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Discussions

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Towards quantifying the increase of rainfall interception during secondary forest succession

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Abstract

Large scale forest regrowth is one aspect of modern land-cover change. Yet, despite the importance of understanding the hydrological consequences of land cover dynamics, the relation 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 modelling 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 comprises 20 natural forest patches regrowing for 3 up to about 130 yr. We sampled each patch with a minimum of 20 funnel-type throughfall collectors over a continuous two-month period that had nearly 900 mm of rain. At the same time and locations, 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 have the strongest influence on the variation of canopy interception. Our analyses provide three main findings. First, canopy interception changes rapidly during forest succession. After only a decade, throughfall volumes approach 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 very young forests. In case entire catchments are subject to forest regrowth, initial stages may be associated with undesirable effects on streamflow generation. Our results further highlight the need to study all forest succession stages, including early ones.

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1 Introduction

Across the tropics, large proportions 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 spreading in tropical regions (Chazdon, 2008; Perz and Skole, 2003). In addition, evidence accumulates 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 of secondary forest cover. Most often, the regrowing forests occur in areas with patches of mature forest, pastures, farmland, settlements, etc., and are thus 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). The original forests, which provide the baseline for evaluating secondary forests' hydrology, differ from 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 forests originates from the 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 successional

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trajectories. For instance, the recovery time, the type of regrowing forest (e.g. invasive plants versus natural succession), and the type and intensity of past land use (e.g. pasture versus slash-and-burn agriculture) 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), it should be evident that we need observations both from forests of different age and from multiple sites within an age class to describe the change of interception during forest regrowth. These observations are, of course, costly to obtain. It would thus be desirable if we could use forest inventory data to predict the change of 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: (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? At the end of the article we also discuss the implications of our findings regarding the hydrological functioning of catchments subject to forest succession.

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2 Methods

2.1 Study area

We studied interception loss in 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 a steep and dissected terrain with a high drainage density. The island of Barro Colorado was isolated from the main land in 1914 after damming the Chagres River 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 a.m.s.l. – above mean sea level) adjacent to the 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 ± 485 mm (mean ±1 standard deviation, $n = 82$, data from 1929 to 2010, data by courtesy of the Environmental Sciences Program, Smithsonian Tropical Research Institute, Republic of Panama), and 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), which covers all of BCI. Vegetation cover in the Agua Salud Project area includes pastures, subsistence agriculture and timber plantations as well as secondary forests of various recovery stages (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). For our study we used forest inventory data from 95 of the SFD plots. For throughfall monitoring we selected 16 of these plots in addition to 4 plots on BCI.

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2.2 Sampling scheme

2.2.1 Site selection

Since our objective was to relate interception to forest structure, which we wanted to tackle with a regression-type analysis (cf. Sect. 2.3), we optimized site selection by spreading the range of succession stages as far as possible and by sampling the distribution of potentially important predictor variables as evenly as possible (Webster and Lark, 2013). That is, we selected both very young forests (the youngest was recovering for three years only) and sites in the mature secondary forest of BCI (Fig. 1d–f); we chose intermediate plots such that the range of site-specific canopy openness, basal area and stem density was covered evenly (this approach was possible thanks to prior information from the SFD study). The sites on BCI are not part of the secondary forest dynamics study but their inclusion was essential because the secondary forests in the ASP area are not older than a few decades. In total, we chose 20 throughfall sampling sites. The SFD plots measured 20 m by 50 m; at two ASP sites and on BCI, plots were 30 m by 60 m.

2.2.2 Age estimates and determination of forest structure and canopy openness

Our sites 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 recovery time (forest age) of our plots by 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 timing of forest succession. For instance, ridges often experience more and longer human impact, e.g. by cattle treading, than do middle or down slope locations. Moreover, most streams and gullies are surrounded by streamside vegetation which, of course, influences secondary succession. Hence,

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recovery time is to be considered a fuzzy variable and not used as an explanatory variable in regression modelling (cf. Sects. 2.3.3 and 2.3.4).

Stand characteristics in the secondary forest dynamics plots are monitored annually. All plots were divided into 5 m by 5 m quadrants. In each quadrant, we identified all tree, shrub, and palm species of all stems with a dbh (diameter at breast height) ≥ 5 cm and measured the dbh of all individuals in this class. The same was done in every other quadrant for all individuals with a dbh ≥ 1 cm.

We took hemispherical photographs (HemiView, Delta-T Devices Ltd) above each throughfall collector during the throughfall measurement campaigns.

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 a throughfall and its closest rainfall site was 360 m on average and 760 m at maximum. At each rainfall site, we placed five to ten collectors. We measured throughfall within each forest plot at several randomly selected locations to estimate the plot mean of throughfall. Because young forests require less sampling effort than old ones (Zimmermann and Zimmermann, 2013), we divided our plots into "young" and "old" forest plots. We set the limit for young plots to a total basal area of 10 $m^2\,ha^{-1}$ because at this point the initially strong decline of canopy openness levels off (van Breugel et al., 2013). Sample sizes in most young and old plots were 20 and 25, respectively; two young ASP plots and the mature secondary forest sites on BCI were sampled with a sample size of 36 (Table 1). Given our sample support of 113 cm^2 and the temporal aggregation of the throughfall data (see below, this subsection), our sampling approach ensures relative error limits of the estimated mean throughfall of 15 %

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(Zimmermann and Zimmermann, 2013). In total, we monitored throughfall at 536 sampling locations.

We monitored throughfall at the ASP sites continuously for two months in the middle and late rainy season of 2011. During this period, average rainfall amounted to 831 ± 35 mm (mean ±1 standard deviation, data from the rainfall sites in the ASP area). We visited each throughfall site at least every fifth 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, 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 of the other two sites on the island had been obtained on event basis during the years 2007 and 2008 (Zimmermann et al., 2009).

Stemflow at two of our throughfall sites on BCI was only 1 % of gross precipitation over a two month period (A. Zimmermann, unpublished data). Other studies in Panamanian secondary and native species plantation forests report similar low stemflow volumes (Macinnis-Ng et al., 2012; Park and Cameron, 2008). We therefore do not consider stemflow in this study.

2.3 Data analysis

2.3.1 Calculation of relative throughfall and of interception loss

First, at each site we added the measured throughfall and rainfall values of the entire measurement period to obtain long-term data (i.e. throughfall and rainfall during several months) and converted these data into mm. Next, we calculated the relative throughfall (t_r) at each site $\boldsymbol{x}_i$ as follows:

$$t_\mathrm{r}(\boldsymbol{x}_i) = \frac{\hat{\hat{T}}(\boldsymbol{x}_i)}{\hat{\hat{R}}(\boldsymbol{x}_i)} \times 100, \tag{1}$$

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where $\widehat{\overline{T}}(\boldsymbol{x}_i)$ is the estimated mean throughfall at the site and $\widehat{\overline{R}}(\boldsymbol{x}_i)$ is the average rainfall of the corresponding rainfall site. Since 100 % t_r equals 0 % interception (i_c) and vice versa, it is straightforward to convert t_r into interception loss. For the ASP sites, we calculated t_r with rainfall data of the nearest rainfall site because the weighted rainfall average of all ASP rainfall sites performed worse in the modelling.

2.3.2 Derivation of explanatory variables

From the forest monitoring data, we derived the following forest structure parameters: basal area and stem density separately for two dbh classes (class 1: dbh between 1 and 5 cm; class 2: dbh > 5 cm), abbreviated with BA_1, SD_1 (class 1) and BA_5, SD_5 (class 2). For dbh-class 2, for which we had species information for all plots, we also calculated the Shannon's diversity index (Magurran, 2004) (diversity hereafter) for trees > 5 cm dbh. We also merged the information on basal area in the two dbh-classes into an index that we defined to be the ratio of BA_1 to the total basal area. This integrated measure, which we called the BA_{ratio}, takes into account that the basal area of the smaller trees is related in a complex way to that of canopy trees (Montgomery and Chazdon, 2001; van Breugel et al., 2012). We anticipated that this relationship between basal area classes might also influence rainfall interception.

We derived the canopy openness (openness hereafter) from the hemispherical photographs. The 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 strongest 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 modelling.

Characteristics of the terrain might also influence canopy interception, particularly in rough terrains like ours. We derived those terrain attributes from a Digital Elevation Model that might influence interception, 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 Bayes 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 BMA approach described below, we used the Root Mean Square Error (RMSE):

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

where $z(\boldsymbol{x}_i)$ is the measured and $\hat{z}(\boldsymbol{x}_i)$ the predicted t_{r} value at location $\boldsymbol{x}_i$. We calculated the RMSE both for the calibration data and the validation data (leave-one-out cross validation).

2.3.4 Modelling framework using multiple parameters

This second step of our analysis was designed to answer the question if the inclusion of all available parameters in a multivariate framework improves predictive accuracy. Since we did not know a priori which combination of forest structure parameters is suited best to predict relative throughfall, we applied Bayesian Model Averaging (BMA) to our data, which is a popular framework to deal with the issue of model uncertainty. In BMA, models are constructed for all possible combinations of explanatory variables and inference is based on a weighted average over all of them. The model weights arise naturally from Bayes' theorem as posterior model probabilities (PMP). 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, and the

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prior probability reflects one's belief about the probability of the model before looking at the data. The prior probability 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. 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 (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 e.g. by the posterior mean and standard deviation.

2.3.5 Predictions at the landscape scale

We applied our modelling framework to predict relative throughfall at the landscape scale using forest structure data from 95 plots of the secondary forest dynamics study. Our calculations involved two steps: (1) we pooled the forest inventory data of the years 2009–2011 within four pre-specified age classes. We then fitted empirical distributions on the forest structure data using Kernel density estimation and sampled these distributions 1000 times each. This procedure provided age-class depended forest structure information which we finally 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 through different age classes of forest succession. (2) Based on forest inventory data of the years 2009–2011 we predicted relative throughfall for all 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 of 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 recovery time

Interception loss in the studied secondary succession gradient amounted to maximal 26 % of gross rainfall (Table 1). In two of the young plots, mean interception was slightly negative (plots 2 and 4, Table 1), which is due to uncertainty in estimating mean relative throughfall – standard errors vary between 2.9 and 5.5 % (Table 1). The coefficients of variation are typical for natural secondary forests in central Panama (Zimmermann and Zimmermann, 2013) and range between 15 % in the youngest and 41 % in the oldest study plots (Table 1). While throughfall data of most sites have a low skewness, 3 plots show a skewness > 1 due to single locations that constantly received particularly large throughfall amounts (Table 1).

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Our data indicate a relationship between interception loss and recovery time 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 at all (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 also with openness and SD_1. Further correlations exist between BA_5 and openness, BA_5 and diversity, BA_1 and SD_1, and between the 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 those variables as predictors which are strongly related to relative throughfall: 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 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 Bayesian Model Averaging with the specifications explained in Sect. 2.3.4 and with the BA_{ratio} instead of BA_1 and BA_5 as a predictor to reduce the number of ex-

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planatory variables, which then amounted to eight. The outcome of the BMA approach highlighted the overall importance of the BA_{ratio} also in the multivariate space: It has a posterior inclusion probability (PIP) of 0.70 (Table 4), its coefficient estimates differ from 0 (Fig. 2), and the model with the highest posterior probability only included this predictor (Fig. 3). In addition, the BA_{ratio} is in almost all models positively related to t_r (Table 4) 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 in the course of forest succession. The PIPs of all other predictors are smaller than 0.5 (Table 4), 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).

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), respectively. 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.

3.5 Variation in canopy interception at the landscape scale

In the following analyses we used the simple linear regression model with the BA_{ratio} as the explanatory variable to predict relative throughfall. In a first step we predicted throughfall within four age classes (Fig. 4a). We then compared the obtained distributions of relative throughfall values within each age class with the mean and the credible interval limits of relative throughfall in mature forests of our study area. This reveals that only the predicted values for the two age classes that cover succession stages in forests younger than a decade clearly differ 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 of all secondary forests plots in our study area. The predicted values still differ from throughfall of mature forest on Barro Colorado Island (BCI), though more than half of the prediction sites already show relative throughfall values which are within the credible interval limits of relative throughfall at the mature forest sites (Fig. 4b).

4 Discussion

4.1 Changes of 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 of canopy interception loss after land-use abandonment occurs during the first decade of forest development (Table 1, Fig. 4a). This is because forest structure changes considerably during early succession which is, for instance, reflected in a strong increase of the basal area (Fig. 1d), a marked decrease of the ratio of the basal area of small stems to the total basal area (Fig. 1e), and a distinct decrease of the canopy openness (Fig. 1f). The large scatter in relative throughfall amounts within a given period (Table 1, Fig. 4a) reflects the tremendous spatial variation of the factors that influence secondary forest regrowth, such as the intensity of past land use, landscape features (e.g. distance to forest), and nutrient availability (Guariguata and Ostertag, 2001; Hölscher et al., 2005).

We envision that the spatio-temporal variation of interception during secondary succession has two important consequences. First, we expect that the influence of forest succession on interception at regional scales is detectable only if very young secondary forest ($\ll 10$ yr) are abundant because only early succession stages show canopy inter-

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ception 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 of catchments. For instance, in areas with compacted soils, such as former pastures, the change in canopy interception during succession clearly predates (Table 1, Fig. 4a) the recovery of soil permeability (Hassler et al., 2011; Zimmermann and Elsenbeer, 2008; Zimmermann et al., 2010). Consequently, the concurrence of pasture-like hydrological flow paths (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 (e.g. Bruijnzeel, 1989; Brown et al., 2005), effects on the hydrologic regime of large watersheds with their typical mixture of land uses are probably difficult to detect in most cases (cf. Beck et al., 2013).

4.2 Modelling 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 is 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 stronger to the underlying physical principle, i.e. 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 is relatively easy to obtain and was 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 value to explain variations in throughfall magnitudes is limited, particularly for large rainfall amounts and long-term data (Zimmermann et al., 2009).

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Moreover, openness and the BA_{ratio} were strongly related, which is why their simultaneous inclusion into the modelling 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 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 modelling instead of applying empirical relationships, which has its own difficulties (e.g. the need to sample small events) there are two avenues to improve the relationship between forest structure and canopy interception. The first is testing alternative data to describe forest structure, most notably from remote sensing. For instance, Nieschulze et al. (2009) successfully modelled canopy interception using satellite image data. Alternatively, airborne light detection and ranging (LiDAR) data with its 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 can be exhaustive, which makes landscape scale predictions entirely feasible. The second and probably equally important potential improvement is in the acquisition of the throughfall and rainfall data themselves. In spite of the several hundred collectors used in our study, standard errors for plot-level relative throughfall are in the range of three to five 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 introduces 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.

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5 Conclusions

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

1. Canopy interception changes rapidly during forest succession. After about a decade of forest recovery, throughfall volumes approach the level that is typical for mature forests. The fast change in canopy interception during forest succession clearly predates the recovery of soil permeability. 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 behaviour 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. 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 stems' basal area, which proved to be valuable for univariate predictions.

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 regions with a substantial fraction of very young forests. The limited detectability of the young forests' interception signal, however, should not be confused with the potential relevance of the changes in canopy interception during forest succession.

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Table 1. Summary statistics of the throughfall data.

Plot	Age (years)	n[1]	Mean t_r (%)	SE[2] (%)	CV[3] (%)	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

[1] Sample size for throughfall; [2] standard error of t_r estimate; [3] coefficient of variation of t_r.

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Table 2. Correlation matrix (Spearman's rank correlation coefficients) for relative throughfall (t_r) and forest structure parameters.

Variable		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

Note: correlations $> |\pm 0.75|$ are shown in bold.

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Table 3. Results of simple linear regression.

Predictor	Slope[1]	CI^{2}_{low}	CI^{3}_{up}	$RMSE^{4}_{cal}$ (%)	$RMSE^{5}_{val}$ (%)
BA_{ratio}	0.19	0.12	0.25	4.39	4.92
openness[6]	14.23	8.23	20.23	4.87	5.37
BA_5	−0.41	−0.63	−0.19	5.48	6.03

[1] Slope of regression model; [2] lower limit of credible interval for slope ($\alpha = 0.05$); [3] upper credible interval for slope; [4] RMSE of calibration data; [5] RMSE of validation data; [6] openness was $\log_{10}$-transformed prior to regression modelling.

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Table 4. Statistics for standardized coefficient estimates.

Predictor	PIP[1]	PM[2]	PSD[3]	Sign[4]
BA_{ratio}	0.70	0.66	0.32	0.96
openness	0.36	0.44	0.26	1.00
SD_1	0.33	0.37	0.23	1.00
$aspect_{sine}$	0.18	0.15	0.16	1.00
slope	0.16	0.15	0.19	1.00
$aspect_{cosine}$	0.15	−0.10	0.16	0.00
diversity	0.14	−0.08	0.23	0.13
SD_5	0.14	0.00	0.27	0.76

[1] Posterior inclusion probability; [2] posterior mean; [3] posterior standard deviation; [4] posterior probability of a positive coefficient expected value conditional on inclusion: 1 = positive, 0 = negative, [> 0 sign < 1] reflects uncertainty about the sign.

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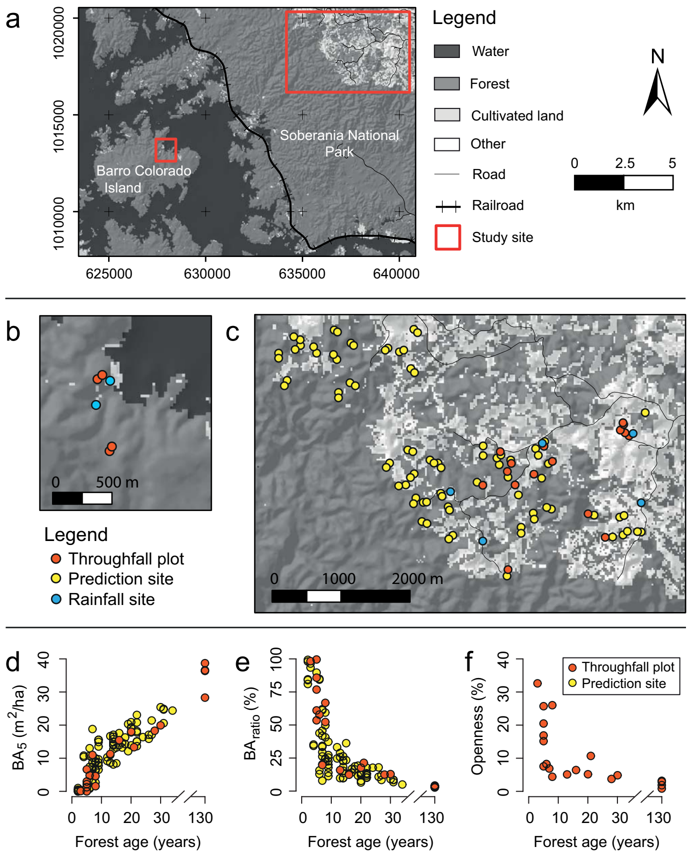

Fig. 1. Location of the study sites in central Panama **(a)**, detailed view at the BCI **(b)** and the ASP study area **(c)**, and relationship between forest age and BA_5 (basal area) **(d)**, between forest age and the BA_{ratio} (ratio of the basal area of small stems to the total basal area) **(e)**,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

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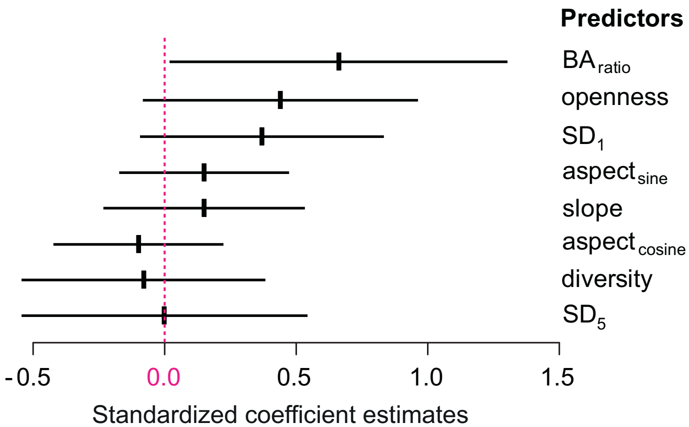

Fig. 2. The standardized coefficient estimates for all predictors resulting from the BMA modelling. The vertical bar at each horizontal line denotes the coefficient's expected value, from which the ends extend to two times the standard deviation derived from the coefficient's posterior distribution. We consider a predictor to be important if these horizontal lines do not include zero. Exact numbers for each coefficient's expected value and its standard deviation are given in Table 4.

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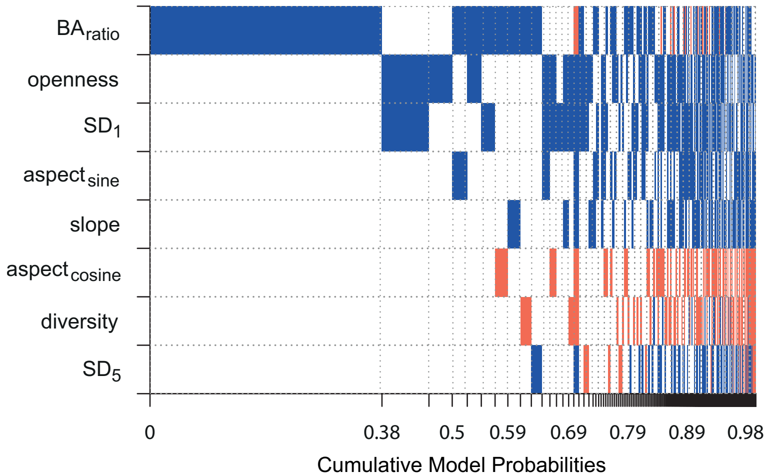

Fig. 3. Cumulative posterior model probabilities resulting from the BMA approach. The colours denote the sign of a coefficient's expected value: blue refers to a positive sign, red to a negative sign. Note: the model with BA_{ratio} as the only predictor clearly has the largest weight.

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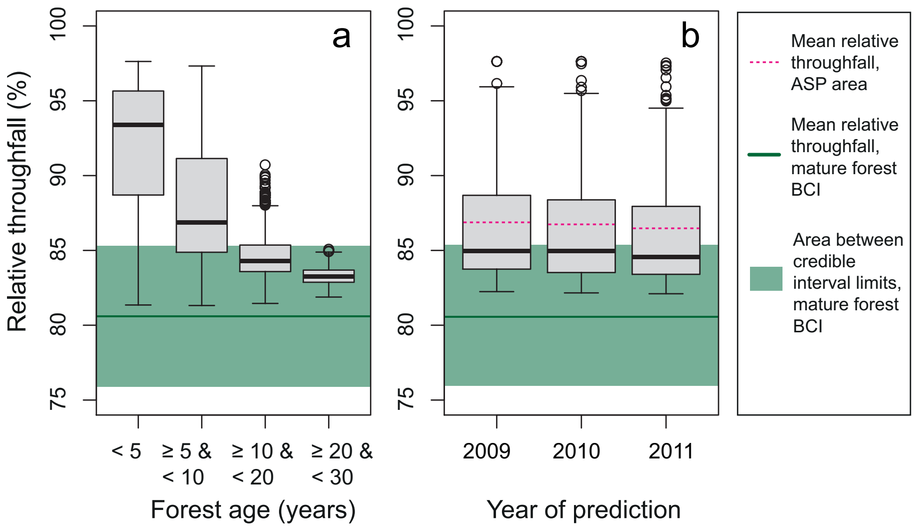

Fig. 4. Relative throughfall as predicted with the simple linear regression model that uses BA_{ratio} as predictor for **(a)** four age classes and **(b)** 95 plots in the ASP study area. The credible interval for the mature forest's mean relative throughfall is based on this study's mature forest throughfall data, as well as on 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).

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