



Area, shape and isolation of tropical forest fragments: effects on tree species diversity and implications for conservation

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Abstract

Aim To quantify the influences of forest *area*, *shape* and *isolation* on tree species diversity in Ghana and to compare their significance with the influences of climate (average annual rainfall) and disturbance (fire burn, logging, agriculture).

Location The forest zone of southern Ghana, West Africa (between 5 and 8° N).

Methods For twenty-two forest fragments (1) bivariate regression analyses of tree species diversity (number and composition) were employed with forest spatial geometry, climate and disturbance variables. (2) Multivariate regression analyses of tree species number and all seven environmental variables were used to determine the variability in tree species number that could be accounted for by these environmental variables.

Results Forest area, shape and isolation accounted for sharply decreasing proportions of variability in tree species diversity. Large forest fragments contained the greatest numbers of tree species and the highest proportions of rare tree species; irregular fragments had high proportions of regenerating, light-demanding pioneers and mature, animal-dispersed species and isolated fragments were floristically similar to less isolated fragments. Fire burn and average annual rainfall accounted for small, but nevertheless significant, proportions of variability in tree species diversity. Logging and agriculture were non-significant variables.

Main conclusions (1) Forest area is the most important consideration when planning tropical forest reserves. (2) Management of disturbance should take priority over management of forest shape if higher levels of tree diversity and species quality are to be maintained. (3) If new reserves are to be designated, they should be located within different climatic zones in order to capture a large fraction of the regional biota. (4) Biogeographers have an important role to play in formulating and testing hypotheses at a broad spatial scale and ultimately, informing conservation management within the tropical biome.

Keywords

Tropical forest, fragmentation, biodiversity, conservation, regression analysis, Ghana.

INTRODUCTION

Fragmentation of tropical forest has been described as the single greatest threat to global biological diversity (Turner,

1996; Laurance, 1999). Research suggests that fragmentation decreases species number and alters community composition as a result of a reduction in forest area, a change in forest shape and an increase in isolation of the remaining forest fragments. The relationship between forest area and species diversity in the tropics is well documented (e.g. Bierregaard *et al.*, 1992; Hill *et al.*, 1994; Laurance & Bierregaard, 1997; Pimm, 1998) and this aspect of fragmentation research continues to dominate (May & Stumpf, 2000; Pimm & Raven,

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Table 1 Tree species diversity, forest spatial geometry and environmental variables examined for twenty-two forest fragments in Ghana

Independent variables	Dependent variables
<ul style="list-style-type: none"> • Forest spatial geometry <ul style="list-style-type: none"> Fragment area Fragment shape Fragment isolation • Forest climate <ul style="list-style-type: none"> Average annual rainfall • Forest disturbance <ul style="list-style-type: none"> Fire burn Logging Agriculture 	<ul style="list-style-type: none"> • Tree species number • Tree species composition <ul style="list-style-type: none"> Rarity Regeneration guild Seed dispersal Phenology

2000; Hill & Curran, 2001). By contrast, fewer empirical studies have examined the ecological effects of forest shape or isolation within this biome, especially for fragments that have been isolated for decades or longer (Forman, 1995; Turner, 1996; Zuidema *et al.*, 1996).

The effect of forest spatial geometry on communities is important as it controls fundamental ecological processes such as speciation, dispersal, migration, competition and extinction and thereby affects both the number and composition of species in a landscape (Turner, 1996; Zuidema *et al.*, 1996; Laurance *et al.*, 2002). As a result of these processes, the fragmented ecosystem usually fails to support species assemblages found in intact ecosystems.

As fragmentation continues in many parts of the tropics, conservation efforts must focus on understanding the effects of forest spatial geometry on species diversity as only then can biodiversity be influenced significantly by managing forest area, shape and isolation. This paper aims to provide a foundation for such understanding by examining diversity–geometry relationships for twenty-two forest fragments in Ghana, West Africa. It is the first published study to quantify the influence of forest spatial geometry on tree species diversity at the landscape level and to compare the significance of geometric variables relative to those of climate and disturbance (Table 1).

METHODS

Study site

Tropical forest in Ghana comprises fragments of differing area and shape, protected largely as extractive reserves and separated mostly by a 'matrix' of agricultural land (Hall & Swaine, 1981). The ecotone between the forest fragments and the surrounding vegetation is generally sharp, with forests harbouring plant species that are mostly distinct from the matrix. The reserves were demarcated by the Ghana Forestry Department in the 1920s and 1930s (Varley & White, 1958) and the distribution of the twenty-two forest fragments used in this study is shown in Fig. 1. The

spatial geometry of the fragments has remained relatively stable for over 100 years, allowing time for the ecosystem to respond.

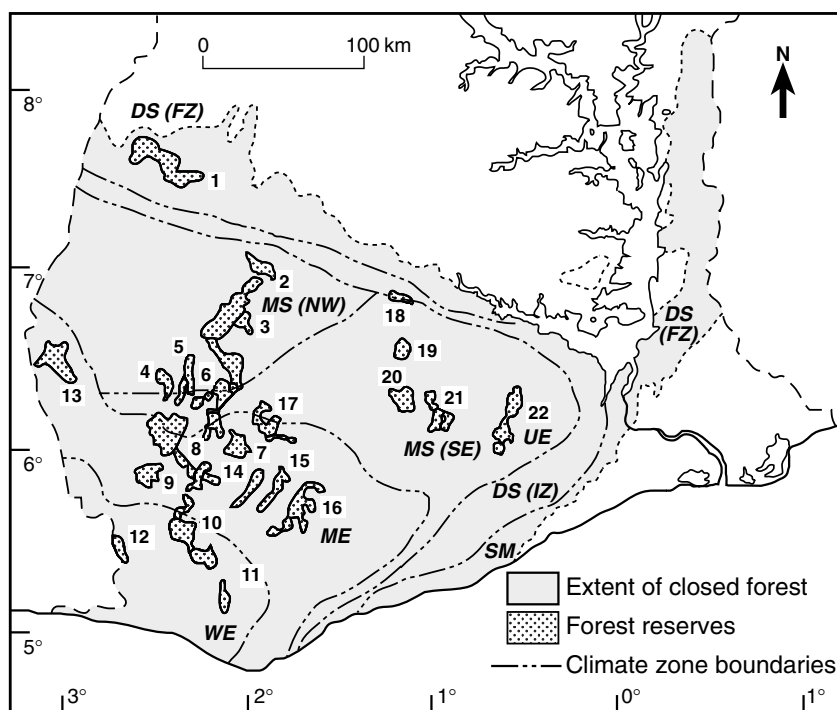
A strong rainfall gradient exists across the forest zone, with the average annual total decreasing from *c.* 2100 mm in the south-west to *c.* 1000 mm in the north-east. This transition modifies forest cover from a closed canopy of predominantly evergreen trees in wetter areas to a more open canopy with higher proportions of deciduous trees in drier areas (Martin, 1991). The upper canopy is usually formed by a fluctuating mixture of species, none of which dominates. Many emergents are timber trees such as *Ceiba*, *Entandrophragma*, *Khaya* and *Triplochiton* (Taylor, 1960). The forest generally overlies low, undulating country but intermittent scarps up to 700 m in height give rise to localized upland associations (Hall & Swaine, 1981).

Disturbance history is a cause of local species variation within the forests. Fire activity has spread from the dry semi-deciduous fire zone (DSFZ) south to both subtypes of moist semi-deciduous (MS) forest (Fig. 1), where it is the cause of most degradation today (Hawthorne, 1994). Its effect does not penetrate into the wet evergreen (WE) and upland evergreen (UE) zones. There is a history of logging in the semi-deciduous zones, but it occurs selectively according to a minimum girth system so that removals amount to only 0.4% of the total biomass per annum (four to five trees per hectare) (Hawthorne, 1993a). The forests were cultivated historically using the taungya plantation system, where crops were grown between rows of trees during the early ages of plantation. This has resulted in scattered blocks of timber trees within more diverse forest (FAO/UNEP, 1981).

Measurement of tree species

The Overseas Development Administration and the Ghana Forestry Department surveyed a random sample of forest reserves in Ghana as part of a Forest Inventory and Management Project (FIMP) initiated in 1986. The total area surveyed was directly proportional to the reserve area within each forest zone (Wong, 1989). Reserve boundaries and fragment names (visible in Fig. 1) show that most of the twenty-two forest fragments used within this study were derived from single isolated reserves, but some were derived from reserve amalgams. This provided a total sample size of forty-one reserves.

Sample plots of 1 ha were laid systematically across the forest reserves on a 2 × 2 km grid. Each grid was aligned with magnetic north and superimposed randomly on 1 : 50,000 scale reserve maps. Plots were located within grids by compass and chain survey from the boundary pillars of reserves. Sample plots were rectangular in shape, measuring 20 × 500 m. Each plot was subdivided into 5 × 0.2 ha subplots, one of which was further subdivided into 2 × 0.05 ha subplots. Trees counted within the sample plots were classified into two categories: ≥30 cm d.b.h. (mature) and <30 cm d.b.h. (regenerating). Diameter at breast height was measured 1.3 m above ground level or 30 cm above buttresses (Wong, 1989). Mature trees were



Forest fragments and their complex perimeter/area ratios

1 Tain Tributaries II (2.02)	12 Jema Asemkrom (1.54)
2 Tinte Bepo (1.74)	13 Bia Tributaries South (1.43)
3 Tano Ofin Group (3.24)	14 Bowiye Range (1.77)
4 Tano Suhien (1.35)	15 Opon Mansi (1.95)
5 Tano Suraw and Extension (1.83)	16 Ben Group (2.89)
6 Afao Hills (1.85)	17 Oda River Group (2.44)
7 Tonton (1.22)	18 Anum Su North (1.65)
8 Suhuma Group (2.34)	19 Dome River (1.10)
9 Tano Anwia (1.30)	20 Pra Anum (1.18)
10 Fure Group (2.20)	21 Mamang River Group (2.31)
11 Ndumfri (1.47)	22 Atewa Range and Extension (2.04)

Figure 1 Geographical distribution of the twenty-two forest fragments across the climate zones of southern Ghana. WE, wet evergreen; ME, moist evergreen; UE, upland evergreen; MS, moist semi-deciduous (NW, north-west subtype; SE, south-east subtype); DS, dry semi-deciduous (FZ, fire zone subtype; IZ, inner zone subtype); SM, southern marginal.

identified and measured over the whole 1 ha sample plot, whereas regenerating trees were enumerated only within the 2×0.05 ha subplots. The sampling intensity across each forest reserve was consequently 0.25% for mature trees and 0.025% for regenerating trees. The total tree flora used in this paper amounts to 384 of the roughly 700 Ghanaian tree species, recorded within 1174 sample plots.

Tree species *number* within each forest fragment was determined using computer programs written specifically to process FIMP data (Hill, 1995). Tree species *composition* was analysed using four schemes of categorization: regeneration guild, rarity, phenology and dispersal. Guild types were based on the abundance of seedlings in extremes of the forest mosaic (gap and mature phases) (Watt, 1947; Whitmore, 1978; Hawthorne, 1993b). Species were divided, according to their germination requirements for sunlight, into pioneers, non-pioneer light

demanders (NPLDs) and shade-tolerators. Pioneers regenerate only under canopy gaps and hence thrive in secondary forest. NPLDs can survive in, or even require shade, as germinating seedlings, but they require canopy gaps to survive beyond the early parts of their life cycle. Shade-tolerant species are found as healthy saplings only in forest shade. Rarity was based on frequency of occurrence of species. Based on a colour code, rarity in Africa or Ghana merited gold or blue star ratings, whilst green star species were common both internationally and locally (Table 2). Information concerning phenology and dispersal was derived from ecological literature (Hutchinson & Dalziel, 1954–1972; Taylor, 1960; Irvine, 1961; Hall & Swaine, 1981; Hawthorne, 1990). Phenology was restricted to leaf shedding (evergreen or deciduous), whilst dispersal categorized the different means by which seeds were carried from the parent (animals or

Category	Descriptor	Average number of degree squares in Africa
Gold	Fairly rare internationally and/or locally	7.8 ± 3.8
Blue	Widespread internationally but rare locally or vice versa	24.5 ± 12.6
Green	Common internationally and locally	69.2 ± 49.8

Source: Hawthorne (1993b).

Table 3 Examples of tree species by biological category

Category	Tree species
Rarity	
Gold	<i>Anisophyllea meniaudii</i> , <i>Dactyladenia dinklagei</i>
Blue	<i>Balanites wilsoniana</i> , <i>Cylicodiscus gabunensis</i>
Green	<i>Celtis</i> spp., <i>Strombosia glaucescens</i>
Guild	
Pioneers	<i>Musanga cecropioides</i> , <i>Trema orientalis</i>
NPLDs	<i>Khaya</i> spp., <i>Entandrophragma</i> spp.
Shade tolerators	<i>Guarea</i> spp., <i>Celtis mildbraedii</i>
Dispersal	
Animal	<i>Celtis mildbraedi</i> , <i>Guarea cedrata</i>
Wind	<i>Ceiba pentandra</i> , <i>Vernonia</i> spp.
Phenology	
Evergreen	<i>Nauclea diderrichi</i> , <i>Celtis</i> spp.
Deciduous	<i>Entandrophragma</i> spp., <i>Triplochiton scleroxylon</i>

NPLDs, non-pioneer light demanders.

wind). Examples of tree species by biological category are given in Table 3.

Measurement of forest spatial geometry

Area data for the forest fragments were derived from Hall & Swaine (1981), but they originate in Ghana Forestry Department statistics. The areas of fragments used in this research ranged between 34.7 and 877.5 km².

Fragment *shape* was quantified using the complex perimeter/area ratio (Patton, 1975). This measure is particularly sensitive to detailed irregularities in the perimeter and, unlike the simple perimeter/area ratio, it is not intrinsically dependent on fragment area (Hill, 1994). The complex ratio compares the total external perimeter of a landscape fragment to the circumference of a circle having the same area and is therefore a measure of shape irregularity. As fragment shape becomes more irregular, the index increases without limit above a value of 1. The complex perimeter/area ratios for the reserves examined in this study are shown in Fig. 1. A weakness of the ratio over the sampled forests, however, was its extrinsic relationship with area, whereby larger fragments were more irregular than smaller ones ($r = 0.64$, $P = 0.001$). The influence of area was consequently controlled for within regression analyses.

Table 2 Definition of rarity categories applied to the tree species of Ghana

The measurements entered into the complex perimeter/area ratio were derived from a 1 : 500,000 scale map of forest fragments (Gold Coast Survey Department, 1949a) digitized within an Arc/Info geographical information system (GIS). Area measurements obtained from the small-scale map did not differ significantly from those measured by ground-based survey (Hall & Swaine, 1981) (Student's *t*-test, $P = 0.001$).

Isolation of forest fragments was examined in terms of their proximity to surrounding forests. A single multi-directional proximity figure was calculated for each fragment within IDRISI GIS. The figure was derived from the average nearest neighbour distance as calculated across four quadrants delimited by the cardinal compass directions. The data ranged from 3 to 18 km and the error was defined by the GIS raster resolution as 500 m.

Measurement of climate and disturbance variables

Average annual rainfall totals were derived from a 1 : 500,000 scale rainfall map (Gold Coast Survey Department, 1949b). Forest fragments were located between isohyets and thus data were categorical. The figures were derived from temporal averages from local meteorological stations and were therefore considered to have minimal levels of measurement error. The measurements ranged from 1200 to 1850 mm. Figures for burn, logging and taungya were taken from percentage visual estimates of their extent within FIMP sample plots (J.L.G. Wong, pers. comm.). Average levels of disturbance across the sampled fragments were 15%, 4% and 10%, respectively, for these variables.

Hypothesis testing for bivariate regressions

Tree species diversity and forest area

It was expected that tree species number would increase with forest area. The positive relationship between species number and area is a fundamental and long accepted aspect of community ecology (Watson, 1859; Arrhenius, 1921; Gleason, 1922; Connor & McCoy, 1979; Dunn & Loehle, 1988; Lomolino, 2001). The relationship has been attributed to ecological processes, explained by island biogeography theory, habitat diversity and successional development and to sampling effects, whereby larger fragments contain more random samples that record more of the community (Hill *et al.*, 1994; Lomolino, 2001). It was also expected that as the area of forest fragments increased, the relative

proportions (percentages of sampled tree species numbers) of rare, shade-tolerant and evergreen species would increase with respect to common, deciduous and pioneer species (Laurance, 1991; Tabarelli *et al.*, 1999). This is because as the area of forest fragments increases, the areas of edge and interior forest increase at differing rates. Thus, the amount of interior compared with edge forest increases with fragment area (Saunders *et al.*, 1991; Collinge, 1996; Turner, 1996). The model chosen to describe these species–area relationships was least-squares linear regression. Nonlinear models were also used and both the pattern of residuals about the regression line and the correlation coefficients were similar to those of the linear model. Calculations were undertaken using Minitab statistical package.

Tree species diversity and forest shape

Tree species were classified into ten biological categories which, when partitioned into regenerating and mature trees, generated twenty shape-related hypotheses (Fig. 2). The primary influence of forest shape on species diversity derives from the ratio of edge to interior environment (Laurance, 1991, 2000; Ranta *et al.*, 1998). Fragmentation increases the proportion of edge zone in the landscape, altering microclimate and the competitive advantage afforded to any species (Kapos *et al.*, 1997; Didham & Lawton, 1999). Typically, forest edges have a large number of pioneer species (Laurance, 1991; Laurance *et al.*, 1998a), whilst forest interiors have a large number of shade-tolerant species (Benitez-Malvido, 1998; Kellman *et al.*, 1998). It was expected, therefore, that the proportion of pioneer and NPLD tree species would increase and the proportion of shade-tolerators would decrease with increasing fragmentation and for-

est irregularity because of the rising ratio of edge to interior environment.

It was expected that the proportion of rare tree species would decrease with increasing forest irregularity because rare species tend to be shade-tolerators which thrive in less-disturbed interiors (Benitez-Malvido, 1998; Brokaw, 1998). Research examining the effect of forest shape on common species is scarce in the literature. This is perhaps because their representation in both light-demanding and shade-tolerant guilds means that their proportions are not dictated by the balance between interior and edge environments. It was hypothesized, therefore, that this category would be unrelated to shape.

Increases in temperature and decreases in relative humidity along forest edges (Kapos *et al.*, 1997) were expected to raise the number of deciduous tree species at the expense of evergreen ones resulting in ‘induced seasonality’ around forest peripheries (Bierregaard *et al.*, 1992).

Two opposing mechanisms allow either a rise or a fall in the expected proportion of animal-dispersed species with increasing irregularity of forest shape. The first mechanism is interception; the movement of birds and mammals across a forest boundary (Game, 1980; Forman, 1995). Interception was expected to increase with fragment irregularity because a longer boundary presents a larger target to mobile animals from most directions and an increase in interception means a larger proportion of animal-dispersed species. The second mechanism, circulation within a forest, acts against interception. A more regular shape can provide sufficient undisturbed interior forest to allow animals to traverse around the area and minimize dispersal distances (Blouin & Connor, 1985; Forman, 1995). An irregular forest, with its high ratio of perimeter to area, will not provide such compact, undisturbed forest and so circulation was expected to decrease with increasing fragment irregularity.

A direct positive relationship with forest shape was hypothesized for tree species with plumed seeds borne by wind. Plumed dispersal enables seeds covered with fine hairs to travel to *c.* 5 km (Augsperger & Franson, 1987; Greene & Johnson, 1989) and forest fragments can intercept seeds over such distances according to the target-area hypothesis (Game, 1980). Consequently, an increase in plumed tree species was expected with increasing forest irregularity.

Relationships between tree species diversity and forest shape were also tested using least-squares linear regression calculated within Minitab. To reduce the influence of area on the dependent variable, the proportion (measured as percent of sampled tree species numbers), rather than the number of species within the biological categories, were used in the analyses.

Tree species diversity and forest isolation

Immigration into a fragment must equal extinction if species diversity is to be maintained (Forman, 1995). Isolation plays a major role in dictating the rate of dispersal towards and immigration into a fragment (MacArthur & Wilson, 1967). Immigrants make demographic and genetic contributions to populations existing in fragments, which increases the size

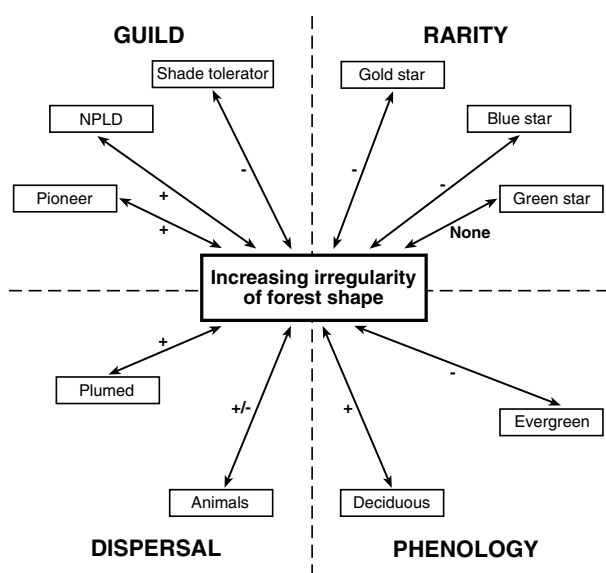


Figure 2 Hypotheses concerning tree species composition and forest shape to be tested by regression analysis. +/-/none refer to a positive, negative or no expected relationship.

and fitness of their populations (Brown & Kodric-Brown, 1977). Tree species numbers in Ghana were consequently expected to be higher in fragments that were in close proximity to others.

Dispersal mechanisms adopted by trees vary in their effectiveness with distance. As such, isolation of forest fragments can be viewed as a filter mechanism dictating the type of dispersal that can occur successfully. Distance constraints tend to be strong for ground-dwelling animals that have to leave forest cover to pass from one fragment to another (Hamrick *et al.*, 1993; Willson, 1993). In contrast, seeds dispersed by birds or carried by wind tend to display weaker effects of distance (Murray, 1988; Hamrick *et al.*, 1993). It was consequently expected that higher proportions of animal-dispersed tree species would be found in proximate forest fragments and this proportion would fall with increasing inter-fragment distance. Conversely, it was expected that the proportions of bird- and wind-dispersed tree species would rise with increasing inter-fragment distance.

Relationships between tree species numbers and forest isolation were again tested using least-squares linear regression calculated within Minitab. To examine individual dispersal mechanisms, the proportion of species within the categories were employed in the regression analyses.

Tree species diversity and climate/disturbance variables

The numbers of tree species recorded in the forest fragments were expected to decline with increasing fire, logging and taungya activity. This is due to direct species loss and altered ecosystem functioning (IUCN, 1988; Hawthorne, 1993a, 1994). Conversely, tree species numbers were expected to increase in forest fragments with high average annual rainfall totals as this reduces the stress of dry seasons (Hall & Swaine, 1981; Terborgh, 1992).

Hypothesis testing for multivariate regressions

Multiple and stepwise multiple regressions were undertaken to ascertain the combined association between tree species number and all environmental variables (spatial geometry, climate, disturbance) and to investigate the relative significance of the variables in accounting for tree species number. Calculations were undertaken using both Minitab and SPSSx statistical packages. It was expected that a significant amount of the variation in tree species number would be accounted for by the environmental variables and that aspects of spatial geometry would feature significantly amongst these.

RESULTS

Bivariate regression analyses

Regression analyses of tree species number and composition on forest fragments of differing area, shape and isolation identified the additional factors of climate and disturbance. Their influence was expressed in regression plots as forest

outliers (variance > 2), so fragments occurring consistently as outliers were investigated and if secondary sources (Hawthorne & Juam Musah, 1993; J.L.G. Wong, pers. comm.) confirmed the influence of climate or disturbance they were removed from the analyses. The number of forests entered into analyses is indicated in the text. To render species–area curves linear, double or semi-logarithmic transformations were undertaken as indicated.

Tree species diversity and forest area

The logarithm of tree species number was related positively to the logarithm of forest area for regenerating trees ($r = 0.96$, $P = 0.005$, $n = 20$). Thus, forest area accounted for 92% of the variation in tree species number. This significant relationship was repeated for mature trees ($r = 0.87$, $P = 0.005$, $n = 20$). The slope values of the regression lines were slightly higher for regenerating trees (0.31) compared with mature trees (0.25). Thus, the rate of increase of tree species with forest area was higher for the regenerating group.

In terms of species composition, the relative proportions of rare (gold and blue star) tree species increased significantly with the logarithm of forest area for the regenerating group ($r = 0.69$, $P = 0.005$ and $r = 0.46$, $P = 0.025$; $n = 21$). This was not the case, however, with the common (green star) species, which provided between 60% and 72% of the total species complement for forests of all areas.

There was a significant increase in the proportion of evergreen tree species with an increase in the logarithm of forest area for mature trees ($r = 0.68$, $P = 0.005$, $n = 19$). The result was reversed for deciduous trees, as they had a significant decrease in their proportion with an increase in the logarithm of forest area ($r = -0.72$, $P = 0.005$, $n = 19$). There was no significant relationship for regenerating trees.

The proportion of NPLD tree species, a group requiring sunlight to grow, decreased significantly with forest area for the mature category ($r = -0.63$, $P = 0.005$, $n = 20$). This contrasted with the closely related pioneer category, which was unrelated to forest area. The proportion of mature shade-tolerators increased significantly with forest area ($r = 0.49$, $P = 0.025$, $n = 20$).

Tree species diversity and forest shape

The proportion of regenerating pioneer trees rose with increasing irregularity of forest shape ($r = 0.57$, $P = 0.005$, $n = 20$) but the relationship for mature pioneers was insignificant. The NPLDs were expected to correspond closely with the pioneers, as both require light early in their life cycle. The proportion of NPLD tree species, however, decreased with increasing irregularity of forest shape. The correlation coefficient was significant for both the regenerating group ($r = -0.67$, $P = 0.005$, $n = 22$) and the mature group ($r = -0.43$, $P = 0.025$, $n = 22$). Shade-tolerators in the mature size group increased their proportions with increasing forest irregularity ($r = 0.45$, $P = 0.025$, $n = 21$), but the regenerating group recorded an insignificant relationship with forest shape.

There was a significant relationship between the proportion of gold star tree species and increasing irregularity of

forest shape for regenerating trees only ($r = 0.47$, $P = 0.025$, $n = 22$). The coefficient of determination derived from this figure was just over 22% and this was lowered substantially by the presence of seven forest fragments that contained no gold star species. These forests were spread across the shape range and had higher residual values with increasing forest irregularity. Thus, superimposed on the general rise in gold star species was a base of forest fragments of differing shape that did not contain this rare species category. Relationships between the proportion of blue star tree species and forest shape were positive for both regenerating and mature trees, but the correlation coefficients were low ($r = 0.38$ and $r = 0.36$, $P = 0.05$, $n = 22$). The ordering of forests about the regression line indicated a possible suppression of the effect of shape on the proportion of blue star species by climate. Those forest fragments with the highest proportion of blue star species were located in the wetter, evergreen zones, indicating the mesic requirements of rare species. The proportions of common species were not related significantly to forest shape for regenerating or mature trees. The proportions of common species remained within a range of 63–72% for regenerating trees and 58–66% for mature trees. Tree species common in Ghana and Africa thereby formed the foundation of communities in forests of all shapes.

The relationship between the proportion of evergreen tree species and the shape of forest fragments was significant only for mature trees. The correlation coefficient ($r = 0.44$, $P = 0.025$, $n = 20$) translated into a coefficient of determination of 19%. Fragment shape therefore accounted for around one-fifth of the variation in the proportion of evergreen tree species, but no significant relationships were found for deciduous species.

There was no significant effect of fragment shape on the proportion of tree species dispersed by animals in the regenerating category, but a significant and positive relationship was found for the mature category ($r = 0.46$, $P = 0.025$, $n = 20$). The coefficient of determination attained a value of 21%. A significant negative relationship was observed between the proportion of mature trees dispersed by plumed seeds and irregularity of forest shape ($r = -0.58$, $P = 0.005$, $n = 22$). Shape therefore accounted for around one-third of the variation in the proportion of plumed tree species. No outstanding residuals were identified and there was no apparent pattern according to climate zone or disturbance condition.

Tree species diversity and forest isolation

Relationships between the logarithm of tree species number and forest proximity were insignificant for the regenerating and mature categories ($P = 0.05$). Insignificant relationships were also found between the proportions of animal, bird and wind-dispersed tree species and the proximity of neighbouring forest fragments.

Tree species diversity and climate/disturbance variables

The number of tree species in forest fragments rose with increasing average annual rainfall for mature trees ($r = 0.57$,

$P = 0.05$), but the relationship was insignificant for regenerating trees. Tree species numbers were also significantly negatively correlated with fire burn for both regenerating and mature trees ($r = -0.8$, $P = 0.001$ and $r = -0.69$, $P = 0.01$, respectively). As the area of fire burn increased within forest fragments, the number of tree species decreased. No significant relationships were recorded between tree species numbers and logging or agricultural activity.

Multivariate regression analyses

Significant relationships were recorded between the logarithms of regenerating and mature tree species numbers and all seven environmental variables ($r = 0.98$ and $r = 0.97$, $P = 0.001$). For regenerating trees, 96% of the variation in species numbers was accounted for by the variables and the value for mature trees was only slightly lower at 94%. The order of importance of the variables was highlighted by their beta weights, which indicate how much change in the dependent variable is produced by a standardized change in each of the independent variables when the others are controlled. For both size groups, the logarithm of fragment area produced the most rapid change in the logarithm of tree species number ($P = 0.001$). The only other significant variables were fire burn for regenerating and mature trees ($P = 0.001$ and $P = 0.01$, respectively) and rainfall for mature trees ($P = 0.05$).

The beta weights from multiple regression analyses indicated that of the seven environmental variables only three proved significant when accounting for variability in the logarithm of tree species number. To elucidate their relative explanatory power, stepwise multiple regression was employed. Results indicated that the logarithm of forest area accounted for 83% of the variation in the logarithm of species number for regenerating trees and when fire activity was added, the coefficient of multiple determination rose to just over 94% ($r = 0.97$, $P = 0.001$) (Table 4). The order of entry of the variables was identical for mature trees, but forest area accounted for only 65% of the variation in tree species number and burn added a further 23.5% to bring the coefficient of multiple determination to 88.5%. Average annual rainfall was also identified as a significant variable for mature trees, raising the coefficient of multiple determination to over 91% ($r = 0.96$, $P = 0.001$) (Table 4).

Table 4 Significant results from stepwise multiple regression of the logarithm of tree species number with seven environmental variables (values of r)

Variable	Log number of tree species (regenerating)	Log number of tree species (mature)
Log area	0.91	0.81
Burn	0.97	0.94
Rainfall		0.96
Significance	$P = 0.001$	$P = 0.001$

DISCUSSION

Tree species diversity and forest area

Area was the most important influence on tree species number and composition in Ghanaian forest fragments. Species–area relationships indicated that large forest fragments contained the greatest number of tree species, attributable to ecological processes and also to sampling effects (Hill *et al.*, 1994; Lomolino, 2001). More regenerating than mature tree species were accumulated per unit increase in area, which bodes well for future persistence. Additionally, extra tree species found within larger forest fragments followed a predictable pattern rather than representing random species drawn from the community. The proportion of rare tree species increased with forest area, whilst common species formed a foundation comprising around two-thirds of the total forest complement. As the area of forest fragments increased, raising the amount of interior compared with edge forest (Collinge, 1996; Turner, 1996), the relative proportions of evergreen and shade-tolerant species increased with respect to deciduous pioneers. Forest fragmentation will thereby cause local extinction, particularly of rare, shade-tolerant, evergreen species.

Tree species diversity and forest shape

Shape was a partially significant variable dictating tree species composition in Ghanaian forest fragments. Half of the relationships tested (Fig. 2) were significant and were used to support or reject hypotheses. A greater number of significant relationships were recorded for mature trees, but when regenerating trees displayed a significant relationship, the correlation was often higher. Thus, the shape of forest fragments influenced species composition to differing degrees depending on tree girth. These contrasts in significance may be explained by the buffering effect of the long life spans (>100 years) of canopy trees (Martinez-Ramos & Alvarez-Buylla, 1998). Initial effects of isolation on trees in a relict fragment are generally expressed more strongly through regenerating populations (Bierregaard *et al.*, 1992; Laurance *et al.*, 1998a; Sizer & Tanner, 1999).

The guild category responded to edges clearly in the regenerating size group because it was defined by the amount of exposure that species require for regeneration (Hawthorne, 1993b). Level of exposure controls inter-specific competition between both seedlings and saplings, allowing a response to be measured quickly (Brokaw, 1985). The relationships may be weaker for the mature trees because the present cohort of individuals is representative of a time when the forest was less fragmented. The forest fragments of Ghana have been isolated for about a century, which is shorter than the life span of many trees (Martinez-Ramos & Alvarez-Buylla, 1998). This might explain some of the insignificant relationships found within the guild category. The time frame is notably longer, however, than the 10–20-year mortality response documented in several studies (Ferreira & Laurance, 1997; Laurance *et al.*, 1998b).

Pioneer species regenerate under canopy gaps, so their response to disturbance around forest edges is immediate

(Laurance & Bierregaard, 1997; Nepstad *et al.*, 1999). This might explain the significant rise in their proportions with increasing forest irregularity. The insignificant response of mature trees might be explained by the short time frame of isolation, where an increase in pioneers may not be registered among the older individuals. The results for the NPLDs are difficult to interpret. They showed a significant decrease in the proportion of species requiring light later in their life cycle with increasing proportions of edge. This relationship cannot be explained with reference to the literature. Shade-tolerators thrive in low light conditions experienced under the forest canopy (Benitez-Malvido, 1998; Kellman *et al.*, 1998), so it was expected that the proportion of regenerating species would decrease with increasing forest irregularity. No significant relationship was found for this size group, however, which is difficult to explain. With respect to mature trees, the rise in the proportion of shade-tolerators may, once again, refer to past conditions before the forests were fragmented. They may have grown under conditions of canopy continuity but persist at edges today due to their long life spans. Studies of species health and mortality are required to test this assertion.

As forests became more irregular in shape the number of rare species increased significantly. This does not support the hypothesis of a decrease in their proportions with increasing forest irregularity (Benitez-Malvido, 1998; Brokaw, 1998), but as most rare species are shade-tolerators, it is in accordance with the positive association recorded between this guild and shape. The lack of significant association with shape displayed by the common species is as expected. Common species are often opportunist and consequently are found in both edge and interior environments, which prevents any significant influence of shape.

The phenology category displayed only one significant relationship with shape. Lack of significant relationships in the regenerating group might be accounted for by the indeterminacy of phenology in young trees. Many rain forest species are evergreen in their early life before adopting a deciduous habit when mature (W.D. Hawthorne, pers. comm.). Thus, categorization according to phenology might not apply until trees reach maturity. By this time, the trees may already be relics, dictated by earlier ecological conditions. They may be actively shedding leaves due to water stress exceeding their physiological tolerances (Laurance *et al.*, 1998b), but no data exist for these forests to test this assertion.

Relationships between the proportion of animal-dispersed tree species and shape supported hypotheses. The lack of significant association in the regenerating group might be due to the operation of both interception and circulation (Blouin & Connor, 1985). These mechanisms oppose one another in the sense that increased interception eventually leads to a larger proportion of animals in irregular shaped forests, whereas increased circulation raises the proportion of animals within more regular shapes. A significantly greater proportion of animal-dispersed tree species occurred among mature individuals in irregularly shaped forests. This suggests that the proportion of species dispersed by animals

in irregular forests has decreased over time. It is unlikely that this is the result of reduced animal dispersal into such forests attributable to a change in their form or isolation because these factors have remained stable over time. The reduction might be explained, however, by an overall loss of animals due to forest fragmentation (Chiarello & de Melo, 2001; Cordeiro & Howe, 2001; Harrington *et al.*, 2001). A decline in animal seed dispersers is a process that requires a longer time to become manifest than edge-driven changes (Turner *et al.*, 1996). The significant results recorded here allude to such ecological change, but no data currently exist to test this theory. The significant decrease in the proportion of mature plumed trees with increasing irregularity is difficult to explain. Their proportion was expected to increase due to greater interception. A possible explanation is that the position of wind-dispersed trees in the canopy overcomes any edge effect. Wind-dispersed trees are located in the upper canopy, where wind speeds are maximized. By filling this niche, the advantage of being situated along edges might be cancelled out.

Tree species diversity and forest isolation

Isolation was not a significant variable dictating tree species number or dispersal composition in Ghanaian forest fragments. Neither the genetic contribution of proximate neighbours to fragmented populations nor the varying distance constraints on dispersal were substantiated. The results may have been influenced by statistical measures such as the choice of proximity index, or ecological reasons such as variation in matrix vegetation (Ricketts, 2001; Vandermeer & Carvajal, 2001; Laurance *et al.*, 2002). A gravity measure could be added to nearest neighbours according to their area, or forests below a specified area could be excluded from the proximity index, as it is unlikely that they will provide significant genetic support to proximate fragments. Research should progress to measuring dispersal directly, quantifying any variations in surrounding matrix vegetation, as this will render equidistant forest fragments incomparable in terms of dispersal ability. The results presented here support the assertion that ecological effects of fragmentation are more varied than simple dispersal models predict (Young *et al.*, 1996; Shafer, 2001).

Tree species diversity and climate/disturbance variables

Fire activity was the second most important variable influencing tree species number across Ghanaian forest fragments. The association between regenerating trees and extent of fire damage was more significant than that between mature trees and extent of fire damage. This can be explained by the sensitivity of saplings and poles to ground fires (Hawthorne, 1994). Average annual rainfall proved to be a factor of tertiary significance for mature trees, despite its signature being dampened by the categorical data. This indicates a response of mature trees to large area factors, whilst regenerating trees are more sensitive to small area disturbance events. Logging and taungya did not signifi-

cantly influence the number of tree species across the sampled forest fragments, which is in accordance with reports of the Ghana Forestry Department (Ghana Timber Export Development Board, 1992).

IMPLICATIONS FOR BIODIVERSITY CONSERVATION

Quantifying the effects of forest area, shape and isolation on tree species diversity, and comparing their impacts with those of other environmental variables, is important in managing forest fragments for conservation. Prioritizing variables of spatial geometry might enable current deforestation to be managed beneficially for diversity maintenance by indicting how much land and what shape and pattern it should assume to maintain key tree species. Additional consideration can then be given to climate and disturbance.

Species–area curves from Ghana showed that large forest fragments contained the greatest number of tree species. The presence of outstanding residuals according to climate and disturbance, however, cautions against the predictive use of species–area curves when the data are collected over a wide geographical area. Diversity figures are augmented by favourable climate and environmental heterogeneity, and this renders prediction both location and scale specific (Harte *et al.*, 1999; Rosenzweig, 1999).

A species–area curve needs to be assessed with respect to the nature of species comprising it. The results presented in this paper indicate that the steep rising limb of such a curve in Ghana is composed of common tree species whilst the flatter section represents increments of rare species. Considering species number alone, it would appear that habitat area can be reduced substantially without the loss of many species, but the lost species are the most rare. Thus, an early question to be asked in conservation planning is whether to conserve representative or rare species. In Ghana, the preservation of maximum species richness has now been shown to preserve a valuable portion of the forest ecosystem: the rare and shade-tolerant species. These species will be safeguarded more effectively by the preservation of maximum species richness within larger forest reserves. Small reserves can, however, provide source areas for re-establishment of more extensive forest in areas that have been heavily degraded (Turner & Corlett, 1996).

The research presented here lends some support to, and certainly does not refute, the assertion that irregularly shaped forest fragments promote gap and building phases along edges. This, in turn, raises the proportions of pioneer species (Laurance *et al.*, 1998a; Sizer & Tanner, 1999). It is important to protect consolidated fragments to ensure that species requiring interior habitat are maintained. This is particularly important in Ghana, especially in the semi-deciduous areas, where fire and dry Harmattan winds can penetrate easily into interior habitat from outside forest boundaries. Fragments with core areas provide safety for sensitive, shade-tolerant species and their genetic diversity (Brokaw, 1998; Kellman *et al.*, 1998). They provide sources of recolonization according to the rescue effect (Brown &

Kodric-Brown, 1977). By maintaining a community of edge species, core species will be protected from altered microclimates and disturbance regimes. This requires consideration of the temporal dynamics of edges. Edge communities will need to be managed to prevent boundary recession, especially when surrounded by harsh matrix vegetation (Gascon *et al.*, 1999, 2000; Mesquita *et al.*, 1999; Cochran, 2001; Laurance & Williamson, 2001). A landscape-level conservation strategy is necessary, which maximizes area to perimeter relationships across a number of reserves, protects reserve edges using buffer zones (managed ecotones) and minimizes matrix harshness. Ecological processes that operate over large distances must not be ignored. They are the processes that situate forest fragments within the landscape. At this scale, edges may not be detrimental, but represent key elements for the restoration of landscapes (Restrepo *et al.*, 1999).

Tropical forest trees can tolerate changed environmental conditions along forest edges until the end of their life cycle (Turner & Corlett, 1996). Such species may persist today as mature trees with little possibility of regenerating *in situ*. They are effectively extinct locally, but are nevertheless recorded in the extant flora. This indicates that forest equilibrium for mature trees may only be achieved over very long time-scales, possibly centuries (Turner *et al.*, 1994, 1996; Laurance *et al.*, 1997, 2000). This can lead to the build up of an 'extinction debt' where the true cost of habitat destruction is manifest only after a long time-lag (Kent, 1987; Tilman *et al.*, 1994). Crucially, fragmentation does not have temporary effects on tree species composition. Forest fragments do not return rapidly to a microcosm of continuous forest but become organized by different processes. This requires a dynamic response by managers to work with new conditions and processes.

In Ghana, the influences of forest shape and isolation on tree species diversity at the landscape level were not as strong as those of climate and disturbance. Thus, the placing of forest reserves across a climatically diverse region is important in maximizing species diversity and these reserves should ideally be larger than a minimum dynamic area (Pickett & Thompson, 1978). This is the smallest area with a natural disturbance regime that maintains recolonization and minimizes extinction. Additionally, small proximate fragments that might not genetically sustain larger forest fragments may, nevertheless, be important as bridges or 'stepping stones' that connect fragments together (Kent, 1987; Ranta *et al.*, 1998).

Five important management statements can be formulated from the results presented here. They are based on conserving maximum tree species number and rarity. Emphasis on other management aspects may modify the statements.

- Forest area is the most important consideration in reserve management. A large forest reserve contains the greatest number of tree species and includes the highest proportion of rare tree species.
- Unless dealing with very small areas, shape is not a crucial consideration for the design of forest reserves. The main-

tenance of similar matrix vegetation immediately surrounding fragmented reserves can act to buffer forests, diminishing edge effects.

- Management of disturbance should be considered in preference to forest shape if higher levels of tree diversity and species quality are to be maintained. Thus, deforestation to produce a fragment may not be as important as internal degradation after it has been isolated. Internal degradation is partly controlled by fragment area.
- If a number of forest reserves are to be designated, they should be located within different forest types according to climate, in order to capture a large fraction of the regional biota.
- No conclusive statement can be made concerning reserve isolation. It is possible, however, that reserves above an area threshold buffer their neighbours and that modification of matrix vegetation may provide opportunities for reducing reserve isolation and thus extinction risk of fragmented tree populations.

Investigation at the landscape level in Ghana highlighted broad patterns of tree species within fragmented forests. The ecological processes that potentially shaped the spatial patterns of tree species number and composition were inferred with reference to the patterns themselves. As the formative mechanisms are essentially demographic, precise predictions about growing conditions, survival rates, mortality and metapopulation dynamics can be tested at local levels by extensive demographic work on the ground. Data are required which measure directly the processes of species loss (e.g. ecosystem relaxation, disturbance) and gain (e.g. immigration) within fragmented forest. This requires the establishment of permanent sample plots that can trace ecosystem development over long periods of time, but at the resolution of individual stems. The research undertaken in this paper highlighted that ecological understanding at the landscape level, provided by the spatially explicit view of the biogeographer, can inform conservation management within the tropics. Ideally, studies of landscape pattern (the geographical approach) and landscape process (the ecological approach) should be integrated (Opdam *et al.*, 2002). Much research remains to be undertaken at both landscape and local levels before the route and ultimate nature of floral re-equilibrium in fragmented tropical forest can be comprehended fully.

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BIOSKETCHES

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