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Terrestrial pteridophytes as indicators of a forest-like environment in rubber production systems in the lowlands of Jambi, Sumatra

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Abstract

Species richness of terrestrial ferns and fern allies (Pteridophyta) may indicate forest habitat quality, as analysed here for a tropical lowland area in Sumatra. A total of 51 standard 0.16 ha plots in primary forest, rubber (*Hevea brasiliensis*) agroforests and rubber plantations was compared for plot level diversity (average number of species per plot) and landscape level diversity (species–area curves). Average plot level species richness (11 species) was not significantly different amongst the three land use types. However at the landscape level the species–area curve for rubber agroforests (also called jungle rubber) had a significantly higher slope parameter than the curve for rubber plantations, indicating higher beta diversity in jungle rubber as compared to rubber plantations. Plot level species richness is thus not fully indicative of the (relative) richness of a land use type at the landscape scale because scaling relations differ between land use types. Terrestrial fern species can serve as indicators of disturbance or forest quality as many species show clear habitat differentiation with regard to light conditions and/or humidity. To assess forest habitat quality in rubber production systems as compared to primary forest, terrestrial pteridophyte species were grouped according to their ecological requirements into 'forest species' and 'non-forest species'. Species–area curves based on 'forest species' alone show that the understorey environment of jungle rubber supports intermediate numbers of 'forest species' and is much more forest-like than that of rubber plantations, but less than primary forest. Species richness alone, without a priori ecological knowledge of the species involved, did not provide this information. Jungle rubber systems can play a role in conservation of part of the primary rain forest species, especially in areas where the primary forest has already disappeared. In places where primary forest is gone, jungle rubber can conserve part of the primary forest species, but large areas of jungle rubber are needed. In places where primary forest is still present, priority should be given to conservation of remaining primary forest patches.

Keywords: Agroforestry; Biodiversity; Jungle rubber; Pteridophyta; Species–area relations; Tropical rain forest

1. Introduction

With the disappearance of undisturbed lowland rain forest habitat the question arises whether disturbed habitat maintains some of the characteristics and functions of the original forest, to what extent it can support survival and reproduction of primary rain forest species and how this function is influenced by management practices. For a complete answer of this question we would have to consider all major taxa of flora and associated fauna. The research reported here compares diversity of terrestrial pteridophyte species, with known habitat requirements, to assess for this group to what extent the understorey habitat in rubber produc-

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tion systems is comparable to the understorey habitat in undisturbed rain forest for the lowland peneplain of Jambi (Sumatra).

1.1. Exploratory research and remaining questions

De Foresta and co-workers were probably the first to study the vegetation of rubber agroforests (also called 'jungle rubber'; Gouyon et al., 1993) to get an impression of species richness. Sampling a 100 m transect line (Michon and De Foresta, 1995) they found almost twice as many herb species in a rubber agroforest as compared to a nearby primary forest (23 versus 12 species) in Jambi Province, Sumatra. Their research was broad in the sense that all vegetation was included, but limited in the fact that vegetation types were represented by a 100 m transect only and that the study was not replicated across the landscape. When a larger number of plots are sampled, will the average number of herb species per plot remain twice as high for jungle rubber as compared to primary forest? Another question that remained after the exploratory work by Michon and De Foresta was whether high diversity found on the plot level is a reflection of high species turnover (beta diversity) on a landscape scale, or not. Data on plot level have been used (Leakey, 1999) to make statements that 'complex, multistrata agroforests contain about 70% of all the regional pool of plant species', apparently assuming that a single transect line is sufficient to characterise a vegetation type and that scaling rules above plot level do not differ between vegetation types.

1.2. Species turnover and species composition

In spite of a high number of species found at the plot level, if the species composition in jungle rubber at the landscape level would be rather repetitive, in other words if the species–area curve for jungle rubber would have a much lower slope parameter than the curve for primary forest, those rubber agroforests would probably not be as interesting an option for biodiversity conservation.

Species richness, regardless of species composition, is often used as a measure in biodiversity studies. If we deal with disturbed ecosystems however, there are risks involved because different taxa react in different ways to disturbance. For many taxa, "diversities peak at intermediate rates of small-scale disturbance" (Rosenzweig, 1995, p. 39). Although species are considered the 'currency' of biodiversity, counting just any species does not help us much when we are interested in conservation of a specific ecosystem. What kind of species do we find? Do the species we find give us some information about the quality of the type of habitat we are interested in? The fact that we can find great diversity of pteridophyte species on the forest floor of rubber agroforests does not tell us that the environment there is comparable to a primary forest and can be expected to support primary forest species.

1.3. Terrestrial pteridophytes as an indicator group

For assessments using an indicator group we should know first of all whether the group of species we are using contains enough species that differ in habitat requirements with respect to the range of the environmental factors that change when a forest is disturbed by human action. If the great majority of pteridophyte species were generalist species that could grow anywhere they would not indicate any changes in forest environment due to disturbance. Enough species with narrow habitat requirements are needed so they can be grouped to indicate different degrees of disturbance. Important environmental factors for life in the understorey of a tropical lowland rain forest that change with disturbance are light conditions (quantity and spectrum) and microclimate (moisture and temperature regime). When species are thus grouped we can assess which part of the total diversity in each land use type is made up by species requiring forest-like conditions, assuming that the bigger the share of those 'forest species', the more forest-like the understorey environment will tend to be.

1.4. Research questions

Summarising the above, the research is focussed on the following questions:

- Can rubber production systems play a role in conservation of primary forest species by providing forest-like habitat?
- Can terrestrial pteridophyte species indicate disturbance level or habitat quality of the forest understorey?

- Is plot level species richness indicative of the (relative) richness of a land use type at the landscape scale, or do scaling relations differ essentially between land use types?
- Is species richness a useful indicator of habitat quality, or is (a priori) ecological information needed on the species involved?

2. Land use change in the Jambi lowlands

The study was carried out in the lowlands of the peneplain area in Jambi Province, Sumatra at elevations of 40–150 m above sea level. For sampling locations see Fig. 1.

The original forests of this area are mixed Dipterocarp rain forests. The physical environment, structure and floristics of these forests and of the derived secondary vegetation types are described by Laumonier (Laumonier, 1997, pp. 88–130). Extensive research on land use and land use changes has been carried out by the 'Alternatives to Slash-and-Burn' project and summarised in two reports (Van Noordwijk et al., 1995; Tomich et al., 1998). Land use types described by the ASB project (Tomich et al., 1998, Table I.2, p. 19) include natural forest, forest extraction (community-based forest management, commercial logging), complex multistrata agroforestry systems (rubber agroforests), simple tree crop systems (rubber, oil palm (*Elaeis guineensis*) and industrial timber monoculture), crop/fallow systems (upland rice (*Oryza sativa*)/bush fallow rotation), continuous annual cropping systems (monoculture cassava degrading to *Imperata cylindrica*), and grasslands/pasture (*I. cylindrica*).

Primary and logged-over forests in the Jambi lowlands are disappearing fast in recent years, they are replaced mainly by plantations (oil palm, rubber, timber) and to a lesser extent by smallholder agroforests (rubber, fruit trees). By the end of the 1990s much of the lowland primary and logged-over forests as shown on Laumonier's 1986 vegetation map (Laumonier, 1997) had already been converted to other land uses (survey by H. Beukema, 1997). Unfortunately an up to date land use map showing these current rapid changes is not available. For generalised maps of land use changes in the Jambi lowlands in the 1980s, see Beukema et al. (1997).

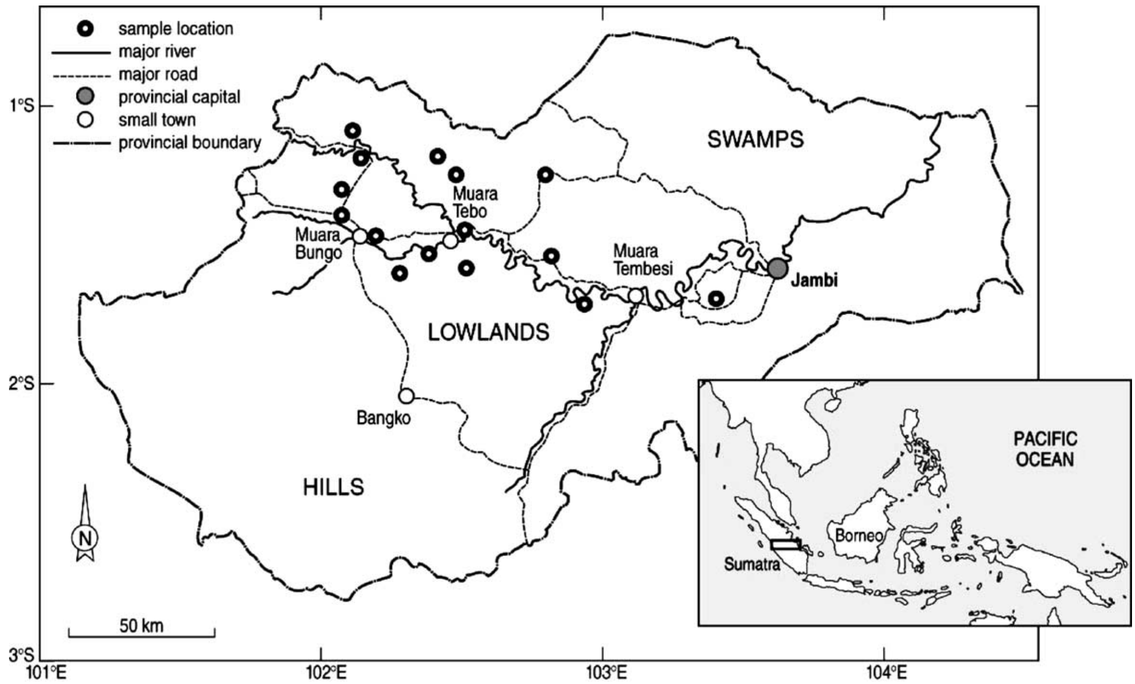

Fig. 1. Sampling locations in the lowland area of Jambi Province, Sumatra.

3. Rubber production systems

In Jambi Province rubber is produced mainly in rubber agroforests and to a lesser extent in more intensively managed monocultural plantations. Both production systems use slash-and-burn to clear land before planting.

In the monocultural plantations rubber (latex) is the only product. The undergrowth below the rubber trees is kept low by using herbicides and by manual weeding, while fertilisers are applied around the rubber trees to stimulate their growth. Tapping starts when the rubber trees are 5–6 years old. Trees remain productive until they are 20–25 years old and a new planting cycle starts.

In the jungle rubber production system there are a number of secondary products next to rubber (latex) that is the main product. Rubber is planted together with rice, vegetables, herbs, and a limited number of useful trees such as fruit trees. Weeds are controlled manually and only during the first 2 or 3 years when rice and vegetables are produced. After that the secondary vegetation that comes in naturally and includes useful species is allowed to grow with the rubber. A dense secondary forest vegetation builds up. Around 9 years after planting, a path between the rubber trees is made and tapping starts. Through natural regeneration of rubber seedlings and active replanting in gaps by the farmer (Wibawa et al., in review), those rubber agroforests can remain productive much longer than rubber plantations. A secondary forest dominated by rubber is the result. In an average 'jungle rubber' agroforest only about 40% of trees with a diameter at breast height (DBH) of over 10 cm are rubber trees. The other trees are mostly natural regrowth while some trees are planted by the farmer.

4. Method

4.1. Plot sampling

Three land use types with associated anthropogenic disturbance levels were sampled: undisturbed rain forest (11 plots), low disturbance jungle rubber (23 plots) and high disturbance rubber plantations (17 plots). The 'undisturbed' rain forest was old growth forest without visible traces of timber cutting and without known history of logging or shifting cultivation, the only human use being limited collection of non-timber forest products and hunting.

Plots were located across the Jambi peneplain, a slightly undulating to flat area of around 200 km × 150 km with rather uniform soils in the centre of Sumatra. The total area of each land use type in the Jambi peneplain is unknown, but the area under jungle rubber is much larger than the area under either rubber plantation or undisturbed forest. In each land use type, the total area sampled is very small compared to the total area of the land use type, so the differences in sampling intensity are probably less important.

Standard plots of 40 m × 40 m (0.16 ha per plot) were subdivided into 16 subplots of 10 m × 10 m each. Counting presence of terrestrial pteridophyte species in the 16 subplots of each plot resulted in a frequency score between 0 and 16 for each species in each plot. For this paper, only presence of species in plots was analysed. Edge effects were avoided by locating the plots away from forest edges and roadsides. Small paths used by rubber tappers however were considered characteristic of jungle rubber systems and therefore not avoided. Plots were located well away from rivers and streams to avoid rheophytes that indicate moisture rather than any level of anthropogenic disturbance.

Only productive rubber systems were sampled. Age of jungle rubber plots varied from 9 to 74 years, while the age of rubber plantation plots was 5–19 years old.

4.2. Pteridophyte grouping

Pteridophyte species were grouped based on ecological notes in literature on Malaysian species (Alston, 1937; Backer and Posthumus, 1939; Fletcher and Kirkwood, 1979; Holttum, 1932, 1938, 1959a,b, 1963, 1966, 1974, 1981, 1991; Holttum and Hennipman, 1978; Kramer, 1971; Page, 1976; Pemberton and Ferriter, 1998; Piggot and Piggot, 1988; Spicer et al., 1985; Wong, 1982). From the literature, it became clear that there is enough habitat differentiation among species to make pteridophytes potentially a suitable indicator group for this study. We would have liked to classify our species by their optima for both light and microclimate conditions, but the available species descriptions (mostly from taxonomical literature) included consistent information on light requirements and preferred habitat only. Nevertheless that information was sufficient to classify the species into ecological groups for the purpose of this study. Based on the literature four levels for light conditions were distinguished: ‘open’ conditions, ‘open/light shade’, ‘light shade’ and ‘shade/deep shade’. In combination with data on preferred habitat the species were assigned to one of two groups arbitrarily named ‘forest species’ and ‘non-forest species’.

‘Forest species’ are all species that require shade or deep shade plus the species that require light shade and grow in forest. ‘Non-forest species’ are all species of open and open/light shade conditions plus the species that require light shade and prefer habitats other than forest (roadsides, forest edges, plantations, etc.). This grouping does not imply that ‘non-forest species’ never grow in the forest. Some of them do occur in forest, especially in gaps, but they are more abundant in open conditions. Species are thus grouped by (inferred) ecological optimum rather than by ecological range.

Of a total of 65 terrestrial pteridophyte species found in the survey, 36 were classified as ‘forest species’ and 26 as ‘non-forest species’ (see Table 1).

Three species remained unclassified because they were not identified to the species level and could not be linked to literature (see Table 1). They were excluded from analyses concerning ‘forest species’. Although species–area curves are of course sensitive to the removal of species from the data, we expect the effects to be limited in this case. Of the three species that were excluded, two unclassified *Cyathea* species (labelled *Cyathea* sp.2 and *Cyathea* sp.3) were most likely not ‘forest species’ in our classification and would not have been included in the analysis anyway. They were not encountered in forest at all. *Cyathea* sp.2 occurred more often in rubber plantations than in jungle rubber: it was found in four rubber plantation plots and in one jungle rubber plot (24 and 4% of those plots, respectively) while *Cyathea* sp.3 occurred in one rubber plantation plot and in one jungle rubber plot. Both species were found to be growing more abundantly in the rubber plantation plots than in the jungle rubber plots. The third species that was excluded was an unclassified *Asplenium* species occurring as a single individual in a jungle rubber plot.

4.3. Data analysis

For statistical analysis the program SPSS Version 10.0 was used.

At the plot level, differences between land use types for average number of (forest) species per plot were tested using one-way ANOVA and Tukey’s HSD test.

At the landscape level, to analyse species–area relations the program EstimateS (Colwell, 1997) was used to randomise plot sequence 100,000 times for each land use type and derive average cumulative richness values.

A logarithmic equation of the form:

$$y = b \ln x + a \quad (1)$$

was fitted through the resulting points, where y is the cumulative number of species, b the scaling relation of species richness (beta diversity), x the cumulative number of 0.16 ha plots (area), and a a constant estimating the average richness for a single plot (alpha diversity).

The ‘area’ in the species–area curves represents a collection of non-adjacent 0.16 ha plots scattered over a vast landscape.

The distances between plots are comparable for forest and jungle rubber: the average distance between plots was for forest plots 42 km (S.E. = 3.6) and for jungle rubber plots 39 km (S.E. = 1.5). Non-parametric tests show that also the distributions of interplot distances are comparable for forest and jungle rubber. However, the interplot distances of the rubber plantation plots were different both in average (as high as 74 km, S.E. = 5.2) and in distribution. This is due to the fact that there are only two large rubber estates in the Jambi lowlands that have rubber trees of the higher age classes that we needed to include in the sampling, and those two estates are far apart (one near Muara Bungo, the other near Jambi town). As a result, long distances are over represented in the rubber plantation sample. This may have caused a slight overestimation of the slope parameters of the species–area curves for rubber plantations, but such overestimation would not seriously affect our main conclusions.

The slope parameters (b) found for the three land use types were compared statistically by linear regression over their common area range of 11 plots (1.76 ha).

Table 1
Species list of terrestrial pteridophyte species found in Jambi lowlands, for classification criteria see text

Family	Species name	Group
Aspleniaceae	*Asplenium glaucophyllum* v.A.v.R.	Non-forest
Aspleniaceae	*Asplenium longissimum* Bl.	Non-forest
Aspleniaceae	*Asplenium pellucidum* Lam.	Forest
Aspleniaceae	*Asplenium* sp.	Not classified
Blechnaceae	*Blechnum finlaysonianum* Hk. & Grev.	Forest
Blechnaceae	*Blechnum orientale* L.	Non-forest
Blechnaceae	*Stenochlaena palustris* (Burm.) Bedd.	Non-forest
Cyatheaceae	*Cyathea* cf. *contaminans* (Hooker) Copel.	Non-forest
Cyatheaceae	*Cyathea moluccana* R. Br.	Forest
Cyatheaceae	*Cyathea* sp.2	Not classified
Cyatheaceae	*Cyathea* sp.3	Not classified
Dennstaedtiaceae	*Lindsaea* cf. *repens* (Bory) Thw.	Forest
Dennstaedtiaceae	*Lindsaea cultrata* (Willd.) Swartz	Forest
Dennstaedtiaceae	*Lindsaea divergens* Hk. & Grev.	Forest
Dennstaedtiaceae	*Lindsaea doryphora* Kramer	Forest
Dennstaedtiaceae	*Lindsaea ensifolia* Swartz	Non-forest
Dennstaedtiaceae	*Lindsaea parasitica* (Roxb. Ex Griffith) Hieron.	Forest
Dennstaedtiaceae	*Microlepia speluncae* (L.) Moore	Non-forest
Dennstaedtiaceae	*Pteridium caudatum* (L.) Maxon subsp. yarrabense (Domin) Parris	Non-forest
Dryopteridaceae	*Diplazium crenatoserratum* (Bl.) Moore	Forest
Dryopteridaceae	*Diplazium malaccense* C. Presl	Forest
Dryopteridaceae	*Diplazium pallidum* Bl.	Forest
Dryopteridaceae	*Diplazium riparium* Holtt.	Forest
Dryopteridaceae	*Diplazium tomentosum* Bl.	Forest
Dryopteridaceae	*Pleocnemia irregularis* (C. Presl) Holtt.	Forest
Dryopteridaceae	*Tectaria barberi* (Hk.) Copel.	Forest
Dryopteridaceae	*Tectaria fissa* (Kunze) Holtt.	Forest
Dryopteridaceae	*Tectaria singaporeana* (Wall. ex Hk. & Gr.) Copel.	Forest
Dryopteridaceae	*Tectaria vasta* (Bl.) Copel.	Forest
Gleicheniaceae	*Dicranopteris linearis* (Burm. f.) Underw. var. linearis	Non-forest
Gleicheniaceae	*Dicranopteris linearis* (Burm. f.) Underw. var. subpectinata (Christ.) Holtt.	Non-forest
Hymenophyllaceae	*Trichomanes javanicum/singaporeanum*	Forest
Hymenophyllaceae	*Trichomanes obscurum* Bl.	Forest
Lomariopsidaceae	*Teratophyllum* cf. *ludens* (Fée) Holtt.	Forest
Lomariopsidaceae	*Teratophyllum* cf. *rotundifoliatum* (R. Bonap.) Holtt.	Forest
Lycopodiaceae	*Lycopodium cernuum* L.	Non-forest
Nephrolepidaceae	*Nephrolepis biserrata* (Sw.) Schott	Non-forest
Ophioglossaceae	*Helminthostachys zeylanica* L. Hook.	Non-forest
Ophioglossaceae	*Ophioglossum reticulatum* L.	Non-forest
Polypodiaceae	*Microsorum scolopendria* (Burm. f.) Copel.	Non-forest
Pteridaceae	*Adiantum latifolium* Lam.	Non-forest
Pteridaceae	*Pityrogramma calomelanos* (L.) Link	Non-forest
Pteridaceae	*Taenitis blechnoides* (Willd.) Sw.	Forest
Schizaeaceae	*Lygodium circinnatum* (Burm. f.) Sw.	Forest
Schizaeaceae	*Lygodium flexuosum* (L.) Sw.	Non-forest
Schizaeaceae	*Lygodium longifolium* (Willd.) Sw.	Non-forest
Schizaeaceae	*Lygodium microphyllum* (Cav.) R.Br.	Non-forest
Schizaeaceae	*Lygodium salicifolium* Presl	Non-forest
Schizaeaceae	*Schizaea dichotoma* (L.) Sm.	Forest
Schizaeaceae	*Schizaea digitata* (L.) Sw.	Forest
Selaginellaceae	*Selaginella caulescens* (Wall.) Spring	Forest
Selaginellaceae	*Selaginella intermedia* (Bl.) Spring	Forest
Selaginellaceae	*Selaginella plana* (Desv.) Hieron.	Forest

Table 1 (*Continued*)

Family	Species name	Group
Selaginellaceae	*Selaginella roxburghii* (Hk. & Gr.) Spring	Forest
Selaginellaceae	*Selaginella willdenowii* (Desv.) Baker	Non-forest
Thelypteridaceae	*Amphineuron* sp.	Non-forest
Thelypteridaceae	*Christella parasitica* (L.) Lév.	Non-forest
Thelypteridaceae	*Christella subpubescens* (Bl.) Holtt.	Non-forest
Thelypteridaceae	*Mesophlebion chlamydophorum* (C.Chr.) Holtt.	Forest
Thelypteridaceae	*Mesophlebion motleyanum* (Hook.) Holtt.	Forest
Thelypteridaceae	*Pronephrium glandulosum* (Bl.) Holtt.	Forest
Thelypteridaceae	*Pronephrium rubicundum* (v.A.v.R.) Holtt.	Forest
Thelypteridaceae	*Pronephrium* sp.	Forest
Thelypteridaceae	*Pronephrium triphyllum* (Sw.) Holtt.	Non-forest
Thelypteridaceae	*Sphaerostephanos heterocarpus* (Bl.) Holtt.	Forest

Families according to Kubitzki (1990).

5. Results

5.1. Plot level results

The average number of terrestrial pteridophyte species per plot in the current study was indeed higher in jungle rubber (on average 11.7 species) than in primary forest (on average 9.4 species), but not twice as high as found by Michon and De Foresta for herbs, and the difference found is not statistically significant.

Applying a priori ecological knowledge about our species, we find that the plot level species richness in jungle rubber and in rubber plantations is largely due to an increase in species that have their optima in environments other than the shady forest understorey, in our classification 'non-forest species'. Fig. 2 shows the differences in average number of species per plot for the three land use types. Differences are small and not statistically significant when all species are considered ($F[2, 48] = 1.846$, $P = 0.169$), while those differences are large and statistically significant when only 'forest species' are considered ($F[2, 48] = 18.112$, $P < 0.0005$; Table 2).

5.2. Landscape level results, all species

Looking at the landscape level, we see that the species–area curves for pteridophytes in primary forest, jungle rubber and rubber plantations are close together (Fig. 3).

We tested for equality of slopes of the regressions for the three land use types, and found that including interactions (which allows for different slopes) significantly improved the model ($F[2, 27] = 4.005$, $P = 0.030$). The slope parameter of the jungle rubber land use type was significantly higher than the slope parameter of the rubber plantations land use type ($t = 2.827$, $P = 0.009$). The slope parameter of the forest was not significantly different from the slope parameters of the jungle rubber land use type and the rubber plantations land use type ($t = -1.534$, $P = 0.137$

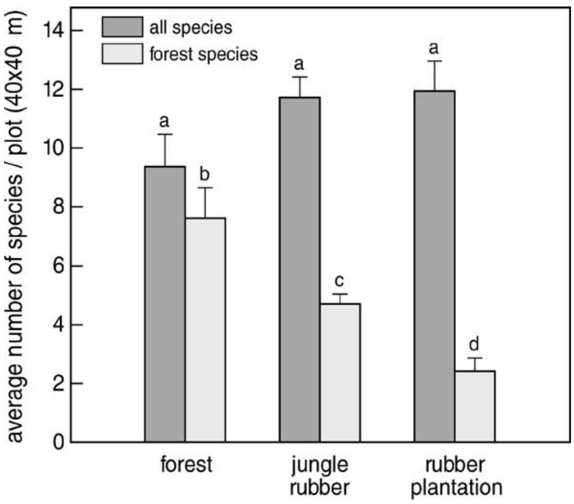

Fig. 2. Number of terrestrial pteridophyte species per 0.16 ha plot. Means and their standard errors for three land use types: forest ($n = 11$), jungle rubber ($n = 23$) and rubber plantations ($n = 17$). Dark bars: all data; light bars: 'forest species' subset. Different letters indicate significant differences between land use types (Tukey's HSD test, $P < 0.05$, see Table 2).

Table 2
Analysis of variance and post-hoc multiple comparisons for data in Fig. 2: number of species per plot (all species, 'forest species')

	N	Mean of all species per plot	S.E. of the mean	Mean of 'forest species' per plot	S.E. of the mean
Forest	11	9.4	1.08	7.6	1.06
Jungle rubber	23	11.7	0.70	4.7	0.36
Rubber plantations	17	11.9	0.99	2.4	0.41
All land use types	51	11.2	0.52		

ANOVA

	Sum of squares	d.f.	Mean square	*F*	Significance
Number of terrestrial pteridophyte species					
Between groups	49.649	2	24.824	1.846	0.169
Within groups	645.528	48	13.448		
Total	695.176	50			
Number of 'forest species'					
Between groups	176.644	2	88.322	18.112	0.000
Within groups	234.062	48	4.876		
Total	410.706	50			

Multiple comparisons (Tukey's HSD). Dependent variable: number of 'forest species'

Land use (*I*)	Land use (*J*)	Mean difference ($I - J$)	S.E.	Significance	95% confidence interval	
					Lower bound	Upper bound
Primary forest	Jungle rubber	2.89*	0.81	0.002	0.94	4.85
	Rubber plantation	5.13*	0.85	0.000	3.07	7.20
Jungle rubber	Primary forest	−2.89*	0.81	0.002	−4.85	−0.94
	Rubber plantation	2.24*	0.71	0.007	0.53	3.95
Rubber plantation	Primary forest	−5.13*	0.85	0.000	−7.20	−3.07
	Jungle rubber	−2.24*	0.71	0.007	−3.95	−0.53

* The mean difference is significant at the 0.05 level.

and $t = 1.292$, $P = 0.207$, respectively). Figs. 2 and 3 and the statistical testing make clear that the pattern at the plot scale is not reflected at the landscape scale. Jungle rubber shows higher beta diversity for terrestrial pteridophytes at the landscape scale than rubber plantations, despite similar plot level diversity.

5.3. Landscape level results, 'forest species'

After grouping species into 'forest species' and 'non-forest species' a second set of species–area curves was constructed based only on 'forest species'. These curves for 'forest species' (Fig. 4) show the part of the total diversity in each land use type (as in Fig. 3) that consists of species that prefer conditions prevalent in undisturbed forest.

Slopes of the regression lines for 'forest species' (Table 3) differ significantly ($F[2, 27] = 352.161$, $P < 0.0005$). The regression line for forest has a steeper slope than the regression lines for jungle rubber and rubber plantations ($t = 17.544$, $P < 0.0005$ and $t = 26.017$, $P < 0.0005$, respectively), and the regression line for jungle rubber has a steeper slope than the regression line for rubber plantations ($t = 8.473$, $P < 0.0005$). The differences between the curves for primary forest (upper line), jungle rubber (middle line) and rubber plantations (lower line) show that the understorey environment of jungle rubber is much more forest-like than that of rubber plantations, but less than primary forest.

The number of jungle rubber plots added up to find the same number of 'forest species' in jungle rubber as in primary forest is progressively larger at the higher

Table 3
Slopes and their standard errors for the species–area regressions (all species, 'forest species') in Figs. 3 and 4

	N	Slope parameter all species	S.E. of the slope	Slope parameter 'forest species'	S.E. of the slope
Forest	11	9.71	0.16	8.34	0.14
Jungle rubber	11	10.11	0.21	5.07	0.11
Rubber plantations	11	9.37	0.18	3.49	0.14

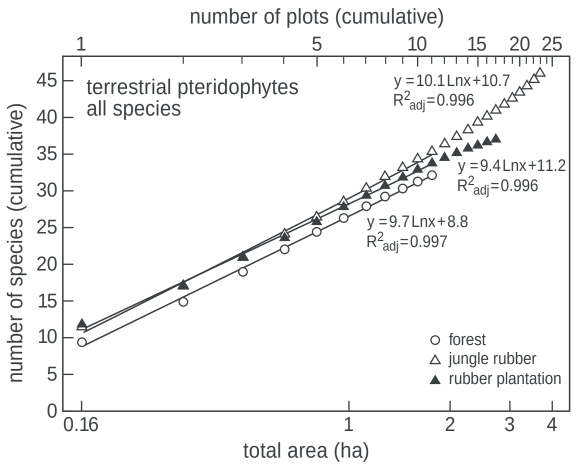

Fig. 3. Species–area curves for terrestrial pteridophytes in forest, jungle rubber and rubber plantations. Plots were 0.16 ha each, non-adjacent and spread over a large area (see Fig. 1). Plots were randomised 100,000 times to remove the effect of plot order.

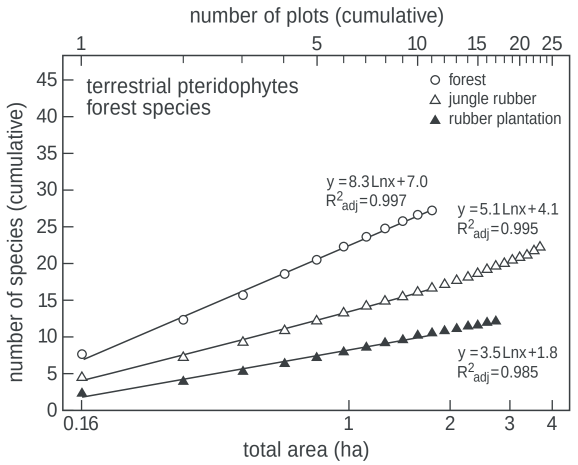

Fig. 4. Species–area curves for 'forest species' subset of terrestrial pteridophytes in forest, jungle rubber and rubber plantations. Plots were 0.16 ha each, non-adjacent and spread over a large area (see Fig. 1). Plots were randomised 100,000 times to remove the effect of plot order.

levels of species richness associated with larger areas. When S represents the number of 'forest species', we find at $S = 15$ we need 3.0 jungle rubber plots for each primary forest plot, at $S = 20$ we need 4.0 and at $S = 25$ we would need 5.3 jungle rubber plots for each primary forest plot.

In addition to the differences in diversity of 'forest species', our data show that some of the 'forest species' that are found in several primary forest plots never show up in jungle rubber plots, even though the sample contains twice as many jungle rubber plots as primary forest plots. It is likely that the absence of those species, e.g. *Teratophyllum* spp. (Lomariopsidaceae) and *Trichomanes* spp. (Hymenophyllaceae), from the jungle rubber plots indicates that some primary forest species will never grow in jungle rubber.

6. Discussion and conclusions

6.1. Scale matters

The data clearly show that scaling relations differ between land use types and that plot level species richness does not directly indicate the (relative) richness of a land use type at the landscape scale. No single ratio can express the relative richness across different scales and conclusions as formulated by Leakey (1999) on the basis of the plot data of Michon and De Foresta (1995) cannot be trusted.

6.2. Conservation and production

Returning to the first question formulated in the introduction, we conclude that rubber production systems can indeed play some role in conservation of primary forest species (apparently providing forest-like habitat), but in places where primary forest is still present, priority should be given to conservation of remaining primary forest patches.

In places where primary forest is gone, jungle rubber can play a role in conservation of part of the primary forest species, while rubber plantations have little conservation value. In areas such as the Jambi lowlands where there is almost no primary forest left and where even logged-over forest is to a large extent already converted to plantations, jungle rubber might provide for intermediate levels of biodiversity while at the same time providing income to farmers (Van Noordwijk et al., 1997). ICRAF is currently working in this area on a project to increase income of smallholders and promote biodiversity conservation by keeping production in old jungle rubber on a profitable level. Techniques of gap replanting and direct grafting in rubber agroforests using genetically improved rubber are developed to extend the lifespan of existing rubber agroforests, at the same time reducing the frequency of slash-and-burn in the landscape (Wibawa et al., in review). With these techniques production could be raised while preserving the biodiversity associated with old jungle rubber.

6.3. Indicator groups

Species richness of terrestrial pteridophytes alone (without knowing the species or their ecological requirements) is not a useful indicator of habitat quality, as it discriminates poorly between the disturbed land use types and primary forest. A priori ecological information on the species involved is needed before terrestrial pteridophyte species can be used to indicate disturbance level or habitat quality of the forest understorey. If we would like to fully answer the question how much primary forest biodiversity is conserved in rubber agroforests we would have to sample most of the major taxonomic groups because different groups react in different ways to disturbance (see e.g. Thiollay, 1995 for birds). For each taxonomic group we would need enough samples to account for the variability in the data, and samples should cover a sufficiently large area to include different scales (plot level to landscape level). In addition, we need to know the ecological position (habitat requirements, guilds, etc.) of the species, as diversity alone does not give enough information for most taxonomic groups. Even so, such data collected within 'homogeneous' land use types cannot directly answer questions about the change in overall biodiversity value that can be expected if some types of land use will decrease, while others increase. The scaling rules within a land use type as given here will have to be (at least) complemented by assessments of species overlap between land use types. In addition assumptions have to be made about the maximum number of species present in each land use type as well as the minimum area required in each land use type to maintain healthy populations of those species.

It is understandable that available data are not compliant with all those requirements. Restricted by time and financial limits, researchers working in jungle rubber had to make choices with regard to the sampling dilemma, either researching all major groups but in small sample sizes and/or a small area, or getting ample information on one taxon and none on others. Difficult taxonomic groups in diverse tropical areas make the problem worse, as typically each sampling effort results in scores of new species to be named and described for the first time and existing ecological knowledge is limited. Pteridophytes proved in this study to be a relatively well-described group suitable to indicate local environmental conditions. Because the spores are wind dispersed their occurrence is not limited by presence of other organisms required for most seed dispersal or pollination. However, this characteristic of pteridophytes makes the group less suitable to represent biodiversity of other taxa. Hunting pressure and habitat fragmentation will affect some taxa more than others. Pteridophytes alone would probably provide us with a too optimistic view on biodiversity in jungle rubber.

As more results on different taxa become available it is no doubt possible to get a general idea of the order of magnitude of the contribution of jungle rubber to biodiversity conservation of tropical rain forest species. However, if the current trend of conversion to more intensively managed rubber or oil palm plantations continues we can be sure that hardly any biodiversity value will be left.

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