The relationship between wood density and mortality in a global tropical forest data set

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Summary

• Wood density is thought to be an important indicator of plant life history because it is coupled to many aspects of whole-plant form and function. We used a hierarchical Bayesian approach to explain variation in mortality rates with wood density, drawing on data for 765 500 trees from 1639 species at 10 sites located across the Old and New World tropics.
• Mortality rates declined with increasing wood density at five of 10 sites. Similar negative trends were detected at four additional sites, while one site showed no relationship. Our model explained 40% of variation in mortality on average. Both wood density and mortality rates show a high degree of phylogenetic conservatism.
• Grouping species by family across sites in a second analysis, we found considerable variation in the relationship between wood density and mortality, with 10 of 27 families demonstrating a strong negative relationship.
• Our results highlight the importance of wood density as a functional trait in tropical forests, as it is strongly linked to variation in survival. However, the relationship varied among families, plots, and even census intervals within sites, indicating that the factors responsible for the relationship between wood density and mortality vary spatially, taxonomically and temporally.

Introduction

A central goal of ecology is to understand how variation in the morphological and physiological characteristics of species relates to differences in growth, survival, and, ultimately, patterns in the distribution and abundance of organisms across landscapes (McGill *et al.*, 2006; Westoby & Wright, 2006). Growing consensus among plant ecologists now permits the quantification of woody plant strategies along several often orthogonal axes of variation related to characteristics of the leaves, seeds, wood, and growth form (Westoby, 1998; Westoby *et al.*, 2002; Cornelissen *et al.*, 2003; Wright *et al.*, 2004). These attributes, or functional traits, are most ecologically meaningful when they correlate with variation in vital rates and performance, both of which contribute to lifetime fitness (Ackerly, 2003; Violle *et al.*, 2007).

Wood density is thought to be an important functional trait because it is directly coupled to many aspects of whole-plant form and function (Cornelissen *et al.*, 2003; Chave *et al.*, 2009). Species with denser wood tend to grow more slowly (in height or diameter) because they invest more carbon in a given volume of stem relative to species with lighter wood, and because high sapwood density is associated with reduced conductance and thus reduced photosynthetic carbon gain (Enquist *et al.*, 1999; Bucci *et al.*, 2004; King *et al.*, 2005; Chave *et al.*, 2009; O'Grady *et al.*, 2009). Species with dense wood tend to occur later in succession than species with low-density wood (ter Steege & Hammond, 2001; Falster & Westoby, 2005). High wood density is known to correlate with resistance to drought-induced embolism, minimum seasonal water potential, mechanical breakage, and attack by pathogens and fungi (Augspurger & Kelly, 1984; Niklas, 1992; Clark & Clark, 2001; Hacke *et al.*, 2001; Ackerly, 2004; Jacobsen *et al.*, 2005; Preston *et al.*, 2006; Alvarez-Clare & Kitajima,

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2007; Chave *et al.*, 2009; Zanne *et al.*, 2010). These benefits of denser wood should lead to reduced mortality.

As causes of mortality may vary among regions, it is reasonable to expect that the relationship between wood density and mortality will differ among sites. Similarly, plant functional traits such as wood density are often broadly conserved within related taxa, so we expect there to be variation in the wood density–mortality relationship across lineages as well (Prinzing *et al.*, 2001; Chave *et al.*, 2006; Swenson & Enquist, 2007; Donoghue, 2008).

A negative relationship between wood density and mortality has been documented at local sites (e.g. Muller-Landau, 2004; Nascimento *et al.*, 2005; King *et al.*, 2006; Chao *et al.*, 2008; Poorter, 2008; Wright *et al.*, In press) and in 140 tree species across five neotropical sites (Poorter *et al.*, 2008), but this relationship has yet to be explored at a pan-tropical scale. Here, we present the results of analyses exploring the relationship between wood density and mortality in over 765 500 trees from 1639 species at 10 long-term forest census plots located across the Old and New World tropics. Our study improves on previous efforts by including a broad range of tropical forests across continents, a large standardized sampling effort within forests, and a single analytic framework.

We use a hierarchical Bayesian modeling approach (e.g. Clark, 2005; Gelman & Hill, 2007), which assumes that process model parameters of interest (such as species' mortality rates) are drawn from broader distributions. One goal of the approach is to produce accurate estimates of the parameters that describe these distributions, as opposed to simply estimating process model parameters directly from the data. There are several advantages to this approach. First, it permits us to incorporate the hierarchical structure of our data into the model, which allows us to separate variation among geographic locations, families and species from sampling error (Clark, 2005); standard frequentist methods often confound these sources of variation and overestimate true variance. Secondly, it permits us to include rare species with sparse sample data in our estimates of species mortality rates (Condit *et al.*, 2006). Recent analyses suggest that rare tree species within tropical forests tend to have functional trait values that are somewhat distinct from those of more common species (Baraloto *et al.*, 2009), indicating that rare species should be included in analyses in order to capture the full spectrum of trait variation within communities. Finally, the ability of hierarchal Bayesian approaches to characterize distributions of parameters at various levels within analyses permits the discussion of both the central tendencies and the degree of variation present within distinct components of our model.

Specifically, we ask three questions. (1) Is there support for a pan-tropical relationship between wood density and mortality rates across forest sites, and, if so, how variable is the relationship across sites? (2) Is there variation in the strength of the relationship across families? Finally, as the evolutionary nonindependence of related taxa can impact correlations between traits when taxa are analyzed out of phylogenetic context (Felsenstein, 1985), we ask (3) does the evolutionary history of taxa included in the study influence the relationship?

Materials and Methods

Data sources

We used previously published forest census data (Condit *et al.*, 2006) from 10 permanent tropical forest dynamics plots that are part of the Center for Tropical Forest Science (CTFS) network. The plots range in size from 20 to 52 hectares (Supporting Information Table S1), and are located in forests largely free from human disturbance. Details of the sites and the census protocols can be found elsewhere (Condit, 1998; Losos & Leigh, 2004; Condit *et al.*, 2006). At three sites (Barro Colorado Island, Panama; Pasoh, Malaysia; Mudumalai, India), data for multiple census intervals were available. We chose to use the longest census interval at these sites, although we present separate analyses of the intermediate census intervals for comparison in case census interval affects mortality rates (Sheil & May, 1996; Lewis *et al.*, 2004). In all analyses we expressed mortality in terms of annual rates. The Ituri forest site in the Democratic Republic of Congo has two plots, Edoro and Lenda, which we treated separately. Mean wood density, defined as the ratio of wood dry mass to fresh volume (Niklas, 1992; Chave *et al.*, 2006; Williamson & Wiemann, 2010), was taken largely from published compilations (Chave *et al.*, 2006, 2009; Zanne *et al.*, 2009) and unpublished data from J. Chave and N. Swenson. These database values are the best estimates of wood density currently available for many of the species in the study, although it may be valuable to revisit these analyses as more locally collected data become available. Only taxa for which we had species-level wood density determinations were included in our analyses; that is, we did not apply genus-level or family-level means to species lacking published wood density data. Species-level wood density estimates were available for 20–72% (mean 43%) of the species present at a site (Table S1).

Model 1: site-based analyses

First, we estimated parameters describing the relationship between wood density and mortality rates across species at each forest site. We used a hierarchical Bayesian approach and Metropolis–Hastings algorithms (e.g. Clark, 2005; Gelman & Hill, 2007) with noninformative (i.e. uniform) priors to estimate parameters describing the relationship between wood density and mortality rates across species at each forest site (cf. Condit *et al.*, 2006; Metz *et al.*, 2008).

Sites were analyzed independently. Across all species i at a site, we modeled a linear relationship with lognormal errors between the mortality rate constants, m_i, and wood density, wd_i, as:

$$m_i = a \cdot \text{wd}'_i + b' + \varepsilon \qquad \text{Eqn 1}$$

For analysis, we subtracted the global mean wood density value (across all species in all sites in the study) from each species' wood density (wd_i) to produce a centered wood density value wd'_i. Once mortality rates were estimated, wood density values were uncentered (as wd_i), and intercepts (b'_j) were adjusted accordingly for presentation (as b_j). We assumed that the species mortality rate constants, m_i, followed a lognormal distribution about a predicted mortality rate, μ_i, for a given wood density, wd_i. The parameters μ_i and σ describe the mean and standard deviation, respectively, of the logarithm of this distribution and capture the residual error ($\varepsilon \sim \text{lognormal}(0, \sigma)$) in the wood density–mortality relationship not captured elsewhere by other components of the model. The predicted mortality rate (μ_i) was not a parameter in the model but was calculated directly using a, wd'_i and b'.

The simple relationship between wood density and mortality described by Eqn 1 is the core of our analysis; however, we also wanted to partition variance in the relationship into several specific sources. By using a hierarchical approach, we are able to estimate parameters that describe variation in the relationship at different levels in the structure of our data: the census level, the family level, and the site level.

Census data In our model, mortality rate estimates (m_i) were assumed to depend both on the relationship of wood density and mortality, described above in Eqn 1, and on the observations of the survival of individual trees across a census period. These observations of tree survival can be subject to high error, particularly for rare species. Instead of using these observations as a direct measure of mortality, we used a probability model in the form of a binomial distribution (Condit *et al.*, 2006). We estimated a survival probability (θ_i) for individuals of each species i, based on the observed number of trees at the beginning of a census, N_i, and the observed number of survivors across the census interval, S_i. The binomial distribution permits the estimation of a finite and nonzero survival probability for a species even if all or none of the starting individuals survive over the census interval, as can be seen by comparing the observed vs fitted mortality rate constants in the supporting data set of a related analysis by Condit *et al.* (2006). This feature allows us to include many rarer species that would be excluded from traditional analyses. The annual survival probability is related to the annual mortality rate by the exponential function ($\theta = e^{-m}$). Thus, the probability of observing S survivors from N individuals for any species i is:

$$P(S_i | N_i, \mu_i, \sigma) = \int \text{Binom}(S_i | N_i, \theta_i) \cdot \text{lognormal}(m_i | \mu_i, \sigma) d\theta \qquad \text{Eqn 2}$$

Family level As preliminary results suggested that there is both a site and a taxonomic component to the relationship between wood density and mortality, we allowed the slope and intercept of the relationship between wood density and mortality to vary across families within a site. Thus, we expanded our model from Eqn 1 to include variation in the relationship attributable to family differences:

$$m_i = a_j \cdot \text{wd}'_i + b'_j + \varepsilon \qquad \text{Eqn 3}$$

Here a_j represents the slope of the relationship for family j to which species i belongs. Similarly , b'_j represents the intercept of the relationship for family j, and is an estimate of the mortality rate of a hypothetical species within the family at the global average wood density. One limitation of our approach is that plant family delineations are somewhat arbitrary, in that they represent clades of different ages. A more natural approach would consider phylogenetic relatedness in a continuous fashion; however, practical modeling constraints limited us to placing species into clades, and families were the most recognizable and tractable level at which to group species.

Site-wide parameters Family-level slopes (a_j) and log-transformed family-level intercepts ($\log_e(b'_j)$) were assumed to be jointly distributed in a bivariate normal distribution across all families at a site. This distribution was described by five plot-wide hyperparameters: the mean (α) and variance (SD_α^2) of the slopes of the families, the mean (β) and variance (SD_β^2) of the logarithms of the intercepts of the families, and the covariance between slope and intercept ($\text{Cov}_{\alpha,\beta}$). The means of this bivariate distribution (α, β) describe the relationship of an average family at a site, while the variances (SD_α^2 and SD_β^2) capture family-to-family variation. If family variation is unimportant at a site, the variances in slope and intercept across families (SD_α^2 and SD_β^2) should be estimated as 0. We assumed that residual unexplained error, σ, first introduced in the description of Eqn 1, was constant across all families at a site.

Thus, variation in the relationship between wood density and mortality is partitioned into several different sources. At the census level, the binomial distribution accounts for sampling error, including cases where species lost all or no individuals in a given census interval. At the site-wide level, the bivariate distribution of family slopes and intercepts allows for variation among families, and the lognormal distribution of mortality rates accounts for variation in mortality at a given wood density.

We ran 101 000 iterations of the Metropolis–Hastings algorithms for each forest over each census interval, discarding the first 1000 iterations (the 'burn-in' period) from the

final analysis. In each step all parameters were updated in turn. The site-wide parameters (α, SD_α^2, β, SD_β^2 and $Cov_{\alpha,\beta}$) were updated using the bivariate normal distribution of family slopes and intercepts that they describe. The family-level parameters (a_j, b_j' and σ) were updated using Eqn 3. The mortality rate constant, m_i, of each species was updated using the census-data level relationship described in Eqn 2.

To ensure that the Metropolis–Hastings algorithms thoroughly explored the range of possible parameter values, the step size used to propose a random new value of each parameter was adjusted during the initial 1000-iteration burn-in period until approx. 25% of the proposed steps were accepted. The step size was then held constant for the following 100 000 iterations, which were used to estimate the posterior distributions of the parameters. Visual inspection of the Markov-chain Monte Carlo (MCMC) chains for each site-wide parameter and the log likelihood values revealed that the posterior distributions had converged well before 1000 iterations.

We ran the Bayesian analyses with data for each site, using all tree species for which wood density data were available. While our plot network data included all trees ≥ 10 mm diameter at breast height (dbh), many tropical forest census plots work exclusively with trees ≥ 100 mm dbh. To check if our results were robust to this difference, we repeated our analysis after removing all stems of 10–99 mm dbh from our data. We also explored running the model with log-transformed mortality rates in order to permit comparisons with prior analyses, many of which have log-transformed mortality observations to meet the assumptions of parametric analyses. All analyses were performed in R version 2.7.2 (R Development Core Team, 2008), and code for Model 1 and a sample dataset are available as Supporting Notes S1 and S2.

Following these analyses, we used the 95% credible intervals of parameter estimates to determine which sites had nonzero slopes (α values) and to compare results across sites. To facilitate comparison with other studies, we evaluated the goodness of fit of the model at each forest by calculating Bayesian R^2 (Gelman & Pardoe, 2006; Gelman & Hill, 2007). This calculation compares the variance in the estimated species' mortality rates (m_i) in a forest to the variance of the residual errors about the predicted linear relationship defined by species' wood density and the corresponding family-level slope (a_j) and intercept (b_j') parameters. It does not account for variation explained at the census data level of the model (Eqn 2). Note that Bayesian R^2 averages over uncertainty in the regression coefficients and therefore usually produces lower estimates of the amount of variance explained by a model relative to a 'traditional' coefficient of determination R^2 (Gelman & Pardoe, 2006).

Finally, for graphical purposes we calculated the 95% confidence interval for the family and site-wide parameter portions of the model by sampling the bivariate normal distribution of family-level slopes and intercepts (defined by α, SD_α^2, β, SD_β^2 and $Cov_{\alpha,\beta}$), calculating predicted mortality at a range of wood density values, and adding within-family variation to each estimate using σ. This process was repeated 10 000 times and the 97.5% and 2.5% quantiles of the resulting distribution were calculated (shaded areas in Fig. 1). This procedure allows us to determine where 95% of randomly chosen species from randomly chosen families would be predicted to fall, and thus provides an estimate of the range of variability in the wood density–mortality relationship.

Model 2: family-based analyses

To address our second question about the role of family-level variation, we ran a second model that grouped species across sites by family. We then conducted a similar analysis for each family as we had done for each plot in Model 1, but Model 2 did not have the site-wide parameter portion of the model. Each family j was analyzed separately. The census data level of the model remains the same, but the family level was simplified to estimate a single slope (a_j), intercept (b_j') and residual error (σ_j). In cases where species occurred at multiple sites, only the data from the site with the most individuals were included, although our main conclusions were insensitive to including these extra observations (results not shown). We chose to restrict our analyses to families with 15 or more species in the data set.

Phylogenetic analyses

As a last step, we explored the phylogenetic component of the relationship between wood density and mortality in two ways. First, we tested the degree of phylogenetic conservatism (Lord et al., 1995; Blomberg et al., 2003) of wood density and estimated mortality rates using the Analysis of Traits (AOT) routine in the program PHYLOCOM (Webb et al., 2008). In order to do this, we created a phylogenetic tree of all taxa using PHYLOMATIC (Webb & Donoghue, 2005) and the angiosperm phylogeny R20050610 (archived at http://svn.phylodiversity.net/tot/megatrees/). Unresolved relationships between genera within families and species within genera were treated as polytomies. We used log-transformed estimates of mortality from Model 1, and averaged mortality rates across sites for species that occurred in multiple locations. Secondly, to control for phylogenetic nonindependence, we tested for a pan-tropical relationship between wood density and mortality with a phylogenetic independent contrasts (PICs) analysis of all taxa in the study (Felsenstein, 1985; Garland et al., 1992), again implemented in the AOT module of PHYLOCOM (Webb et al., 2008).
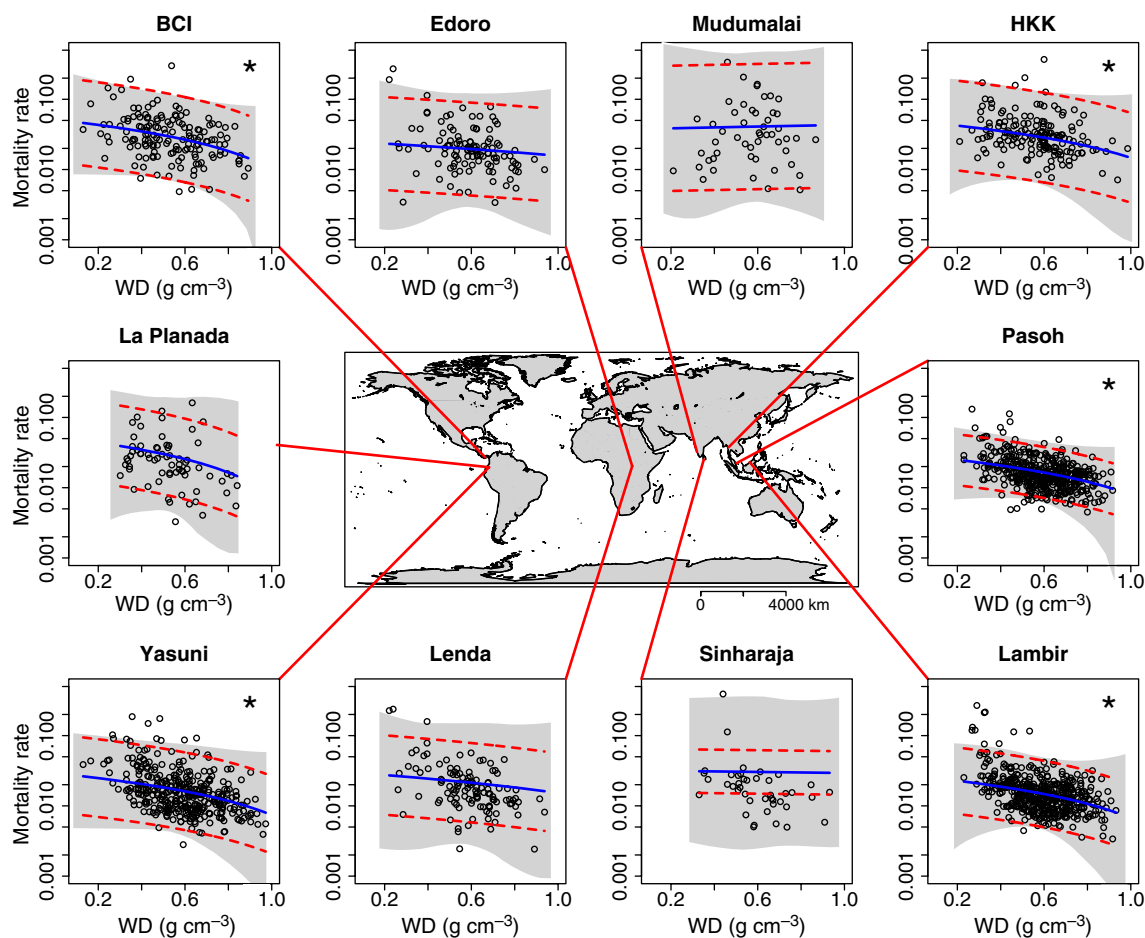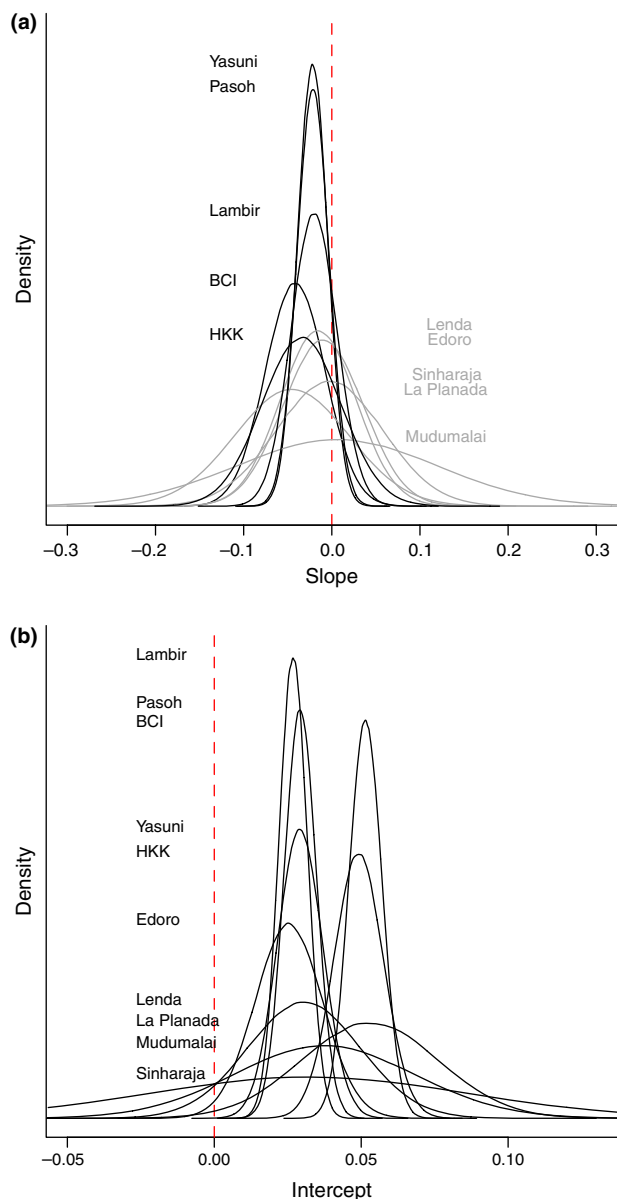
Fig. 1 The relationship between wood density (WD) and annual mortality rates for individual species (black points) from 10 forest census plots across the tropics, as described by Model 1. The solid line indicates the average family relationship as described by the site-wide slope α and intercept β; lines curve because the *y*-axis has been log-transformed for presentation. Dashed lines denote ± 2σ (within-family error) around the average family relationship. The shaded area indicates the 95% confidence interval in the model, reflecting variation both within and across families. At some sites the shaded area contracts around the global mean wood density (0.58 g cm^{-3}), reflecting the fact that data were centered on this value before analysis. An asterisk (*) denotes plots where site-wide slope (α) 95% credible interval estimates do not overlap 0 (see Tables 1 and S4). Note that the intercept of the average family relationship at Sinharaja is strongly influenced by two species, each the sole representative of their family (Melastomataceae and Vitaceae), with elevated mortality rates relative to the rest of the plot.

Results

Mortality rates declined with increasing wood density at five of the 10 sites in our study (Figs 1 and 2), where the 95% credible interval (CI) of the plot-wide slope (α) was < 0 (Table 1). Almost all of the individual families at these five sites (95–100%) had negative slope parameter (a_j) estimates (Fig. 3). Four sites (Edoro and Lenda in the Democratic Republic of Congo, Sinharaja in Sri Lanka, and La Planada in Colombia) had negative plot-wide slope (α) estimates, but the 95% CI included 0. At these four sites the majority of families (52–100%) had negative slopes (Fig. 3). One site (Mudumalai, India) had a positive plot-wide slope with a 95% CI including 0 (Table 1). The slope of the relationship was indistinguishable among the five sites with clear

negative relationships (all slope 95% CIs for α overlapped; Table 1, Fig. 2a), although these sites did differ in the plot-wide intercept (β) of the relationship (Table 1, Fig. 2b). Specifically, BCI (Panama) and HKK (Thailand) had higher intercepts (corresponding to higher mortality rates at the global mean wood density) than Lambir (Malaysia), Pasoh (Malaysia), and Yasuní (Ecuador) (Table 1, Fig. 2b). These main results were also seen in an alternative version of the model operating on log-transformed mortality rates (Table S5 and Fig. S2).

Site-based Model 1 explained an average of 40% of the variation in mortality rates across all sites (Bayesian R^2; Table 1), ranging from 13% at BCI to 83% at Sinharaja. Several of the sites with weak plot-wide relationships (α CI estimates include 0) had high Bayesian R^2 values relative to

Fig. 2 A comparison of the fitted hyperdistributions of family slopes (a) and intercepts (b) of the relationship between wood density and mortality rates from the 10 forest plots in our study, as described by Model 1. Gaussian curves are plotted using the slope mean and standard deviation (α and SD_α) in (a) and the intercept mean and standard deviation (β and SD_β) in (b). The area underneath each normalized curve sums to 1. Intercepts have been converted to a normal scale for presentation. Dashed lines indicate a slope or intercept of 0. Labels are placed at the same height as the apex of each distribution. Broader distributions indicate a greater family-to-family variation in the relationship at a given site. In (a), forests with slope hyperdistribution means (α) with 95% credible intervals that did not include 0 are plotted and labeled in black; those that did include 0 are plotted and labeled in gray. Note that the credible intervals themselves are not depicted in the figure – see Table 1.

other sites (e.g. Sinharaja). If just the five sites with a clear site-wide negative relationship are considered, the average Bayesian R^2 is lower (0.31).

The three sites with multiple censuses exhibited noticeable variation in the wood density–mortality relationship among sample intervals (Table S2). For example, the goodness of fit (Bayesian R^2) at BCI was the highest in our study in the initial 1982–1985 census interval (0.32), which corresponds to a period of elevated mortality associated with the severe 1983 El Niño-driven drought (Condit *et al.*, 1995), but declined steadily in subsequent censuses to 0.22 in the most recent (2000–2005) interval (Table S2). The slopes did not show a clear trend across intervals. In contrast, the relationship between wood density and mortality at Pasoh became more strongly negative (lower α estimates) over the three census intervals in our data set. Restricting our analysis to trees of $\geq$ 100 mm dbh produced comparable estimates of the relationship between wood density and mortality (Table S3), albeit with larger credible intervals on some parameters, which is not surprising given the smaller number of species and individuals present in this reduced sample.

When we grouped species by family instead of site in Model 2, we found considerable variation in the relationship between wood density and mortality. Ten of the 27 most species-rich families in our study (with $\geq$ 15 species) had a negative relationship (a_j 95% CIs < 0), with Euphorbiaceae and Melastomataceae having the most negative slopes. Two families (Ebenaceae and Combretaceae) had a moderately positive slope (Figs 4 and S1; Table 2) and one (Myrtaceae) had a flat slope. The remaining 14 families had negative estimated slopes with a CI including 0 (Table 2). The average Bayesian R^2 across families was 13%.

Our phylogenetic analyses found strong phylogenetic conservatism of both wood density (PHYLOCOM AOT test, $P = 0.001$) and mortality rate constants ($P = 0.001$). The analysis of phylogenetic independent contrasts (PICs) revealed that the pan-tropical relationship between wood density and mortality remained significantly negative after accounting for phylogenetic relationships (PHYLOCOM PICS test: 447 contrasts, 168 positive, sign test $P < 0.0001$, correlation coefficient of contrasts = -0.295).

Discussion

Our results show that there is support across the tropics for a negative relationship between wood density and annual mortality rates within forest communities (Figs 1–3). An average of 31% of the variation in mortality at a site with a negative relationship can be explained by variation in wood density (Table 1). In addition to the five sites with significantly negative plot-wide slopes, four sites exhibited negative trends with CIs on the slope that included 0. Within these four sites the majority of individual families had negative relationships (Fig. 3). It should be noted that there was a geographic pattern to the strength of the relationship; the patterns were strongest at sites in South America and

Table 1 Site-wide parameter estimates and measures of goodness-of-fit (Bayesian R^2) for the relationship between wood density and mortality at 10 sites as described in Model 1

Site	Country	Year	α	SD_α	β	SD_β	$Cov_{\alpha,\beta}$	σ	Bayesian R^2
Barro Colorado Island (BCI)	Panama	1982–2005	−0.041 (−0.068 to −0.016)	0.034 (0.012 to 0.067)	0.0512 (0.047 to 0.0578)	0.0056 (0.0017 to 0.014)	0 (−0.004 to 0.003)	0.698 (0.604 to 0.807)	0.14
Huai Kha Kaeng (HKK)	Thailand	1993–1999	−0.034 (−0.067 to 0)	0.045 (0.016 to 0.086)	0.0488 (0.0428 to 0.0583)	0.0084 (0.0024 to 0.0217)	0 (−0.007 to 0.006)	0.735 (0.606 to 0.888)	0.20
Ituri-Edoro	Democratic Republic of Congo	1994–2000	−0.01 (−0.042 to 0.025)	0.046 (0.013 to 0.092)	0.0255 (0.018 to 0.0454)	0.0115 (0.0018 to 0.053)	−0.003 (−0.022 to 0.011)	0.761 (0.561 to 0.992)	0.39
Ituri-Lenda	Democratic Republic of Congo	1994–2000	−0.015 (−0.048 to 0.016)	0.043 (0.01 to 0.102)	0.0303 (0.0203 to 0.06)	0.0192 (0.0043 to 0.0996)	−0.004 (−0.026 to 0.013)	0.651 (0.458 to 0.869)	0.56
La Planada	Colombia	1997–2003	−0.046 (−0.102 to 0.003)	0.065 (0.018 to 0.135)	0.0532 (0.0399 to 0.0979)	0.0233 (0.0048 to 0.1558)	0.002 (−0.031 to 0.038)	0.661 (0.507 to 0.862)	0.46
Lambir	Malaysia	1992–1997	−0.02 (−0.032 to −0.009)	0.026 (0.015 to 0.04)	0.0267 (0.0246 to 0.0298)	0.0048 (0.0026 to 0.0089)	−0.001 (−0.004 to 0.002)	0.544 (0.488 to 0.603)	0.39
Mudumalai	India	1988–2000	0.006 (−0.096 to 0.114)	0.113 (0.029 to 0.282)	0.0373 (0.0163 to 0.1331)	0.0306 (0.0041 to 0.3219)	0 (−0.065 to 0.069)	1.026 (0.749 to 1.379)	0.26
Pasoh	Malaysia	1987–2000	−0.021 (−0.03 to −0.012)	0.018 (0.01 to 0.028)	0.029 (0.0269 to 0.0319)	0.0054 (0.0033 to 0.009)	−0.001 (−0.003 to 0.001)	0.417 (0.378 to 0.46)	0.44
Sinharaja	Sri Lanka	1995–2001	−0.003 (−0.062 to 0.043)	0.061 (0.015 to 0.141)	0.0322 (0.0107 to 0.1781)	0.0538 (0.0061 to 1.1745)	−0.007 (−0.067 to 0.044)	0.356 (0.061 to 0.811)	0.83
Yasuni	Ecuador	1996–2003	−0.022 (−0.032 to −0.011)	0.017 (0.007 to 0.032)	0.0293 (0.0258 to 0.035)	0.0077 (0.0037 to 0.0162)	−0.001 (−0.005 to 0.002)	0.637 (0.564 to 0.718)	0.39

Site-wide parameters include the mean (α) and standard deviation (SD_α) of the family slopes, the mean (β) and standard deviation (SD_β) of the family intercepts (converted to a normal scale for presentation here), and the covariance ($Cov_{\alpha,\beta}$) between slope and intercept. The parameter σ describes the residual error in log annual mortality rates about each family's relationship. Parameters were estimated using the longest interval of survival data available at each site. Values are the mean of the posterior distributions for each parameter, estimated using Metropolis–Hastings algorithms in a Bayesian hierarchical model. The 95% credible interval for each parameter's distribution is given in parentheses. Slopes (a_j) and intercepts (b_j) for individual families within plots are shown in Supporting Information Table S4.
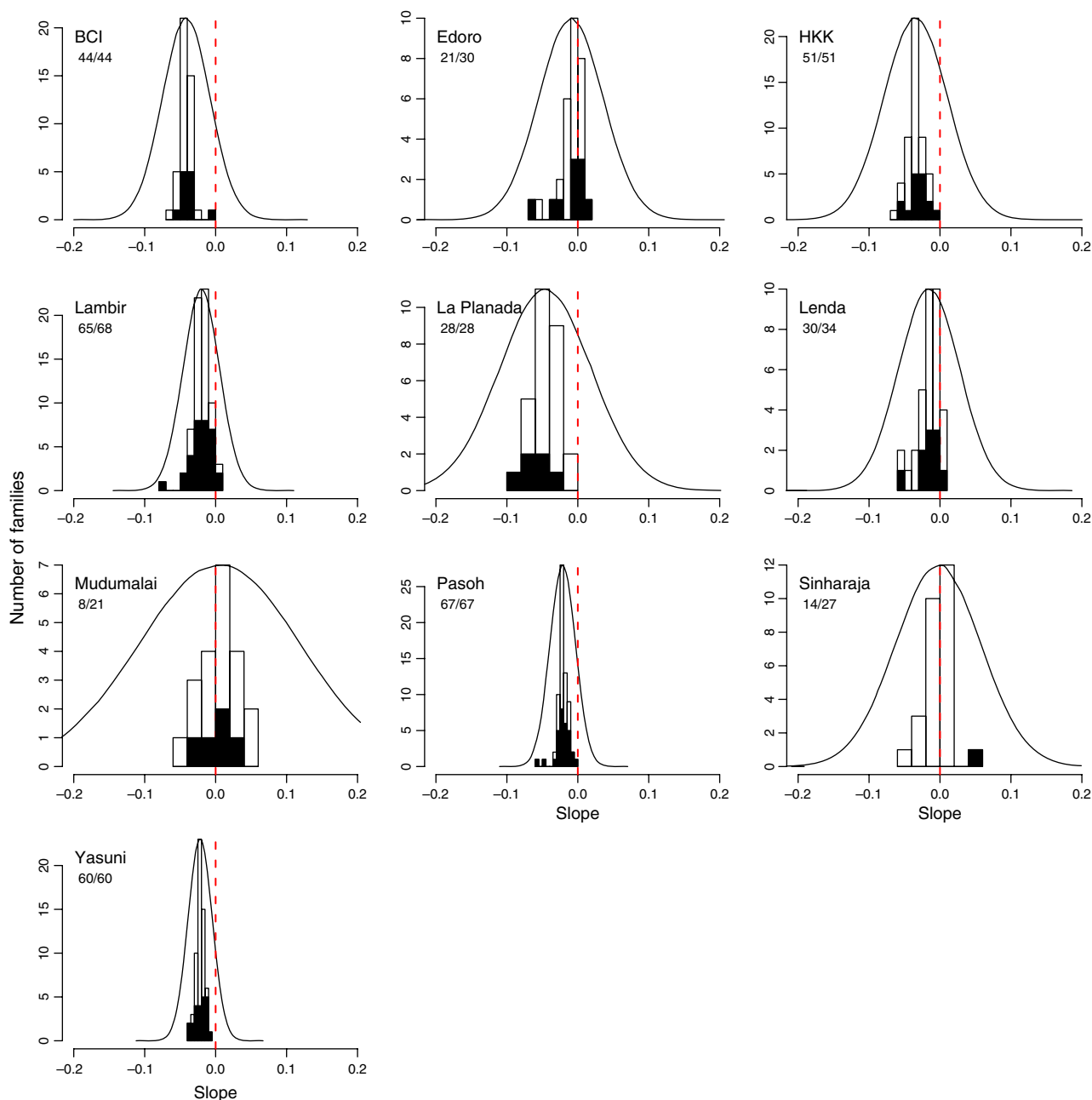
Fig. 3 Summary of family-to-family variation in the slope of the wood density–mortality relationship across 10 different forest plots, as described by Model 1. Histograms of the family-level slope (a_i) estimate for families with four or more species at the site are shown as filled bars; additional families with fewer species are shown as open bars. The fitted hyperdistribution of family slopes (see Fig. 2a), described by α and SD_α, is traced above each histogram, and a slope of 0 is indicated by the dashed line. Note that the scale of the y-axis differs across panels. The proportion of families with negative slope (a_i) estimates is indicated underneath the site label for each panel. Note that at three sites (La Planada, Edoro and Lenda) the majority of families were estimated as having negative slopes (a_i), even though the credible interval on the mean of the hyperdistribution of slopes (α) included 0 (see Table 1).

Southeast Asia, intermediate in Africa, and weakest on the Indian subcontinent (Fig. 1). This variation may be attributable to differences in sample size among sites that mirrored these trends (Table S1, although the correlation between richness and plot-wide slope or richness and Bayesian R^2 was not significant), or to real differences in

mortality agents and mechanisms across forests. For example, the biggest outlier in our study, Mudumalai in India (Fig. 1), has a set of mortality agents that is unique relative to other sites in our study, including frequent fires that disproportionately kill small trees (Sukumar et al., 1998) and a very high density of large browsing mammals such as the
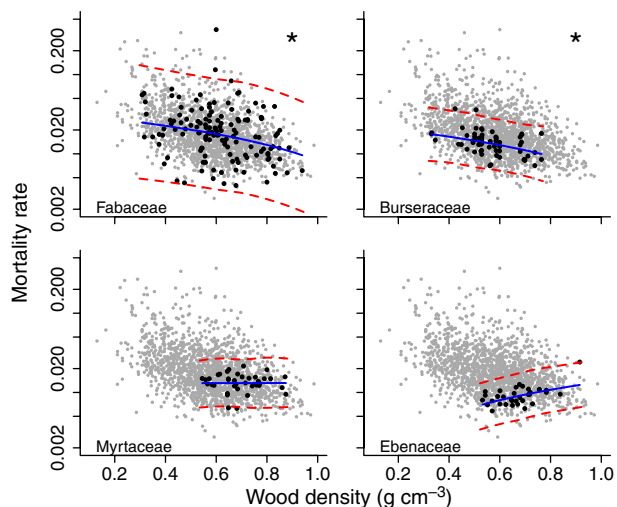
Fig. 4 Examples of the variation in the relationship between wood density and mortality for species in four families (black points), as estimated by Model 2. Gray points represent the entire global data set. The solid line indicates the family relationship as described by the slope (a_i) and intercept (b_i) parameters; dashed lines indicate the 95% confidence interval of the model, reflecting within-family variation (σ). Lines curve because the y-axis has been log-transformed for presentation. An asterisk (*) denotes families where slope (a_i) 95% credible interval estimates do not overlap 0 (see Tables 2). For additional families see plots in Supporting Information Fig. S1 and parameter estimates in Table 2.

Asian elephant (Sukumar *et al.*, 2004). The sites in our study vary in climatic conditions such as mean annual rainfall and length of dry season (Losos & Leigh, 2004), and, while there was no significant relationship between these attributes and the slope or Bayesian R^2 values from Model 1 (linear regression, $P > 0.05$), it would be valuable to re-examine this relationship as data from more sites become available.

While there are some obvious limitations (see discussion in Materials and Methods) to grouping species into families within sites and allowing families to vary, as we did in Model 1, we would argue that the limitations are out-weighed by our ability to include some evolutionary infor-mation in our estimation of the relationship between wood density and mortality at individual sites. It is important to note that our model was free to estimate that individual family distinctions were unimportant; were this the case, the distribution of family slopes and intercepts within a site would have no variance (SD_α^2 and SD_β^2 would be esti-mated as 0). This was not the case in our results – Model 1 estimated a range of family relationships within plots (e.g. Figs 2 and 3), and many families had slope (a_j) or intercept (b_j) estimates that differed from the overall plot slope (α) and intercept (β) estimates (Tables 1 and S4). Simplifying Model 1 to remove family effects entirely did not signifi-cantly alter the plot-wide results presented here (results not shown).

Mechanisms

The relationship that we observed may occur because wood density is an indicator of features of the stem that reduced mortality risk, or because wood density is a correlate of other traits beyond the stem itself that impact mortality rates. Several lines of evidence support the former, more direct connection. Species with dense wood are thought to have reduced vulnerability to the mortality agents of drought-induced embolism (Hacke *et al.*, 2001; Jacobsen *et al.*, 2005), pathogen attack (Augspurger & Kelly, 1984), and mechanical breakage (Niklas, 1992). In tropical forests, wood density is often relatively uncorrelated with other key functional traits such as leaf economics traits and seed size (with the exception of leaf size; see Wright *et al.*, 2007; Kraft *et al.*, 2008), further suggesting a direct, mechanistic connection between wood density and mortality.

The negative relationship between wood density and tree mortality may occur as a result of different constraints oper-ating on opposing corners of the bivariate space defined by wood density and mortality. That species do not have both low wood density and low mortality rates (Figs 1 and 4) may result from the increased susceptibility light-wooded species have to a range of mortality agents, as outlined in the preceding paragraph. In contrast, the lack of species demonstrating both high wood density and high mortality rates may reflect a physiological constraint; dense wood is expensive (in terms of carbon) to construct. Species with a high mortality rate, and therefore a short life, would have little time to accumulate the carbon to invest in the con-struction of dense wood, and would do so at the expense of allocating resources to reproduction or other strategies to offset the fitness costs of high mortality.

Evolutionary history

The relationship between wood density and mortality that we observed at the plot level (Table 1) was generally more consistent than the within-family relationships (Table 2). Some families exhibited strong negative relationships that mirrored our plot-level results (e.g. Euphorbiaceae and Fabaceae), and many exhibited a weak negative relationship (e.g. Annonaceae and Clusiaceae). However, in certain families mortality is apparently insensitive to variation in wood density (e.g. Myrtaceae and Sapotaceae). This result is also reflected in the fact that the hyperdistribution of family slopes for each site from Model 1 crosses zero (Fig. 2), indicating that our model estimated that there are families at each site (whether or not they were measured in our data set) that do have a flat or moderately positive rela-tionship between wood density and mortality. The lack of relationship within certain families may result from higher within-family susceptibility to mortality agents that are unrelated to wood density (e.g. herbivory pressure), from

Table 2 Parameter estimates, species per family (N) and measures of goodness-of-fit (Bayesian R^2) for the relationship between wood density and mortality rates for species grouped by families across 10 tropical forest sites, as described by Model 2

Order	Family	N	a	b	σ	Bayesian R^2	Slope group
Ericales	Ebenaceae	34	0.014 (0.029 to 0)	−0.0004 (0.0014 to −0.002)	0.341 (0.509 to 0.219)	0.14	n.s.
	Lecythidaceae	18	−0.005 (0.019 to −0.028)	0.0117 (0.0166 to 0.0082)	0.617 (1.105 to 0.306)	0.10	n.s.
	Sapotaceae	68	−0.002 (0.01 to −0.014)	0.0103 (0.0125 to 0.0084)	0.452 (0.596 to 0.336)	0.01	n.s.
Fabales	Fabaceae	138	−0.024 (−0.005 to −0.043)	0.0322 (0.0355 to 0.0292)	0.828 (0.962 to 0.711)	0.05	a,b
Gentianales	Apocynaceae	21	−0.027 (−0.003 to −0.053)	0.0273 (0.0315 to 0.0242)	0.355 (0.721 to 0.046)	0.49	a,b
	Rubiaceae	52	−0.01 (0.027 to −0.046)	0.0244 (0.0293 to 0.0201)	0.68 (0.88 to 0.523)	0.00	n.s.
Lamiales	Bignoniaceae	16	−0.028 (0.026 to −0.082)	0.0378 (0.0543 to 0.0275)	0.973 (1.65 to 0.596)	0.14	n.s.
	Lamiaceae	19	−0.03 (0.029 to −0.078)	0.0368 (0.0503 to 0.0288)	0.842 (1.466 to 0.426)	0.14	n.s.
Laurales	Lauraceae	95	−0.032 (−0.02 to −0.04)	0.0353 (0.0373 to 0.0335)	0.44 (0.542 to 0.353)	0.29	a,b
Magnoliales	Annonaceae	54	−0.017 (0.003 to −0.036)	0.0251 (0.0283 to 0.0222)	0.68 (0.851 to 0.539)	0.05	n.s.
	Myristicaceae	43	−0.006 (0.015 to −0.024)	0.0158 (0.0183 to 0.0137)	0.428 (0.58 to 0.31)	0.00	n.s.
Malpighiales	Chrysobalanaceae	19	−0.044 (0.002 to −0.09)	0.0494 (0.0609 to 0.0394)	0.509 (0.827 to 0.303)	0.21	n.s.
	Clusiaceae	42	−0.035 (0.005 to −0.069)	0.0411 (0.0483 to 0.0353)	0.845 (1.118 to 0.643)	0.08	n.s.
	Euphorbiaceae	61	−0.093 (−0.064 to −0.123)	0.0789 (0.0847 to 0.0739)	0.792 (0.986 to 0.638)	0.39	a,c
	Phyllanthaceae	44	−0.03 (0.022 to −0.082)	0.0395 (0.0466 to 0.034)	0.656 (0.876 to 0.487)	0.03	n.s.
	Salicaceae	27	−0.038 (0.079 to −0.157)	0.0525 (0.0679 to 0.041)	0.728 (1.057 to 0.496)	−0.01	n.s.
Malvales	Dipterocarpaceae	89	−0.034 (−0.016 to −0.053)	0.039 (0.0421 to 0.0363)	0.613 (0.743 to 0.506)	0.16	a,b
	Malvaceae	77	−0.029 (−0.005 to −0.051)	0.0302 (0.034 to 0.0272)	0.845 (1.036 to 0.691)	0.09	a,b
Myrtales	Combretaceae	17	0.015 (0.071 to −0.035)	0.0022 (0.0114 to −0.004)	0.659 (1.174 to 0.359)	0.05	n.s.
	Melastomataceae	26	−0.106 (−0.009 to −0.204)	0.1128 (0.1408 to 0.0935)	1.046 (1.467 to 0.755)	0.18	a,b,c
	Myrtaceae	38	0 (0.023 to −0.024)	0.0131 (0.0168 to 0.01)	0.358 (0.518 to 0.239)	−0.01	n.s.
Oxalidales	Elaeocarpaceae	15	−0.033 (0.031 to −0.075)	0.0381 (0.0494 to 0.0307)	0.739 (1.326 to 0.399)	0.19	n.s.
Rosales	Moraceae	105	−0.045 (−0.029 to −0.058)	0.0442 (0.048 to 0.0409)	0.833 (1.013 to 0.68)	0.22	a,b
Sapindales	Anacardiaceae	37	−0.015 (0.006 to −0.032)	0.0213 (0.025 to 0.0184)	0.623 (0.875 to 0.441)	0.07	n.s.
	Burseraceae	60	−0.018 (−0.001 to −0.034)	0.0237 (0.0253 to 0.0221)	0.391 (0.503 to 0.302)	0.11	a,b
	Meliaceae	95	−0.017 (0.008 to −0.042)	0.0274 (0.0306 to 0.0246)	0.631 (0.765 to 0.522)	0.03	n.s.
	Sapindaceae	36	−0.06 (−0.026 to −0.097)	0.0605 (0.0683 to 0.0543)	0.604 (0.888 to 0.403)	0.32	a,b,c

Only families with ≥ 15 species are presented here. We estimated the slope (a), intercept (b) and standard deviation of the logarithm of annual mortality rates (σ) using Metropolis–Hastings algorithms in a Bayesian hierarchical model. Values are the mean of the posterior distributions for each parameter with the 95% credible interval (CI) for each parameter's distribution shown in parentheses. Families with nonzero overlapping slope CIs are grouped by letters; an n.s. in this column indicates that the slope CIs include 0.

low within-family variation in wood density (e.g. Salicaceae), or from consistently low mortality rates across the family. For example, both Myrtaceae and Sapotaceae are composed of species with relatively high wood density and generally low mortality rates that may be attributable in part to additional investment in defenses (cytotoxic organic compounds in Myrtaceae and latex borne in phloem canals in Sapotaceae; McNair, 1932; Regnault-Roger, 1997; Smith *et al.*, 2004). A lack of a relationship may also be attributable to poor statistical power resulting from low within-family species sampling; however, the fact that some of the most species-rich families (e.g. Sapotaceae) had slopes that were indistinguishable from 0 suggests that power was not the culprit in all cases. Further, we would not expect to see the observed variation in the family-level parameter estimates in the plot-wide analyses (Fig. 3) if variation in sample size was the sole cause of variation among families. Rather, family-level estimates would collapse to the side-wide mean estimate, and variation attributable to sample size would be accounted for elsewhere.

Finally, it should be noted that many families occupied a distinct and relatively restricted portion of the bivariate space defined by wood density and mortality (Figs 4 and S1), a pattern that is consistent with the high degree of phylogenetic conservatism that we detected for both traits. Taken together, our family-level analysis suggests that the consistent negative relationship we observed within communities results from two related but distinct family-level components: negative wood density–mortality relationships within many families, and turnover across families where mortality varies little with wood density.

Future directions

As plant ecology moves toward an increasing emphasis on functional traits, there is a growing need to solidify our understanding of connections between traits and variation in plant performance. Our results indicate that wood density is a functional trait that is well worth considering in studies focused on life history strategies, even though wood density was not a component of some early plant strategy schema (e.g. Westoby, 1998). Collecting wood density data may require increased effort relative to other commonly measured functional traits (Cornelissen *et al.*, 2003; Williamson & Wiemann, 2010), but these data are correlated with substantial variation in demographic rates among species.

Here we have outlined a straightforward application of a hierarchical Bayesian approach to a relatively focused question at the intersection of functional ecology and demography. As additional trait and demographic data become available, this type of analysis can easily be applied to them separately or in a multivariate context. It remains to be seen whether other commonly measured functional traits are as strongly related to mortality as wood density, although several analyses with multiple traits suggest that wood density may be a better predictor than many other traits (Poorter *et al.*, 2008; Wright *et al.*, In press). Large geographic-scale analyses will play an important role in efforts to characterize strategy variation among plant species.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Plots of all 27 family-level relationships from Model 2.

Fig. S2 Alternative version of selected panels of Fig. 1 for Model 1, run with log mortality rates.

Table S1 Details of forest censuses used in this analysis

Table S2 Site-wide parameter estimates and measures of goodness-of-fit (Bayesian R^2) for the relationship between wood density and mortality (as described in Model 1) for intermediate census intervals at sites where data for more than one census interval were available

Table S3 Mean site-wide parameter estimates and measures of goodness-of-fit (Bayesian R^2) for the relationship between wood density and mortality rates for large trees at all sites as described in Model 1

Table S4 Family slope (a) and intercept (b) parameters for each site in Model 1

Table S5 Alternative version of Table 1 for Model 1 run with log-transformed mortality data, showing site-wide parameter estimates and measures of goodness-of-fit (Bayesian R^2) for the relationship between wood density and mortality at 10 sites

Notes S1 Code to run Model 1 in R.

Notes S2 Sample data set for Notes S1.

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The relationship between wood density and tropical tree mortality in a

global dataset

Nathan J. B. Kraft, Margaret R. Metz, Richard S. Condit, Jérôme Chave

Tables S1-S5, including details about each of the forest census plots, additional parameter estimates from Model 1, and results of alternative analyses

Figs S1 (2 files) and S2

Notes S1 R code for model 1

Notes S2 Sample dataset for Notes S1.

Table S1 Details of forest censuses used in this analysis, including the number of species and stems at each forest dynamics plot in each census period, and the number of species and stems for which wood density estimates were available for use in these analyses.

Site	Location	Interval	Plot Size (ha)	Plot Richness	Analysis Richness	Species Analyzed (%)	Plot Stems	Analysis Stems	Stems Analyzed (%)	Mean stems per species (range)
BCI	Panama	82-05	50	304	152	50.00%	235,275	171,803	73.02%	1,130 (1 - 39,829)
		82-85	50	304	152	50.00%	234,675	171,375	73.03%	1,127 (1 - 39,745)
		85-90	50	303	152	50.17%	241,560	176,878	73.22%	1,164 (1 - 41,013)
		90-95	50	302	155	51.32%	243,710	181,053	74.29%	1,168 (1 - 40,398)
		90-05	50	302	155	51.32%	243,914	181,198	74.29%	1,103 (1 - 36,060)
		95-00	50	301	156	51.83%	228,952	172,112	75.17%	1,027 (1 - 31,928)
		00-05	50	299	157	52.51%	213,709	161,232	75.44%	229 (1 - 5,491)
HKK	Thailand	93-99	50	292	167	57.19%	78,775	38,296	48.61%	288 (1 - 15,843)
Ituri- Edoro	Dem. Rep. of Congo	94-00	20	363	116	31.96%	161,687	33,457	20.69%	196 (1 - 10,292)
Ituri- Lenda	Dem. Rep. of Congo	94-00	20	349	118	33.81%	135,961	23,169	17.04%	657 (1 - 4,254)
La Planada	Colombia	97-03	25	179	69	38.55%	98,312	45,329	46.11%	330 (1 - 8,403)
Lambir	Malaysia	92-97	52	1179	482	40.88%	330,104	159,045	48.18%	390 (1 - 5,175)
Mudumalai	India	88-00	50	71	51	71.83%	25,924	19,889	76.72%	390 (1 - 5,170)
		88-92	50	71	51	71.83%	25,927	19,891	76.72%	243 (1 - 2,677)
		92-96	50	68	51	75.00%	17,999	12,416	68.98%	217 (1 - 2,603)
		92-00	50	68	51	75.00%	18,014	12,425	68.97%	423 (1 - 6,459)
		96-00	50	65	49	75.38%	15,686	10,626	67.74%	425 (1 - 6,501)
Pasoh	Malaysia	87-00	50	811	447	55.12%	332,656	189,097	56.84%	413 (1 - 6,359)
		87-90	50	811	447	55.12%	334,828	190,132	56.78%	424 (1 - 6,726)
		90-95	50	811	448	55.24%	325,147	185,061	56.92%	440 (1 - 5,986)
		90-00	50	811	448	55.24%	323,993	184,565	56.97%	184 (1 - 2,320)
		95-00	50	815	448	54.97%	334,633	189,853	56.73%	1,130 (1 - 39,829)
Sinharaja	Sri Lanka	95-01	25	205	42	20.49%	205,088	18,496	9.02%	1,127 (1 - 39,745)
Yasuní	Ecuador	96-03	25	1104	364	32.97%	143,901	66,971	46.54%	1,164 (1 - 41,013)

Table S2 Site-wide parameter estimates and measures of goodness-of-fit (Bayesian R^2) for the relationship between wood density and mortality (as described in Model 1) for intermediate census intervals at sites where data for more than one census interval were available. Site-wide parameters include the mean (α) and standard deviation (sd_α) of the family slopes, the mean (β) and standard deviation (sd_β) of the family intercepts, and the covariance ($Cov_{\alpha,\beta}$) between slope and intercept. The parameter σ describes the residual error in log annual mortality rates about each family's relationship. Values are the mean of the posterior distributions for each parameter, estimated using Metropolis-Hastings algorithms in a Bayesian hierarchical model. The 95% credible interval for each parameter's distribution is given in parentheses.

Site	country	year	α	sd_α	β	sd_β	$Cov_{\alpha,\beta}$	σ	Bayesian R^2
Barro Colorado Island	Panama	82-85	-0.057 (-0.087 - -0.029)	0.04 (0.015 - 0.077)	0.0601 (0.0551 - 0.0681)	0.0067 (0.0013 - 0.0179)	0 (-0.006 - 0.005)	0.679 (0.575 - 0.801)	0.32
		85-90	-0.041 (-0.062 - -0.021)	0.027 (0.009 - 0.052)	0.044 (0.0402 - 0.0501)	0.0054 (0.0015 - 0.0139)	0 (-0.005 - 0.003)	0.702 (0.592 - 0.829)	0.29
		90-95	-0.044 (-0.067 - -0.022)	0.032 (0.007 - 0.062)	0.0485 (0.044 - 0.0554)	0.0061 (0.0015 - 0.0157)	0 (-0.005 - 0.004)	0.705 (0.601 - 0.824)	0.29
		95-00	-0.051 (-0.083 - -0.023)	0.044 (0.017 - 0.082)	0.0589 (0.0537 - 0.0669)	0.0079 (0.0027 - 0.0188)	0 (-0.007 - 0.006)	0.656 (0.558 - 0.768)	0.22
		00-05	-0.044 (-0.072 - -0.016)	0.042 (0.015 - 0.078)	0.0509 (0.0462 - 0.0584)	0.0063 (0.0019 - 0.0163)	0 (-0.006 - 0.004)	0.729 (0.618 - 0.857)	0.22
Mudumalai	India	88-92	0.017 (-0.104 - 0.143)	0.132 (0.033 - 0.325)	0.0507 (0.0118 - 0.3358)	0.0698 (0.0076 - 1.656)	-0.003 (-0.114 - 0.096)	0.957 (0.655 - 1.345)	0.39
		92-96	-0.024 (-0.179 - 0.121)	0.153 (0.021 - 0.404)	0.0646 (0.0365 - 0.2191)	0.0381 (0.0048 - 0.5626)	-0.002 (-0.105 - 0.094)	1.225 (0.852 - 1.694)	0.17
		96-00	-0.019 (-0.117 - 0.073)	0.096 (0.022 - 0.252)	0.0457 (0.0248 - 0.1935)	0.0319 (0.0032 - 0.685)	-0.002 (-0.071 - 0.06)	1.189 (0.779 - 1.695)	0.24
Pasoh	Malaysia	87-90	-0.011 (-0.018 - -0.004)	0.013 (0.006 - 0.021)	0.0177 (0.0163 - 0.0197)	0.0032 (0.0017 - 0.0056)	0 (-0.002 - 0.001)	0.414 (0.362 - 0.472)	0.39
		90-95	-0.019 (-0.028 - -0.011)	0.017 (0.01 - 0.027)	0.0264 (0.0244 - 0.0292)	0.005 (0.0028 - 0.0084)	-0.001 (-0.003 - 0.001)	0.419 (0.374 - 0.468)	0.44
		95-00	-0.026 (-0.038 - -0.012)	0.027 (0.015 - 0.042)	0.0351 (0.0325 - 0.0385)	0.0059 (0.0033 - 0.0101)	-0.001 (-0.005 - 0.002)	0.459 (0.411 - 0.512)	0.41

Table S3 Mean site-wide parameter estimates and measures of goodness-of-fit (Bayesian R^2) for the relationship between wood density and mortality rates for large trees (>100 mm dbh) at all sites as described in Model 1. Site-wide parameters include the mean (α) and standard deviation (sd_α) of the family slopes, the mean (β) and standard deviation (sd_β) of the family intercepts, and the covariance ($Cov_{\alpha,\beta}$) between slope and intercept. The parameter σ describes the residual error in log annual mortality rates about each family's relationship. Values are the mean of the posterior distributions for each parameter, estimated using Metropolis-Hastings algorithms in a Bayesian hierarchical model. The 95% credible interval for each parameter's distribution is given in parentheses.

Site	year	α	sd_α	β	sd_β	$Cov_{\alpha,\beta}$	σ	Bayesian R^2
Barro Colorado Island	82-85	-0.035 (-0.066 - -0.004)	0.04 (0.012 - 0.081)	0.0471 (0.0393 - 0.0617)	0.0133 (0.0044 - 0.038)	0 (-0.01 - 0.011)	0.609 (0.461 - 0.779)	0.39
	82-05	-0.029 (-0.055 - -0.001)	0.032 (0.009 - 0.068)	0.043 (0.0359 - 0.0561)	0.0122 (0.004 - 0.0336)	0 (-0.009 - 0.007)	0.748 (0.62 - 0.896)	0.21
	85-90	-0.028 (-0.051 - -0.005)	0.031 (0.011 - 0.062)	0.035 (0.0282 - 0.0509)	0.0117 (0.0029 - 0.0451)	0 (-0.01 - 0.009)	0.775 (0.6 - 0.979)	0.37
	90-95	-0.021 (-0.042 - 0)	0.028 (0.008 - 0.058)	0.0297 (0.0238 - 0.042)	0.0106 (0.0034 - 0.0338)	0 (-0.009 - 0.009)	0.656 (0.504 - 0.826)	0.43
	95-00	-0.024 (-0.048 - 0)	0.034 (0.01 - 0.065)	0.0337 (0.029 - 0.0421)	0.0074 (0.0022 - 0.0202)	0 (-0.006 - 0.007)	0.596 (0.46 - 0.75)	0.30
	00-05	-0.022 (-0.047 - 0.002)	0.032 (0.01 - 0.065)	0.0345 (0.0291 - 0.0446)	0.0088 (0.0027 - 0.0244)	0 (-0.007 - 0.006)	0.65 (0.503 - 0.815)	0.24
Huai Kha Kaeng	93-99	-0.001 (-0.021 - 0.017)	0.024 (0.01 - 0.045)	0.0152 (0.0111 - 0.0226)	0.0063 (0.0021 - 0.0181)	0 (-0.005 - 0.005)	0.67 (0.485 - 0.877)	0.31
Ituri- Edoro	94-00	-0.004 (-0.037 - 0.028)	0.038 (0.008 - 0.088)	0.0172 (0.008 - 0.0697)	0.0148 (0.0016 - 0.2491)	-0.002 (-0.024 - 0.017)	0.7 (0.196 - 1.191)	0.60
Ituri- Lenda	94-00	-0.001 (-0.025 - 0.023)	0.027 (0.008 - 0.06)	0.0128 (0.0067 - 0.0322)	0.0081 (0.0012 - 0.0542)	0 (-0.011 - 0.01)	0.776 (0.447 - 1.204)	0.37
La Planada	97-03	-0.012 (-0.049 - 0.017)	0.037 (0.01 - 0.082)	0.0254 (0.0148 - 0.0738)	0.0205 (0.0036 - 0.2172)	0.003 (-0.02 - 0.032)	0.632 (0.419 - 0.899)	0.53
Lambir	92-97	-0.01 (-0.019 - 0.001)	0.018 (0.009 - 0.029)	0.0154 (0.0136 - 0.0181)	0.0029 (0.0011 - 0.0065)	0 (-0.003 - 0.002)	0.638 (0.521 - 0.77)	0.33
Mudumalai	88-92	0.014 (-0.05 - 0.084)	0.066 (0.013 - 0.181)	0.0171 (-0.0011 - 0.2256)	0.0317 (0.0024 - 1.7889)	0 (-0.06 - 0.059)	1.045 (0.693 - 1.526)	0.36

	88-00	0.015 (-0.059 - 0.098)	0.081 (0.021 - 0.215)	0.0172 (0.0025 - 0.1004)	0.0204 (0.0023 - 0.3131)	0.001 (-0.052 - 0.057)	1.165 (0.838 - 1.586)	0.15
	92-96	-0.006 (-0.101 - 0.088)	0.091 (0.021 - 0.251)	0.0336 (0.0164 - 0.135)	0.0248 (0.0029 - 0.3853)	-0.001 (-0.068 - 0.06)	1.232 (0.858 - 1.732)	0.16
	96-00	-0.002 (-0.076 - 0.072)	0.073 (0.016 - 0.195)	0.0287 (0.0102 - 0.2334)	0.0295 (0.0023 - 1.3706)	-0.001 (-0.059 - 0.051)	1.487 (0.975 - 2.146)	0.18
Pasoh	87-90	-0.007 (-0.017 - 0.004)	0.014 (0.006 - 0.025)	0.015 (0.0128 - 0.0184)	0.0036 (0.0012 - 0.0084)	0 (-0.002 - 0.002)	0.488 (0.356 - 0.627)	0.36
	87-00	-0.017 (-0.028 - -0.005)	0.017 (0.006 - 0.03)	0.0278 (0.025 - 0.0318)	0.0062 (0.0032 - 0.0118)	0 (-0.003 - 0.002)	0.461 (0.4 - 0.529)	0.36
	90-95	-0.014 (-0.025 - -0.003)	0.016 (0.006 - 0.03)	0.0227 (0.0205 - 0.026)	0.004 (0.0014 - 0.0085)	0 (-0.002 - 0.002)	0.459 (0.366 - 0.559)	0.32
	95-00	-0.015 (-0.031 - 0.001)	0.026 (0.011 - 0.047)	0.0279 (0.0247 - 0.0327)	0.006 (0.0025 - 0.0128)	0 (-0.004 - 0.003)	0.488 (0.41 - 0.575)	0.38
Sinharaja	95-01	0.003 (-0.038 - 0.04)	0.041 (0.009 - 0.092)	0.0137 (0.0027 - 0.1681)	0.018 (0.0013 - 1.5805)	-0.004 (-0.036 - 0.022)	0.277 (0.022 - 0.791)	0.87
Yasuní	96-03	-0.014 (-0.025 - -0.002)	0.015 (0.006 - 0.028)	0.0224 (0.0192 - 0.0278)	0.0063 (0.0027 - 0.0141)	0 (-0.003 - 0.002)	0.576 (0.461 - 0.705)	0.42

Table S4 Family slope (*a*) and intercept (*b*) parameters for each site in Model 1. Values are the mean of the posterior distributions for each parameter, estimated using Metropolis-Hastings algorithms in a Bayesian hierarchical model. The 95% credible interval (CI) for each parameter's distribution is given in parentheses. The direction of the slope estimate is summarized using codes: (-) for a negative slope, (-*) for a negative slope where the 95% CI does not overlap 0, and (+) for a positive slope.

Site	year	family	N	*a*	*a* direction	*b*
Barro Colorado Island	1982-2005	Acanthaceae	1	-0.05 (-0.135 - 0.019)	-	0.0586 (0.0477 - 0.0768)
		Anacardiaceae	4	-0.035 (-0.081 - 0.02)	-	0.0472 (0.0384 - 0.0585)
		Annonaceae	5	-0.045 (-0.092 - 0.006)	-	0.0552 (0.0467 - 0.0673)
		Apocynaceae	1	-0.028 (-0.103 - 0.059)	-	0.0411 (0.0307 - 0.0525)
		Araliaceae	2	-0.044 (-0.123 - 0.027)	-	0.0536 (0.0432 - 0.0689)
		Arecaceae	3	-0.057 (-0.129 - -0.001)	-*	0.057 (0.0477 - 0.0669)
		Bignoniaceae	3	-0.036 (-0.083 - 0.021)	-	0.0474 (0.0386 - 0.0585)
		Boraginaceae	3	-0.046 (-0.121 - 0.02)	-	0.0549 (0.0449 - 0.0694)
		Brassicaceae	1	-0.046 (-0.129 - 0.029)	-	0.0527 (0.0426 - 0.065)
		Burseraceae	4	-0.037 (-0.095 - 0.024)	-	0.0481 (0.0397 - 0.0591)
		Cannabaceae	2	-0.063 (-0.152 - 0.001)	-	0.0664 (0.056 - 0.0838)
		Chrysobalanaceae	3	-0.036 (-0.087 - 0.022)	-	0.0482 (0.039 - 0.0601)
		Clusiaceae	6	-0.044 (-0.11 - 0.018)	-	0.056 (0.0471 - 0.0697)
		Combretaceae	2	-0.041 (-0.105 - 0.026)	-	0.0502 (0.041 - 0.0618)
		Euphorbiaceae	6	-0.033 (-0.095 - 0.029)	-	0.0471 (0.0385 - 0.059)
		Fabaceae	21	-0.008 (-0.052 - 0.049)	-	0.0301 (0.024 - 0.0371)
		Lacistemataceae	1	-0.043 (-0.123 - 0.033)	-	0.053 (0.0426 - 0.0681)
		Lauraceae	6	-0.051 (-0.126 - 0.01)	-	0.0572 (0.0483 - 0.0692)
		Lecythidaceae	1	-0.041 (-0.123 - 0.038)	-	0.0492 (0.039 - 0.0609)
		Lythraceae	1	-0.039 (-0.113 - 0.036)	-	0.0504 (0.0402 - 0.065)
		Malvaceae	15	-0.035 (-0.082 - 0.009)	-	0.0451 (0.0359 - 0.0549)
		Melastomataceae	1	-0.05 (-0.136 - 0.02)	-	0.0591 (0.0483 - 0.078)
		Meliaceae	5	-0.042 (-0.111 - 0.023)	-	0.0516 (0.0433 - 0.0627)
		Moraceae	13	-0.05 (-0.086 - -0.01)	-*	0.0565 (0.0492 - 0.0661)
		Myristicaceae	3	-0.032 (-0.103 - 0.042)	-	0.0443 (0.0347 - 0.0559)
		Myrsinaceae	1	-0.04 (-0.121 - 0.038)	-	0.0513 (0.0413 - 0.0661)
		Ochnaceae	1	-0.041 (-0.123 - 0.038)	-	0.0524 (0.0419 - 0.0684)
		Olacaceae	1	-0.048 (-0.133 - 0.028)	-	0.0528 (0.0428 - 0.0641)
		Phyllanthaceae	1	-0.038 (-0.114 -	-	0.0504 (0.04 - 0.0667)

				0.038)		
		Piperaceae	1	-0.042 (-0.117 - 0.025)	-	0.0519 (0.0413 - 0.0667)
		Polygonaceae	1	-0.041 (-0.12 - 0.035)	-	0.0509 (0.0407 - 0.0649)
		Putranjavaceae	1	-0.046 (-0.128 - 0.027)	-	0.0528 (0.0431 - 0.0651)
		Rhamnaceae	1	-0.038 (-0.11 - 0.037)	-	0.05 (0.0397 - 0.0657)
		Rhizophoraceae	2	-0.032 (-0.1 - 0.043)	-	0.0462 (0.0367 - 0.0592)
		Rubiaceae	9	-0.037 (-0.096 - 0.025)	-	0.0473 (0.0397 - 0.0562)
		Rutaceae	2	-0.044 (-0.123 - 0.029)	-	0.0538 (0.0437 - 0.069)
		Salicaceae	8	-0.042 (-0.112 - 0.026)	-	0.0549 (0.0463 - 0.0673)
		Sapindaceae	1	-0.04 (-0.119 - 0.038)	-	0.0517 (0.0414 - 0.0678)
		Sapotaceae	3	-0.032 (-0.088 - 0.033)	-	0.0463 (0.037 - 0.0587)
		Simaroubaceae	2	-0.045 (-0.119 - 0.022)	-	0.053 (0.043 - 0.0662)
		Tapisciaceae	1	-0.048 (-0.127 - 0.017)	-	0.0561 (0.0456 - 0.0718)
		Urticaceae	1	-0.052 (-0.135 - 0.011)	-	0.0585 (0.0477 - 0.0755)
		Violaceae	1	-0.037 (-0.112 - 0.041)	-	0.0501 (0.0401 - 0.0656)
		Vochysiaceae	1	-0.047 (-0.129 - 0.022)	-	0.0559 (0.0453 - 0.0727)
Huai Kha Kaeng	1993-1999	Anacardiaceae	3	-0.034 (-0.117 - 0.041)	-	0.0484 (0.0348 - 0.0674)
		Annonaceae	4	-0.015 (-0.106 - 0.079)	-	0.036 (0.025 - 0.0507)
		Apocynaceae	2	-0.032 (-0.125 - 0.055)	-	0.047 (0.0329 - 0.0667)
		Bignoniaceae	5	-0.028 (-0.091 - 0.041)	-	0.0443 (0.0334 - 0.059)
		Boraginaceae	2	-0.011 (-0.109 - 0.106)	-	0.036 (0.023 - 0.0556)
		Burseraceae	2	-0.033 (-0.135 - 0.069)	-	0.0491 (0.0353 - 0.071)
		Cannabaceae	3	-0.05 (-0.153 - 0.035)	-	0.0638 (0.0487 - 0.0931)
		Celastraceae	2	-0.038 (-0.147 - 0.065)	-	0.0466 (0.0331 - 0.0628)
		Clusiaceae	3	-0.016 (-0.099 - 0.083)	-	0.0421 (0.0279 - 0.0657)
		Combretaceae	3	-0.048 (-0.145 - 0.046)	-	0.0534 (0.0405 - 0.0692)
		Cornaceae	2	-0.052 (-0.154 - 0.031)	-	0.0616 (0.0469 - 0.0866)
		Dilleniaceae	2	-0.039 (-0.144 - 0.061)	-	0.0533 (0.0387 - 0.0779)
		Dipterocarpaceae	7	-0.033 (-0.099 - 0.045)	-	0.0426 (0.0325 - 0.0538)
		Ebenaceae	3	-0.017 (-0.077 - 0.058)	-	0.0389 (0.0258 - 0.0575)
		Elaeocarpaceae	1	-0.031 (-0.133 - 0.072)	-	0.0461 (0.0323 - 0.0665)
		Euphorbiaceae	5	-0.053 (-0.136 - 0.021)	-	0.0625 (0.0509 - 0.0801)
		Fabaceae	14	-0.059 (-0.117 - 0)	-*	0.0698 (0.0584 - 0.0861)
		Fagaceae	1	-0.035 (-0.141 -	-	0.0476 (0.0333 - 0.0668)

					0.069)
		Icacinaceae	1	-0.035 (-0.143 - 0.073)	-	0.0492 (0.0346 - 0.0712)
		Irvingiaceae	1	-0.041 (-0.105 - 0.031)	-	0.0516 (0.0385 - 0.0697)
		Juglandaceae	1	-0.027 (-0.127 - 0.084)	-	0.0434 (0.0294 - 0.0629)
		Lamiaceae	7	-0.036 (-0.135 - 0.053)	-	0.0491 (0.0375 - 0.0649)
		Lauraceae	5	-0.027 (-0.11 - 0.064)	-	0.0419 (0.0311 - 0.0555)
		Lecythidaceae	1	-0.023 (-0.084 - 0.064)	-	0.0432 (0.0287 - 0.0654)
		Lythraceae	5	-0.035 (-0.129 - 0.061)	-	0.0473 (0.0365 - 0.0607)
		Magnoliaceae	1	-0.034 (-0.135 - 0.066)	-	0.0486 (0.0346 - 0.07)
		Malvaceae	7	-0.006 (-0.087 - 0.087)	-	0.0322 (0.0205 - 0.0482)
		Meliaceae	10	-0.032 (-0.108 - 0.048)	-	0.0511 (0.0404 - 0.0662)
		Moraceae	13	-0.021 (-0.094 - 0.053)	-	0.037 (0.0255 - 0.0498)
		Myristicaceae	1	-0.038 (-0.143 - 0.063)	-	0.0522 (0.0375 - 0.0753)
		Myrtaceae	5	-0.033 (-0.12 - 0.058)	-	0.0463 (0.0353 - 0.0599)
		Oleaceae	1	-0.037 (-0.14 - 0.064)	-	0.0492 (0.0355 - 0.0686)
		Opiliaceae	1	-0.03 (-0.123 - 0.072)	-	0.0472 (0.0337 - 0.0679)
		Phyllanthaceae	6	-0.022 (-0.114 - 0.084)	-	0.0422 (0.0305 - 0.0586)
		Podocarpaceae	1	-0.033 (-0.137 - 0.073)	-	0.0481 (0.0333 - 0.0701)
		Polygalaceae	1	-0.039 (-0.147 - 0.063)	-	0.049 (0.0363 - 0.0657)
		Putranjavaceae	1	-0.048 (-0.163 - 0.051)	-	0.0536 (0.0403 - 0.0709)
		Rhizophoraceae	1	-0.043 (-0.154 - 0.059)	-	0.0504 (0.0372 - 0.0669)
		Rosaceae	2	-0.04 (-0.131 - 0.049)	-	0.0492 (0.0371 - 0.0658)
		Rubiaceae	2	-0.04 (-0.134 - 0.057)	-	0.0525 (0.0395 - 0.0718)
		Rutaceae	5	-0.026 (-0.093 - 0.055)	-	0.0482 (0.0357 - 0.0671)
		Sabiaceae	1	-0.036 (-0.138 - 0.06)	-	0.0502 (0.0358 - 0.0718)
		Salicaceae	5	-0.019 (-0.103 - 0.08)	-	0.0417 (0.0293 - 0.0594)
		Sapindaceae	9	-0.042 (-0.115 - 0.029)	-	0.0539 (0.0441 - 0.0671)
		Simaroubaceae	2	-0.043 (-0.14 - 0.04)	-	0.0553 (0.0412 - 0.0769)
		Styracaceae	1	-0.038 (-0.142 - 0.063)	-	0.0524 (0.0376 - 0.0772)
		Tapisciaceae	1	-0.043 (-0.147 - 0.05)	-	0.0562 (0.0416 - 0.0816)
		Tetramelaceae	1	-0.064 (-0.177 - 0.016)	-	0.0717 (0.055 - 0.1059)
		Tetrameristaceae	1	-0.03 (-0.133 - 0.078)	-	0.0537 (0.037 - 0.0896)
		Theaceae	1	-0.034 (-0.14 - 0.074)	-	0.0487 (0.0341 - 0.071)
		Ulmaceae	2	-0.032 (-0.137 - 0.072)	-	0.0494 (0.035 - 0.0737)
Ituri- Edoro	1994-2000	Achariaceae	1	0 (-0.098 - 0.116)	+	0.0124 (0.0036 - 0.0263)
		Anacardiaceae	2	-0.015 (-0.109 - 0.069)	-	0.0277 (0.0141 - 0.0542)

		Family				
		Annonaceae	4	0.012 (-0.05 - 0.066)	+	0.0081 (-7e-04 - 0.0215)
		Apocynaceae	3	-0.005 (-0.099 - 0.093)	-	0.0209 (0.0096 - 0.0398)
		Bignoniaceae	3	-0.012 (-0.103 - 0.055)	-	0.0242 (0.0129 - 0.0446)
		Burseraceae	2	0.004 (-0.078 - 0.078)	+	0.0123 (0.0023 - 0.0275)
		Cannabaceae	4	0.009 (-0.067 - 0.104)	+	0.0069 (-5e-04 - 0.0173)
		Chrysobalanaceae	2	0.002 (-0.086 - 0.104)	+	0.0219 (0.0069 - 0.0488)
		Clusiaceae	5	-0.001 (-0.088 - 0.104)	-	0.0211 (0.0073 - 0.0479)
		Combretaceae	1	0.002 (-0.091 - 0.114)	+	0.0235 (0.0067 - 0.0628)
		Euphorbiaceae	3	-0.052 (-0.165 - 0.033)	-	0.065 (0.0395 - 0.1303)
		Fabaceae	20	-0.029 (-0.078 - 0.016)	-	0.0346 (0.0275 - 0.0445)
		Icacinaceae	1	-0.006 (-0.109 - 0.108)	-	0.0323 (0.0137 - 0.0786)
		Irvingiaceae	3	-0.007 (-0.062 - 0.053)	-	0.021 (0.009 - 0.0403)
		Ixonanthaceae	1	-0.013 (-0.102 - 0.081)	-	0.0239 (0.0128 - 0.0425)
		Lauraceae	2	-0.011 (-0.116 - 0.094)	-	0.0255 (0.0136 - 0.0477)
		Malvaceae	3	0.008 (-0.079 - 0.113)	+	0.0095 (0.0017 - 0.021)
		Meliaceae	14	0.009 (-0.057 - 0.085)	+	0.0126 (0.005 - 0.0231)
		Moraceae	8	-0.062 (-0.146 - 0.011)	-	0.0692 (0.0505 - 0.1082)
		Myristicaceae	3	-0.022 (-0.081 - 0.035)	-	0.0277 (0.0184 - 0.0416)
		Olacaceae	2	-0.015 (-0.09 - 0.06)	-	0.0251 (0.0143 - 0.0407)
		Pandaceae	1	-0.002 (-0.102 - 0.111)	-	0.0287 (0.0087 - 0.0873)
		Phyllanthaceae	4	0 (-0.093 - 0.109)	+	0.0362 (0.0143 - 0.0816)
		Rhizophoraceae	1	-0.01 (-0.082 - 0.068)	-	0.0233 (0.0109 - 0.0441)
		Rubiaceae	8	-0.002 (-0.079 - 0.07)	-	0.0154 (0.0087 - 0.0246)
		Rutaceae	1	-0.008 (-0.113 - 0.103)	-	0.0244 (0.0119 - 0.0495)
		Salicaceae	2	-0.004 (-0.092 - 0.098)	-	0.0217 (0.0081 - 0.0492)
		Sapindaceae	5	-0.04 (-0.117 - 0.033)	-	0.0406 (0.0318 - 0.0548)
		Sapotaceae	6	-0.008 (-0.059 - 0.061)	-	0.0184 (0.0092 - 0.0317)
		Simaroubaceae	1	-0.013 (-0.108 - 0.063)	-	0.0271 (0.0127 - 0.0592)
Ituri- Lenda	1994-2000	Achariaceae	1	0.006 (-0.082 - 0.127)	+	0.0033 (-0.002 - 0.0141)
		Anacardiaceae	2	-0.035 (-0.15 - 0.046)	-	0.0471 (0.0255 - 0.0972)
		Annonaceae	5	-0.013 (-0.073 - 0.046)	-	0.0218 (0.0121 - 0.0394)
		Apocynaceae	4	-0.011 (-0.098 - 0.076)	-	0.0191 (0.0097 - 0.0355)
		Bignoniaceae	2	-0.02 (-0.12 - 0.051)	-	0.0317 (0.0173 - 0.0627)
		Burseraceae	2	-0.041 (-0.159 - 0.036)	-	0.0465 (0.0296 - 0.0801)
		Cannabaceae	3	-0.031 (-0.154 - 0.059)	-	0.0305 (0.0225 - 0.0453)
		Chrysobalanaceae	2	0.006 (-0.082 - 0.125)	+	0.0275 (0.0046 - 0.0694)
		Clusiaceae	4	0.004 (-0.074 - 0.107)	+	0.0138 (0.0031 - 0.0297)

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		Combretaceae	1	-0.022 (-0.127 - 0.072)	-	0.0271 (0.0158 - 0.0521)
		Ebenaceae	1	-0.01 (-0.081 - 0.072)	-	0.0245 (0.0091 - 0.0572)
		Euphorbiaceae	2	-0.054 (-0.193 - 0.035)	-	0.0841 (0.0395 - 0.1927)
		Fabaceae	20	-0.027 (-0.064 - 0.006)	-	0.0307 (0.0251 - 0.038)
		Icacinaceae	1	-0.016 (-0.124 - 0.088)	-	0.0293 (0.0124 - 0.0764)
		Irvingiaceae	2	-0.012 (-0.07 - 0.042)	-	0.0224 (0.0099 - 0.0455)
		Ixonanthaceae	1	-0.009 (-0.097 - 0.085)	-	0.0229 (0.0096 - 0.0476)
		Lauraceae	2	0.009 (-0.081 - 0.122)	+	0.0018 (-0.004 - 0.0131)
		Lecythidaceae	1	-0.016 (-0.118 - 0.087)	-	0.0278 (0.0123 - 0.0694)
		Malvaceae	4	-0.001 (-0.075 - 0.069)	-	0.0142 (0.0067 - 0.0253)
		Meliaceae	15	-0.005 (-0.078 - 0.081)	-	0.0234 (0.0155 - 0.0339)
		Melianthaceae	1	-0.008 (-0.105 - 0.105)	-	0.0369 (0.0109 - 0.1188)
		Moraceae	7	-0.057 (-0.207 - 0.031)	-	0.0819 (0.0457 - 0.1373)
		Myristicaceae	2	-0.019 (-0.085 - 0.04)	-	0.0363 (0.0223 - 0.0614)
		Olacaceae	2	-0.011 (-0.087 - 0.061)	-	0.0218 (0.0105 - 0.0389)
		Pandaceae	1	-0.009 (-0.11 - 0.102)	-	0.0373 (0.0114 - 0.1186)
		Phyllanthaceae	2	-0.004 (-0.092 - 0.107)	-	0.0302 (0.0122 - 0.0651)
		Rhamnaceae	1	-0.027 (-0.131 - 0.053)	-	0.0394 (0.0199 - 0.0894)
		Rhizophoraceae	2	-0.009 (-0.081 - 0.065)	-	0.0223 (0.0089 - 0.0459)
		Rubiaceae	8	-0.007 (-0.061 - 0.047)	-	0.0163 (0.0097 - 0.0266)
		Rutaceae	1	-0.012 (-0.119 - 0.098)	-	0.0445 (0.0186 - 0.105)
		Salicaceae	1	-0.007 (-0.092 - 0.089)	-	0.0241 (0.0086 - 0.0545)
		Sapindaceae	5	-0.024 (-0.099 - 0.044)	-	0.0348 (0.0242 - 0.0511)
		Sapotaceae	9	-0.018 (-0.046 - 0.012)	-	0.02 (0.0145 - 0.028)
		Simaroubaceae	1	-0.015 (-0.099 - 0.054)	-	0.026 (0.0118 - 0.0575)
La Planada	1997-2003	Actinidiaceae	2	-0.077 (-0.23 - 0.045)	-	0.0786 (0.0516 - 0.1296)
		Annonaceae	3	-0.044 (-0.156 - 0.04)	-	0.044 (0.0333 - 0.0619)
		Asteraceae	1	-0.058 (-0.229 - 0.084)	-	0.0646 (0.0418 - 0.1114)
		Boraginaceae	1	-0.066 (-0.245 - 0.076)	-	0.0955 (0.0518 - 0.1995)
		Cannabaceae	1	-0.04 (-0.184 - 0.069)	-	0.0454 (0.0267 - 0.0899)
		Chrysobalanaceae	3	-0.043 (-0.146 - 0.031)	-	0.0455 (0.0296 - 0.07)
		Clusiaceae	3	-0.024 (-0.153 - 0.114)	-	0.0666 (0.0376 - 0.1139)
		Elaeocarpaceae	1	-0.046 (-0.188 - 0.087)	-	0.0454 (0.0306 - 0.0722)
		Euphorbiaceae	4	-0.024 (-0.128 -	-	0.0375 (0.0246 - 0.0577)

				0.072)		
		Fabaceae	6	-0.072 (-0.239 - 0.056)	-	0.0587 (0.0517 - 0.0686)
		Icacinaceae	1	-0.039 (-0.193 - 0.114)	-	0.0491 (0.0318 - 0.083)
		Lauraceae	8	-0.069 (-0.192 - 0.025)	-	0.0532 (0.0454 - 0.0639)
		Lecythidaceae	1	-0.028 (-0.135 - 0.063)	-	0.0397 (0.0212 - 0.0717)
		Malvaceae	2	-0.028 (-0.146 - 0.094)	-	0.0282 (0.0189 - 0.0435)
		Melastomataceae	4	-0.042 (-0.188 - 0.097)	-	0.0756 (0.0497 - 0.1143)
		Meliaceae	4	-0.047 (-0.149 - 0.046)	-	0.0375 (0.0292 - 0.0508)
		Moraceae	9	-0.091 (-0.175 - -0.012)	-*	0.0716 (0.0626 - 0.088)
		Myristicaceae	1	-0.017 (-0.12 - 0.089)	-	0.026 (0.0127 - 0.0503)
		Myrtaceae	3	-0.005 (-0.079 - 0.063)	-	0.0162 (0.0052 - 0.0333)
		Rubiaceae	1	-0.055 (-0.211 - 0.081)	-	0.0568 (0.0383 - 0.0927)
		Salicaceae	2	-0.056 (-0.208 - 0.082)	-	0.0496 (0.0374 - 0.0692)
		Sapindaceae	2	-0.056 (-0.207 - 0.075)	-	0.0592 (0.0399 - 0.0918)
		Sapotaceae	1	-0.034 (-0.165 - 0.093)	-	0.0424 (0.0252 - 0.0749)
		Siparunaceae	1	-0.027 (-0.176 - 0.133)	-	0.0529 (0.027 - 0.1052)
		Styracaceae	1	-0.037 (-0.155 - 0.068)	-	0.0412 (0.0246 - 0.0733)
		Symplocaceae	1	-0.056 (-0.222 - 0.08)	-	0.0619 (0.0399 - 0.1084)
		Tapisciaceae	1	-0.036 (-0.172 - 0.079)	-	0.0419 (0.024 - 0.0823)
		Urticaceae	1	-0.063 (-0.22 - 0.059)	-	0.0662 (0.0408 - 0.134)
Lambir	1992-1997	Achariaceae	4	-0.02 (-0.067 - 0.028)	-	0.0253 (0.0201 - 0.0319)
		Anacardiaceae	11	-0.026 (-0.057 - 0.007)	-	0.0278 (0.0241 - 0.0326)
		Anisophylleaceae	2	-0.018 (-0.065 - 0.032)	-	0.0246 (0.0186 - 0.0329)
		Annonaceae	13	-0.019 (-0.046 - 0.006)	-	0.0231 (0.02 - 0.0269)
		Apocynaceae	4	-0.018 (-0.064 - 0.023)	-	0.0247 (0.0183 - 0.0341)
		Aquifoliaceae	1	-0.019 (-0.072 - 0.032)	-	0.0257 (0.0188 - 0.0363)
		Araliaceae	1	-0.026 (-0.077 - 0.021)	-	0.031 (0.0234 - 0.0434)
		Asteraceae	1	-0.038 (-0.093 - 0.007)	-	0.0403 (0.0313 - 0.0565)
		Bonnetiaceae	1	-0.016 (-0.057 - 0.035)	-	0.0249 (0.0172 - 0.0374)
		Boraginaceae	1	-0.018 (-0.072 - 0.036)	-	0.0262 (0.0193 - 0.0369)
		Brassicaceae	1	-0.02 (-0.075 - 0.034)	-	0.0267 (0.0192 - 0.0393)
		Burseraceae	25	-0.005 (-0.032 - 0.024)	-	0.0139 (0.0115 - 0.0167)
		Cannabaceae	4	-0.05 (-0.104 - -0.007)	-*	0.0455 (0.0381 - 0.0564)

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Celastraceae	3	-0.027 (-0.081 - 0.022)	-	0.0287 (0.0238 - 0.0354)
Chrysobalanaceae	3	-0.006 (-0.04 - 0.032)	-	0.0189 (0.0119 - 0.0281)
Clusiaceae	16	-0.011 (-0.04 - 0.018)	-	0.0188 (0.0153 - 0.0232)
Combretaceae	3	-0.02 (-0.074 - 0.034)	-	0.027 (0.0199 - 0.0381)
Cornaceae	5	-0.008 (-0.048 - 0.033)	-	0.0215 (0.0154 - 0.0304)
Ctenolophonaceae	1	-0.019 (-0.063 - 0.027)	-	0.0257 (0.0192 - 0.035)
Dilleniaceae	5	0 (-0.045 - 0.048)	+	0.0121 (0.0074 - 0.0183)
Dipterocarpaceae	60	-0.019 (-0.036 - -0.002)	-*	0.0275 (0.025 - 0.0303)
Ebenaceae	20	-0.003 (-0.026 - 0.022)	-	0.0109 (0.008 - 0.0143)
Elaeocarpaceae	6	-0.023 (-0.074 - 0.027)	-	0.0271 (0.021 - 0.0355)
Euphorbiaceae	22	-0.074 (-0.101 - -0.05)	-*	0.0649 (0.0602 - 0.0706)
Fabaceae	15	-0.017 (-0.042 - 0.007)	-	0.0248 (0.0206 - 0.0301)
Fagaceae	5	0 (-0.046 - 0.051)	+	0.0217 (0.0129 - 0.0347)
Gentianaceae	2	-0.003 (-0.045 - 0.046)	-	0.0199 (0.012 - 0.0318)
Gnetaceae	1	-0.017 (-0.07 - 0.037)	-	0.0274 (0.0197 - 0.0398)
Icacinaceae	1	-0.018 (-0.071 - 0.035)	-	0.0251 (0.0178 - 0.0365)
Irvingiaceae	1	-0.013 (-0.048 - 0.029)	-	0.023 (0.0156 - 0.0338)
Juglandaceae	1	-0.019 (-0.072 - 0.035)	-	0.0259 (0.0186 - 0.0378)
Lamiaceae	4	-0.034 (-0.075 - 0.002)	-	0.0328 (0.028 - 0.0392)
Lauraceae	35	-0.036 (-0.06 - -0.009)	-*	0.0358 (0.0325 - 0.0397)
Lecythidaceae	2	-0.021 (-0.076 - 0.034)	-	0.0256 (0.0194 - 0.0342)
Magnoliaceae	1	-0.02 (-0.075 - 0.034)	-	0.0255 (0.0192 - 0.0348)
Malvaceae	19	-0.019 (-0.045 - 0.01)	-	0.0236 (0.0204 - 0.0274)
Melastomataceae	5	-0.032 (-0.073 - 0.009)	-	0.0347 (0.0288 - 0.0427)
Meliaceae	25	-0.007 (-0.036 - 0.023)	-	0.0183 (0.0144 - 0.023)
Monimiaceae	1	-0.023 (-0.078 - 0.031)	-	0.0302 (0.0225 - 0.043)
Moraceae	17	-0.034 (-0.071 - 0.002)	-	0.0372 (0.0317 - 0.0445)
Myristicaceae	15	-0.006 (-0.045 - 0.033)	-	0.0125 (0.0094 - 0.0162)
Myrsinaceae	2	-0.022 (-0.075 - 0.029)	-	0.0284 (0.021 - 0.0406)
Myrtaceae	6	-0.027 (-0.056 - 0.003)	-	0.0294 (0.0241 - 0.0364)
Ochnaceae	2	-0.012 (-0.06 - 0.04)	-	0.0233 (0.0167 - 0.033)
Olacaceae	3	-0.017 (-0.058 - 0.025)	-	0.0245 (0.0182 - 0.0327)
Oleaceae	1	-0.021 (-0.072 - 0.03)	-	0.0264 (0.0201 - 0.0355)
Oxalidaceae	2	-0.02 (-0.075 - 0.034)	-	0.0262 (0.0198 - 0.0355)
Pentaphylacaeae	5	-0.029 (-0.084 - 0.022)	-	0.0353 (0.0284 - 0.0452)
Phyllanthaceae	18	-0.014 (-0.047 - 0.02)	-	0.0232 (0.0194 - 0.0279)

		Family				
		Polygalaceae	9	-0.028 (-0.051 - 0)	-*	0.0296 (0.0246 - 0.0354)
		Polyosmaceae	1	-0.021 (-0.077 - 0.033)	-	0.0299 (0.0219 - 0.0433)
		Proteaceae	1	-0.017 (-0.07 - 0.038)	-	0.0223 (0.0164 - 0.0306)
		Putranjavaceae	4	-0.028 (-0.08 - 0.021)	-	0.029 (0.0244 - 0.0349)
		Rhamnaceae	1	-0.023 (-0.079 - 0.03)	-	0.0315 (0.0226 - 0.0479)
		Rhizophoraceae	4	-0.012 (-0.055 - 0.031)	-	0.0246 (0.0182 - 0.0337)
		Rosaceae	3	-0.02 (-0.07 - 0.028)	-	0.0288 (0.0214 - 0.0394)
		Rubiaceae	10	-0.009 (-0.046 - 0.028)	-	0.0227 (0.0172 - 0.0296)
		Rutaceae	2	-0.026 (-0.072 - 0.013)	-	0.0305 (0.0231 - 0.0424)
		Salicaceae	3	-0.011 (-0.056 - 0.038)	-	0.0262 (0.0181 - 0.0387)
		Sapindaceae	9	-0.026 (-0.059 - 0.009)	-	0.0304 (0.0253 - 0.0371)
		Sapotaceae	18	-0.004 (-0.022 - 0.017)	-	0.0124 (0.0094 - 0.0161)
		Simaroubaceae	3	-0.007 (-0.057 - 0.039)	-	0.0161 (0.0103 - 0.0238)
		Stemonuraceae	3	0.006 (-0.03 - 0.05)	+	0.0107 (0.005 - 0.0187)
		Symplocaceae	2	-0.039 (-0.091 - 0.004)	-	0.0395 (0.0316 - 0.0517)
		Tapisciaceae	1	-0.017 (-0.07 - 0.035)	-	0.0244 (0.0173 - 0.0349)
		Tetrameristaceae	1	-0.02 (-0.074 - 0.034)	-	0.0264 (0.0198 - 0.0365)
		Thymelaeaceae	4	-0.044 (-0.095 - -0.003)	-*	0.0368 (0.0315 - 0.0439)
		Vitaceae	1	-0.037 (-0.096 - 0.013)	-	0.0443 (0.033 - 0.0666)
Mudumalai	1988-2000	Anacardiaceae	3	0.053 (-0.139 - 0.256)	+	0.0054 (-0.0201 - 0.051)
		Apocynaceae	1	0.006 (-0.229 - 0.218)	+	0.0314 (0.0034 - 0.086)
		Boraginaceae	1	-0.021 (-0.323 - 0.236)	-	0.0605 (0.0239 - 0.1522)
		Burseraceae	1	-0.003 (-0.279 - 0.262)	-	0.0394 (0.0104 - 0.1013)
		Combretaceae	4	0.007 (-0.095 - 0.128)	+	0.0159 (6e-04 - 0.0417)
		Dipterocarpaceae	1	0.014 (-0.267 - 0.322)	+	0.0579 (0.0091 - 0.2096)
		Ebenaceae	1	-0.005 (-0.212 - 0.21)	-	0.035 (0.0091 - 0.0831)
		Euphorbiaceae	1	0.01 (-0.273 - 0.3)	+	0.0415 (0.0066 - 0.128)
		Fabaceae	9	0.019 (-0.122 - 0.146)	+	0.0321 (0.0114 - 0.0665)
		Lamiaceae	4	-0.028 (-0.212 - 0.135)	-	0.0525 (0.0294 - 0.0959)
		Lecythidaceae	1	0.024 (-0.209 - 0.296)	+	0.0266 (-0.0051 - 0.0971)
		Malvaceae	3	0.021 (-0.232 - 0.301)	+	0.0536 (0.0102 - 0.1458)
		Meliaceae	1	0.003 (-0.281 - 0.289)	+	0.0335 (0.0042 - 0.1007)
		Moraceae	5	0.024 (-0.077 - 0.118)	+	0.0091 (-0.0098 - 0.0401)
		Myrtaceae	1	-0.031 (-0.316 - 0.208)	-	0.0423 (0.0229 - 0.0781)
		Oleaceae	1	0.032 (-0.212 - 0.327)	+	0.0296 (-0.0073 - 0.1209)
		Phyllanthaceae	3	0.002 (-0.237 - 0.244)	+	0.0364 (0.0122 - 0.0838)
		Rhamnaceae	2	-0.002 (-0.247 - 0.258)	-	0.0442 (0.0134 - 0.1085)
		Rubiaceae	4	-0.012 (-0.221 - 0.163)	-	0.0439 (0.0225 - 0.082)
		Salicaceae	2	0.056 (-0.161 - 0.365)	+	0.0046 (-0.0233 - 0.0605)

		Family				
		Sapindaceae	2	-0.051 (-0.231 - 0.108)	-	0.0683 (0.0433 - 0.1177)
Pasoh	1987-2000	Achariaceae	2	-0.024 (-0.062 - 0.014)	-	0.0329 (0.0258 - 0.0431)
		Anacardiaceae	17	-0.008 (-0.029 - 0.016)	-	0.0163 (0.0139 - 0.0192)
		Annonaceae	18	-0.027 (-0.045 - -0.01)	-*	0.0317 (0.0287 - 0.035)
		Apocynaceae	5	-0.022 (-0.047 - 0.004)	-	0.0247 (0.021 - 0.0295)
		Araliaceae	1	-0.027 (-0.064 - 0.008)	-	0.0346 (0.0255 - 0.0494)
		Asparagaceae	1	-0.021 (-0.058 - 0.017)	-	0.0278 (0.0209 - 0.0377)
		Asteraceae	1	-0.033 (-0.071 - 0.001)	-	0.041 (0.0305 - 0.0581)
		Bignoniaceae	2	-0.02 (-0.058 - 0.018)	-	0.0278 (0.0197 - 0.0404)
		Boraginaceae	1	-0.021 (-0.058 - 0.019)	-	0.0299 (0.0221 - 0.0416)
		Brassicaceae	1	-0.021 (-0.06 - 0.017)	-	0.0284 (0.0205 - 0.0412)
		Burseraceae	22	-0.021 (-0.043 - 0.003)	-	0.0261 (0.0237 - 0.0287)
		Cannabaceae	4	-0.024 (-0.059 - 0.01)	-	0.0289 (0.0227 - 0.0369)
		Celastraceae	3	-0.019 (-0.047 - 0.011)	-	0.0249 (0.0197 - 0.0315)
		Chrysobalanaceae	6	-0.026 (-0.055 - 0.004)	-	0.0342 (0.0283 - 0.0415)
		Clusiaceae	16	-0.018 (-0.036 - 0.001)	-	0.0273 (0.0236 - 0.0315)
		Combretaceae	4	-0.023 (-0.06 - 0.014)	-	0.0261 (0.0206 - 0.0337)
		Cornaceae	5	-0.023 (-0.052 - 0.007)	-	0.0318 (0.0257 - 0.0401)
		Crypteroniaceae	1	-0.021 (-0.059 - 0.017)	-	0.0285 (0.0211 - 0.0397)
		Ctenolophonaceae	1	-0.021 (-0.055 - 0.014)	-	0.0281 (0.0215 - 0.0373)
		Dilleniaceae	3	-0.018 (-0.054 - 0.021)	-	0.0292 (0.0223 - 0.0385)
		Dipterocarpaceae	29	-0.046 (-0.065 - -0.027)	-*	0.0484 (0.0451 - 0.0521)
		Ebenaceae	14	-0.013 (-0.036 - 0.01)	-	0.0185 (0.0155 - 0.0218)
		Elaeocarpaceae	6	-0.027 (-0.065 - 0.009)	-	0.0394 (0.0318 - 0.049)
		Euphorbiaceae	21	-0.055 (-0.075 - -0.036)	-*	0.0495 (0.0464 - 0.0531)
		Fabaceae	21	-0.01 (-0.021 - 0)	-	0.0159 (0.014 - 0.0183)
		Fagaceae	8	-0.013 (-0.047 - 0.024)	-	0.0343 (0.0267 - 0.0438)
		Gentianaceae	1	-0.019 (-0.057 - 0.019)	-	0.0295 (0.0218 - 0.0408)
		Gnetaceae	1	-0.022 (-0.06 - 0.017)	-	0.0286 (0.0221 - 0.038)
		Icacinaceae	1	-0.022 (-0.059 - 0.014)	-	0.0296 (0.0213 - 0.042)
		Irvingiaceae	1	-0.024 (-0.051 - 0.003)	-	0.0293 (0.0226 - 0.0377)
		Ixonanthaceae	2	-0.016 (-0.047 - 0.018)	-	0.0279 (0.0201 - 0.0385)
		Juglandaceae	1	-0.02 (-0.056 - 0.017)	-	0.0275 (0.0199 - 0.0386)
		Lamiaceae	4	-0.02 (-0.054 - 0.015)	-	0.023 (0.0184 - 0.029)
		Lauraceae	28	-0.029 (-0.054 - -0.005)	-*	0.0339 (0.0306 - 0.0377)

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		Family				
		Lecythidaceae	3	-0.028 (-0.063 - 0.006)	-	0.0272 (0.0233 - 0.0323)
		Magnoliaceae	1	-0.021 (-0.058 - 0.017)	-	0.0282 (0.021 - 0.0387)
		Malvaceae	18	-0.022 (-0.042 - -0.003)	-*	0.0261 (0.0235 - 0.0291)
		Melastomataceae	8	-0.03 (-0.059 - -0.004)	-*	0.0399 (0.0341 - 0.0469)
		Meliaceae	20	0 (-0.026 - 0.027)	-	0.0161 (0.0125 - 0.0203)
		Monimiaceae	1	-0.021 (-0.06 - 0.017)	-	0.0284 (0.0208 - 0.0396)
		Moraceae	16	-0.028 (-0.054 - -0.003)	-*	0.0293 (0.0259 - 0.0332)
		Myristicaceae	13	-0.018 (-0.051 - 0.016)	-	0.0246 (0.0212 - 0.0287)
		Myrsinaceae	1	-0.024 (-0.063 - 0.013)	-	0.0326 (0.0238 - 0.0462)
		Myrtaceae	20	-0.01 (-0.033 - 0.016)	-	0.0209 (0.0173 - 0.025)
		Ochnaceae	2	-0.016 (-0.052 - 0.024)	-	0.0299 (0.0221 - 0.0409)
		Olacaceae	3	-0.021 (-0.052 - 0.009)	-	0.0289 (0.0226 - 0.0372)
		Oleaceae	2	-0.015 (-0.051 - 0.026)	-	0.0352 (0.025 - 0.0506)
		Opiliaceae	1	-0.022 (-0.058 - 0.014)	-	0.0286 (0.0222 - 0.0376)
		Passifloraceae	1	-0.026 (-0.063 - 0.011)	-	0.0287 (0.0232 - 0.0362)
		Phyllanthaceae	19	-0.018 (-0.043 - 0.007)	-	0.027 (0.0234 - 0.0311)
		Polygalaceae	7	-0.018 (-0.04 - 0.006)	-	0.0239 (0.0194 - 0.0291)
		Polyosmaceae	1	-0.022 (-0.06 - 0.016)	-	0.0312 (0.0221 - 0.0466)
		Putranjavaceae	4	-0.024 (-0.057 - 0.008)	-	0.0279 (0.0233 - 0.0335)
		Rhizophoraceae	3	-0.013 (-0.048 - 0.026)	-	0.0255 (0.0194 - 0.0337)
		Rosaceae	3	-0.025 (-0.062 - 0.011)	-	0.0357 (0.0275 - 0.0477)
		Rubiaceae	11	-0.023 (-0.054 - 0.006)	-	0.0341 (0.0291 - 0.0401)
		Rutaceae	3	-0.028 (-0.063 - 0.003)	-	0.0345 (0.0269 - 0.0449)
		Salicaceae	4	-0.016 (-0.05 - 0.02)	-	0.0274 (0.0205 - 0.0355)
		Sapindaceae	9	-0.011 (-0.038 - 0.016)	-	0.0234 (0.0181 - 0.0296)
		Sapotaceae	13	-0.014 (-0.037 - 0.012)	-	0.0212 (0.0178 - 0.0253)
		Simaroubaceae	1	-0.014 (-0.051 - 0.027)	-	0.0198 (0.0145 - 0.0268)
		Stemonuraceae	1	-0.022 (-0.06 - 0.017)	-	0.0291 (0.021 - 0.0421)
		Styracaceae	1	-0.028 (-0.067 - 0.009)	-	0.0393 (0.0289 - 0.0564)
		Symplocaceae	1	-0.024 (-0.064 - 0.013)	-	0.0342 (0.0251 - 0.0489)
		Tapisciaceae	1	-0.02 (-0.058 - 0.02)	-	0.0281 (0.02 - 0.0413)
		Theaceae	1	-0.025 (-0.063 - 0.012)	-	0.0338 (0.0253 - 0.0468)
		Thymelaeaceae	2	-0.014 (-0.047 - 0.019)	-	0.0227 (0.017 - 0.0303)
Sinharaja	1995-2001	Apocynaceae	1	-0.015 (-0.167 - 0.093)	-	0.0339 (0.0101 - 0.119)
		Clusiaceae	3	0.002 (-0.021 - 0.024)	+	0.0046 (0.0013 - 0.0122)

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		Family				
		Cornaceae	1	-0.021 (-0.196 - 0.116)	-	0.0378 (0.0169 - 0.0646)
		Dilleniaceae	1	0.005 (-0.147 - 0.161)	+	0.0271 (0.009 - 0.0554)
		Dipterocarpaceae	1	0.002 (-0.133 - 0.145)	+	0.0213 (4e-04 - 0.0981)
		Euphorbiaceae	1	0.014 (-0.102 - 0.108)	+	0.0067 (-0.0069 - 0.0313)
		Fabaceae	1	0.001 (-0.118 - 0.088)	+	0.0143 (3e-04 - 0.0505)
		Lamiaceae	1	-0.001 (-0.116 - 0.083)	-	0.0124 (0.0016 - 0.0338)
		Lauraceae	3	-0.006 (-0.134 - 0.107)	-	0.0247 (0.0121 - 0.0398)
		Malvaceae	2	-0.025 (-0.144 - 0.038)	-	0.0227 (0.0166 - 0.0337)
		Melastomataceae	1	-0.013 (-0.19 - 0.133)	-	0.3079 (0.0516 - 0.5981)
		Meliaceae	2	0.017 (-0.12 - 0.177)	+	0.0116 (-0.0013 - 0.031)
		Moraceae	2	-0.051 (-0.185 - 0.046)	-	0.0452 (0.0307 - 0.0759)
		Myristicaceae	1	-0.019 (-0.137 - 0.086)	-	0.0324 (0.0128 - 0.0707)
		Myrtaceae	4	0.046 (-0.03 - 0.119)	+	-0.0203 (-0.0249 - -0.0112)
		Ochnaceae	1	0.006 (-0.123 - 0.104)	+	0.0091 (-0.0021 - 0.0292)
		Pentaphylacaeae	1	-0.012 (-0.188 - 0.13)	-	0.0404 (0.0184 - 0.0718)
		Phyllanthaceae	2	-0.015 (-0.168 - 0.119)	-	0.0287 (0.0126 - 0.0521)
		Putranjavaceae	1	-0.012 (-0.123 - 0.067)	-	0.0152 (0.0077 - 0.0292)
		Rhizophoraceae	1	0.008 (-0.137 - 0.155)	+	0.0087 (-0.0032 - 0.0324)
		Rubiaceae	1	0.013 (-0.124 - 0.16)	+	0.0187 (-0.0055 - 0.0888)
		Rutaceae	1	-0.007 (-0.182 - 0.139)	-	0.0171 (0.0085 - 0.0322)
		Salicaceae	1	0.007 (-0.134 - 0.13)	+	0.0094 (-0.0024 - 0.0319)
		Sapindaceae	2	0.017 (-0.083 - 0.144)	+	0.0044 (-0.0075 - 0.0245)
		Sapotaceae	2	0.016 (-0.055 - 0.072)	+	0.0025 (-0.0089 - 0.0276)
		Symplocaceae	3	-0.006 (-0.18 - 0.141)	-	0.026 (0.011 - 0.0432)
		Vitaceae	1	-0.022 (-0.214 - 0.117)	-	0.106 (0.0344 - 0.1893)
Yasuní	1996-2003	Achariaceae	2	-0.022 (-0.059 - 0.014)	-	0.0252 (0.0183 - 0.0359)
		Anacardiaceae	4	-0.02 (-0.045 - 0.008)	-	0.0253 (0.0191 - 0.0344)
		Annonaceae	10	-0.022 (-0.046 - 0.001)	-	0.0285 (0.0232 - 0.0357)
		Apocynaceae	5	-0.027 (-0.061 - 0.006)	-	0.0302 (0.0235 - 0.0402)
		Araliaceae	2	-0.022 (-0.06 - 0.014)	-	0.0289 (0.0199 - 0.0438)
		Arecaceae	5	-0.028 (-0.062 - 0.002)	-	0.0318 (0.0212 - 0.0446)
		Bignoniaceae	5	-0.026 (-0.051 - -0.003)	-*	0.031 (0.0244 - 0.0404)
		Boraginaceae	3	-0.022 (-0.058 - 0.013)	-	0.0283 (0.02 - 0.0408)
		Brassicaceae	1	-0.023 (-0.062 - 0.015)	-	0.0275 (0.019 - 0.0419)
		Burseraceae	12	-0.017 (-0.044 - 0.013)	-	0.0216 (0.0176 - 0.027)
		Cannabaceae	2	-0.028 (-0.069 - 0.006)	-	0.0376 (0.0261 - 0.0591)
		Cardiopteridaceae	1	-0.023 (-0.063 - 0.014)	-	0.0258 (0.0184 - 0.0379)

Caricaceae	1	-0.025 (-0.065 - 0.01)	-	0.0346 (0.0223 - 0.0572)
Caryocaraceae	2	-0.018 (-0.054 - 0.022)	-	0.0373 (0.0227 - 0.0654)
Chrysobalanaceae	4	-0.017 (-0.048 - 0.018)	-	0.0255 (0.0172 - 0.0373)
Clusiaceae	5	-0.033 (-0.072 - -0.001)	-*	0.0418 (0.0307 - 0.0607)
Combretaceae	5	-0.02 (-0.052 - 0.014)	-	0.0269 (0.0193 - 0.0374)
Ebenaceae	1	-0.022 (-0.061 - 0.017)	-	0.0285 (0.0188 - 0.0455)
Elaeocarpaceae	3	-0.016 (-0.041 - 0.013)	-	0.0205 (0.0148 - 0.0283)
Euphorbiaceae	11	-0.038 (-0.081 - -0.007)	-*	0.0395 (0.0327 - 0.0493)
Fabaceae	48	-0.029 (-0.051 - -0.007)	-*	0.0361 (0.0323 - 0.0403)
Lacistemataceae	1	-0.021 (-0.06 - 0.019)	-	0.0268 (0.0175 - 0.0436)
Lamiaceae	1	-0.016 (-0.048 - 0.022)	-	0.0298 (0.0173 - 0.0549)
Lauraceae	19	-0.017 (-0.032 - 0.003)	-	0.0227 (0.0189 - 0.0274)
Lecythidaceae	8	-0.015 (-0.034 - 0.006)	-	0.018 (0.0137 - 0.0234)
Magnoliaceae	1	-0.023 (-0.061 - 0.015)	-	0.031 (0.0208 - 0.0486)
Malpighiaceae	1	-0.022 (-0.06 - 0.017)	-	0.0272 (0.019 - 0.0409)
Malvaceae	20	-0.035 (-0.064 - -0.012)	-*	0.0289 (0.0254 - 0.0335)
Melastomataceae	9	-0.024 (-0.062 - 0.011)	-	0.0563 (0.0403 - 0.0777)
Meliaceae	22	-0.021 (-0.048 - 0.006)	-	0.0272 (0.0232 - 0.0321)
Moraceae	40	-0.032 (-0.047 - -0.017)	-*	0.034 (0.0307 - 0.038)
Myristicaceae	11	-0.015 (-0.044 - 0.018)	-	0.0196 (0.0157 - 0.0248)
Myrtaceae	6	-0.014 (-0.044 - 0.019)	-	0.0237 (0.0165 - 0.0329)
Nyctaginaceae	1	-0.023 (-0.061 - 0.016)	-	0.0268 (0.0195 - 0.0386)
Ochnaceae	2	-0.018 (-0.05 - 0.018)	-	0.0276 (0.0184 - 0.0429)
Olacaceae	2	-0.02 (-0.053 - 0.015)	-	0.0265 (0.0189 - 0.0376)
Opiliaceae	1	-0.02 (-0.053 - 0.015)	-	0.0275 (0.0184 - 0.0431)
Phyllanthaceae	1	-0.018 (-0.054 - 0.021)	-	0.0321 (0.0205 - 0.0532)
Piperaceae	2	-0.023 (-0.061 - 0.012)	-	0.0299 (0.0197 - 0.0483)
Polygonaceae	2	-0.02 (-0.055 - 0.019)	-	0.0241 (0.0176 - 0.0343)
Proteaceae	1	-0.025 (-0.059 - 0.009)	-	0.0277 (0.0202 - 0.0411)
Putranjavaceae	2	-0.021 (-0.056 - 0.016)	-	0.0282 (0.0203 - 0.0404)
Rhizophoraceae	3	-0.018 (-0.054 - 0.02)	-	0.0291 (0.0201 - 0.0431)
Rubiaceae	13	-0.008 (-0.034 - 0.024)	-	0.0187 (0.0136 - 0.0251)
Rutaceae	1	-0.021 (-0.06 - 0.018)	-	0.028 (0.018 - 0.0468)
Salicaceae	11	-0.015 (-0.048 - 0.025)	-	0.0298 (0.0225 - 0.0397)
Sapindaceae	2	-0.021 (-0.06 - 0.018)	-	0.0336 (0.0225 - 0.0536)

Sapotaceae	27	-0.012 (-0.029 - 0.009)	-	0.0168 (0.0128 - 0.0214)
Simaroubaceae	3	-0.013 (-0.046 - 0.024)	-	0.0187 (0.0122 - 0.0284)
Siparunaceae	3	-0.019 (-0.056 - 0.02)	-	0.0262 (0.0193 - 0.0361)
Solanaceae	1	-0.031 (-0.074 - 0.004)	-	0.05 (0.0293 - 0.0985)
Staphyleaceae	1	-0.024 (-0.062 - 0.013)	-	0.0316 (0.0208 - 0.0515)
Stemonuraceae	1	-0.022 (-0.06 - 0.017)	-	0.0278 (0.0192 - 0.0423)
Styracaceae	1	-0.019 (-0.056 - 0.02)	-	0.0258 (0.0165 - 0.0422)
Tapisciaceae	1	-0.028 (-0.067 - 0.007)	-	0.0366 (0.0243 - 0.0602)
Theaceae	1	-0.022 (-0.06 - 0.017)	-	0.0291 (0.0185 - 0.0498)
Ulmaceae	1	-0.019 (-0.054 - 0.02)	-	0.0299 (0.0198 - 0.0476)
Urticaceae	1	-0.027 (-0.066 - 0.004)	-	0.0343 (0.0226 - 0.0566)
Violaceae	5	-0.019 (-0.052 - 0.019)	-	0.0232 (0.0182 - 0.0302)
Vochysiaceae	3	-0.028 (-0.067 - 0.006)	-	0.0321 (0.0237 - 0.0462)

Table S5 Alternative version of Table 1 for Model 1 run with log-transformed mortality data, showing site-wide parameter estimates and measures of goodness-of-fit (Bayesian R^2) for the relationship between wood density and mortality at 10 sites. Site-wide parameters include the mean (α) and standard deviation (sd_α) of the family slopes, the mean (β) and standard deviation (sd_β) of the family intercepts (converted to a normal scale for presentation here), and the covariance ($\text{Cov}_{\alpha,\beta}$) between slope and intercept. The parameter σ describes the residual error in log annual mortality rates about each family's relationship. Parameters were estimated using the longest interval of survival data available at each site. Values are the mean of the posterior distributions for each parameter, estimated using Metropolis-Hastings algorithms in a Bayesian hierarchical model. The 95% credible interval for each parameter's distribution is given in parentheses.

Site	country	year	a	SD(a)	b	SD(b)	covar(a,b)	σ	Bayesian R^2
Barro Colorado Island	Panama	1982-2005	-2.059 (-3.255 - -0.977)	1.62 (0.51 - 3.163)	-2.4879 (-2.6555 - -2.3204)	0.2372 (0.0852 - 0.4477)	-0.001 (-0.222 - 0.228)	0.692 (0.597 - 0.802)	0.18
Huai Kha Kaeng	Thailand	1993-1999	-1.649 (-3.038 - -0.215)	2.129 (0.775 - 4.008)	-2.6832 (-2.886 - -2.4967)	0.3094 (0.1226 - 0.5693)	0.002 (-0.323 - 0.353)	0.736 (0.602 - 0.893)	0.21
Ituri- Edoro	Democratic Republic of Congo	1994-2000	-0.317 (-3.352 - 3.218)	5.473 (2.621 - 9.747)	-3.9924 (-4.3452 - -3.6511)	0.5528 (0.1733 - 1.0133)	-0.096 (-2.09 - 1.768)	0.666 (0.491 - 0.885)	0.59
Ituri- Lenda	Democratic Republic of Congo	1994-2000	-1.831 (-4.182 - 0.937)	3.922 (1.549 - 7.393)	-3.1698 (-3.5485 - -2.8265)	0.669 (0.2722 - 1.1535)	-0.098 (-1.584 - 1.383)	0.568 (0.38 - 0.786)	0.66
La Planada	Columbia	1997-2003	-1.581 (-4.248 - 1.121)	3.373 (1.006 - 6.947)	-3.0031 (-3.3974 - -2.623)	0.6894 (0.3624 - 1.1506)	0.192 (-1.211 - 1.905)	0.68 (0.527 - 0.873)	0.44
Lambir	Malaysia	1992-1997	-1.832 (-2.754 - -0.88)	2.396 (1.495 - 3.566)	-3.2318 (-3.3465 - -3.1109)	0.2873 (0.1738 - 0.4233)	-0.037 (-0.296 - 0.217)	0.501 (0.448 - 0.559)	0.47
Mudumalai	India	1988-2000	0.652 (-4.446 - 5.884)	6.789 (2.109 - 14.153)	-3.8269 (-4.4463 - -3.2295)	0.8698 (0.2695 - 1.6946)	0.274 (-4.574 - 5.872)	0.981 (0.666 - 1.362)	0.39
Pasoh	Malaysia	1987-2000	-1.724 (-2.386 - -1.022)	1.498 (0.923 - 2.226)	-3.151 (-3.2651 - -3.033)	0.3466 (0.2413 - 0.4716)	-0.038 (-0.239 - 0.149)	0.388 (0.351 - 0.428)	0.53
Sinharaja	Sri Lanka	1995-2001	-2.623 (-6.904 - 1.918)	6.185 (2.285 - 11.464)	-2.668 (-3.1413 - -2.2231)	0.7428 (0.3018 - 1.3036)	-0.772 (-4.167 - 1.902)	0.417 (0.128 - 0.808)	0.80
Yasuni	Ecuador	1996-2003	-2.572 (-3.708 - -1.415)	2.397 (1.201 - 3.955)	-2.7647 (-2.9602 - -2.5717)	0.4991 (0.3427 - 0.702)	-0.066 (-0.531 - 0.349)	0.568 (0.499 - 0.643)	0.53

Fig. S1 (**2 files**) Relationship between wood density and mortality for species within the most species-rich families in our dataset (black points), as predicted by model 2. Families are arranged by taxonomic order, given in parentheses. Grey points represent the entire dataset. Blue solid line indicates the family relationship as described by the slope (*a*) and intercept (*b*) parameters, red dashed lines indicate the 95% confidence interval of the model, reflecting within-family variation (*s*). Lines curve because the Y-axis has been log transformed for presentation. An asterisk (*) denotes families where slope 95% (*α)* 95% credible interval estimates do not overlap 0 (see Table 2).

Fig. S2 Alternative set of panels for Figure 1 for Model 1 run with log transformed mortality data, showing the relationship between wood density and annual mortality rates for individual species (black points) from ten forest census plots across the tropics. Solid line indicates the average family relationship as described by the site-wide slope α and intercept β. Dashed lines denote $\pm 2\ \sigma$ (within-family error) around the average family relationship. Shaded area indicates the 95% confidence interval in the model, reflecting variation both within and across families. At some sites the shaded area contracts around the global mean wood density (0.58 g/cm^3), reflecting the fact that data were centered on this value prior to analysis. An asterisk (*) denotes plots where site-wide slope (*α)* 95% credible interval estimates do not overlap 0 (see Table S5).
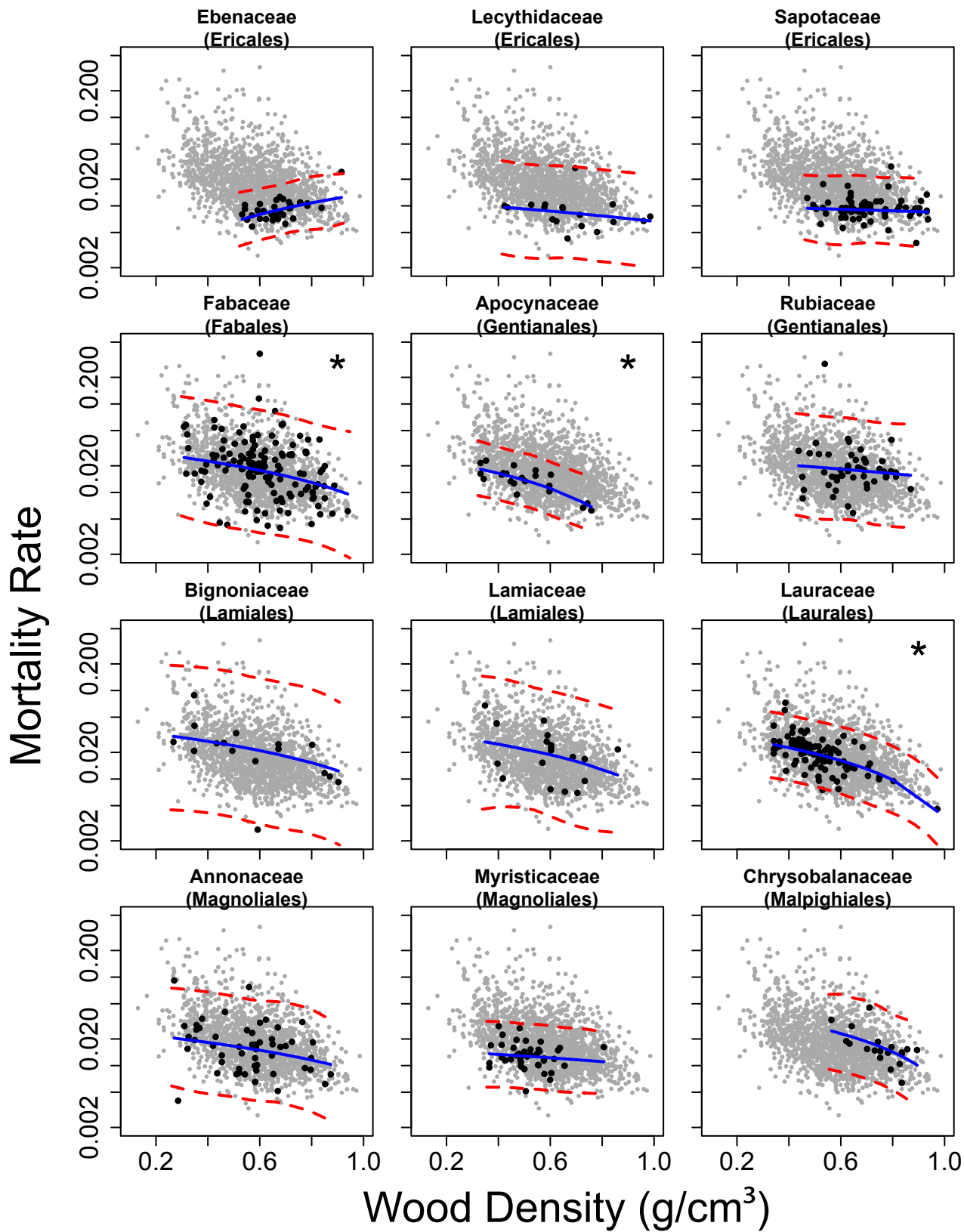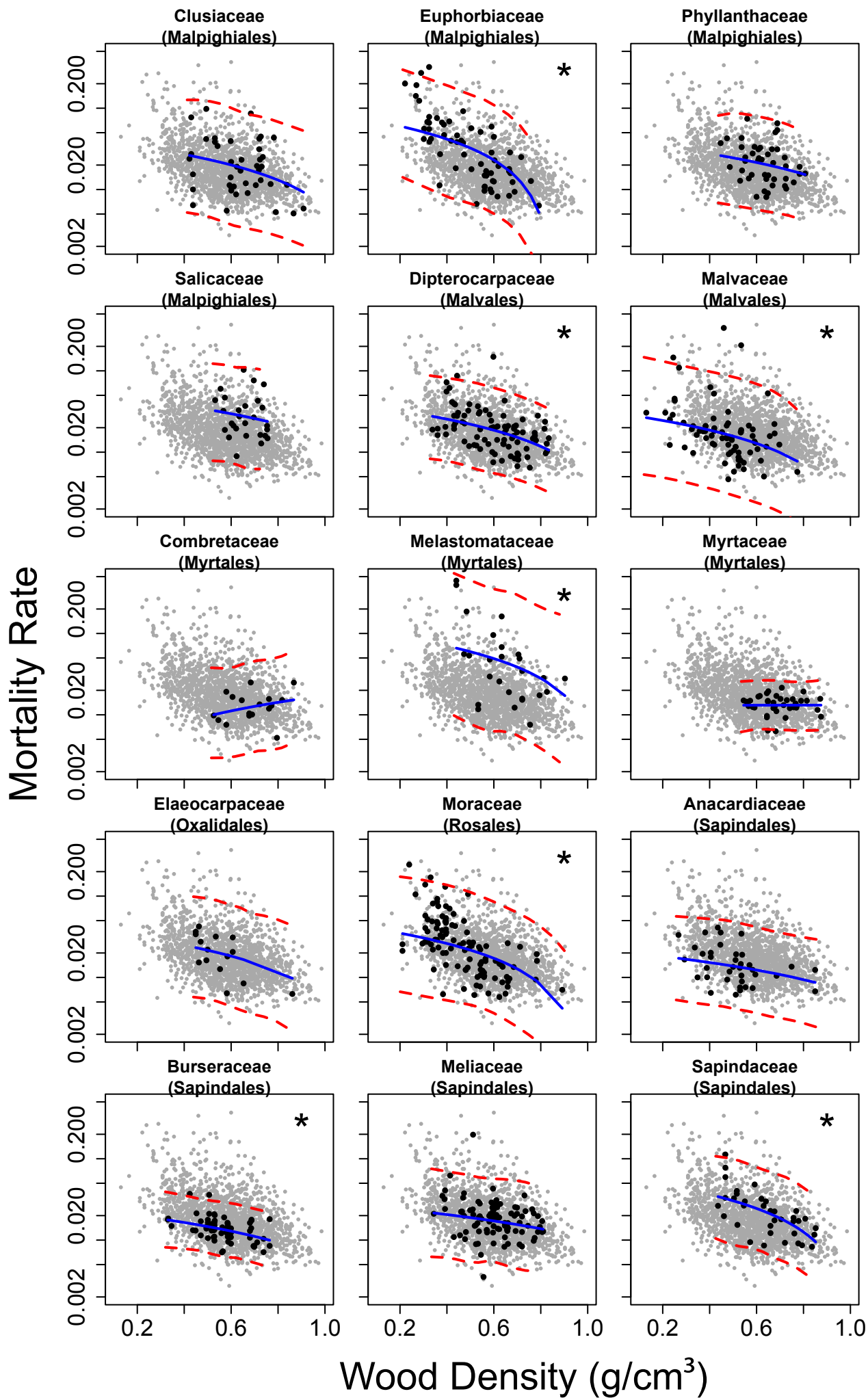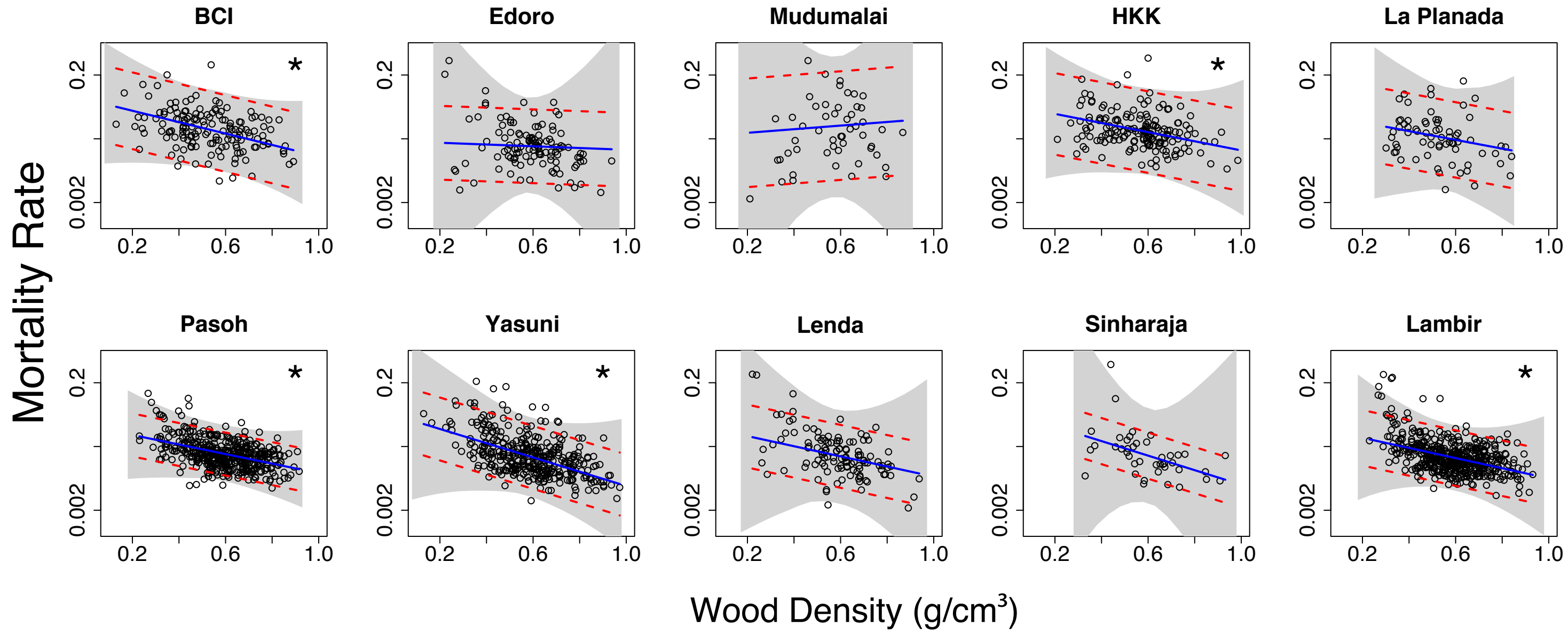
Figure S1A

Figure S1B

Figure S2

Notes S1 Code to run Model 1 in R


```
#######################################################
###
###   Master function - Wood density & mortality
###
###   Calls and runs functions for Bayesian analysis of
###      model with slopes and intercepts
###      varying by family, using Gibbs Sampler
###
###   Sets up file names, R environment,
###      prepares datasets, calls Gibb Sampler,
###      saves output as .Rdata files, one for each
### site/census.
###
###   Source this file to load all functions.
###
###   to run analysis, use run.density.mortality()
###      with inputs described below
###
###   Note: must have package "mvtnorm" loaded
###
#######################################################



#######################################################
###
###   DATA FORMAT:
###      Each species is a row, and all species
###         (from all censuses/sites) are in one dataframe.
###      Columns must include the following:
###         plotCensus - unique code for plot/census
###         sp - code for species
###         N - no. of individuals in species at census start
###         S - number of individuals surviving census interval
###         time - length of census interval in years
###         site - site code
###         wd - wood density
###         wd_detlevel - source of wood density estimate
###            (e.g. from a measurement of the species or
###            from a genus or family mean); function will
###            only choose species where the value is
###            "species" (i.e. estimates are from measures
```

```
###                    on that species and not from a family/genus
mean)
###             fam - family the species belongs to.
###
###########################################################


###########################################################
###
###   INPUTS
###       Input either file or name of a comma-separated data
###           file (data=mydataframe or use path="directorypath"
###           and datafile="mydata.csv").  Path term is also
###           where results will be saved
###
###       Other inputs are for running of Gibbs Sampler:
###           reps - the total number of iterations (including the
burn-in)
###           reps.wanted - the desired range of the iterations
###               (i.e. the last xxx iterations, which follow the
###               burn-in iterations)
###           adjust - the number (slightly > 1) used in the self-
adjustment
###               phase for the size of the Metropolis jumps
###           scale.burnin - the number of steps the scale
parameter can
###               self-adjust (should be the same as the burn-in
iterations
###               to limit adjustment to the burn-in period).
###           start.pars - starting values of a (slope) and b
(intercept),
###               in that order
###           scale.start - starting values for scale (sd)
parameterS of
###               a, b, sigma, and Mi (in that order); used in
Metropolis
###               algorithm
###
###########################################################


###########################################################
###
###   OUTPUTS two lists, all steps in the parameter
```

```
###       chains and mean parameter estimates with
###       95% credible intervals
###
###
###   "results" list contains data at every iteration:
###       reps.wanted - chosen # of iterations following burn-in
###       slope.families - rows are families, columns
###           are the slope value at each iteration
###           (matrix of family x reps)
###       interc.families - rows are families, columns
###           are the intercept value at each iteration
###           (matrix of family x reps)
###       sigma - sigma values at each iteration (vector)
###       slope.mean - mean of distribution of family slopes
###           at each iteration (vector)
###       slope.sd - standard deviation of distribution of
###           family slopes at each iteration (vector)
###       interc.mean - mean of distribution of family intercepts
###           at each iteration (vector)
###       interc.sd - standard deviation of distribution of
###           family slopes at each iteration (vector)
###       covar - covariance between family slopes and intercepts
###           at each iteration (vector)
###       mort.rates - rows are species, columns are species'
###           mortality rate estimates at each iteration
###           (matrix of species x reps)
###
###
###   "summary.results" list contains parameter summaries (mean,
2.5%,
###       97.5%) for the iterations beyond the burn-in (i.e. for
###       "reps.wanted")
###           slope.families - matrix with rows as families
###           interc.families - matrix with rows as families
###           hyperparameters - rows are site-level model
parameters
###           mort.rates - matrix with rows as species
###
###
#######################################################


## MAIN FUNCTION that runs analysis for all sites/species and
```

saves output in directory specified by "path".

```r
run.density.mortality=function(data=NULL, datafile="mydata.csv",
path="", reps=11000, reps.wanted=1001:11000, adjust=1.01,
scale.burnin=1000, start.pars=c(-0.05, 0.15), scale.start=c(0.01,
0.01, 0.01, 0.01))
{
    cat(date(),"\n")
    on.exit(cat(date(),"\n"))

    require(mvtnorm)
    if(is.null(data))
data=read.csv(paste(path,datafile,sep=""),as.is=T,row.names=1)

    ### prepare datasets ###

    global=find.global.mean.wd(data)
    alldata=prep.data(data, global)
    censnames=names(alldata)
        # alldata is a list with each item the data from one
census from one plot


    ### Gibbs Sampler iterations ###

    for(m in 1:length(alldata)) # Loop over all sites/censuses #
    {
        cat("Running sampler for plot and census interval ",
censnames[m], "\n")

        results=dens.mort.Gsampler(alldata[[m]], reps=reps,
reps.wanted=reps.wanted, adjust=adjust,
scale.burnin=scale.burnin, start.pars=start.pars,
scale.start=scale.start)

        results$wd.centered=alldata[[m]]$wd
        results$wd.orig=alldata[[m]]$wd.orig

    names(results$wd.centered)=names(results$wd.orig)=rownames(al
ldata[[m]])


    summary.results=list(slope.families=t(apply(results$slope.fam
ilies[,results$reps.wanted], 1, CI)),
```

```r
  interc.families=t(apply(results$interc.families[,results$reps.wan
  ted], 1, CI)),
  hyperparameters=rbind(sigma=CI(results$sigma[results$reps.wanted]
  ), slope.mean=CI(results$slope.mean[results$reps.wanted]),
  slope.sd=CI(results$slope.sd[results$reps.wanted]),
  interc.mean=CI(results$interc.mean[results$reps.wanted]),
  interc.sd=CI(results$interc.sd[results$reps.wanted]),
  covar=CI(results$covar[results$reps.wanted])),
  mort.rates=t(apply(results$mort.rates[,results$reps.wanted], 1,
  CI)))

        save(results, summary.results,
  file=paste(path,censnames[m], ".Rdata", sep=""))

        alldata[[m]]=NA
        rm(results, summary.results)

        for(q in 1:20) gc()

            }


        rm()
        for(m in 1:20) gc()


        } # end run.density.mortality()




############################################################
###
### Data Preparation functions
###
###       for wood density / mortality analyses
###
############################################################


##########################################
# Find the global mean wood density to use in centering wood
density values for later analysis
```

```r
find.global.mean.wd=function(data)
{

    # only use species where wood density obtained from
measurement on that species and not genus/family mean
    data=subset(data, wd_detlevel=="species" & !is.na(time))

    # use single census datasets to find global average
    # and use unique combo of species x wsg measurement
    # this way species in multiple censuses (with the same wsg
value) are not counted twice

    return(mean(unique(data[,c("sp","wd")])[,2], na.rm=T))
    }


#########################################
# Separate tree data into list with each item representing one
plot/census.
    # filename is name of datafile
    # global is the global mean wood density, calculated using
above function

prep.data=function(data, global)
{

    site.censname=unique(data$plotCensus)

    # reduce to species-level wood density determinations
    data=subset(data, wd_detlevel=="species" & !is.na(time))

    # center wood density data across whole dataset.
    data$wd.orig=data$wd
    data$wd=data$wd.orig-global

    alldata=list()

    for(i in 1:length(site.censname))
    {
        alldata[[i]]=subset(data, plotCensus==site.censname[i])
        names(alldata)[i]=site.censname[i]
    }
```

```
        return(alldata)
}

##############################
# find mean and 95% credible intervals of posterior
distributions.

CI=function(x)
{
    results.summary=c(mean=mean(x), quantile(x, prob=c(0.025,
0.975)))
    return(results.summary)
    }




####################################################
###
###   Wood density & mortality Gibbs Sampler
###
###       called by master.wd.mortality.family.analyses.R
###
###       fits model for a given plot/census
###           using Metropolis-Hastings algorithms
###           and calls likelihood functions listed below
###
###       returns chains for mortality rates,
###           model parameter estimates, etc.
###
####################################################


dens.mort.Gsampler=function(data,reps=11000,
reps.wanted=1001:11000, adjust=1.01, scale.burnin=1000,
start.pars=c(-0.05, 0.15), scale.start=c(0.1, 0.1, 0.01, 0.01))
{

    #### set observed values ####

    S=data$S
    N=data$N
    time=data$time
```

```r
wd=data$wd
fam=data$fam
families=sort(unique(data$fam))
spp=data$sp


####  set initial mortality values ####

Mi=matrix(data=NA, nrow=length(data$sp),ncol=reps)
rownames(Mi)=data$sp
Mi[,1]=(log(N)-log(S))/time
Mi[(Mi[,1]==0 | is.na(Mi[,1])),1] = 0.01
Mi[is.infinite(Mi[,1]),1]=0.9


    #### set initial values of hyperparameters ####
slope.mean=start.pars[1]
interc.mean=log(start.pars[2])
slope.sd = abs(slope.mean/3)
interc.sd = abs(interc.mean/3)
sigma=sd(log(Mi[,1]))

    #### set initial values of family-level parameters ####

a=b=matrix(data=NA, nrow=length(families),ncol=reps)
rownames(a)=rownames(b)=families
a[,1]=rnorm(dim(a)[1], mean=slope.mean, sd=slope.sd)
b[,1]=rlnorm(dim(b)[1], meanlog=interc.mean, sdlog=interc.sd)

    #### set initial slope/intercept covariance ####
covar = cov(a[,1], log(b[,1]))


    #### set start for scale parameters, updated throughout,
but then held frozen after burn-in ####
    a.scale=rep(scale.start[1], length(families))
    b.scale=rep(scale.start[2], length(families))
    sigma.scale=scale.start[3]

    slope.mean.scale = slope.sd.scale = 0.01
    interc.sd.scale = interc.mean.scale = .1
    covar.scale = 0.001

    Mi.scale=rep(scale.start[4], dim(Mi)[1])
```

```r
#### clear some memory before analysis ####
 rm(data); for(z in 1:10) gc() ; rm(z)



       #### Update each parameter in turn ####

    for(i in 2:reps)
    {
        # loop over families...
        for(k in 1:length(families))
        {
            # update a (slope) for a family
            step=metrop1step(a.fam.likelihood,
start.param=a[k,i-1], scale.param=a.scale[k], adjust=adjust,
target=0.25, adjust.scale=(i<=scale.burnin),
wd=wd[fam==families[k]] , b=b[k,i-1], Mi=Mi[fam==families[k],i-
1], sigma=sigma[i-1], slope.mean=slope.mean[i-1],
slope.sd=slope.sd[i-1])
            a[k,i]=step[1]
            a.scale[k]=step[2]

            # update b (intercept) for a family
            step=metrop1step(b.fam.likelihood,
start.param=b[k,i-1], scale.param=b.scale[k],
adjust=adjust,target=0.25, adjust.scale=(i<=scale.burnin),
wd=wd[fam==families[k]] , a=a[k,i], Mi=Mi[fam==families[k],i-1],
sigma=sigma[i-1], interc.mean=interc.mean[i-1],
interc.sd=interc.sd[i-1])
            b[k,i]=step[1]
            b.scale[k]=step[2]

        } #end loop over families

        # update sigma (constant among families)
        step=metrop1step(sigma.likelihood,
start.param=sigma[i-1], scale.param=sigma.scale, adjust=adjust,
target=0.25, adjust.scale=(i<=scale.burnin), Mi=Mi[,i-1],
a=a[match(fam, families),i], wd=wd, b=b[match(fam, families),i])
            sigma[i]=step[1]
            sigma.scale=step[2]
```

```
#### update hyperparameters ####

# update slope/intercept distribution means
step=metrop1step(slope.mean.likelihood,
start.param=slope.mean[i-1], scale.param=slope.mean.scale,
adjust=adjust, target=0.25, adjust.scale=(i<=scale.burnin),
int.mean=interc.mean[i-1], slope.sd=slope.sd[i-1],
int.sd=interc.sd[i-1], covar=covar[i-1], slopes.ints=cbind(a[,i],
log(b[,i])))
        slope.mean[i]=step[1]
        slope.mean.scale=step[2]

step=metrop1step(interc.mean.likelihood,
start.param=interc.mean[i-1], scale.param=interc.mean.scale,
adjust=adjust, target=0.25, adjust.scale=(i<=scale.burnin),
slope.mean=slope.mean[i], slope.sd=slope.sd[i-1],
int.sd=interc.sd[i-1], covar=covar[i-1], slopes.ints=cbind(a[,i],
log(b[,i])))
        interc.mean[i]=step[1]
        interc.mean.scale=step[2]

# update variance/covariance terms
step=metrop1step(slope.sd.likelihood,
start.param=slope.sd[i-1], scale.param=slope.sd.scale,
adjust=adjust, target=0.25,
adjust.scale=(i<=scale.burnin),slope.mean=slope.mean[i],
int.mean=interc.mean[i],  int.sd=interc.sd[i-1], covar=covar[i-
1], slopes.ints=cbind(a[,i], log(b[,i])))
        slope.sd[i]=step[1]
        slope.sd.scale=step[2]

step=metrop1step(interc.sd.likelihood,
start.param=interc.sd[i-1], scale.param=interc.sd.scale,
adjust=adjust, target=0.25, adjust.scale=(i<=scale.burnin),
slope.mean=slope.mean[i], int.mean=interc.mean[i],
slope.sd=slope.sd[i], covar=covar[i-1], slopes.ints=cbind(a[,i],
log(b[,i])))
        interc.sd[i]=step[1]
        interc.sd.scale=step[2]

step=metrop1step(covar.likelihood, start.param=covar[i-
1], scale.param=covar.scale, adjust=adjust, target=0.25,
adjust.scale=(i<=scale.burnin), slope.mean=slope.mean[i],
```

```
        int.mean=interc.mean[i],  slope.sd=slope.sd[i],
        int.sd=interc.sd[i], slopes.ints=cbind(a[,i], log(b[,i])))
              covar[i]=step[1]
              covar.scale=step[2]


              # update Mortality Rate estimates for each species
              for(j in 1:(dim(Mi)[1]))
              {
                    step=metrop1step(m.likelihood, start.param=Mi[j,i-
        1], scale.param=Mi.scale[j], adjust=adjust, target=0.25,
        adjust.scale=(i<=scale.burnin), a=a[families==fam[j],i],
        b=b[families==fam[j],i],wd=wd[j],sigma=sigma[i],time=time[j],
        N=N[j], S=S[j])
                    Mi[j,i]=step[1]
                    Mi.scale[j]=step[2]
                    } # end loop over each species' mortality rate

        } # end loop Gibbs Sampler iterations



        #### assemble final data for output  ####

        all.results=list(reps.wanted=reps.wanted, slope.families=a,
        interc.families=b, sigma=sigma, slope.mean=slope.mean,
        slope.sd=slope.sd, interc.mean=interc.mean, interc.sd=interc.sd,
        covar=covar, mort.rates=Mi)

        return(all.results)
        } # end dens.mort.Gsampler




        #################################################################
        ###
        ###  Metropolis Hastings algorithm for 1 step in Gibbs Sampler
        ###
        #################################################################

        metrop1step=function(func,start.param,scale.param,adjust,target,
```

```r
adjust.scale=T, ...)
{
    origlike=func(start.param,...)
    newval=rnorm(1,mean=start.param,sd=scale.param)
    newlike=func(newval,...)
    newscale=scale.param
    # scale term is only changed during the burn-in period, then
held fixed.

    AdjExp=(1-target)/target

    if(newlike>=origlike)
    {
        if(adjust.scale==T) newscale=scale.param*adjust^AdjExp
        return(c(newval,newscale,1))
    }
    else likeratio=exp(newlike-origlike)

    if(runif(1)<likeratio)
    {
        if(adjust.scale==T) newscale=scale.param*adjust^AdjExp
        return(c(newval,newscale,1))
    }
    else
    {
        if(adjust.scale==T) newscale=scale.param*(1/adjust)
        return(c(start.param,newscale,0))
    }

}




####################################################
###
###   Likelihood Functions
###
###   Model has slopes and intercepts varying by family
###
###
###       functions used in Metropolis algorithm
```

```
###              to assess likelihood of current
###              and proposed steps in the MCMC chain
###
###        called by functions in wsg.mort.family.model.v3.R
###
###########################################################




##############################
####   a.fam.likelihood    ####
##############################

# Likelihood function for the slope for the wood density /
mortality relationship within one family.
    # a - family slope term
    # wd - vector of wood density values, one for each species in
family
    # b - family intercept term
    # Mi - vector of mortality rates, one for each species in
family
    # sigma - lognormal scatter around fitted line
    # slope.mean - mean of all family slope terms
    # slope.sd - standard deviation of all family slope terms
a.fam.likelihood=function(a,wd,b,Mi,sigma, slope.mean, slope.sd)
{
    m.norm=(a*wd)+b
    if(length(m.norm[m.norm<=0 | is.na(m.norm)])>0) return(-Inf)

    mu=log(m.norm)

    # log likelihoods
    part1=sum(dlnorm(Mi,meanlog=mu,sdlog=sigma,log=T))
    # log likelihood of mortality rates being drawn from a
distribution centered around a mortality rate estimated using
family slope and intercept term
    part2=dnorm(a, mean=slope.mean, sd=slope.sd, log=T)
    # log likelihood of family slope term being drawn from a
distribution centered on the mean of all family slopes

    return(part1+part2)
}
```

```
############################
####   b.fam.likelihood   ####
############################

# Likelihood function for the intercept for the wood density /
mortality relationship within one family.
    # b - family intercept term
    # wd - vector of wood density values, one for each species in
family
    # a - family slope term
    # Mi - vector of mortality rates, one for each species in
family
    # sigma - lognormal scatter around fitted line
    # interc.mean - mean of all family intercept terms
    # interc.sd - standard deviation of all family intercept
terms

b.fam.likelihood=function(b,wd,a,Mi,sigma, interc.mean,
interc.sd)
{
    if(b<=0) return(-Inf)

    m.norm=(a*wd)+b
    if(length(m.norm[m.norm<=0 | is.na(m.norm)])>0) return(-Inf)

    mu=log(m.norm)

    # log likelihoods
    part1=sum(dlnorm(Mi,meanlog=mu,sdlog=sigma,log=T))
        # log likelihood of mortality rates being drawn from a
distribution centered around a mortality rate estimated using
family slope and intercept term
    part2=dlnorm(b, mean=interc.mean, sd=interc.sd, log=T)
        # log likelihood of family intercept term being drawn
from a distribution centered on the mean of all family intercepts

    return(part1+part2)
}
```

```
##############################
####   sigma.likelihood    ####
##############################

# Likelihood function for the variance around the wood density /
mortality relationship, uniform across all families.
    # sigma - lognormal scatter around fitted line
    # Mi - vector of mortality rates, one for each species in
family
    # a - family slope term
    # wd - vector of wood density values, one for each species in
family
    # b - family intercept term

sigma.likelihood=function(sigma,Mi,a,wd,b) #using vectors of mi
and wd
{
    if(sigma<=0) return(-Inf)

    m.norm=(a*wd)+b
    if(length(m.norm[m.norm<=0 | is.na(m.norm)])>0) return(-Inf)

    mu=log(m.norm)

    return(sum(dlnorm(Mi,meanlog=mu, sdlog=sigma,log=T)))
    # log likelihood of mortality rates being drawn from a
lognormal distribution centered around a mortality rate estimated
using family slope and intercept term, with sigma as standard
deviation
}




#########################
####   m.likelihood    ####
#########################

# Likelihood function for a species mortality rate.
    # m - mortality rate estimate (single species)
    # b - family intercept term
    # wd - vector of wood density values, one for each species in
```

family
```
    # a - family slope term
    # sigma - lognormal scatter around fitted line
    # time - time between censuses
    # S - number of survivors over census interval
    # N - number of individuals at start of census interval

m.likelihood=function(m,b,wd,a,sigma,time,S,N)  #using single
values of wd and m
{
    m.norm=(a*wd)+b
        if(length(m.norm[m.norm<=0 | is.na(m.norm)])>0) return(-
Inf)

    mu=log(m.norm)
    if(sigma<=0) return(-Inf)

    part1=dlnorm(m,meanlog=mu,sdlog=sigma,log=T)
    # Likelihood from lognormal dist of morality rates

    theta=exp(-m*time)
    # theta is annual survival probability, and m is annual
mortality rate constant
        if(theta<=0 | theta>=1) return(-Inf)

    part2=dbinom(S,size=N,prob=theta,log=T)
    # Likelihood of S survivors from N individuals given annual
survival probability theta

    return(part1+part2)
}
```


         ########### HYPERPARAMETERS ###########


```
################################
####   slope.mean.likelihood   ####
################################

# Likelihood function for mean slope across families.
    # slope.mean - mean of all family slope terms
    # int.mean - mean of all family intercept terms (term is log
```

transformed)
```
    # slope.sd - standard deviation of all family slope terms
    # int.sd - standard deviation of all family intercept terms
    # covar - covariance of intercept and slope
    # slopes.ints - two column matrix listing slopes and
intercepts (intercepts are log-transformed before passing to this
function)

slope.mean.likelihood=function(slope.mean, int.mean, slope.sd,
int.sd, covar, slopes.ints)
{
    means=c(slope.mean, int.mean)
    sigmas=matrix(data=c(slope.sd^2, covar, covar, int.sd^2),
nrow=2)

    return(sum(dmvnorm(x=slopes.ints, mean=means, sigma=sigmas,
log=T)))
    }




####################################
####   interc.mean.likelihood   ####
####################################

# Likelihood function for mean intercept across families.
    # int.mean - mean of all family intercept terms (term is log
transformed)
    # slope.mean - mean of all family slope terms
    # slope.sd - standard deviation of all family slope terms
    # int.sd - standard deviation of all family intercept terms
    # covar - covariance of intercept and slope
    # slopes.ints - two column matrix listing slopes and
intercepts (intercepts are log-transformed before passing to this
function)

interc.mean.likelihood=function(int.mean, slope.mean, slope.sd,
int.sd, covar, slopes.ints)
{
    means=c(slope.mean, int.mean)
    sigmas=matrix(data=c(slope.sd^2, covar, covar, int.sd^2),
nrow=2)
```

```
    return(sum(dmvnorm(x=slopes.ints, mean=means, sigma=sigmas,
log=T)))
    }




###############################
####   slope.sd.likelihood   ####
###############################

# Likelihood function for sd of family slopes.
    # slope.sd - standard deviation of all family slope terms
    # slope.mean - mean of all family slope terms
    # int.mean - mean of all family intercept terms
    # int.sd - standard deviation of all family intercept terms
    # covar - covariance of intercept and slope
    # slopes.ints - two column matrix listing slopes and
intercepts (intercepts are log-transformed before passing to this
function)

slope.sd.likelihood=function(slope.sd, slope.mean, int.mean,
int.sd, covar, slopes.ints)
{
    if(slope.sd<=0) return(-Inf)

    means=c(slope.mean, int.mean)
    sigmas=matrix(data=c(slope.sd^2, covar, covar, int.sd^2),
nrow=2)

    # do not permit var/cov matrices resulting in negative
eigenvalues
        tmp=eigen(sigmas, symmetric = TRUE, only.values =
TRUE)$values
        if(length(tmp[tmp<=0])>0) return(-Inf)

    return(sum(dmvnorm(x=slopes.ints, mean=means, sigma=sigmas,
log=T)))
    }


###############################
####   interc.sd.likelihood   ####
###############################
```

```r
# Likelihood function for sd of family intercepts.
    # int.sd - standard deviation of all family intercept terms
    # slope.mean - mean of all family slope terms
    # int.mean - mean of all family intercept terms
    # slope.sd - standard deviation of all family slope terms
    # covar - covariance of intercept and slope
    # slopes.ints - two column matrix listing slopes and
intercepts (intercepts are log-transformed before passing to this
function)

interc.sd.likelihood=function(int.sd, slope.mean, int.mean,
slope.sd, covar, slopes.ints)
{
    if(int.sd<=0) return(-Inf)

    means=c(slope.mean, int.mean)
    sigmas=matrix(data=c(slope.sd^2, covar, covar, int.sd^2),
nrow=2)

    # do not permit var/cov matrices resulting in negative
eigenvalues
        tmp=eigen(sigmas, symmetric = TRUE, only.values =
TRUE)$values
        if(length(tmp[tmp<=0])>0) return(-Inf)

    return(sum(dmvnorm(x=slopes.ints, mean=means, sigma=sigmas,
log=T)))
    }




############################
####   covar.likelihood   ####
############################

# Likelihood function for sd of family intercepts.
    # covar - covariance of intercept and slope
    # slope.mean - mean of all family slope terms
    # int.mean - mean of all family intercept terms
    # slope.sd - standard deviation of all family slope terms
    # int.sd - standard deviation of all family intercept terms
    # slopes.ints - two column matrix listing slopes and
intercepts (intercepts are log-transformed before passing to this
function)
```

```r
covar.likelihood=function(covar, slope.mean, int.mean,  slope.sd,
int.sd, slopes.ints)
{
    means=c(slope.mean, int.mean)
    sigmas=matrix(data=c(slope.sd^2, covar, covar, int.sd^2),
nrow=2)

    # do not permit var/cov matrices resulting in negative
eigenvalues
        tmp=eigen(sigmas, symmetric = TRUE, only.values =
TRUE)$values
        if(length(tmp[tmp<=0])>0) return(-Inf)

    return(sum(dmvnorm(x=slopes.ints, mean=means, sigma=sigmas,
log=T)))
    }
```