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# Changes in rainfall interception along a secondary forest succession gradient in lowland Panama

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**Abstract.** Secondary forests are rapidly expanding in tropical regions. Yet, despite the importance of understanding the hydrological consequences of land-cover dynamics, the relationship between forest succession and canopy interception is poorly understood. This lack of knowledge is unfortunate because rainfall interception plays an important role in regional water cycles and needs to be quantified for many modeling purposes. To help close this knowledge gap, we designed a throughfall monitoring study along a secondary succession gradient in a tropical forest region of Panama. The investigated gradient comprised 20 forest patches 3 to 130 yr old. We sampled each patch with a minimum of 20 funnel-type throughfall collectors over a continuous 2-month period that had nearly 900 mm of rain. During the same period, we acquired forest inventory data and derived several forest structural attributes. We then applied simple and multiple regression models (Bayesian model averaging, BMA) and identified those vegetation parameters that had the strongest influence on the variation of canopy interception. Our analyses yielded three main findings. First, canopy interception changed rapidly during forest succession. After only a decade, throughfall volumes approached levels that are typical for mature forests. Second, a parsimonious (simple linear regression) model based on the ratio of the basal area of small stems to the total basal area outperformed more complex multivariate models (BMA approach). Third, based on complementary forest inventory data, we show that the influence of young secondary forests on interception in real-world fragmented landscapes might be detectable only in regions with a substantial fraction of young forests. Our results suggest that where entire catchments undergo forest regrowth, initial stages of succession may be associated with a substantial decrease of streamflow generation. Our results further highlight the need to study hydrological processes in all forest succession stages, including early ones.

## 1 Introduction

Across the tropics, large parts of mature forests have been cleared and converted into agricultural land. Increasingly, however, some of these cultivated areas lie fallow or are abandoned due to declining productivity or rural–urban migration (Aide and Grau, 2004; Wright and Samaniego, 2008). As a consequence, secondary forests are rapidly expanding in tropical regions (Chazdon, 2008; Perz and Skole, 2003). In addition, there is evidence that climate change might amplify some natural forest disturbances, such as droughts, fires, and hurricanes (Elsner, 2006; Malhi et al., 2009; Overpeck et al., 1989), leading to further increases in secondary forest cover. Most often, regrowing forests are found alongside patches of mature forest, pastures, farmland, settlements, etc., and thus they are part of fragmented landscapes, which are now a typical feature of many tropical regions worldwide (Laurance and Bierregaard, 1997).

Given the extent of secondary forests, their effect on hydrological processes as well as their role within the hydrological cycle of fragmented landscapes merits attention (Giambelluca, 2002). Mature forests, which provide the baseline for evaluating secondary forest hydrology, differ from

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agriculturally used areas in two hydrologically significant ways: they have high rates of evapotranspiration and their soils usually allow rapid infiltration of rain water (Bruijnzeel, 2004; Giambelluca, 2002). Part of the high evapotranspiration rate of mature forests originates from the high rainfall interception storage of their canopies. For tropical and warm temperate forests, Schellekens et al. (2000) suggested that rainfall interception (wet canopy evaporation) makes up at least 20–25 % of the total evapotranspiration and may increase to 60–75 % in regions where annual rainfall exceeds 2000 mm.

Because of the importance of rainfall interception, reliable predictions of this component of the water cycle are vital for an assessment of the impact of secondary forest succession on water resources. Unfortunately, this seemingly simple task rapidly turns into a complex problem because of the multitude of factors that influence forest structure and composition. For instance, regrowth stage, the composition of the regrowing forest (e.g., invasive plants versus natural succession), and the type and intensity of past land use (e.g., pasture versus shifting cultivation) determine structural characteristics of secondary forests (Guariguata and Ostertag, 2001; Hölscher et al., 2005). These variables, in turn, likely influence canopy interception and hence the hydrological functioning of a particular secondary forest. Given the structural diversity among secondary forests (Guariguata and Ostertag, 2001; van Breugel et al., 2006), we need observations both from forests of different ages and from multiple sites within an age class to describe the change in interception during forest regrowth. These observations are of course costly to obtain. Ideally, forest inventory data could be used to predict the change in interception during forest recovery. Established relationships between forest structure and throughfall (e.g., Dietz et al., 2006; Ponette-González et al., 2009) suggest the feasibility of this approach, which would also permit the prediction of interception at the landscape scale.

Our main objective in this study is to relate canopy interception to secondary forest succession. We are interested both in the general trend of interception loss during forest recovery and in the relative influence of several forest structure parameters on the variation of interception across secondary forests. More specifically, we ask the following questions: (1) how long does it take for canopy interception to approach a value that characterizes mature forest? (2) Which forest structure parameters are most appropriate to describe the change in interception during forest succession? (3) To which extent can we detect the influence of young secondary forests on interception in (real-world) fragmented landscapes? We also discuss the implications of our findings with regard to the hydrological functioning of catchments subject to forest succession.

## 2 Methods

### 2.1 Study area

We studied interception loss along a gradient of secondary forest succession in the central part of the Panama Canal Watershed with sites on Barro Colorado Island (BCI) and in the area of the Agua Salud Project (ASP) (Fig. 1a–c). Both areas have steep and dissected terrain with high drainage densities. The island of Barro Colorado was isolated from the mainland in 1914 after the Chagres River was dammed to form Lake Gatun, which is part of the Panama Canal. The Agua Salud area is located about 10 km northeast of BCI on a strongly dissected pre-Tertiary basalt plateau (elevation between 53 and 331 m above mean sea level) adjacent to Soberanía National Park (Fig. 1a). While BCI has been a nature reserve since 1923, the ASP area is used by local farmers for small-scale agriculture.

The climate of central Panama is tropical with a distinct dry season from mid-December to April. According to long-term records from BCI (Fig. 1a), annual rainfall averages $2641 \pm 485$ mm (mean $\pm 1$ standard deviation, $n = 82$; data from 1929 to 2010, courtesy of the Environmental Sciences Program, Smithsonian Tropical Research Institute, Republic of Panama). Mean daily temperature varies little throughout the year and averages 27 °C (Dietrich et al., 1996).

The natural vegetation of the central Panama Canal Watershed is classified as semideciduous lowland forest (Foster and Brokaw, 1996). This vegetation type covers all of BCI. The ASP area consists of pastures, subsistence agriculture and timber plantations, as well as secondary forests in varying stages of recovery (Fig. 1c). Within the framework of the ASP, a secondary forest dynamics (SFD) study was established in 2008 with randomly selected permanent sample plots (van Breugel et al., 2013), which together with the forests on BCI provide the basis for setting up our throughfall monitoring campaign (cf. Sect. 2.2.1). For more information on botanical characteristics of the plots selected for throughfall monitoring (cf. Sect. 2.2.1), we provide information on the most abundant species, their share on the total basal area, and information on deciduousness (Supplement S1). The deciduousness data are provided for descriptive purposes only as all species were fully foliated during our throughfall monitoring campaign.

### 2.2 Sampling scheme

#### 2.2.1 Site selection

For the purpose of this study, we used forest inventory data from 95 of the permanent sample plots of the SFD study (cf. Sect. 2.1). In the following, these 95 plots are denoted by SFD plots. For throughfall monitoring, we selected 16 of the SFD plots, in addition to 4 plots on BCI; we refer to these 20 plots as throughfall plots. We adapted the selection of

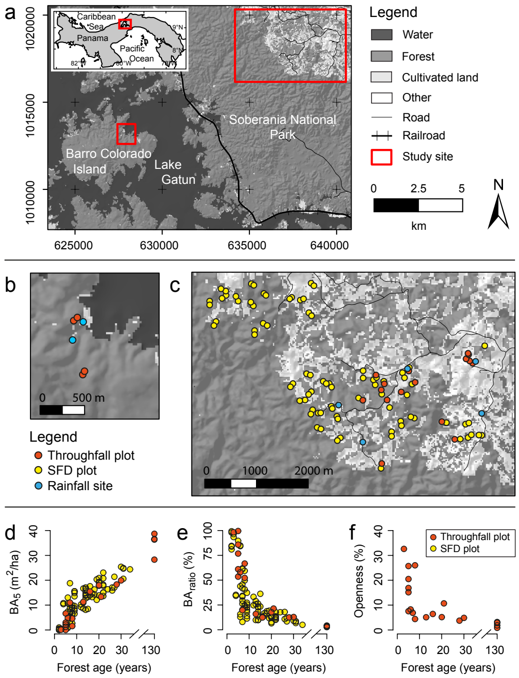


**Fig. 1.** Location of the study sites in central Panama **(a)**, detailed view at the BCI **(b)** and the ASP study area **(c)**, and relationship between forest age and $BA_5$ (basal area) **(d)**, between forest age and the $BA_{ratio}$ (ratio of the basal area of small stems to the total basal area) **(e)**, and between forest age and canopy openness **(f)**. Note: for a description of SFD plots and throughfall plots, refer to Sects. 2.1 and 2.2.1; for an in-depth description of the forest structure variables, refer to Sect. 2.3.2.

throughfall plots to our objective, which was to relate interception to forest structure using a regression-type analysis (cf. Sect. 2.3); that is, we optimized site selection by including very young forests (< 5 yr old) as well as sites in the mature forest of BCI, and by choosing intermediate plots such that the range of site-specific canopy openness, basal area, and stem density was covered evenly. The intermediate plots included young forests (≥ 5 yr and < 10 yr) and older forests (≥ 10 yr). The mature forest sites on BCI are not part of the secondary forest dynamics study but their inclusion was essential because even the older secondary forests in the ASP area are no older than a few decades.

All selected throughfall plots in the ASP area were surrounded by forest. The SFD plots measured 20 m × 50 m; at two throughfall plots in the ASP area and on BCI, plots were 30 m × 60 m. Plot sizes differed because the larger plots were also part of another study.

### 2.2.2 Age estimates and determination of forest structure and canopy openness

Our throughfall plots on BCI are located in secondary forest of more than 130 yr of age (Foster and Brokaw, 1996; Kenoyer, 1929). In the ASP area, we determined the forest age of the SFD plots through interviews with the former land owners. It is important to note that land use on any given farm in the ASP area is traditionally dynamic, which results in small-scale local differences in the stage of forest succession. For instance, ridges often experience more and longer human impact (e.g., by cattle treading) than middle or downslope locations. Moreover, most streams and gullies are surrounded by streamside vegetation, which influences secondary succession (e.g., by promoting tree dispersal). Hence, forest age is considered a fuzzy variable and not used as an explanatory variable in regression modeling (cf. Sects. 2.3.3 and 2.3.4).

Stand characteristics in the SFD plots are monitored annually. All plots were divided into 5 m × 5 m subplots. In each subplot, we identified all tree, shrub, and palm species with a dbh (diameter at breast height) ≥ 5 cm and measured the dbh of all individuals in this class. In every other subplot, all individuals with dbh ≥ 1 cm were identified and measured.

During the throughfall measurement campaigns, we took hemispherical photographs above each throughfall collector at approx. 0.5 m height. All photos were taken during overcast sky conditions in the early morning or late afternoon using a Canon EOS50D camera equipped with a SIGMA Circular Fisheye 4.5 mm 1 : 2.8 lens. At each position we obtained a series of photos with varying exposure and selected the picture for further analysis that showed an optimal histogram of the brightness (cf. Beckschäfer et al., 2013). All selected pictures were analyzed using the software HemiView v8 (Delta-T Devices Ltd).

### 2.2.3 Rainfall, throughfall, and stemflow measurements

We estimated interception loss on the basis of rainfall and throughfall data. For both rainfall and throughfall measurements, we used funnel-type collectors, which consisted of a 2 L polyethylene bottle and a funnel. The receiving area of each collector was 113 $cm^2$. A polyethylene net with a 0.5 mm mesh at the bottom of the funnel minimized measurement errors due to organic material and insects.

Rainfall was measured at five sites in the ASP area and at two sites on BCI (Fig. 1b–c). The distance between each throughfall and its closest rainfall site was 360 m on average and 760 m maximum. At each rainfall site, we placed 5 to 10 collectors to obtain an estimate of mean rainfall. We measured throughfall within each throughfall plot at several randomly selected locations to estimate the plot mean of throughfall. Because simply structured forests require less sampling effort to obtain reliable throughfall estimates than complex-structured ones (Zimmermann A. and Zimmermann B., 2013), we divided our throughfall plots into two groups.

We set the limit for simply structured forest plots to a total basal area of $10\,\mathrm{m^2\,ha^{-1}}$ because at this point the initially strong decline in canopy openness levels off (van Breugel et al., 2013) and forests start to develop a layered and diverse canopy structure. Sample sizes in most simply structured and complex-structured plots were 20 and 25, respectively; two throughfall plots in the ASP area and the throughfall plots in the mature forest on BCI were sampled with 36 collectors (Table 1). Given our collector surface area of $113\,\mathrm{cm^2}$ and the temporal aggregation of the throughfall data (see below, this subsection), our sampling approach ensures relative error limits of estimated mean throughfall of 15 % (Zimmermann A. and Zimmermann B., 2013). In total, we monitored throughfall at 536 sampling locations.

We monitored throughfall at the throughfall plots in the ASP area continuously for two months (2 September–7 November) in the middle and late rainy season of 2011. During this period, average rainfall amounted to $831 \pm 35$ mm (mean $\pm 1$ standard deviation, data from the rainfall sites in the ASP area). We visited each throughfall plot at least every fifth day and each rainfall site at least every second day. When a throughfall plot was visited, the closest rainfall site was also sampled. If rainfall started during sampling, then the plot was revisited the day after. At the same time, we sampled throughfall and rainfall on an event basis at two of the BCI plots. Data from the other two throughfall plots on the island had been obtained on an event basis during 2007 and 2008 (Zimmermann et al., 2009).

Stemflow measured at two of our throughfall plots on BCI was only 1 % of gross precipitation over a 2-month period (Supplement S2). Other studies in Panamanian secondary and native species plantation forests report similarly low stemflow volumes (Macinnis-Ng et al., 2012; Park and Cameron, 2008). We therefore consider stemflow to be negligible in this study.

## 2.3 Data analysis

### 2.3.1 Calculation of relative throughfall and interception loss

At each site, we added measured throughfall and rainfall values of the entire period and converted these data into mm. Next, we calculated the relative throughfall ($t_\mathrm{r}$) at each throughfall plot $x_i$ as follows:

$$t_\mathrm{r}(x_i) = \frac{\hat{\overline{T}}(x_i)}{\hat{\overline{R}}(x_i)} \cdot 100, \tag{1}$$

where $\hat{\overline{T}}(x_i)$ is the estimated plot mean throughfall and $\hat{\overline{R}}(x_i)$ is the average rainfall of the corresponding rainfall site. Since 100 % $t_\mathrm{r}$ equals 0 % interception ($i_\mathrm{C}$) and vice versa (when stemflow is considered negligible), it is straightforward to convert $t_\mathrm{r}$ into interception loss. For the throughfall plots in the ASP area, we calculated $t_\mathrm{r}$ with rainfall data of the nearest rainfall site because the weighted rainfall average of all ASP rainfall sites performed worse in the modeling.

### 2.3.2 Derivation of explanatory variables

From the forest inventory data, we derived the following forest structure parameters: basal area and stem density for two dbh classes (class 1: dbh between 1 and 5 cm; class 2: dbh > 5 cm), abbreviated as $\mathrm{BA_1}$, $\mathrm{SD_1}$ (class 1) and $\mathrm{BA_5}$, $\mathrm{SD_5}$ (class 2). For dbh-class 2, we had species information for all plots. Therefore, we calculated the Shannon diversity index (Shannon and Weaver, 1949) (hereafter diversity) for trees > 5 cm dbh. This index is a common measure of diversity and depends on the number of species as well as on their relative abundance (Magurran, 2004). We also merged the information on basal area in the two dbh classes into an index that we defined as the ratio of $\mathrm{BA_1}$ to the total basal area. This integrated measure, which we call the $\mathrm{BA_{ratio}}$, takes into account that an increasing basal area of trees with a dbh > 5 cm results in a decrease of the basal area of smaller trees (cf. van Breugel et al., 2012).

We derived the canopy openness (hereafter openness) from the hemispherical photographs. Openness is defined as the percentage of the hemisphere that is not blocked by vegetation and is calculated per zenith angle. Zimmermann et al. (2009) showed that small zenith angles correlated most strongly with throughfall data from small collectors. In our case, a zenith angle of 2.5° correlated best with throughfall; hence we used openness calculated from this zenith area for modeling.

Characteristics of the terrain might also influence canopy interception, particularly in rough terrain like our study site. We derived terrain attributes that might influence interception from a 10 m resolution digital elevation model: slope and aspect (Crockford and Richardson, 2000). The latter was transformed with the sine and the cosine function: transformation to sine results in dissimilarities of east and west, while north and south differ after the cosine transformation.

### 2.3.3 Simple linear regression models

As a first step, we modeled the dependency of relative throughfall on forest structure parameters using simple Bayesian linear regression models and uninformed priors for the regression parameters. We limited this approach to the strongest relationships (see Sect. 3.3). To assess the predictive ability of the simple linear models and of the Bayesian model averaging (BMA) approach described below, we used the root-mean-square error (RMSE):

$$\mathrm{RMSE} = \sqrt{\frac{1}{n}\sum_{i=1}^{n}(z(x_i) - \hat{z}(x_i))^2}, \tag{2}$$

where $z(x_i)$ is the measured and $\hat{z}(x_i)$ the predicted $t_\mathrm{r}$ value at location $x_i$. We calculated the RMSE both for the

**Table 1.** Summary statistics of the throughfall data.

| Plot | Age (years) | n[a] | Mean $t_r$ (%) | SE[b] (%) | CV[c] (%) | Skewness | Mean $i_c$ (%) |
|---|---|---|---|---|---|---|---|
| 1 | 3 | 20 | 95.3 | 3.2 | 15.1 | 0.61 | 4.7 |
| 2 | 5 | 20 | 101.6 | 3.5 | 15.6 | 1.48 | −1.6 |
| 3 | 5 | 20 | 87.5 | 3.9 | 19.8 | −0.75 | 12.5 |
| 4 | 5 | 20 | 101.2 | 4.0 | 17.5 | 0.43 | −1.2 |
| 5 | 5 | 36 | 87.6 | 3.0 | 20.7 | 0.36 | 12.4 |
| 6 | 5 | 36 | 92.6 | 3.7 | 24.0 | 1.18 | 7.4 |
| 7 | 6 | 25 | 91.0 | 4.8 | 26.2 | 0.59 | 9.0 |
| 8 | 7 | 25 | 87.3 | 3.5 | 20.1 | 0.24 | 12.7 |
| 9 | 8 | 20 | 89.8 | 3.8 | 18.7 | 0.58 | 10.2 |
| 10 | 8 | 20 | 99.2 | 5.5 | 24.6 | 0.64 | 0.8 |
| 11 | 13 | 25 | 73.7 | 4.7 | 31.7 | 0.00 | 26.3 |
| 12 | 16 | 25 | 84.2 | 5.4 | 31.9 | 0.25 | 15.8 |
| 13 | 20 | 25 | 80.3 | 2.9 | 15.1 | 0.61 | 19.7 |
| 14 | 21 | 25 | 87.5 | 3.4 | 19.5 | −0.60 | 12.5 |
| 15 | 28 | 25 | 82.5 | 4.8 | 28.8 | −0.28 | 17.5 |
| 16 | 30 | 25 | 89.5 | 3.6 | 20.1 | −0.84 | 10.5 |
| 17 | 130 | 36 | 80.3 | 5.4 | 40.6 | 1.03 | 19.7 |
| 18 | 130 | 36 | 84.8 | 3.4 | 24.1 | −0.07 | 15.2 |
| 19 | 130 | 36 | 78.2 | 4.7 | 36.1 | 0.97 | 21.8 |
| 20 | 130 | 36 | 79.0 | 5.1 | 38.6 | −0.24 | 21.0 |

[a] Sample size for throughfall, [b] standard error of $t_r$ estimate, [c] coefficient of variation of $t_r$.

calibration data and the validation data (leave-one-out cross validation).

#### 2.3.4 Modeling framework using multiple parameters

This second step of our analysis was designed to examine whether the inclusion of all available parameters in a multivariate framework would improve predictive accuracy. As parameters we used the explanatory variables given in Sect. 2.3.2 except for $BA_1$ and $BA_5$ (which are included in the $BA_{ratio}$): $SD_1$, $SD_5$, $BA_{ratio}$, diversity, openness, slope, and the sine and cosine of aspect. Since we did not know a priori which combination of forest structure parameters was best suited to predict relative throughfall, we applied BMA to our data, which is a popular framework to deal with the issue of model uncertainty. In Bayesian model averaging (BMA), regression models are constructed for all possible combinations of explanatory variables and inference is based on a weighted average of all of them. The model weights arise naturally from Bayes' theorem as posterior model probabilities (PMP). That is, a model's posterior probability is proportional to its marginal likelihood times its prior probability. The marginal likelihood, in turn, is the probability of the data given the model; hence, it depends only on the actual sample. The prior probability, in contrast, reflects one's belief about the probability of the model before looking at the data. It refers to both the model size (i.e., number of parameters) and to the regression coefficients and needs to be specified first. As to the former, we chose a default prior model size of $K/2$ ($K =$ number of parameters) and a beta-binomial specification (Ley and Steel, 2009), which resulted in a completely flat prior over all model sizes. That is to say, with this prior a model size of 1 (one explanatory variable) is considered as likely as a model size of 8 (all explanatory variables included). Next, we chose the prior for the regression coefficients. This prior needs to be specified for all parameters (explanatory variables) conditional to each possible model. Since we have 256 possible models (number of possible models = 2 raised by the number of explanatory variables), it is impossible to specify coefficient priors separately for each model. We therefore adopted a literature suggestion of using a hyper-g prior; for more details, refer to Liang et al. (2008). In summary, our prior both on model size and on the regression coefficients reflects our lack of prior knowledge.

The BMA approach is not only superior to many other strategies in terms of predictive ability (e.g., Fernández et al., 2001; Liang et al., 2008; Raftery, 1995) but also facilitates the interpretation of the results. For instance, it provides the posterior inclusion probabilities (PIP) for each explanatory variable, which is the sum of the PMPs of all models that include the variable. Since the PMPs of all models sum up to 1, a large (i.e., close to 1) PIP means that the variable was included in models with high posterior probabilities and hence is an important predictor. Another advantage is that the averaging allows for consulting the entire posterior distribution of coefficients, which reveals the uncertainty of the coefficient estimates. Finally, the employed models give rise to predictive densities; that is, we predict a distribution instead of just a single value, which we can then summarize, for example, with the posterior mean and standard deviation.

#### 2.3.5 Predictions at the landscape scale

Based on forest structure data from the SFD plots, we obtained landscape-scale predictions of relative throughfall. Because the $BA_{ratio}$ turned out to be a valuable predictor of relative throughfall (cf. Sects. 3.3 and 3.4) we used this forest structure parameter for our calculations, which involved two steps: (1) we pooled the $BA_{ratio}$ data of the years 2009–2011 within four prespecified age classes. We then fitted empirical distributions on the $BA_{ratio}$ data using kernel density estimation and sampled these distributions 1000 times each. This procedure provided age-class-dependent forest structure information which we used to obtain a distribution of predicted relative throughfall values for each age class. This step of our analysis enabled us to assess the change and spread of relative throughfall across different age classes of forest succession. (2) Based on $BA_{ratio}$ data for the years 2009–2011, we predicted relative throughfall for all SFD plots and individual years, respectively. Subsequently, we calculated the mean relative throughfall of these plots for each year, which enabled us to derive landscape-scale estimates of relative throughfall input to the secondary forests in the study area.

#### 2.3.6 Software

For all statistical analysis, we used the software R, version 2.14.0 (R Development Core Team, 2011). Straightforward application of the BMA approach was possible thanks to the R package BMS (Feldkircher and Zeugner, 2009).

## 3 Results

### 3.1 Characteristics of throughfall data and relationship to forest age

Interception loss in the studied secondary forest plots amounted to a maximum of 26 % of gross rainfall (Table 1). In two of the young throughfall plots, mean interception was slightly negative (plots 2 and 4 in Table 1), which is due to uncertainty in estimating mean relative throughfall. The standard errors varied between 2.9 and 5.5 % (Table 1). The coefficients of variation are typical for secondary forests in central Panama (Zimmermann A. and Zimmermann B., 2013) and range between 15 % in the youngest and 41 % in the oldest throughfall plots (Table 1). While throughfall data of most plots had a low skewness, three plots showed a skewness > 1 due to the influence of single locations that constantly received particularly large throughfall amounts (Table 1).

Our data indicate a relationship between interception loss and forest age but the variation is considerable. The most striking feature of this relationship is a mean interception loss below 10 % in forests younger than a decade and above 15 % in older forests (Table 1). Consequently, canopy interception of secondary forests seems to differ from that of mature forests only within the first decade of forest recovery.

### 3.2 Univariate relationships between throughfall and canopy structure

In the univariate space, the $BA_{ratio}$, $BA_5$, and openness have the largest impact on throughfall, while the terrain attributes do not seem to have an influence (Table 2). Many of the explanatory variables are correlated among themselves: the $BA_{ratio}$ is of course heavily associated with $BA_1$ and $BA_5$, but it is also associated with openness and $SD_1$. Further correlations exist between $BA_5$ and openness, $BA_5$ and diversity, $BA_1$ and $SD_1$, and between $SD_5$ and diversity. Slope is correlated quite strongly to $BA_5$, and the only variables with merely weak associations to other predictors are the sine and cosine of the aspect. This multicollinearity is suboptimal for a multiple regression problem (see Sect. 3.4).

### 3.3 Univariate prediction of relative throughfall

We built simple regression models using the variables most strongly related to relative throughfall as predictors: $BA_{ratio}$, $BA_5$, and openness (Table 2). The strength of the linear relationships between each of the three predictors and relative throughfall is reflected by the credible intervals for the slopes, which do not include zero (Table 3). Using the $BA_{ratio}$ as an explanatory variable provided the highest predictive accuracy as indicated by an RMSE of the validation data of 4.92 % (Table 3).

### 3.4 Multivariate prediction of relative throughfall

We applied BMA with the specifications explained in Sect. 2.3.4. The outcome of the BMA approach highlighted the overall importance of the $BA_{ratio}$ also in multivariate space: it has a posterior inclusion probability (PIP) of 0.70, its coefficient estimates differ from 0 (Fig. 2), and the model with the highest posterior probability only included this predictor (Fig. 3). In addition, in almost all models, the $BA_{ratio}$ is positively related to $t_r$ (Fig. 3), which is expected: relative throughfall decreases (i.e., interception loss goes up) as the basal area of small stems gradually contributes less to the total basal area over the course of forest succession. The PIPs of all other predictors are smaller than 0.5, and their coefficient densities include zero (Fig. 2). The posterior expected model size, i.e., the average number of included predictors, is 2.2. This low number indicates, in addition to the already mentioned high mass of the model that only contains the $BA_{ratio}$, the preference of parsimonious models (cf. Fig. 3).

**Table 2.** Correlation matrix (Spearman's rank correlation coefficients) for relative throughfall ($t_r$) and forest structure parameters. Note: correlations < −0.75 and > 0.75 are shown in bold.

| Variable[a] | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $t_r$ | 1 | 1 | **0.76** | 0.73 | **−0.78** | 0.75 | −0.65 | **0.85** | −0.74 | 0.47 | 0.35 | −0.26 |
| *openness* | 2 | **0.76** | 1 | 0.64 | **−0.90** | 0.68 | −0.52 | **0.90** | −0.66 | 0.45 | 0.23 | −0.16 |
| $BA_1$ | 3 | 0.73 | 0.64 | 1 | −0.72 | **0.95** | −0.35 | **0.82** | −0.48 | 0.43 | 0.18 | 0.09 |
| $BA_5$ | 4 | **−0.78** | **−0.90** | −0.72 | 1 | −0.75 | 0.64 | **−0.95** | **0.76** | −0.67 | −0.11 | 0.20 |
| $SD_1$ | 5 | 0.75 | 0.68 | **0.95** | −0.75 | 1 | −0.43 | **0.84** | −0.55 | 0.49 | 0.14 | −0.01 |
| $SD_5$ | 6 | −0.65 | −0.52 | −0.35 | 0.64 | −0.43 | 1 | −0.63 | **0.82** | −0.43 | −0.39 | 0.29 |
| $BA_{ratio}$ | 7 | **0.85** | **0.90** | **0.82** | **−0.95** | **0.84** | −0.63 | 1 | −0.74 | 0.60 | 0.27 | −0.12 |
| *diversity* | 8 | −0.74 | −0.66 | −0.48 | 0.76 | −0.55 | **0.82** | −0.74 | 1 | −0.43 | −0.22 | 0.39 |
| *slope* | 9 | 0.47 | 0.45 | 0.43 | −0.67 | 0.49 | −0.43 | 0.60 | −0.43 | 1 | −0.11 | 0.08 |
| $aspect_{sine}$ | 10 | 0.35 | 0.23 | 0.18 | −0.11 | 0.14 | −0.39 | 0.27 | −0.22 | −0.11 | 1 | −0.04 |
| $aspect_{cosine}$ | 11 | −0.26 | −0.16 | 0.09 | 0.20 | −0.01 | 0.29 | −0.12 | 0.39 | 0.08 | −0.04 | 1 |

[a] For a description of the variables, refer to Sect. 2.3.2.

**Table 3.** Simple linear regression results.

| Predictor | Slope[a] | $CI^b_{low}$ | $CI^c_{up}$ | $RMSE_{cal}$ (%)[d] | $RMSE_{val}$ (%)[e] |
|---|---|---|---|---|---|
| $BA_{ratio}$ | 0.19 | 0.12 | 0.25 | 4.39 | 4.92 |
| openness[f] | 14.23 | 8.23 | 20.23 | 4.87 | 5.37 |
| $BA_5$ | −0.41 | −0.63 | −0.19 | 5.48 | 6.03 |

[a] Slope of regression model, [b] lower limit of credible interval for slope ($\alpha = 0.05$), [c] upper credible interval for slope, [d] RMSE of calibration data, [e] RMSE of validation data. [f], openness was $\log_{10}$-transformed prior to regression modeling.

The performance of the BMA approach was not superior to that of the simple linear regression model with the $BA_{ratio}$ as the predictor, as indicated by an RMSE of 4.16 % (calibration data) and 5.22 % (validation data). We also tried several other predictor combinations including two-predictor-ensembles to mitigate the problem of multicollinearity (cf. Sect. 3.2), but none of them was able to improve predictive performance as the RMSE for those trials varied between 5 and 6.5 %. Hence, the BMA approach is outperformed by a simple linear regression model that only needs basic forest inventory data.

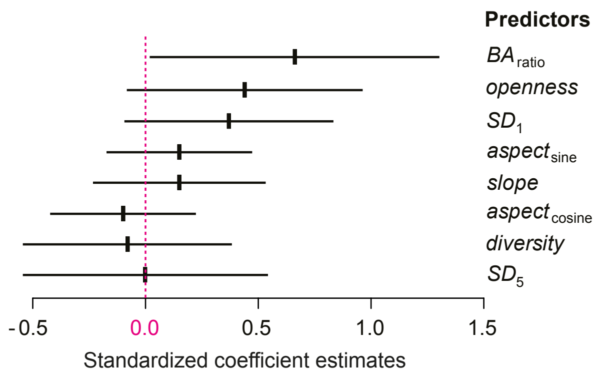


**Fig. 2.** The standardized coefficient estimates for all predictors resulting from the BMA modeling. The vertical bar at each horizontal line denotes the coefficient's expected value, from which the ends extend to two times the standard deviation derived from the coefficient's posterior distribution. We consider a predictor to be important if these horizontal lines do not include zero.

### 3.5 Variation in canopy interception at the landscape scale

In a first step of this analysis we compared predicted throughfall within four age classes with the mean and the credible interval limits of relative throughfall in mature forests of our study area (Fig. 4a). This revealed that only the predicted values for the two age classes that cover succession stages in forests younger than a decade clearly differed from mature forest in terms of canopy interception, which confirms the empirical results (cf. Sect. 3.1).

In a next step of our analysis we predicted relative throughfall input to all SFD plots in our study area. The predicted values still differ from throughfall of mature forest on BCI, though more than half of the SFD plots already show relative throughfall values that are within the credible interval limits of relative throughfall at the mature forest sites (Fig. 4b).

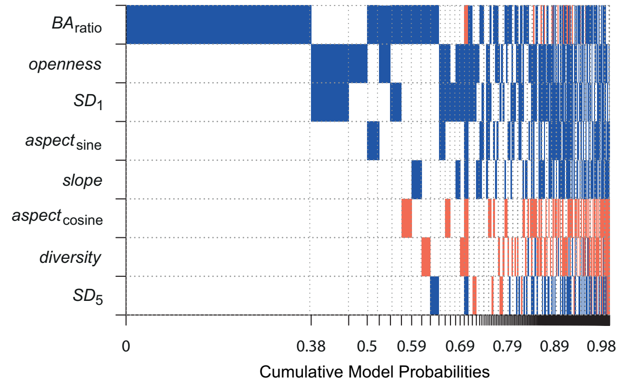


**Fig. 3.** Cumulative posterior model probabilities resulting from the BMA approach. The colors denote the sign of a coefficient's expected value: blue refers to a positive sign (indicating a positive relationship with relative throughfall) and red to a negative sign (indicating a negative relationship with relative throughfall). Note: the model with $BA_{ratio}$ as the only predictor clearly has the largest weight.

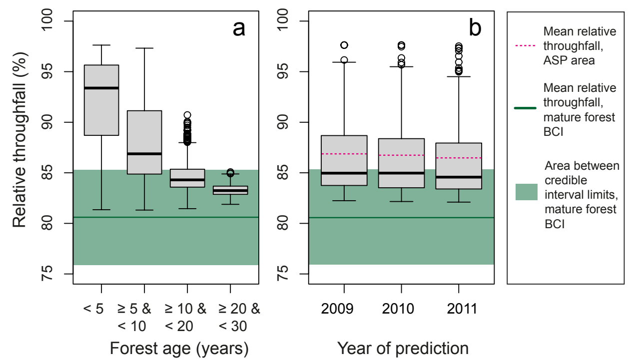


**Fig. 4.** Relative throughfall as predicted with the simple linear regression model that uses $BA_{ratio}$ as predictor for **(a)** four age classes and **(b)** the 95 SFD plots in the ASP study area. The credible interval for the mature forest's mean relative throughfall is based on this study's mature forest throughfall data as well as prior information derived from previous studies in tropical lowland rainforests (e.g., Asdak et al., 1998; Cuartas et al., 2007; Hutjes et al., 1990; Vernimmen et al., 2007). Note that a $(1-\alpha) \times 100\,\%$ Bayesian credible interval is defined as an interval that has a posterior probability of $1-\alpha$ of containing the parameter of interest, in our case the mean (Bolstad, 2007). We set $\alpha$ to 0.05.

## 4 Discussion

### 4.1 Changes in canopy interception during forest succession: timing and consequences

In many tropical landscapes young secondary forests are an important component of the land-use mosaic (Perz and Skole, 2003; Wright and Samaniego, 2008). We showed that the major change in canopy interception loss after land abandonment in lowland forests in Panama occurs during the first decade of forest development (Table 1, Fig. 4a). This is because forest structure changes considerably during early succession, as is reflected in a strong increase in basal area (Fig. 1d), a marked decrease in the ratio of the basal area of small stems to the total basal area (Fig. 1e), and a distinct decrease in the openness (Fig. 1f). The large scatter in relative throughfall amounts within a given period (Table 1, Fig. 4a) reflects the tremendous spatial variation in forest structure, as well as the underlying factors that influence secondary forest regrowth, including the intensity of past land use, landscape features such as the occurrence of remnant trees, and nutrient availability (Guariguata and Ostertag 2001; Hölscher et al., 2005). However, research in Mexican and Costa Rican montane cloud forests (Holwerda et al., 2010; Hölscher et al., 2010; Muñoz-Villers et al., 2012) indicates that changes in canopy interception during secondary succession do not necessarily occur as rapidly as in our study area. At a montane cloud forest site in Mexico, for instance, canopy interception loss of a 20 yr old secondary forest amounted to only 50 % of the value estimated for an adjacent mature forest, which was explained by the slow recovery of the epiphyte biomass (Holwerda et al., 2010).

For regions of the lowland tropics that undergo rapid forest succession (Ewel, 1980; Guariguata and Ostertag, 2001; Hölscher et al., 2005), we envision that the spatio-temporal variation of interception has two important implications. First, we expect that the influence of forest succession on interception at the landscape scale is detectable only if secondary forests < 10 yr are abundant because only early successional stages show canopy interception values that are consistently lower than those of mature forests (cf. Fig. 4). Second, we suppose that the rapid increase of canopy interception during the first decade of forest recovery (Table 1, Fig. 4a) may have potentially undesirable consequences for the entire flow regime. For instance, in areas with compacted soils, such as former pastures, the change in canopy interception during succession (Table 1, Fig. 4a) clearly predates the recovery of soil permeability observed in other studies (Fig. 5). Consequently, the concurrence of pasture-like hydrological flow paths (i.e., the predominance of overland flow; Germer et al., 2010) and strongly rising evapotranspiration rates during the first decade of recovery might temporarily decrease groundwater recharge even beyond pasture levels, leading to further reductions in dry-season flow (cf. Jackson et al., 2005). However, while secondary forest succession might clearly influence the flow regime of small catchments with one dominant land use or forest age (e.g., Bruijnzeel, 1989; Brown et al., 2005), effects on the hydrologic regime of large watersheds with their typical mixture of land uses and secondary forest ages are likely difficult to detect in most cases (cf. Beck et al., 2013).

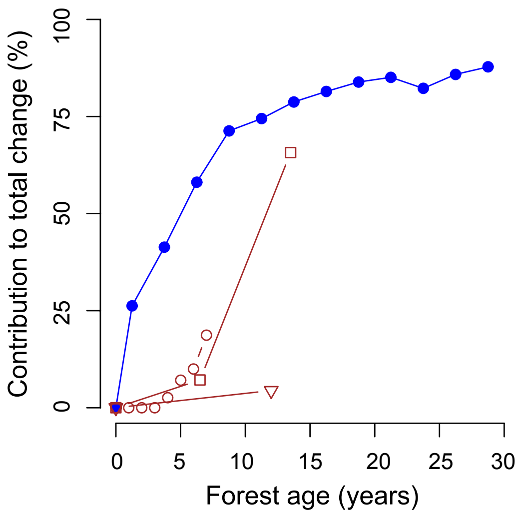


**Fig. 5.** Change in canopy interception (blue filled circles) and recovery of soil permeability (red open symbols) during secondary forest succession. The plot shows the contribution to total change, which is calculated using data from pastures and old-growth forests as end members. The change in canopy interception is calculated based on predictions of relative throughfall using a simple linear regression model and $BA_{ratio}$ data from the 95 SFD plots (forest inventories of the years 2009–2011). The change in soil permeability is calculated based on data from secondary forests located in (1) the ASP area (red open squares; from Table 2a in Hassler et al., 2011), (2) southwestern Amazonia (red open circles, from Fig. 1 in Zimmermann et al., 2010), and (3) eastern Amazonia (red open triangles; from de Moraes et al., 2006).

### 4.2 Modeling canopy interception using forest inventory data

This study shows that common forest structure parameters can predict changes in rainfall interception reasonably well. We found that the increase of total basal area during succession was less efficient for predicting the change in canopy interception than the $BA_{ratio}$, which gives the contribution of the basal area of small stems to the total basal area. Hence, the $BA_{ratio}$ seems to relate more strongly to the development of the canopy structure during forest succession. Other common attributes for describing canopy structure are tree height and canopy openness. We used the latter in our analysis because openness data are relatively easy to obtain and were found to be associated with throughfall in previous studies (e.g., Dietz et al., 2006; Zimmermann et al., 2009). However, because openness does not take the leaf area density into account, its potential to explain variations in throughfall magnitudes is limited, particularly for large rainfall amounts and long-term data (Zimmermann et al., 2009). Moreover, openness and the $BA_{ratio}$ were strongly related, which is why their simultaneous inclusion into the modeling framework did not improve predictive accuracy. Interestingly, the incorporation of additional vegetation parameters did not help either, most likely because of the pervasive correlations among them (Table 2). The parsimonious two-parameter (tree height and leaf area index) model that Dietz et al. (2006) reported to be the "best" model out of an extensive set of candidate models is in line with the results of our BMA approach, i.e., the large posterior probability of one- or two-parameter models (Fig. 3).

### 4.3 Directions for future research

Given the considerable error attached to our throughfall predictions, what should be done in future studies? Apart from using interception modeling instead of applying empirical relationships, which has its own difficulties (e.g., the need to sample small events), we see two avenues to improve models that apply forest structure parameters for predicting canopy interception. The first is testing alternative data to describe forest structure, most notably from remote sensing. For instance, Nieschulze et al. (2009) successfully modeled canopy interception using satellite image data. Alternatively, airborne light detection and ranging (LIDAR) data, with their potential to capture fine-scale three-dimensional forest structures (Asner et al., 2011), might prove valuable for predicting interception. The remotely sensed information provides the additional advantage that it usually has a good spatial coverage, which makes landscape-scale predictions feasible. The second and probably equally important potential improvement is in the acquisition of the throughfall and rainfall data themselves. In spite of the 536 collectors used in our study, standard errors for plot-level relative throughfall are in the range of 3 to 5 % percent (Table 1), which is considerable given the small range of total variation (approx. 25 %) in relative throughfall along our 130 yr chronosequence. Moreover, some of our throughfall plots were several hundred meters away from their rainfall site, which likely introduced further errors. Hence, sampling efforts in future investigations need to be increased even further if land-use-related changes of interception need to be quantified.

## 5 Conclusions

We conclude our study by answering the three research questions posed in the introduction.

1. Canopy interception changes rapidly during forest succession in tropical lowland regions in Panama. After about a decade of forest recovery, throughfall volumes approach the level that is typical for mature tropical lowland forests. The fast change in canopy interception during forest succession predates the recovery of soil permeability (de Moraes et al., 2006; Hassler et al., 2011; Zimmermann et al., 2010). We expect that this temporal asymmetry can have important consequences for the flow regime of small catchments.

2. Forest structure parameters are considerably correlated with each other. In a multiple regression framework, this behavior leads to a large degree of multicollinearity and hence a large uncertainty in estimated regression coefficients. Simple linear regression is therefore better suited to model canopy interception than multiple regression. Forest inventories that include measurements of small stems are beneficial in this respect because they enable the calculation of the ratio between small- and large-stem basal areas, which proved to be most useful for predictions in this study.

3. Given the uncertainties associated with throughfall predictions and the inherently large variation of throughfall during early forest succession, the influence of young secondary forests on interception in real-world fragmented landscapes might be detectable only in tropical lowland regions with a substantial fraction of forests < 10 yr. This is because in tropical lowland regions, only forests in early successional stages show canopy interception values that are consistently lower than those of mature forests.

**Supplementary material related to this article is available online at http://www.hydrol-earth-syst-sci.net/17/4659/2013/hess-17-4659-2013-supplement.pdf.**

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