Wood Density as a Conservation Tool: Quantification of Disturbance and Identification of Conservation-Priority Areas in Tropical Forests

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Abstract: *Inventories of tree species are often conducted to guide conservation efforts in tropical forests. Such surveys are time consuming, demanding of expertise, and expensive to perform and interpret. Approaches to make survey efforts simpler or more effective would be valuable. In particular, it would be good to be able to easily identify areas of old-growth forest. The average density of the wood of a tree species is closely linked to its successional status. We used tree inventory data from eastern Borneo to determine whether wood density can be used to quantify forest disturbance and conservation importance. The average density of wood in a plot was significantly and negatively related to disturbance levels, with plots with higher wood densities occurring almost exclusively in old-growth forests. Average wood density was unimodally related to the diversity of tree species, indicating that the average wood density in a plot might be a better indicator of old-growth forest than species diversity. In addition, Borneo endemics had significantly heavier wood than species that are common throughout the Malesian region, and they were more common in plots with higher average wood density. We concluded that wood density at the plot level could be a powerful tool for identifying areas of conservation priority in the tropical rain forests of Southeast Asia.*

Keywords: forest disturbance, priority conservation areas, species range, species diversity, tree inventories, tropical forest conservation, wood density

Densidad de Madera como una Herramienta de Conservación: Cuantificación de la Perturbación e Identificación de las Áreas Prioritarias para la Conservación en Bosques Tropicales

Resumen: *Los inventarios de árboles a menudo son llevados a cabo para guiar los esfuerzos de conservación en bosques tropicales. Tales inventarios consumen tiempo, demandan profesionalismo y su realización e interpretación son costosas. Métodos para que los esfuerzos fueran más simples o más efectivos serían muy valiosos. En particular, sería bueno poder identificar áreas de bosque maduro fácilmente. La densidad promedio de madera de una especie de árbol se relaciona estrechamente con el estatus sucesional. Utilizamos datos del inventario de árboles de Borneo oriental y de densidad de madera para determinar sí la densidad de la madera se puede utilizar para cuantificar la perturbación del bosque y su importancia para la conservación. La densidad promedio de madera en una parcela se relacionó significativa y negativamente con los niveles de perturbación, las parcelas con las mayores densidades de madera ocurrieron casi exclusivamente en los bosques maduros. La densidad promedio de madera se relacionó unimodalmente con la diversidad de especies*

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de árboles, lo que indica que la densidad promedio de madera en una parcela puede ser un mejor indicador de un bosque maduro que la diversidad de especies. Adicionalmente, las especies endémicas de Borneo tenían madera significativamente más pesada que las especies que son comunes en la región Malesiana, y fueron más comunes en parcelas con mayor densidad promedio de madera. Concluimos que la densidad de madera a nivel de parcela pudiera ser una herramienta poderosa para la identificación de áreas de prioridad para la conservación en los bosques tropicales lluviosos del sureste de Asia.

Palabras Clave: áreas prioritarias para la conservación, conservación de bosques tropicales, densidad de madera, diversidad de especies, inventarios de árboles, perturbación de bosques, rango de distribución de especies

Introduction

Old-growth forests in the tropics are important for conservation because they frequently harbor a higher proportion of vulnerable (disturbance-sensitive) and restricted species (plants and animals) than can be found elsewhere (Chua et al. 1998). Such forests are becoming increasingly rare and fragmented and their extent, especially in Asia, is already surpassed by areas that have been logged over or have regrown following full or partial clearance (e.g., Murali & Hedge 1997; Sayer et al. 2000; Brooks et al. 2001). These disturbed forests form a mosaic of heavily to moderately disturbed patches at different stages of recovery. Such large disturbances are not new: many areas have been subjected to significant destructive human or natural impacts for many millennia (Goldammer 1989; Gathorne-Hardy et al. 2002; Gemerden et al. 2003). In addition, there are flash floods, landslides, wind throws, and tree falls that operate continuously throughout tropical rain forests (Brokaw 1982; Myster & Walker 1997; Whitmore & Burslem 1998; Douglas et al. 1999; Proctor et al. 2001; Pitman et al. 2005; Restrepo & Alvarez 2006). Thus, instead of being one uniform stable habitat, tropical rainforests form a large mosaic of disturbance histories that vary over space and time. Although recent histories are often available, older impacts remain less readily identified. Nevertheless, if one were able to assess forest communities on the basis of successional status of the constituent species, many of these disturbance patterns might become clearer.

We explored the possibility of using tree inventories in combination with data on wood density of tree species to assess the conservation value of a forested area. We examined wood density because it correlates strongly with the successional status of trees (e.g., Steege & Hammond 2001; King et al. 2005; Slik 2005), is relatively easy to measure in the field (Chave 2005), and is already known for many tropical tree species in our research area (Oey 1990). Because stems that have less dense wood are likely to represent early-successional, light-demanding, fast-growing tree species and stems that have denser wood are likely to represent slow-growing, shade-tolerant, late-successional species, we hypothesized that the average wood density of coexisting tree species provides information on the successional status of the sampled forest area. Earlier research in which species of *Macaranga* and *Mallotus* (Euphorbiaceae) were classified as pioneers or nonpioneers on the basis of plant functional traits showed that such a classification in combination with inventory data is effective in identifying disturbed forest areas (Slik 2005).

We also explored the relationship between average wood density of trees sampled within a forest area and the diversity of tree species of that area. On the basis of the intermediate disturbance hypothesis, the highest diversity should be reached at intermediate levels of disturbance (or time since disturbance) because both early- and late-successional species can coexist (Connell 1978; Molino & Sabatier 2001; Sheil & Burslem 2003). Therefore, assuming that wood density is indeed a good proxy of forest disturbance, we expected the highest diversity in forests with intermediate wood density. Such a pattern is especially interesting given that a primary conservation concern is with “old growth,” but many researchers currently give weight to species richness per se, whereas others argue that high richness and old growth are not necessarily the same thing (Sheil et al. 1999; Molino & Sabatier 2001; Sheil & Burslem 2003).

Our principle aim was to determine whether average wood density of trees in a forest can be used as a measure of disturbance and specifically as a means to identify areas of intact old-growth forest with high conservation value. Our secondary aim was to show that inventory lists of tree species from tropical forests can be used more effectively for conservation purposes when combined with relatively easy to determine plant traits, such as wood density.

Methods

Field Sites

We carried out our study at 3 spatial scales, local, landscape, and regional, within East Kalimantan Province, eastern Borneo, Indonesia. Each level had its own plot layout and inventory protocol. At the local scale (approximately 200 km^2), we used data from the Sungai Wain–Samboja area near the city of Balikpapan. This area consisted of a mixture of old-growth and burned forests (see Supporting Information). The landscape-scale study (approximately 10,000 km^2) included only old-growth forests of Gunung Meratus, Gunung Lumut and Sungai Wain (Supporting Information), and the regional study (approximately 125,000 km^2) consisted of old-growth, logged, and burned forest from 3 main sites that covered a large part of East Kalimantan Province (Supporting Information). If available, we included heavily disturbed areas to allow for better overall characterization of the shape of the disturbance–wood density relationship.

All plots were established in lowland dipterocarp forests ranging in elevation between 30 and 500 m asl. The rainfall in the study locations is comparable and fairly constant (approximately 2500 mm/year), although the period from June till October is usually slightly drier than the other months of the year (Walsh 1996). Occasionally very dry years occur, associated with the El Niño Southern Oscillation (Walsh 1996). Temperatures range between a minimum of 24 °C at night and a maximum of 31 °C during daytime. All selected forest areas were, floristically, examples of the mixed dipterocarp forests of Indonesian Borneo, although the Berau area showed additional affinities with forests in Sarawak, East Malaysia (Slik et al. 2003).

Plot Layout

For the local study we surveyed plots of 10 × 10 m (0.01 ha) in old-growth, once-burned (1998), and twice-burned (1983 and 1998) lowland dipterocarp rainforest in the Sungai Wain–Samboja area. Fires in the burned forests here were associated with extreme El Niño–related droughts, but actual ignition was probably caused by human activities in the surrounding agricultural areas. For detailed information on the burned and old-growth forests in this location, refer to Slik and Eichhorn (2003). The plots were established between December 2004 and April 2005 along 120 transects that extended 300 m on either side of the burned–unburned forest boundary. These transects were spaced 10 m (Wanariset Samboja: 60 transects) or 20 m (Sungai Wain: 60 transects) apart. Each transect contained 2 plots at a random distance from the unburned–burned forest boundary (1 plot at the same distance on either side of the boundary), with the restriction that in each location each distance to the boundary (10-m intervals) was permitted to occur only twice. These plots provided a representative sample of the area (which consisted mainly of infertile sandy soils), including swamps, river valleys, hillsides, and ridges and covered an elevational range between 30 and 110 m. In these plots we enumerated all trees with diameter at breast height (dbh) $\geq$5 cm, whereas trees with a dbh <5 cm but taller than 1.3 m were sampled in 5 × 5 m subplots. Because our diversity measure was based on rarefaction of similar stem numbers in each plot (explained below), we used only the 159 plots (of 240) that contained 20 or more stems.

For the landscape-scale study, we used 90 plots of 10 × 10 m (0.01 ha) each, established between December 2004 and March 2005, from 3 locations: Gunung Lumut, Gunung Meratus, and Sungai Wain (Supporting Information). In these plots, we enumerated all trees taller than 1.3 m. The plots in each location were placed at 50-m intervals along 3 transects (each 500 m long and consisting of 10 plots) that originated from a central point and were arranged at 120° angles to each other. These plots covered an elevational range of 110 to 190 m (Gunung Meratus), 240 to 420 m (Gunung Lumut), and 40 to 80 m (Sungai Wain) and included alluvial sites, hill slopes, and ridges at all 3 locations. The 3 locations differed in soils, with the Sungai Wain area having the least fertile soils.

For the regional study, we established another independent set of plots between October 2000 and April 2001 in old-growth, selectively logged, once-burned, and twice-burned forest in 3 main sites covering a large part of the Province of East Kalimantan (Supporting Information). These plots were also 10 × 10 m, but here we enumerated all trees with a dbh $\geq$10 cm in the entire plots, trees with a dbh <10 cm but >5 cm in 5 × 5 m subplots, and all trees with a dbh $\leq$5 cm but taller than 1.3 m in 2 × 2 m subplots. These plots were established along line transects of 900 m length (one per forest type), each containing 30 plots spaced at 50-m intervals to cover as much of the local variation in terrain as possible. The locations differed in soils and elevation. The Balikpapan area consisted mainly of slightly undulating terrain, varying between 30 and 150 m asl, with poor sandy soils. The sampled area in Berau consisted mainly of a mosaic of very poor, almost white, sandy soils on ridges and relatively rich clay soils in alluvial sites. The area was slightly undulating, varying between 50 and 200 m asl. The Meratus area also covered a lot of different soil types, from very poor (almost white) sandy soils on high plateaus to rich clay soils in alluvial sites. The area consisted of very steep and pronounced hills, varying in elevation between 150 and 500 m asl. In total 480 plots were established; however, due to our rarefaction method with which we calculated diversity (explained below), we only used plots that contained at least 10 trees, which reduced the number of usable plots to 199. Sampled trees from all locations were identified in the field and later verified through herbarium collections. Vouchers were deposited in the National Herbarium Nederland, Leiden University, The Netherlands.

Wood Density

We based wood density on data from published studies (Oey 1990), which provided air-dried (containing approximately 12% moisture) average wood densities for several thousand Indonesian tree species (wood density defined as "air dried mass / air dried volume"). We found wood densities for approximately 50% of the tree species in our study area. We based the wood density of the remaining species on the average of known densities of other species in the genera to which these species belonged. Because wood density in tropical trees is strongly phylogenetically conserved (approximately 70% of variance explained at genus level in Indonesian trees), this provides a reliable estimate of species-specific wood density (Slik 2006*a*). We then calculated the average wood density by averaging the wood density of all individual stems in each plot.

We calculated the average wood density and 95% confidence intervals of the plots in each location of the regional East Kalimantan data set ($n = 30$ plots of 0.01 ha/location). These locations covered twice-burned ($n = 3$), once-burned ($n = 3$), logged ($n = 5$), and undisturbed ($n = 5$) forests. Subsequently, the locations were sorted from low to high average wood density to check how this order corresponded with the known disturbance history of the locations.

Based on the literature (Kessler et al. 1994; Slik 2005) and information on herbarium labels, we identified pioneer tree species in our plots (Supporting Information). Species were considered pioneers if more than one-third of the collections that contained detailed habitat information were made in degraded, open forest types (on the basis of species with more than 10 herbarium collections). We then calculated the percentage of pioneer trees in the plots on a per-stem basis for the local (Sungai Wain–Samboja) data set. The relationship between average wood density and percentage of pioneer trees in a plot was then tested with linear regression analysis.

To determine whether wood density was related to species distribution ranges, we checked whether the wood density of Borneo endemics differed from those of species occurring throughout the Malesian region (from Peninsular Malaysia to New Guinea). We used the local Samboja–Sungai Wain data set to do this because the species distributions of all the tree species in that data set are known (Slik 2006*b*). The average wood density of the Borneo endemics in this data set was compared to that of the Malesian species with a Kolomogorov–Smirnov test.

To determine whether average wood density in a plot could be used as an indicator of old-growth forest, we classified the plots from the local Samboja–Sungai Wain data set as disturbed (sampled in the burned forest) and old-growth (sampled in the unburned forest). We then used logistic regression to test the relationship between average wood density and disturbance in a plot.

Plot Diversity

We based diversity in the plots on the average number of species present in 5 random draws of 20, 35, and 10 individuals per plot in the local, landscape, and regional data sets, respectively. The number of individuals used per plot to calculate diversity differed among the data sets due to differences in sampled plot surface area and thus stems included in the plots. Five random draws per plot provided a mean diversity value that was reliable enough for this study. We chose this rarefaction method of calculating diversity because it excludes effects of sample size (number of stems) differences between plots on the resulting diversity of those plots (Slik et al. 2003). Indeed, a general-linear, quantitative regression model applied to the local data set failed to identify any significant relationship between total stem density in the plots and their rarefied diversity (df $= 158$, $R^2 = 0$, F ratio $= 0.28$, $p = 0.627$).

Relationship between Diversity and Wood Density

We expected a rise-and-fall (unimodal) relationship between average wood density and diversity in a plot (i.e., first a rise in diversity with increasing average wood density to a diversity maximum followed by a decline in diversity with a further increase in average wood density). Nevertheless, statistics for evaluating the validity of rise-and-fall relationships are not well developed in ecology. Molino and Sabatier's (2001) approach to detecting a unimodal diversity relationship (in their case per sample diversity against per sample proportion of light-demanding [heliophile and/or pioneer] versus shade-tolerant species) required a considerable quantity of data and the application of a series of linear regressions for short intervals along the x-axis. These regressions shifted from markedly positive to markedly negative. Although persuasive, the approach is ad hoc and inefficient.

Fortunately, there have been a number of relevant statistical developments, such as in the dose–response relationships in medical statistics (Ulm 1991; Muggeo 2003), of which some have already been applied in ecology (Drake et al. 2005). We initially found one of these approaches promising (Ulm 1991), which, by assuming 2 linear relations separated by a break point, provides an elegant refinement of Molino and Sabatier's (2001) idea for testing a unimodal relationship. The approach finds the breakpoint where 2 lines can be best fit to the underlying relationship. If the left-hand line increases while the right-hand line declines and both trends are significant but simultaneously allow for the uncertainty in locating the breakpoint, the case for a unimodal form is made. Nevertheless, it remained unsatisfying because we knew the true underlying relationship was a curve, not 2 straight lines. We decided to test for unimodal patterns by applying regression splines in combination with a Monte Carlo bootstrapping test.

Regression Splines

The relationship between diversity and average wood density in a plot was modeled with regression splines

(Hastie & Tibshirani 1990). Regression splines can be thought of as a compromise between (global) polynomial regression and local smoothing approaches. These splines combine the flexibility of a local smoothing approach in modeling localized features while maintaining the regression-like equation for relating the independent and dependent variables. In most applications, regression splines are defined by K piecewise-cubic functions with the different pieces separated by $(K-1)$ points called *knots*. In our application, we used B-splines basis functions (Boor 1978) because these allow fast computation but do not affect the estimated splines curve. The regression function is given by:

$$y_i = \sum_{j=1}^{K+4} e^{-\alpha_j} B_j(x_i; \gamma) + \varepsilon_i,$$

where y_i is the diversity index from site $-i$, B_j is the jth B-splines basis function evaluated at $x_{i.}$, K is the number of knots, γ is the knot position, $e^{-\alpha j}$ is the weight for the jth basis function, and $\varepsilon \sim N(0,\sigma^2)$.

Upon examining the scatterplots of diversity versus average wood density for our data sets, we decided that the data could be modeled with 2 piecewise-cubic functions; hence only one knot (θ) was needed. Model parameters were estimated with maximum likelihood.

Testing the Unimodal Relationship

To test whether the relationship between diversity and average wood density in a plot was significantly unimodal (i.e., there is a wood density for which the diversity is at maximum and for higher or lower average wood densities the diversity declines), we used a Monte-Carlo-based bootstrap test. To demonstrate a well-supported unimodal shape, it is sufficient to prove that the location of x for which the diversity is maximum lies between the minimum observed value ($x_{\min}$) and maximum observed value ($x_{\max}$) of x at a suitable level of confidence. The following is the Monte Carlo bootstrap procedure we used to conduct this test.

1. We estimated θ and its variance-covariance matrix from the data and denoted these estimates as $\hat{\theta}$ and $\hat{V}(\theta)$, respectively.
2. According to standard statistical theory $\hat{\theta} \sim N(\theta, \hat{V}(\theta))$; hence, we generated $\theta^{(1)}$ from a multivariate normal distribution with mean $\hat{\theta}$ and variance–covariance matrix $\hat{V}(\theta)$. With $\theta^{(1)}$, our estimated splines function is

$$f^{(1)}(x_i) = \left(\sum_{j=1}^{5} Exp\left(-\alpha_j^{(1)}\right) B_j\left(x_i; \gamma^{(1)}\right) \right).$$

The average wood density in a plot for which diversity is maximized was estimated by the x value for which $f^{(1)}(x_i)$ is maximized. We denoted this estimate as $x^{(1)}_{d_{\max}}$.
3. We repeated step 2 for 10,000 times, each time denoting the estimated x value for which the estimated diversity is maximized as $x^{(j)}_{d_{\max}}, j = 1, 2, \ldots 10{,}000$.
4. We sorted the $x^{(j)}_{d_{\max}}$ values and determined 95% confidence intervals as the 250th smallest and 250th largest values.
5. If the confidence interval did not contain minimum or maximum values of x, we concluded that there existed an average wood density for which the diversity is maximized and that for higher or lower average wood densities the diversity declines.

All statistical analyses were performed with Stat-Graphics Plus for Windows 2.1 (Statistical Graphics, Herndon, Virginia) and R version 2.2.1 (http://www.r-project.org).

Results

The average air-dried wood density in plots corresponded strongly with known disturbance history of the locations. Average wood densities increased progressively from twice-burned, once-burned, selectively logged, and old-growth forests (Fig. 1). The relationship between average wood density in plots and the percentage of pioneer trees in the plots was significantly negative (Fig. 2). In addition, the higher the average wood density of a plot, the higher the chance the plot was in old-growth forest, with the turning point located at a wood density of approximately 0.60 g/cm^3 (i.e., above that value the chance that a plot was in old-growth forest was >50%) (Fig. 3). This chance increased to nearly 100% for plots with an average wood density $\geq$0.70 g/cm^3.

The Borneo endemics that were co-occurring with widespread Malesian species in the Samboja–Sungai Wain plots had significantly heavier wood than the widespread species, 0.69 versus 0.63 g/cm^3, respectively (Fig. 4). They were also significantly more common (percentage of individuals) in plots with higher average wood density (Fig. 5).

All 3 data sets showed a significant unimodal relationship between average wood density and tree species diversity in a plot (Table 1; Fig. 6), with highest diversity at average wood density of approximately 0.68 g/cm^3.

Discussion

Wood Density, Disturbance, and Borneo Endemics

Our results show that inventory lists when combined with tree species air-dried wood density values can be used to quantify forest disturbance on a continuous scale in lowland dipterocarp rain forests. Old-growth forests

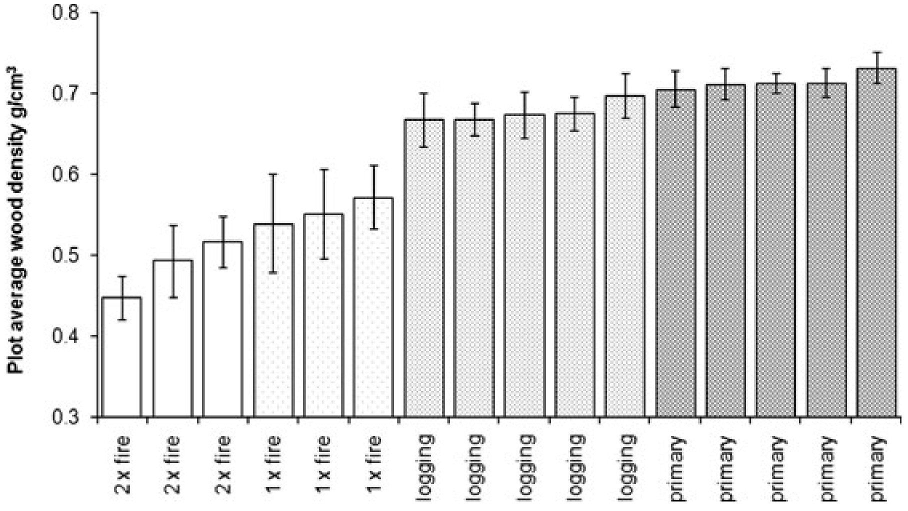

Figure 1. The 16 transects (each with n = *30 plots) from the regional data set ranked from low to high average wood densities in a plot (± CI).*

were all characterized by high average wood density values, whereas disturbed forests showed lower average wood densities that decreased significantly with increasing disturbance severity. This outcome is useful for conservation purposes because it implies that species inventory lists in combination with data on tree wood density can be used to map disturbance levels in an area or to spatially and temporally monitor forest regeneration. Average wood density in a plot can also be used to identify priority conservation areas in lowland dipterocarp forests because we found that forest plots with high average wood density contained significantly more endemics than plots with low average wood density. Nevertheless, our results indicate that disturbance contributes to local-, landscape-, and regional-scale patterns of wood density, but wood density also varies with soil properties, moisture availability, and seasonality (e.g., Wiemann & Williamson 2002; Baker et al. 2004; Steege et al. 2006). These factors, and the small plot sizes, could be a factor in the unexplained variation we observed in the relationship between average wood density and diversity of tree species. This means care has to be taken when our results are applied to forest types other than lowland dipterocarp forests because these might differ in average wood density.

Wood Density, Species Diversity, and the Intermediate Disturbance Hypothesis

The diversity of tree species in an area showed a unimodal relationship with average wood density of coexisting trees. Diversity was highest for plots with average wood densities around 0.68 g/cm^3 and declined with decreasing and increasing average wood densities. This overall pattern conforms to the intermediate disturbance hypothesis. The declining diversity in plots with high average wood density in combination with the fact that such plots are mainly found in old-growth forests is

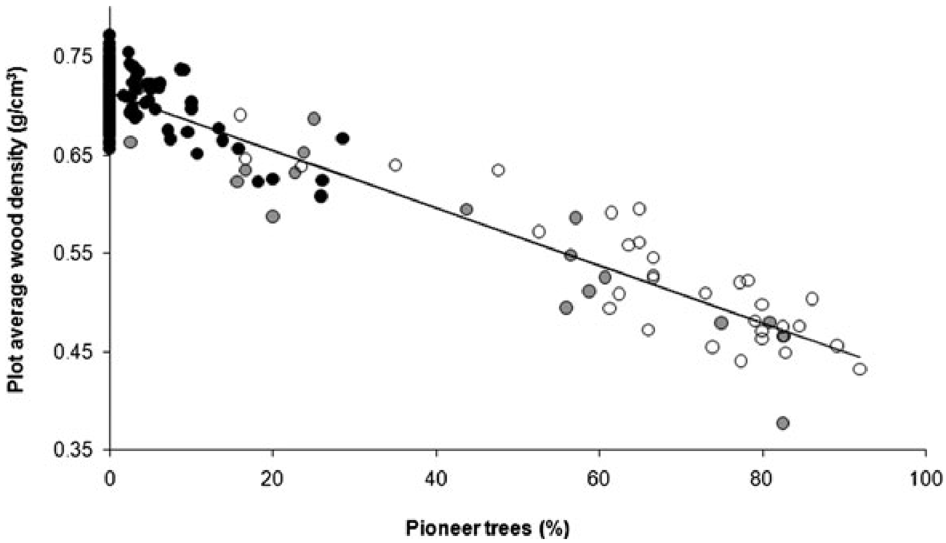

Figure 2. Relationship between average air-dried wood density and percentage of pioneer trees in 159 plots of 0.01 ha in the local Samboja-Sungai Wain data set (correlation coefficient of −0.95, R^2 *of 90.3%, df = 158,* $p < 0.0001$*; undisturbed plots, black dots; once-burned plots, gray dots; twice-burned forest, open dots).*

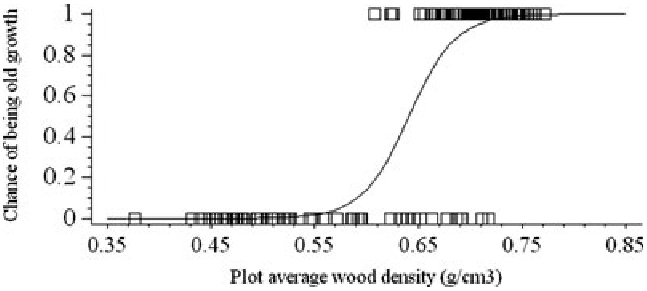

Figure 3. Relationship between average wood density in a plot and the chance that a plot is located in old-growth forest for the local Samboja-Sungai Wain data set, determined with logistic regression (odds ratio 2.20; deviance explained 62.4%; df = 1; χ^2 = 130.3, $p < 0.0001$*; disturbed forest plots, 0; old-growth forest, 1).*

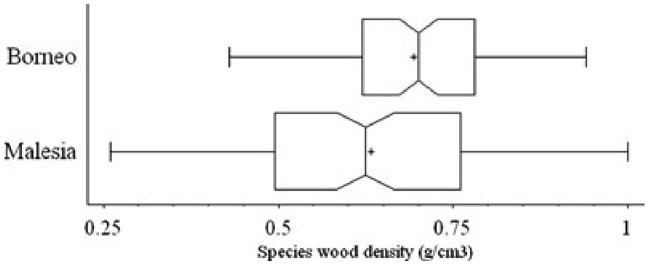

Figure 4. Difference in wood density of Borneo endemic species versus species occurring throughout the Malesian region (determined with a Kolmogorov–Smirnov [K-S] test; $n = 178$*, df = 1, K-S statistic 1.71,* $p = 0.005$*).*

especially notable because it implies that in the absence of sufficient disturbance tree diversity is reduced by competition. This competition selectively excludes light-wooded fast-growing tree species with high turnover rates. This is in accordance with observations from the Guianas (South America) that link the relatively low regional diversity of species and high average wood density in that region to its biogeographical and environmental stability (Steege & Hammond 2001) and with studies that report increased tree-species diversity following logging throughout the tropics (Cannon et al. 1998; Sheil et al. 1999; Molino & Sabatier 2001). The unimodal relationship we found between average wood density and diversity also means plots with the highest species diversity do not automatically identify plots with the lowest disturbance. This matters because, as our results also showed, range-restricted endemics are characterized by high wood densities, implying that areas with high average wood density are more likely to contain these species and should be protected against disturbance and conversion.

Wood Density, Competition, and Monodominance

Our results indicate that plots with very high average wood density are rare in tropical forests of Southeast Asia. In principle, plots could reach an average wood density of 1.08 g cm^{-3} (on the basis of wood density of the species with the heaviest wood in our research area). Nevertheless, such high average wood densities in a plot could only be reached under cases of near monodominance because few species possess such heavy wood. Apparently, disturbance levels, probably in combination with density-dependent mortality, are sufficient to prevent such monodominance from occurring in old-growth forests. In our study area this might be explained by the long history of drought and fire (e.g., Goldammer & Siebert 1989; Whitmore & Burslem 1998; Hope et al. 2005). Evidence shows the occurrence of droughts and fires in the wider region for at least 20,000 years (Haberle & Ledru 2001; Tudhope et al. 2001). Climatic variability, especially the intensification of El Niño–related drought, also affects patterns of tree diversity (Haberle & Ledru 2001) and composition in eastern Borneo (Slik 2004; Nieuwstadt & Sheil

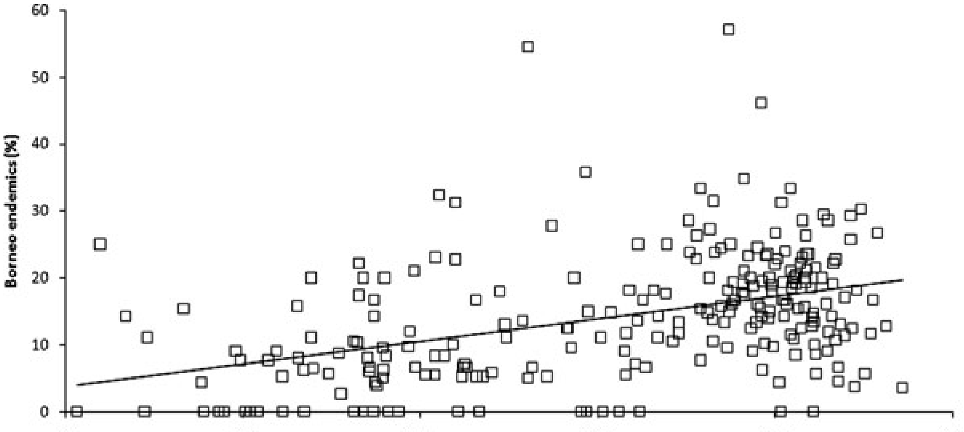

Figure 5. Relationship between percentage of trees that are Borneo endemics in plots from the local Samboja-Sungai Wain data set and average wood density in a plot (R^2 *= 17.0%,* F *ratio 48.7,* $p < 0.0001$*,* $n = 240$*).*

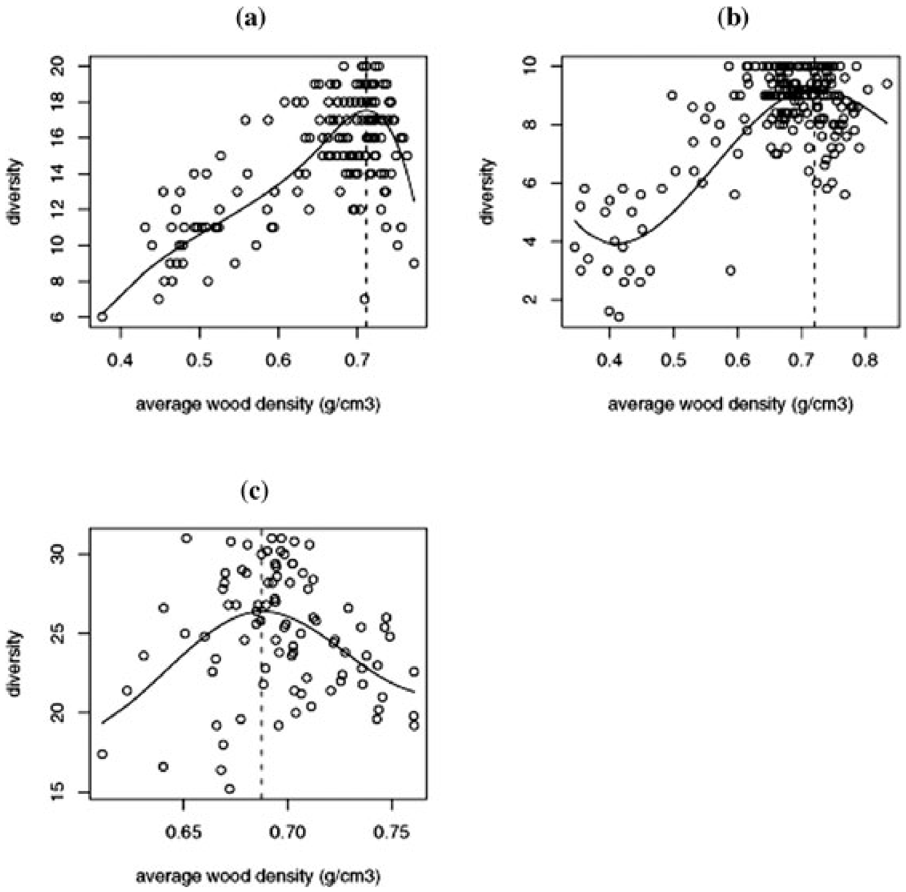

Figure 6. Relationship between average wood density and rarefied diversity of tree species in a plot for (a) local, (b) regional, and (c) landscape scales.

2005). In addition there are flash floods, landslides, wind throws, and tree falls that operate continuously throughout tropical rain forests (e.g., Brokaw 1982; Myster & Walker 1997; Whitmore & Burslem 1998; Douglas et al. 1999; Proctor et al. 2001; Pitman et al. 2005; Restrepo & Alvarez 2006). Thus, instead of being one uniform, stable habitat, tropical rain forests form a large mosaic of disturbance histories that vary both in space and time. These conditions promote the coexistence of both early- and late-successional tree species and prevent monodominance of heavy-wooded species.

Table 1. Results of the tests of the unimodal relationship between average wood density and tree-species diversity in a plot for the local-, landscape-, and regional-scale data sets.*

Data set	*Mean* $x_{d_{max}}$	*95% CI of* $x_{d_{max}}$	x_{min}	x_{max}	*Conclusion*
Local	0.692	(0.672; 0.719)	0.377	0.772	unimodal
Landscape	0.693	(0.666; 0.703)	0.611	0.761	unimodal
Regional	0.673	(0.640; 0.695)	0.346	0.834	unimodal

**A unimodal relationship is significant if the detected mean air-dried wood density at which diversity is maximized ($x_{d_{max}}$) and its 95% CI values fall within the entire range of available values of wood density (x_{min} and x_{max}).*

Conclusions

Although our methods can be improved upon, our results demonstrate the usefulness of combining species inventory lists with plant functional traits such as wood density. The methodology we developed to identify the unimodal relationship between average wood density and diversity in a plot offers a more effective means to detect such relationships than has been seen in previous ecological studies. The detected unimodal relationship between average wood density and diversity in a plot with this methodology has an important implication, namely that the highest diversity does not automatically equal the highest conservation value. Old-growth forests with the highest average wood density might have less diversity yet contain higher abundances of range-restricted (endemic) species. The ability of our method to identify such areas is its main contribution to conservation biology in the tropics.

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Supporting Information

Locations of research sites (Appendices S1 and S3) and a list of pioneer species and their wood densities (Appendix S2) are available as part of the on-line article. The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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