**Water inundation shapes species distributions in tropical forests**

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**Variation among tree species in their environmental tolerances can contribute to species coexistence through niche partitioning**1**. Topographical distributions of tropical tree species have long been associated with local soil water requirements**2–5**, but clear evidence for traits influencing these patterns is not forthcoming. Decreasing water availability at higher elevations appears to impose an upper barrier to many tree species distributions**2,4,6–9**, but factors mediating lower elevational limits remain unresolved**3,10**. We show that water inundation episodes constrain species distributions at lower elevational gradients in tropical forests. Estimates of species-specific seedling responses to water inundation accurately predicted adult tree distributions in a large-scale forest dynamics plot. Our analysis also indicates that water inundation provides an additional niche axis that may partially explain the occurrence of high wood density species within wet low-lying areas of tropical forests. Higher adult wood density predicted tolerance of water inundation as seedlings. However, we found that seedling wood density values were unrelated to tolerance. In a separate experiment, we found that increasing frequencies of inundation typically increased the wood density seedlings by 20% across the gradient. Moreover, adult wood density values predicted the plasticity. Our results suggest that the distribution of higher wood density species on low lying nutrient-rich alluvial forest is perhaps related to the seedlings capacity to grow high wood density under stressful conditions, rather that providing tolerance itself. This may be interpreted as the capacity to grow heavier wood under reduced decline carbon intake during periods of stress. The differential seedling responses to water inundation captures larger scale filtering processes that determine adult topographical distributions of species. However, may also point towards as a potential trade-off between tolerances across the soil water gradient. Given our findings, increasingly variable rainfall amplitude in the region**11 **is likely to affect the spatial structure, species composition, and diversity of future forests.**

Hundreds of tree species can coexist within a single hectare of wet tropical forests, in apparent contradiction of the competitive exclusion principle1,12. One important mechanism that has been proposed to explain species coexistence in tropical forests is niche differentiation at varying spatial scales13,14. At the finer end of the spectrum, the effects of micro-topographical variation are largely unknown, even though it has the potential to explain a substantial component of species distributions. Early life stages are likely most sensitive to niche processes15, and the availability of suitable environmental conditions may provide an initial and lasting advantage. One axis of niche-differentiation among tropical forest trees that varies across macro and micro scales is soil water. As a result, differential seedling survival along water-availability gradients might substantially shape the distributions of adults and facilitate species coexistence.

Water availability on hilltops is often limited16, and the capacity of episodic droughts to restrict the upper elevational distribution of tropical trees is well established2,4,6–9. Here, at the drier end of the spectrum, slower growing speciesare generally more dominant, and this is reflected in their higher than average wood densities17,18. This suggests that wood density should increase with elevation, with fast-growing lower wood density species at an advantage at lower elevation, wetter and nutrient-rich sites. We find no studies explicitly testing a within-site elevation relationship with wood density, although many provide analysis on these components2,4,8,19,20. Nevertheless, under this ecologically compelling model of species distributions, higher wood densities are predicted to be associated with higher elevations.

The extent to which micro-topography interacts with episodic water inundation to constrain species distributions in *terra firme* forest remains largely unexplored. Recent research has shown that species differ in seedling responses to ephemeral water inundation events3, although it is uncertain whether such differences relate to species partitioning10. Moreover, there is little information on how differential responses to micro-topographical variation contributes to species distributions at larger spatial scales. Discovering what limits species at lower elevations prone to waterlogging in tropical forests could help explain niche partitioning across the entire soil water gradient.

We phylogenetically constrained our study to a single family, the Dipterocarpaceae, to reduce uncertainties that could be introduced by including more species from more families. Large-scale (macro-topographical) adult distributions of species (n = 16) and general trends in the wood density distribution (n = 36). We additionally quantified water inundation sensitivities of the 16 dipterocarp species using 2048 seedlings in a fully randomised experiment within the alluvial habitat of Sepilok Forest Reserve, Sabah (Fig. 1a, b & d).

We evaluated both large-scale (macro-topographical) adult distributions and micro-topographical niche segregation among seedlings of 16 species of Dipterocarpaceae, and the extent to which seedling sensitivities to waterlogging reflect adult distributions. We phylogenetically constrained our study to a single family, the Dipterocarpaceae, to reduce uncertainties that could be introduced by including more species from more families. We additionally quantified seedling water inundation sensitivities of 16 dipterocarp species in a fully randomised experiment within the alluvial habitat of Sepilok Forest Reserve, Sabah (Fig. 1a, b & d). Alluvial habitats characteristic of large valleys and riverine areas in lowland dipterocarp forests are common throughout Borneo21–24, and we expect our sites to be representative of much of Borneo’s rainforests. Seedling responses and wood density were used to predict the larger scale (macro-topographical) adult distributions on elevational scales of tens of metres.

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| Figure 1 I.png |
| **Figure 1 | Macro to micro topographical variation within Sepilok Forest Reserve, and community compositional variation at the macro scale.** Topographical digital terrain model of 3375 ha (ca. 75%) of SFR **(a)**, with the 160ha forest plot outlined and the distribution of the four 4 ha plots (and one 2 ha plot) for analysis. **(b)** The distribution of two example species, *Shorea leprosula* (white, diamond) and *S. beccariana* (grey, circle), indicating partitioning along topographical gradients within the 160ha plot. **(c)** Dissimilarity in dipterocarp community compositions reflected by colour variations across the 160ha plot, extracted from axis 1 of a non-metric multi-dimensional scaling analysis of 12 elevational bands. **(d)** Micro-topographical variation within three example plots, mean water inundation height expressed as the transparent blue (Fig. S1 – pictures of water inundation). |

The sixteen species’ elevational distribution were modelled with a unique intercept for each species and quadratic relationship with the environmental gradient. The peak of the probability distribution varied among species (Fig. 2a), with different species occurring at different elevations. Species formed a continuum of elevation associations (Fig. 2a), from *Shorea beccariana*, with a probability of occurrence peaking at an elevation of 114.6 m asl (95% Credible Interval Crl = 111.3 – 120.3, Table S2), to *S. seminis,* which peaked at 48.5 m (95% Crl = 55.8 – 65.4, Table S2).

For 42 tree species we found that the adult tree wood density is non-random (Fig 2b). Overall mean species’ wood density values in ¼ ha areas increase with elevation gradients (GLS, β = 107.69, 95% CI = 92.20 – 130.49, Fig 2b). This confirms the traditional view that higher elevations have typically have higher wood density. However, the reality is more complex. We found a quantile regression reveals a triangular relationship between wood density and elevation: at low elevations both high and low wood density species occur (βQ=0.025 = 4.57, 95% CI = -1.697 – 16.17, Fig. 2c); at higher elevation higher wood densities are more dominant (βQ=0.975 = 159.81, 95% CI = 88.60 – 247.48, Fig. 2c). We therefore suggest that adult wood density variables may have a role in predicting species distributions.

Species varied in their tolerances to water inundation. A model comparison between having the species interaction with water inundation and one without showed the model containing the interaction to explain significantly more variation (χ2 = 34.96, df = 15, *P* = 0.002). At one extreme, seedlings of *Shorea seminis* showed no difference in the probability of mortality between inundated and non-inundated areas (Fig. 2c). *Shorea beccariana*, representing the other end of the response gradient,had an absolute risk increase in mortality of 40.9% when inundated (Fig. 2c). Seedling mortality was not affected by soil pH, soil texture, light, or flash floods (178 mm of rainfall in 6 hours; *see Methods*), nor did inclusion of any of these predictors remove the relationship between seedling mortality and inundation. We refer to the difference in seedling mortality (*Δp(mortality)*) with respect to water inundation as “inundation sensitivity”.

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| **Figure 2 | Adult elevational distribution at landscape scales of 4 species (a), wood density distribution along elevation gradients (b), quantile regression slop coefficients with bootstrap, and interaction between species and water inundation on the probability of seedling mortality at micro-topographical scales (b). (a)** The elevation distribution of adult dipterocarps within a 160ha forest plot using the Integrated Nested Laplace Approximation. The 95% credible intervals (n=5000) were extracted from the posterior distribution. Grey shading of the panel for below (light blue) and above (dark blue) average wood densities. **(b)** Species differ in seedling sensitivity to water inundation along micro-topographical gradients within the alluvial zone. Points are ordered by the most likely elevation the adults are found, and grouped by below and above average wood densities for these species. 95% confidence intervals are bootstrapped (n = 5000). **(c)** quantile regression (0.025, 0.1, 0.5, 0.9, 0.975) typical wood density vs. typical elevation (m asl) of ¼ ha plots (n = 675). |

Investigating the inundation sensitivity of the 9 species that were only affected by inundation we find that there is a tight correlation between sensitivity to flooding and elevational distributions (r2 = 0.66, βinundation sensitivity = 0.00391, 95% CI = 0.00213 – 0.00806, Fig SX). To understand this further we decided to take into account wood density, as this is non-randomly dispersed around the plot…

Inundation sensitivity explained 37.7% of interspecific variation in species elevation distribution (βinundation sensitivity = 146.31, 95% CI = 63.8 – 209.5, Fig. 3a), indicating that tolerant individuals occur where areas with inundation episodes. Our model also predicts a positive relationship between wood density and elevation (βwood density =107.0, 95% CI = 1.06 – 214.8, Fig. 3b). As water inundation is controlled for, this suggests that species with high wood density as adults coexist on the alluvial plain partly because of water inundation episodes. We tested these predicted values were a tight fit to median elevational associations outside the large plot, and found that for every 1 m increase in the predicted elevation the actual elevation was raised 0.86 m (95% CI = 0.27 – 1.45). The median elevation of a species was predicted with an r2 of 0.51 from the model and accounted for 59.2% of variation in the 297 individuals.

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| **Figure 3 | Estimated adult elevation distribution predicted by inundation sensitivity (a) and wood density (b) against the estimated adult elevation distribution (m).** Lines and 95% Confidence intervals were predicted from the model. Sixteen species were included in the analysis. Red dashed lines indicate the univariate analysis. Percentage variance for each variable from an ANOVA test. |

High wood density may provide an advantage within wetter areas. We tested this relationship with a log-log model and found adult wood density predicts seedling inundation sensitivity. Increasing wood density by 1% causes inundation sensitivity to declines by 2.4% (βlog(wood density) =2.37, 95% CI = -3.06 – -1.78, n = 16). However, using wood density values collected as saplings wood density does not confer to tolerance to inundation (βwood density =-0.805, 95% CI = -2.715 – 1.192, n = 16), nor does seedling wood density provide tolerance (βwood density = -0.7417, 95% CI = -1.6409 – 0.4471, n = 9). At these three ontogenic stages, we found a convergence on adult values. Seedling-adult values were the least similar with an (r2 = 0.21, Fig. 4a), seedlings were more similar to saplings (r2 = 0.50, Fig. 4a), and sapling were closest to adults (r2 = 0.64, Fig. 4a). We conducted a nursery experiment on 10 species of dipterocarps (9 overlapping species). Here too, we found that seedling wood density values were not correlated to inundation effects (βwood density = -1.07, 95% CI = -2.18 – 0.048). As wood density clearly does not provide tolerance to inundation, we questioned whether water inundation itself could cause changes in wood density.

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| **Figure 4 | Ontogenic convergence on adult values, changes in wood density through inundation and biomass.** **(a)** r-squared values for wood density on the three life history stages. **(b)** the change in wood density predicted by inundation frequency. **(c)** quadratic relationship between inundation frequency and the fit between inundated seedlings and adults. **(d)** allometic scaling showing the carbon intake per unit biomass, predicting the change in wood density. Points are partial residuals where. Bootstrapped confidence intervals **(b, d)**, whereas **(c)** is predicted form the model. |

Increasing the frequency of water inundation typically increased wood density values by 0.1 g cm-3, equating to an average increase 22.2 % (βlog(treatment + 1) = 0.032, 95% CI = 0.027– 0.036, Fig. 4b). Furthermore, the values non-linearly converged on the adults before declining in similarity at extreme ends of flooding (Fig. 4c). Previous research has indicated that high wood density maybe a response to stress relating to lowering the carbon intake per unit biomass. Therefore, we created an allometric model for carbon intake per total biomass of each seedling and the carbon intake per plant and found that as carbon declines wood density increases (βcarbon intake per unit biomass = -5.656, 95% CI = -7.297 – -4.797, Fig. 4d). Thus, some species may grow into adult values within wet zones as a response to inundation, as a result of period of low carbon intake as a response to inundation episodes.

As a general trend species with high wood density as adults are tolerant to water inundation. These species may have the plasticity to grow into these high wood density values and be enabled to do and we provide some evidence that this could be a result of internal carbon budgeting, whereby species with the plasticity to grow high wood density convergence on adult values. High wood density species are present across the elevation gradient, the ability to exist on a low carbon budget is useful along the entire gradient from drought, shading, water inundation – thus we may not expect to see variable distributions. Nevertheless, the quality of inundation sensitivity can be allowed through another mechanisms (here not stated) as some low wood density species also are able to withstand inundation episodes. Co-occurrence of low- and high-density species is possible in low elevation flooded areas if they include micro-topographical refuges from waterlogging (Fig. 1) where, we conjecture, fast growing low-density species have a competitive advantage over slower growing high-density species3. Thus, in the absence of a flooding regime, species are expected to segregate along gradients of wood density associated with soil water and nutrient responses, but where lower elevations are bounded by floodplains, a triangular relationship is observed (Fig. 3d).

Our understanding of species partitioning across the soil water gradient in tropical forests has been driven almost exclusively from the perspective of species being restricted by limited water availability associated with higher elevations2,4,6–8. We can interpret this as a result of species sorting among seedlings across the soil water gradient that ultimately determines adult spatial distributions. It has been suggested that tropical saplings have developed distribution patterns similar to that exhibited by their adults on reaching a size of 1 cm diameter26. Alternatively, these patterns might be explained as the result of evolved differential adaptations to soil water conditions acting on later (post-seedling) life history stages, which happen to be ontogenetically reflected in seedling populations. Thus, while species sorting among seedlings appears to occur along the soil water gradient, we cannot attribute the distribution of adult populations solely to this process. Nonetheless, there is remarkable congruence between differential seedling responses to inundation at micro-topographical scales and the macro-topographical distribution of adults.

Our results suggest a soil water balance trade-off among dipterocarp species expressed from small-scale micro-topographical differences of a few centimetres that affect seedling survival, to larger scale distributions of adult trees over topographical ranges of tens or hundreds of metres. Yet high wood density species occur across the entire soil water gradient. Thus, a direct trade-off among species may not be forthcoming, as high wood density provides species with some tolerance to both drought16 and, as we show here, water inundation.

Given the increasing evidence that soil water availability constrains species distributions, altered precipitation patterns11 could have an extensive impact on tropical tree communities. The implications of climate change for the vegetation of the lowland tropics of Southeast Asia are poorly understood27, but current understanding suggests that some reorganisation of tree communities is likely as a result of the increasingly variable precipitation predicted for the region.

**Methods Summary**

Seedlings of 16 dipterocarp (Dipterocarpaceae) tree species were tested for their tolerances to flooding on lowland alluvial flats in Sepilok Forest Reserve. The Dipterocarpaceae contributes around 50% of canopy trees in the lowland tropical forests of Borneo28,29. Rainfall peaks from November to February (Fig. S2), during which time ephemeral shallow pools can form in the alluvial valley bottoms of lowland forests creating a heterogeneous landscape. We planted 2048 seedlings within 32 plots over the micro-topographical gradient of the alluvial zone. Seedlings were 3-4 months old when planted, at a stage shortly after loss of cotyledons and emergence of the first true leaves. Seedlings were censused every three months for one year. We mapped micro-topography using a laser lever at all plots and used mean flooding depth during the wetter period of the year (November to February) as a relative baseline for comparison among plots. We determined soil pH, and soil texture at the plot level. During periods of water inundation, depth of inundation was measured for each individual seedling.

All adult dipterocarps in the 160ha plot and four and a half 4 ha plots were mapped and tagged, with distributions being overlaid on a digital terrain model. For the main 160 ha forest plot, we used a quadratic equation to model the probability of occurrence of each species along elevation and hydrological gradients. Integrated Nested Laplace Approximation and Stochastic Partial Differential Equations (INLA-SPDE) were used for the analysis to account for spatial auto-correlation in the data using a matern correlation function30,31. The conditional predictive ordinate was used to select the most parsimonious model32.

Wood density measurements were determined from the global wood density database33. We combined the two analyses presented to understand the relationship between seedling mortality, adult distribution and community composition. Flooding sensitivity was calculated for each species by subtracting the probability of mortality of seedlings that were not flooded from those that were flooded (the statistic: absolute risk increase)34. The maximum peak of the quadratic equation describing the relationship with elevation was used to assign where adults of each species were most likely to be found along the elevation gradient. We ran regressions and ANOVA models weighted with species abundances to investigate the effects of wood density and flooding sensitivity on adult distributions (Fig. 2).

We tested the predictions of statistical model against the median elevation of 13 co-occurring species in the 18 ha of forest outside the 160ha plot. Each 4ha forest plot was at least 260 m apart, and we suggest plots are independent. The predicted elevations of each species from our statistical model were used to explain the variation in the median elevation a species was found at in these areas, weighted by the abundance. We calculated the r2 for the weighted mean elevation (n = 13) and for all individuals (n = 304).

Traditional ideas on wood density distribution throughout the landscape combined with our results suggests that wood density is distributed as a wedge shape along elevation distributions. To test this hypothesis we carried out a quantile regression on all the plot data we have (178 ha) for adult dipterocarps (species = 36). We convert all plots into a ¼ ha lattice of subplots, with the mean value of wood density, and elevation for each ha (n = 720 quarter ha quadrats).

Community similarity map (Fig. 1c) used the same 12 elevation bands as above. Non-metric multidimensional scaling35 was used to calculate the dissimilarity of each elevation band using all individual in the plot (species = 42), and axis 1 was used to create the map. We provide data and code for analysis found at *github.com/t03jam8* in the *ForestFloodingSensitivityAnalysis* repository.

**Methods**

**Site.** Sepilok Forest Reserve (SFR) is a 4475ha patch of mostly pristine lowland dipterocarp forest located on the Northeast coast of Borneo in Sabah, Malaysia (5° 10ʹ N, 117° 56ʹ E). The reserve has a highly variable topography, vegetation, flooding frequency and soil characteristics that are partly derived from differential parent materials (Fig. 1a, *for a description of SFR see*36–39). Sepilok Forest Reserve has a mean annual rainfall of 3136 (±921 SD) mm and a mean annual temperature of 27.3°C39. Sabah's climate is commonly described as aseasonal3,39,40, however there are relatively consistent wetter and drier periods throughout the year (Fig. S2). Climate also varies year on year, with these supra-annual fluctuations attributable to variation in the El Niño Southern Oscillation (ENSO)41.

**Seed collection.** Sixteen species from 3 dipterocarp genera were selected for this study (Table S3) based on their variable adult distributions and seed availability during the 2014 general flowering event. Dipterocarps flower every 2 – 10 years42 often in association with major ENSO events43,44, and as a result seedling recruitment is intermittent42. Moreover, seeds have a short period of viability and germinate within days of falling from the parent tree leaving no seed bank6. As the first year is one of the most sensitive life stages to environmental disturbances15, our study replicated the first year of life as close as possible with the first period of water inundation occurring ca. six months after germination.

All seeds were collected during the mast flowering in 2014 (July-August) with 13 species harvested directly from SFR and three species (*Shorea waltonii, Dryobalanops lanceolata* and *S. pauciflora*) sourced from nearby forest reserves. These three species are found in SFR and remain in the same floristic region within Borneo29. To control for maternal heritage, the seeds were collected directly from the mother tree by shaking the outer fruit-bearing branches using a ‘bigshot’ catapult and rope. Species had variable numbers of mothers due to the availability of fruiting individuals, ranging from 1 to 9, with a total of 51 different mother trees used in this experiment. Seeds were germinated in wet jute sacks, transplanted into cylindrical polythene bags 9 x 15 cm filled with a mixture of sawdust and locally sourced alluvial topsoil. After germination, seedlings were grown for 3 months under 10% ambient light, typical of nursery conditions recreating a medium sized forest gap3,45 and watered daily before being transplanted into the forest after discarding their cotyledons and first true leaves had developed.

**Experimental Design.** A total of 2048 seedlings were planted in a stratified randomized block design in October 2014, ensuring that seedlings derived from different mother trees were evenly distributed among the plots and blocks. To ensure that mortality caused by transplanting seedlings from the nursery to the forest was not a source of error, we replaced any dead or damaged seedlings before the start of the experiment in December. Two alluvial flood plains in SFR, separated by a ca. 800 m formation of mudstone hills, were used to equitably distribute the blocks in natural gaps > 100 m apart (Fig 1a & b). Within each block there were two plots in close proximity < 50 m apart in gap conditions. Each plot was in either high or low topographical positions to capture variation in meso-topography and hydrology. We surveyed for prospective blocks fitting these criteria, and from an assortment of possible locations the final blocks were randomly selected. Each of the 16 each species (Table S3) were represented by four individuals from a range of mothers in every plot. Plots were 2.4m2 and contained 64 seedling positions spaced at 30 cm apart. Using the aforementioned criteria, each position within all plots was assigned a random seedling.

**Environmental Variables.** Micro-topography was measured for each plot using a laser level, which was attached to a pole and positioned ensuring both horizontal tubular bubbles were true. We used a fan angled laser level which projected a horizontal beam over the plot, and measured down from the laser to each seedling in the plot using a tape measure. Using these measurements, we calculated the relative elevation of each seedling in the plot. The difference in elevation of plots within blocks was measured using the laser level. Relative seedling elevations within blocks were determined by adding the difference between the plot elevations to the higher plot.

The water levels within flooded plots during the rainy season were measured at the lowest seedling 13 times during the wettest 24 day period. By knowing the relative elevation of all seedlings in every plot we can calculate the typical flooding depth of water inundation for every seedling within a block, and hence mean flood levels for each block can be linked together. This is more desirable than measuring the exact altitude of each plot, as observations indicated that ground water levels did not play a significant role in determining whether a plot was flooded. Furthermore, we found evidence of gleying (mottled oranges and greys, Fig. S3) in many of the plots, indicating that these areas may experience anaerobic conditions although well above river levels.

Flash floods occurred several times during January 2015 in SFR with the most intense rainfall in the morning of January 14th, when 178.3 mm fell within a 6 hour period (January’s daily mean precipitation was 12.3 mm 95% CrI = 11.0 – 13.8 mm, Fig. S2). Nineteen plots showed complete and eight plots showing partial submergence (27 out of 32) during this event. However, rivers and surface runoff drained sites quickly, freeing the seedlings from submergence in < 5 hours (mean drainage rate: 26.6 ± 17.5 cm hour-1; n = 4 locations).

Four soil samples were taken from each plot using a soil auger at two corners corresponding to a maximum and minimum elevation with each plot, and two depths (0-15 and 30-50 cm46). Soil was air dried for 3 months and the samples from each depth homogenized, leaving 32 from the surface and 32 from the lower layer of soil. Soil pH was determined by measuring samples after mixing with distilled water47. Soil texture was used as an edaphic variable to provide a proxy for soil fertility48,49. We used the pipet method to determine the three soil texture fractions, clay, silt and sand at the plot level50. Organic matter was digested using ammonia solution and hydrogen peroxide with a hot plate. The contents was transferred to a 1L measuring cylinder, filled with distilled water and boiled. Exploiting the differences in settling time of the soil fractions clay, silt and sand; we were able to pipet out the solutions and calculate mean percentage of clay, silt and sand per plot.

The light environment for each plot was measured using a spherical densiometer. The densiometer was held level in the centre of each plot ca. 30 cm above the ground. We counted the number of quarter grid cells on the concave mirror that were reflecting open canopy as the value of canopy openness45,51.

**Seedling Census.** The first seedling census of the plots was taken during in December 2015, after which, a re-census of the seedlings were taken every three months for one year giving a total of four census intervals. During each census we measured diameter and noted the mortality of seedlings. Diameters were measured twice perpendicular at the same marked point 5 cm above the soil with digital callipers. A seedling was considered dead when there was no green phloem tissue remaining under the stem.

**Digital Terrain Model.** Airborne laser scanning (ALS) data for SFR were collected during a survey undertaken by NERC’s Airborne Research Facility in November of 2014. The sensor used was a Leica ALS50-II LiDAR on a Dornier 228-201 and was flown over the 160 ha permanent forest plot. It emitted pulses at 83.1 Hz, has a field of view of 12° and an impression of about 40 cm. The average point density was 7.3 m-2. The point cloud data were processed to produce a digital elevation model (DEM), a digital terrain model (DTM). Data were processed in LAStools (http:// rapidlasso.com/lastools/). For a full description of the methods used see Jucker *et al.* (2017).

**160 ha Forest plot.** The 160 ha forest plot was establish in Sepilok by the end of 2010. All adult dipterocarps were tagged, identified to species level and mapped (n = 5587). Minimum diameter limits were selected based on an estimated size that a species would flower, and were dependent on the expected adult size. For sub-canopy dipterocarps species > 30cm DBH (n species = 2) were selected, for large emergents 50 cm DBH (n species = 13) and for those with a strategy somewhere in the middle 40cm DBH (n species = 1) was selected (Table S3). When investigating the adult distributions, using different minimum diameter sizes is more appropriate than setting a common minimum limit for all species, as it takes into account differences in maximum size. Elevation (asl m) were assigned to each individual adult dipterocarps from the DTM.

**Four ha plots.** Within SFR, nine 4 ha forest plots were established from 2000 to 2001. Of these, 6 plots (24 ha) were within lowland dipterocarps forest, and 4 ½ (18 ha) where outside the 160 ha forest plot. All individuals ≥ 5 cm are tagged and have their DBHs measured. The most recent census of the plots were from 2013 to 2015. Each 4 ha plot is divided into a lattice 10m2, and individuals were located to within one of these. A differential GPS was used to geo-locate the corners (Geneq SXBlue II), and the layout was used to calculate the approximate position of each tree. We calculate and assigned the mean elevation (asl m) from the DTM for each 10m2 area.

**Seedling mortality data analysis.** To test the hypothesis that species respond differently to water inundation we used a generalized linear mixed effects model assuming a binomial error distribution from the lme4 package52 in R v3.3.153. The flooded explanatory variable had two levels: individuals that typically experienced water inundation during the wet period from November to February were flooded, and the control indicating individuals that were on micro-topographical locations that experienced no water inundation. The interaction between flooded and species was key to addressing our hypothesis. In the final model, we controlled for census interval, micro-topography, and the natural logarithm of diameter of the seedlings as fixed effects. Two random effects were also included: plot, which was allowed to vary with census interval, and mother controlling for maternal heritage. Other variables considered for inclusion in the model were site, block, pH, soil texture, light and maximum flash flood levels, and up to all second order interactions. We removed all variables from the final model that did not reduce the AIC by > 4 points. The model was evaluated using a modified version of the binnedplot function54 from the arm package in R v3.3.1. to check for normality and independence of binned residuals, and that random effects were normally distributed. The focal effect of this model was the difference between the inundated and non-inundated plants, as this could provide inference on a species’ inundation sensitivity. We defined a species seedling’s sensitivity to flooding was defined as the absolute risk increase (ARI; also known as the absolute risk reduction). The ARI calculation is the difference between the probability of mortality in the treated group (water inundated individuals) and the probability of mortality in the control group (not inundated)34. As the size of the ARI is the effect size of water inundation on mortality, we hence fourth refer to this as the “inundation sensitivity”.

**Habitat association within 160 ha plot.** Species relationships with elevation were analysed using the Integrated Nested Laplace Approximation (INLA) Bayesian framework with Stochastic Partial Differential Equation (SPDE) fitted to spatial point-referenced data. INLA executes direct numerical calculation of posterior densities and is a computationally effective substitute to MCMC30,31. These tools allowed us to model the probability of a species’ presence or absence at each of the 5587 locations of adult dipterocarp stems in the 160 ha forest plot whilst accounting for spatial auto correlation between individuals of the same species. More specifically, the model used to describe the spatial autocorrelation was the Matern correlation function, which depends on a scale parameter and a smoothness parameter. These parameters were estimated by INLA from flat priors. We constructed a model using species and elevation as the explanatory variables, fitted with the elevation quadratic term, testing five combinations of interactions. For mode selection we used the conditional predictive ordinate (CPO), which computes the density of the posterior predictive distribution at an observation used to select the models which measures the fit through predictive density , essentially a Bayesian leave-one-out cross-validatory predictive check. We checked for possible failures and recomputed these values in accordance with Blangiardo and Cameletti (2015). Thereafter models were compared by calculating . We selected three models based on hypothesis about the shape of the probability of a species occurrence along an elevation gradient, presenting the results of the model with the lowest CPO. The final model for elevation was:

Credible intervals (95%) were calculated by sampling from the posterior distribution 5000 times.

For each species’ adult elevational, the derivative of each species quadratic equation parameters was taken and set to zero . This gives us the elevational position at which a species most probably occurs. Simplifying a species’ adult distribution to its most probable elevational position gives us a single number to use in the linear model and works as a good proxy for the overall distribution.

**Seedling sensitivity wood density.** We tested the hypothesis that wood density could explain variation in flooding sensitivity, with the expectation that higher wood densities are more resilient. A linear model with inundation sensitivity as the response variable, and wood density split into high and low portions (than the mean). This is reflected in Fig 2a where we partition species responses to wood density. Residuals were not equally distributed, as there was an order of magnitude of variation in the low wood density group. Hence, we log transforming the response variable.

We constructed a weighted regression model with the response of elevational distribution. The explanatory variables were wood density and water inundation sensitivity. Model weights we set as the frequency of individuals within the 160ha forest plot area ≥ 50 cm DBH. We ran a global model with the interaction between these two variables. We tested all combinations of this global model and presented the model with the lowest AIC. An ANOVA type II test was used to calculate the variance explained by each variable (Fig. 3a & b). Weighted models sometimes create instability within an analysis, as some high abundant species may have an unduly large effect on the result. To certify that this was not the case, we ran the model with each species removed and found all models were similar to the results presented here.

**Verifying the statistical model.** We tested if our statistical model was able to predict the mean elevations of species in the 4 ha plots species distribution outside the 160ha plot area. We used the mean elevation as low absolute numbers of individuals for some species made modelling this data with a spatial effect impossible. A linear model with elevation (m asl, based on the wood density and flooding sensitivity of a species) as the explanatory variable, responding to the mean elevation a species was found at in the 4 ha plots (calculated by accounting for spatial autocorrelation). We weight this model by abundances. An additional r2 value was calculated for all the elevations of individuals against the species’ predicted values.

**Wood density’s elevational distribution.** We tested the hypothesis that the wood density distribution across the elevation gradient was not linearly consistent. High wood density maybe distributed across the elevation gradient at low and high elevations, whereas low wood density species were distributed predominantly in lower elevations. We partition the full data set from all plots (178 ha), into quarter hectare units (50 m2). The mean elevation and mean wood density within each unit was calculated (n = 720; 648 from 160 ha plot, and 72 from the 4 ½ four ha plots). We used a quantile regression, with wood density as the predictor and elevation as the response. Quantile regression allows us to calculate the conditional quantile function for a response variable, thus enabling a more complex relationship to be shown. The model calculated five quantiles, shown in Fig. 3d (0.025, 0.1, 0.5, 0.9, 0.975). To calculate the confidence around the coefficients we bootstrap the data (n = 5000).

**Community similarity analysis.** To analyses dipterocarps community composition across elevation gradients we partitioned the maps into 12 elevation bands so that there were approximately equal densities of dipterocarps within each band55 (mean number of trees in each band was 465.25 ± 80.9 SD). In addition, using the same elevation bands, we conducted a non-metric multi-dimensional scaling analysis56 of the communities and extracted axis 1 values to map of how the community similarity changes with elevation (Fig. 1c). Non-metric multi-dimensional scaling collapses information from multiple dimensions into few dimensions similar to Principal Components Analysis, however uses rank order rather than Euclidian distances. Although, this method does not account for spatial auto-correlation it does provide some inference as to how communities partition along the elevation gradients.

All linear and ANOVA model residuals had an expectation of zero, equality of variance, independence and were normally distributed – unless specified prior. Analyses were conducted in R v3.3.153 and the analysis can be found in the github repository (<https://github.com/t03jam8/ForestFloodingSensitivityAnalysis>)

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