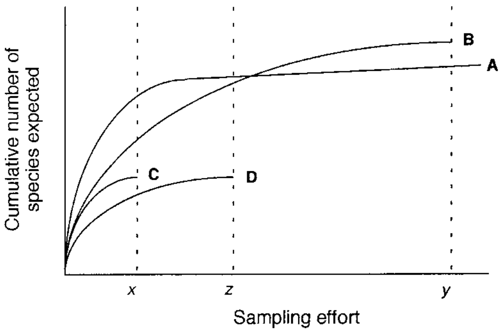

Figure 3. Hypothetical illustration of how smoothed species richness functions might vary with sampling effort across four forests. See text for details.

then calculated as the geometric mean of all such pairwise values. A site of average richness would have mean richness score of one, while sites of above or below average richness would have relative richness scores of greater or less than one, respectively.

We applied Prendergast *et al.*'s method to the fern dataset, first generating smoothed accumulation functions using Krebs' (1989) rarefaction algorithm (see Fig. 2b). The resulting relative richness scores ranged from 0.07 for the poorest forest (Kasagala) to 2.45 for the richest (Kibale). Because in this particular study we sampled our sites relatively evenly, these relative richness scores were in practice closely correlated with our unadjusted recorded richness totals (Pearson's correlation: $r = 0.99$, $N = 12$ forests, $p < 0.001$). Nevertheless, because of the general importance of controlling for differences in sampling effort, we used relative species richness scores for analysing the correlates of fern diversity.

Correlates of species richness

We compared our measures of relative species richness with 14 abiotic attributes of the sampled forests: area (in km^2), mean annual rainfall in the wettest and driest parts of the forest (both in mm), mean length of the longest dry season (in months), mean annual number of days of rain in the wettest and driest parts, highest and lowest altitudes and the difference between them (all in m), number of vegetation types (from Langdale-Brown *et al.*, 1964), distance from the putative East Zaire core area (in km; see Fig. 1), and mean soil pH, C/N ratio, and total cation concentration (the sum of concentrations of Ca, K, Mg and Na, in mg/100 g). Rainfall and altitude data were taken from the *Atlas of Uganda* (Uganda Department of Land and Surveys, 1962). We considered the number of vegetation types because, *a priori*, one might except species richness to increase with habitat heterogeneity. Soil chemistry was assessed from 15 cm cores of topsoil taken at the beginning, middle and end of each transect and analysed by the Department of Soil Science, Makerere University, Kampala. Prior to statistical analysis, all variables which were not approximately normally distributed were $\log_{10}$- or square root-transformed as appropriate.

Bivariate analyses revealed that the relative richness of Ugandan forests for ferns was related to both rainfall and soil fertility (see Table 1; note that none of the probability values here have been corrected for multiple comparisons; Rice, 1989). Fern richness increased with the mean number of rainy days in the wettest part of the forest, which may be a more sensitive indicator of average soil moisture content than total rainfall. Relative species

Table 1. Bivariate relationships between relative species richness of forests for ferns and climatic and edaphic variables. $N = 12$ for all analyses

Forest at tribute	r^2	p
Area (km^2)[a]	−0.09	NS
Mean annual rainfall in wettest part (mm)	−0.05	NS
Mean annual rainfall in driest part (mm)	−0.07	NS
Mean length of longest dry season (months)	−0.10	NS
Mean no. of days of rain in wettest part	0.49	< 0.01
Mean no. of days of rain in driest part	0.11	NS
Highest altitude (m)[b]	−0.07	NS
Lowest altitude (m)	−0.08	NS
Altitudinal range (m)[b]	−0.03	NS
No. of vegetation types	0.02	NS
Distance from refugium (km)	0.21	< 0.10
Mean soil pH	−0.10	NS
Mean soil C/N ratio	0.55	< 0.01
Mean total cation concentration (mg/100 mg)	0.14	NS

[a] Log$_{10}$-transformed.
[b] Square root-transformed.
NS: $p > 0.10$.

richness was also negatively related to soil C/N ratios. Since a low C/N ratio is indicative of high soil fertility (Swaine, 1996), this suggests fern communities tend to be richest on fertile soils. Unsurprisingly, there was no relationship between the relative richness recorded in the sample plots and forest size. Lastly, there was a weak tendency for relative species richness to decline with increasing distance from the nearest Pleistocene refugium.

However, interpreting such bivariate relationships is hampered by strong correlations between many of the climatic and edaphic variables (see Table 2). In particular, as well as close relationships among the different measures of rainfall or topography, forests with high scores for number of rainy days generally had soils with high cation concentrations and low C/N ratios. These results, though strong, are somewhat surprising in that elsewhere in the tropics, high rainfall is frequently associated with pronounced leaching and generally low soil fertility (Hall and Swaine, 1976; Huston, 1980; Clinebell *et al.*, 1995). Moreover, they suggest that the independent relationships between fern species richness and abiotic variables are best explored via multiple regression.

The best multiple regression model contained just two predictor variables which between them accounted for fully 75% of the variance in relative species richness scores (Table 3). Fern species richness was independently and negatively related to both soil C/N ratio and distance from the East Zaïre core area (Fig. 4). After inclusion of these two terms in the model, residual variance in relative species richness was unrelated to all remaining abiotic variables. Moreover, the model could not be improved by replacing either significant term with any of the other climatic or edaphic measures.

Discussion

The field and analytical methods described here enabled us to assess the species richness of ferns in a sample of Uganda's forests rapidly and, we believe, reliably. Field and her-

Table 2. Pearson correlation coefficients describing the bivariate relationships between abiotic attributes of the 12 study forests

	Area (km$^{2)}$	Mean annual rainfall in wettest part (mm)	Mean annual rainfall in driest part (mm)	Mean length of longest dry season (months)	Mean no. of days of rain in wettest part	Mean no. of days of rain in driest part	Highest altitude (m)	Lowest altitude (m)	Altitudinal range (m)	No. of vegetation types	Distance from refugium (km)	Mean soil pH	Mean soil C/N ratio
Mean annual rainfall in wettest part (mm)	−0.11												
Mean annual rainfall in driest part (mm)	−0.27	0.73**											
Mean length of longest dry season (months)	0.07	−0.58*	−0.60*										
Mean no. of days of rain in wettest part	0.37	0.07	0.06	0.14									
Mean no. of days of rain in driest part	0.20	−0.50(*)	−0.31	0.42	0.72**								
Highest altitude (m)	−0.25	0.19	−0.15	−0.14	0.22	0.11							
Lowest altitude (m)	−0.33	0.22	−0.12	−0.19	0.12	0.06	0.99**						
Altitudinal range (m)	0.21	−0.14	−0.41	0.12	0.50(*)	0.46	0.81**	0.74**					
No. of vegetation types	0.77**	−0.22	−0.32	0.38	0.50(*)	0.47	0.01	−0.07	0.45				
Distance from refugium (km)	−0.13	0.24	0.57(*)	−0.28	−0.36	−0.46	−0.37	−0.35	−0.41	−0.39			
Mean soil pH	0.41	−0.54(*)	−0.13	0.43	0.36	0.58*	−0.50(*)	−0.56(*)	0.01	0.43	0.21		
Mean soil C/N ratio	−0.10	−0.37	−0.46	0.09	−0.82**	−0.45	0.03	0.07	−0.07	−0.14	0.12	−0.28	
Mean total cation concentrating (mg/100 mg)	0.40	−0.34	0.03	0.31	0.69*	0.76**	−0.30	−0.36	0.13	0.59*	−0.14	0.83**	−0.61*

(*)$p < 0.10$; *$p < 0.05$; **$p < 0.01$; variables transformed to approximate normally as in Table 1.

Table 3. Significant terms in a multiple regression model predicting relative species richness of forests for ferns. All other terms entered into the model were not significant at $p < 0.10$

Forest attribute	Coefficient	Statistic	p
Distance from refugium (km)	−0.002	$t = 2.78$	< 0.05
Mean soil C/N ratio	−0.26	$t = 4.55$	< 0.01
Overall model		$r^2 = 0.75$	< 0.001

barium work together took a team of two scientists and two to four field assistants an average of 2 weeks per forest, and analyses summarized elsewhere suggest a series of shortcuts which would enable future fieldwork to be further streamlined (Balmford and Lwanga, in prep.). Once a rarefaction programme had been developed working up the raw data to calculate an index of relative species richness which controls for differences in sampling effort took less than a week for the entire dataset. Most interestingly, our regression analyses suggest that a large portion of the variance in the importance of forests for ferns can in principle be predicted from just two environmental variables.

The strongest single predictor of fern species richness was soil C/N ratio: the number of fern species present in a forest was positively related to soil fertility. This result is rather surprising, since evidence from many other tropical forests indicates that plant diversity

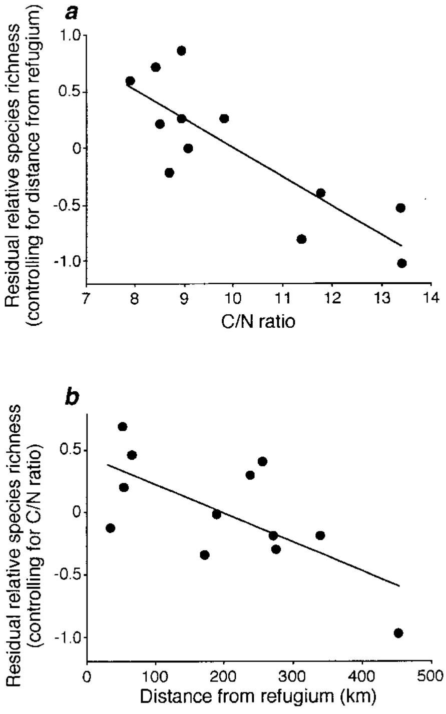

Figure 4. Significant relationships in a multiple regression model predicting relative species richness (a) Relative species richness (controlling for distance from refugium) versus mean soil C/N ratio; (b) relative species richness (controlling for C/N ratio) versus distance from refugium. For statistics, see Table 3.

commonly decreases with increasing soil fertility (Hall and Swaine, 1976; Huston, 1980, 1994; Tuomisto *et al.*, 1995; Tuomisto and Poulsen, 1996). However, the general form of the relationship between species diversity and fertility (and indeed of the determinants of productivity) is complex, with some consensus emerging that when comparing widely dispersed sites, species richness is a unimodal or hump-shaped function of increasing fertility (Grime, 1973; Huston, 1994; Rosenzweig, 1995). Negative diversity/fertility plots are thus explained as sampling the right hand part of this general relationship. In an analogous way, the positive line we observed could be accounted for if all our sites are distributed on the left-hand, rising part of the humped relationship. The generally high fertility of Ugandan soils somewhat undermines this argument. Nevertheless, a similar positive diversity/fertility relationship for pteridophytes (as well as other plants) has recently been reported for 28 forest plots distributed across the neotropics (Tuomisto *et al.*, 1995; Tuomisto and Poulsen, 1996), suggesting that the pattern reported here may not be uncommon.

Two other explanations for the observed link between fertility and diversity suggest that it may actually be driven by a third variable. One possibility is that high fertility sites are associated with relatively dense stands of trees, where deep shade, high humidity and readily available stumps and fallen logs offer ideal conditions for gametophyte establishment (J.P. Grime, pers. comm.). Another explanation is that fern species richness is driven by rainfall (as in Rwanda and Zambia) (Dwzonko and Kornas, 1978, 1994; Kornas, 1993; Clinebell *et al.*, 1995), and in Uganda wet sites happen to have generally fertile soils (Table 2). This last argument is weakened by the broad range of rainfall measures we considered as potential predictors of species richness, and the fact that annual rainfall at all our forests was close to or above the 1100 mm threshold separating sites of low and high pteridophyte diversity elsewhere in Africa (Dwzonko and Kornas, 1978, 1994; Kornas, 1993). On the other hand, it could be argued that none of our rainfall variables measured soil moisture content directly, and all were based on data collected at least 40 years ago (and that since then, finescale variation in rainfall patterns may have changed considerably). It seems clear that unambiguous interpretation of the relationships between fertility, rainfall and species richness may only be achieved through experimental manipulations of soil composition (see also Swaine, 1996).

Controlling for differences in soil fertility, relative species richness was also negatively but weakly correlated with distance from the East Zaïre core area. Similar results have already been reported for Ugandan angiosperms and primates (Hamilton, 1974, 1981; Struhsaker, 1981), but these earlier studies did not control for other potentially confounding variables. A correlation (even a weak one) between distance from a refugium and local fern diversity is perhaps unexpected. Ferns are successful colonists of remote or newly formed islands (Bush and Whittaker, 1991; Given, 1993; Kramer, 1993). Their spores are capable of dispersing at least 1600 km (Tryon, 1985; Barrington, 1993)–over three times the distance of any of our sites from the East Zaïre core area (see Fig. 4b). However, if during periods of forest contraction, ferns became adapted to wet, high altitude conditions of the refugium itself, it is possible that their present-day distribution may be constrained not by dispersal, but by their inability to survive in the less mesic, lowland forests of east and central Uganda (for similar arguments see Tryon, 1985). An alternative and simpler explanation is that the present result is driven largely by low species richness of the easternmost site (West Bugwe; see Fig. 4b), parts of which are highly disturbed. We know relatively little about the extent of historical disturbance in our other study areas, but rather than signalling past range contractions, the paucity of ferns in West Bugwe at least may well reflect the general inability of pteridophytes to cope with human disturbance (Grime, 1985).

Whatever the causal mechanisms driving the relationships we observed, it is striking that three-quarters of the variance in fern species richness can be predicted from readily measured attributes of their environment. Though this figure is high, similarly strong relationships have been reported in many correlational analyses of species richness patterns (see review by Gaston and Williams, 1996). In such cases the ability of carefully selected environmental variables to act as low-cost surrogates for assessing the distribution of biological diversity may be considerable (see Faith and Walker, 1996; Balmford and Lwanga, in prep.).

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