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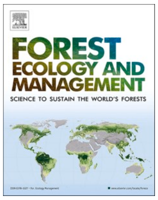

Intra-annual variation in microclimatic conditions in relation to vegetation type and structure in two tropical dry forests undergoing secondary succession

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ABSTRACT

Microclimate acts as a strong filter on species performance in restored and regenerating forests, particularly in seasonally dry tropical forests (SDTF). Yet few studies have measured microclimate patterns across succession in SDTF. Furthermore, although dynamic vegetation models simulate microclimate, evaluation of these simulated variables with field observations has been relatively uncommon. Here, we investigated the seasonal patterns of soil temperature and soil water in naturally regenerated and planted successional vegetation in SDTF in Costa Rica and Puerto Rico, using complementary approaches of intensive field observations and simulation modeling with the Ecosystem Demography model. We found that plots representing later successional stages were wetter on average, but only during the dry season. During the wet season, mean soil water did not differ across vegetation types, but open, early successional vegetation experienced more frequent extreme wet and dry conditions than older forest and plantations. Soil temperature tended to decline with forest structure, and later successional vegetation also experienced less extreme daily temperature fluctuations. Basal area and leaf area index were the best predictors of differences in soil water and temperature across plots. Model simulations were consistent with observations of wet season soil temperature and soil water, but the model failed to reproduce dry season soil moisture dynamics, suggesting that further work is needed to reduce model biases in microclimate variables. Collectively, our results imply that common assumptions about how microclimates influence successional processes in SDTF should be revisited.

1. Introduction

Naturally regenerated and restored tropical second growth forests are expected to make major contributions to climate change mitigation (Chazdon et al., 2016) and biodiversity conservation (Rozendaal et al., 2019). Given the global importance of tropical second-growth forests, much recent work has been devoted to understanding the mechanisms of tropical forest succession, and in particular the environmental filters that affect species performance in restored and regenerating forests (Powers & Marín-Spiotta, 2017; Uriarte et al., 2016). Shifts in microclimate conditions, such a temperature, light, and water availability as secondary forests mature are commonly invoked to explain successional patterns of changes in forest community composition and functional traits (Derroire et al., 2016; Lebrija-Trejos et al., 2010; Lohbeck et al., 2013). However, the necessary measurements needed to evaluate these shifts are rarely collected and/or collected over short time scales that do not fully capture seasonal dynamics (Anten and Selaya, 2011; Jucker et al, 2020).

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Feedbacks between forest successional changes and microclimate could take several possible forms (Fig. 1). First, under dense, tall, closed canopies, light is lower and temperatures tend to be cooler than under more open canopies (De Frenne et al., 2019, 2021; Jucker et al., 2020). Temperatures have been observed to be cooler under old-growth forests compared to plantations with similar canopy height and cover, suggesting an important role for structural complexity, biomass, and species diversity in influencing microclimate (Frey et al., 2016). All else being equal, lower temperatures should result in less evaporation from the soil and/or transpiration from trees, maintaining higher levels of soil moisture under more mature forest canopies (Jucker et al., 2018). This process is often assumed to be the main mechanism of forest structure-microclimate feedbacks and supports observations that soil and air conditions are often cooler and wetter under more closed canopies in late-successional and less-disturbed forests (Frey et al., 2016).

However, other ecological and biophysical processes hinder broad generalizations because microclimatic conditions are also affected by vegetation water use (Anten & Selaya, 2011). Larger trees transpire more water (Meinzer et al., 2004), and so as stand-level biomass increases with succession, the volume of transpiration fluxes may also increase, which depletes soil water. Varying vertical root profiles can also affect soil water. Larger trees may also transpire more subsurface water, potentially resulting in higher surface soil water due to hydraulic redistribution (Neumann & Cardon, 2012). Moreover, successional shifts in species composition can also influence transpiration rates, feeding back to soil water (Bazzaz & Pickett, 1980). Increased leaf area that accompanies succession may also affect soil moisture via changes in rainfall interception (Calvo-Alvarado et al., 2018; Zimmermann et al., 2013). Last, the balance between processes that increase or deplete soil water might vary geographically among sites in relation to topography, soil properties such as texture, and plant species traits that affect transpiration (Kunert et al., 2010). These processes can also vary seasonally, especially in forests that are dominated by deciduous tree species. How the magnitude of these processes, (i.e., vegetation structure, energy and water fluxes, etc.) and their contrasting effects on soil water differ along successional gradients are not well known.

Feedbacks between forest structure and soil water conditions over succession are thought to be particularly important in seasonally dry tropical forests (SDTF), where stressful conditions during dry periods potentially serve as a strong filter on forest composition and function (Hasselquist et al., 2010; Maza-Villalobos et al., 2013). Yet, these feedbacks are often inferred from observations of forest structure and associated shifts in functional traits. For example, shifts from conservative to acquisitive traits over succession in a dry forest in Mexico imply a transition from hot and dry conditions in early succession, to wetter and cooler conditions late in succession (Lebrija-Trejos et al., 2010; Lohbeck et al., 2013), but only a few studies have measured microclimate patterns across succession in SDTF to assess the consistency with which these environmental shifts occur. Moreover, these studies consider mean conditions only, measuring microclimate at only one time point per season or considering only one site per forest age along chronosequences (e.g., Hasselquist et al., 2010; Lebrija-Trejos et al., 2011; (Pineda-García et al., 2013). This lack of data hampers our understanding of the temporal dynamics of microclimate variables and makes generalizing across studies difficult. Resolving these patterns in SDTF ecosystems and understanding which processes are responsible for their dynamics are essential to advancing successional theory and for predicting forest responses to climate change. This is particularly true in SDTF where trees might be operating close to their hydrological limits (Allen et al., 2017).

One tool for predicting forest responses to climate and successional changes are dynamic vegetation models, which try to predict the

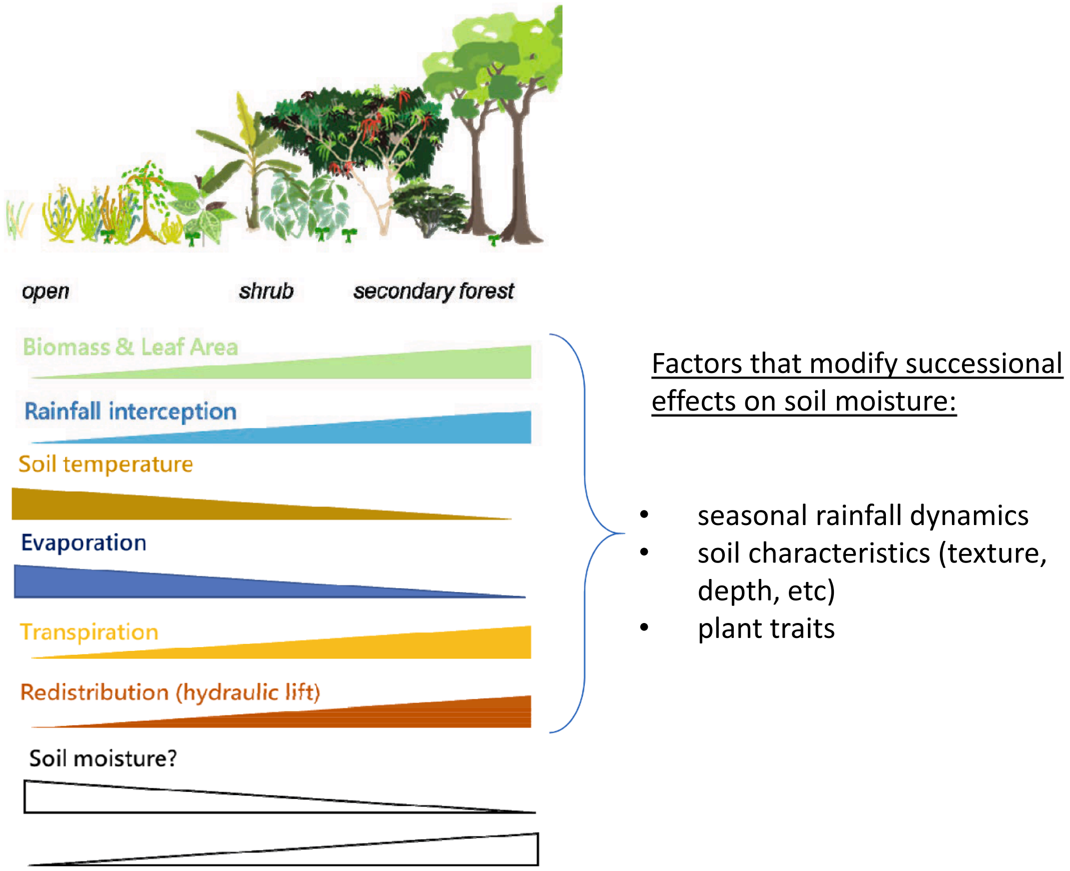

Fig. 1. Conceptual model of hypothesized changes in forest structure, and microclimatic variables during secondary forest succession.

distributions, dynamics, and characteristics of vegetation from physiological principles (Fisher et al., 2018). Implicit in these models are spatial and/or temporal feedbacks between forest structure and microclimate: these models typically simulate soil temperature, throughfall, and soil water content because these quantities directly affect plant-available water, root respiration rates, and organic matter decomposition rates. However, evaluation of simulated microclimatic variables has been relatively uncommon. One such model, is the Ecosystem Demography model (version 2.2; hereafter ED2, Longo et al., 2019a; Longo et al., 2019b), a cohort-based model which has been successfully parameterized to simulate successional change in SDTF (Xu et al., 2016). In the most recent version of this model simulated microclimate variables were not evaluated at all, despite a significant re-vamping of the processes that control these quantities. Determining the circumstances under which models fail to accurately simulate microclimate would indicate important areas for future model improvements.

Here we investigated the seasonal patterns of microclimatic variables in replicated plots representing a gradient of vegetation structure of managed and naturally regenerated second growth forests in dry forest regions in Costa Rica and Puerto Rico, using complementary approaches of intensive field observations and simulation modeling. Our overarching goal was to determine if there are systematic differences in microclimate conditions and their dynamics over the course of the wet and dry seasons in different stages of dry forest succession. Specifically, we asked:

1) How do seasonal average microclimate conditions differ across vegetation types representing a gradient of forest structure?
2) How does within-season variability in microclimate differ across vegetation types?
3) What forest structure and soil characteristics are associated with variation in microclimate conditions?
4) What aspects of microclimate are well-simulated in a dynamic vegetation model, and what processes likely need improved representation?

We hypothesized that early successional vegetation would have lower surface soil moisture compared to later successional vegetation during both the wet and dry seasons, due to elevated temperatures and associated enhanced evapotranspiration in early successional vegetation. As succession proceeds and forest biomass and leaf area increase, we expected these changes to decrease soil temperature and lead to higher soil moisture values.

To test these hypotheses, we measured soil temperature and surface soil moisture across several vegetation types representing a gradient of forest structure in two seasonally dry tropical forests. We complemented our field data with simulations using the ED2 model to simulate microclimatic conditions under a variety of vegetation and soil types, which allowed us to evaluate the model's representation of processes.

2. Methods

2.1. Study sites and plot design

Our primary study site was at Estación Experimental Forestal Horizontes (10.718 N, 85.594 W), which is a part of Área de Conservación Guanacaste in northwestern Costa Rica. Mean annual temperature is ~ 25C° and ~ 35 year mean annual rainfall at a nearby meteorological station is 1761 mm with a distinct 5-to-6-month dry season with little to no rainfall (Waring et al., 2021). The dry season typically starts in late December and continues until mid-May. Soils included both Andic and Typic Haplustepts (Waring et al, 2019) and Vertisols (Werden et al, 2018), and topography is relatively flat. Land at Horizontes was previously used for crops and grazing, and the current land cover includes early successional grasslands that are no longer cropped but are occasionally grazed by cattle, secondary forests aged ~ 30–40 years, and tree plantations (Werden et al., 2017). Because many of the changes in soil properties and canopy cover during secondary forest succession happen rapidly, i.e. within the first ten years (Powers & Marín-Spiotta, 2017), we used replicated patches of early and later successional vegetation instead of chronosequence sampling. All plots were 15 × 20 m.

To encompass large variation in microclimatic conditions and potential drivers across the landscape, we established three plots each in four different vegetation types for a total of 12 plots (Figure S1). Plots vegetation types represent a gradient of forest structure: plots on open land (O) had few trees and were dominated by C4 grasses and/or herbaceous plants. Shrub (S) plots represent early successional patches with more short statured trees, but understories dominated by grass and/or forbs. Mature secondary forest (F) plots consist of mostly deciduous tree species that were likely 40 + years old. Plantation (P) plots were each about 30 years old, and were dominated by different species (one plantation with both *Hymenea courbaril* and *Enterolobium cyclocarpum* (Jacq.) Griseb., and two single-species plantations with *Ateleia Herbert-smithii* Pittier or *Swietenia macrophylla* King). We included plantations because we expected them to have higher biomass than secondary forests. The understories of all tree plantations receive no management except for occasional cattle grazing, and contain variable amounts of naturally recruited trees, shrubs, and lianas.

We added a second study site in Guánica State Forest in Puerto Rico (17.9715° N, 66.8687° W). Although logistical constraints prevented us from sampling as many plots or as frequently as the other study site, as most other studies report data from only one location, we used this additional site to qualitatively assess the generality of results from the location in Costa Rica. In Puerto Rico we sampled only three plots, one in each of the following land cover types: open, mature secondary forest, and plantation. Annual rainfall in Guánica is ~ 825 mm with a 7 to 10 month dry season and mean average temperature is ~ 25.8 °C (Waring et al., 2021). All plots were on level or gently sloping ground. The open plot was likely cleared ~ 100 years ago and is maintained as a C4 grassland with sporadic deciduous trees through fire (Wolfe et al., 2019 and Wolfe and Van Bloem., 2012). The forest plot is > 120 years old and is dominated by semi-deciduous tree species (Skip Van Bloem, pers. comm.). The plantation plot consists of ~90-yr old *Swietenia mahagoni* (L.) Jacq., a deciduous species which was planted in the 1930 s, and now also contains a diverse understory and overstory canopy of naturally recruited trees.

2.2. Forest structure and soil properties

We measured the diameter at 1.3 m (dbh) of all trees or shrubs ≥ 5 cm diameter dbh. Multiple stemmed trees that forked below 1.3 m were treated as separate stems. We calculated basal area per ha (m^2 ha^{-1}) from the diameter measures, and stem density as the total number of stems > 5 cm dbh, scaled to stems per hectare. We measured fine root mass (defined as roots ≤ 2 mm diameter) once during the wet season by extracting soil cores with an 8 cm diameter root corer to 15 cm depth in mineral soil as a potential proxy for differences in transpiration (Ewers et al., 2005). Eight root cores were taken per plot, one at each of the four corners and four samples separated by 5 m in the central portion of the plot. Samples were washed clean of soil, dried at ~ 60 °C for at least 4 days, and then weighed. Leaf area index (LAI) was measured once during the wet season (July 2, 2018) and once during the dry season (February 26, 2019) using a LI-COR Plant Canopy Analyzer LAI 2200-C (Lincoln, NE, U.S.A.). We took three readings ~ 1.5 m above each of the 20 sampling points per plot. Soil samples (8 to 10 2.5 cm cores haphazardly located across each plot) were taken from the 0–10 cm layer of mineral soil, bulked per plot, and shipped to the University of Minnesota. We measured soil particle-size distribution on bulked samples per plot using a Malvern Mastersizer 3000 (Malvern Panalytical Ltd, Cambridge, U.K.), after pretreatment with 0.5% sodium hexametaphosphate and 0.5% sodium hypochlorite to remove organic matter following methods described in (Waring et al, 2021).

At the Puerto Rico site, we quantified basal area and stem density, and soil texture with the same methods as in the Costa Rica plots. We quantified canopy cover once in May 2018 for five points per plot using the default camera app on an iOS 11.3.1 iPhone 7 (Apple, Inc., Cupertino, CA U.S.A.). Photos were exported to ImageJ (Schneider et al., 2012) and converted to a binary image (black and white pixels) to determine canopy cover.

2.3. Microclimate data

In all plots at both sites, soil water content was measured at 20 sampling points along a 15 × 20 m grid marked every 5 m (Figure S1). Plots in Costa Rica were sampled 32 times each from May 21, 2018 to May 23, 2019: approximately every ten days during the wet season and approximately monthly during the dry season. The plots in Puerto Rico were sampled 11 times from May 22 to November 17, 2018 (Table S1). Soil water content in units of volumetric water content (m^3 m^{-3}) was quantified in the top 5 cm of mineral soil with a Delta-T SM150T Soil Moisture Sensor (Cambridge, U.K.). During each sampling event, two measurements of soil water content were taken within 10 cm of each other at each sampling point and then averaged to yield 20 points per plot per sampling event. The order in which plots were sampled during the day was varied throughout the study, and sampling all plots typically took <2 h. For each sampling event, we calculated the mean and standard deviation of soil water content within each plot from the 20 sampling points for use in subsequent analysis.

In the Costa Rica plots, we also measured soil temperature and throughfall interception. Hourly soil temperature at 2 cm soil depth was measured continuously at two points at opposite ends of each plot using iButton thermochron data loggers (Maxim Integrated Inc., San Jose, CA, USA; Model DS1921G). Hourly measurements were summarized to calculate daily mean temperatures and daily temperature range (maximum – minimum temperatures). We estimated throughfall interception by installing one manual rain gauge on a post ~ 1.5 m off the ground in each plot that was recorded and emptied approximately weekly during the wet season on the same days that soil moisture was measured from August 8th to December 13th, 2018, and then measured twice again during the start of the wet season in 2019.

2.4. Weather data

Ambient meteorological data (air temperature at 2 m, precipitation) at the Horizontes field station for the study period were collected with one HOBO U30 weather station (Onset, Massachusetts, USA) logging every 5 min. We defined the onset of the dry season at the first pentad with rainfall below 2 mm/day, provided that 6 of the preceding 8 pentads exceeded 4.5 mm/day, and 6 of the 8 following pentads fell below 3.5 mm/day (Marengo et al., 2001). For the Puerto Rico site, we obtained weather data from the USGS National Water Information System (https://help.waterdata.usgs.gov/).

2.5. Statistical analyses

2.5.1. Costa Rica dataset

Data from Costa Rica and Puerto Rico were analyzed separately as the number of plots and sampling intensity varied between these locations. In the Costa Rica site, we used analysis of variance (ANOVA) to determine whether stem basal area, fine root mass, wet season LAI, dry season LAI, soil clay concentrations, and total throughfall over the measurement period in the rain gauges differed among vegetation types, treating each plot as replicate (n = 12). To determine whether microclimate variables differed with vegetation type, we fit linear mixed effects models. Response variables were plot-level mean and standard deviation of soil water content for each sampling event, and plot-level daily mean and range (maximum – minimum) of soil temperature. Models of standard deviation of soil water content were intended to assess how spatial variability of soil water content within plots differs across vegetation types. We included vegetation type as a fixed effect and included plot as a random effect to account for repeated measures within plots. Models were fit separately for wet and dry season data. With these models, we conducted pairwise comparison of estimated marginal means using the Sidak adjustment for multiple comparisons (Searle et al., 1980). We also calculated temperature offsets as the average difference between mean, minimum, and maximum daily temperatures at the tree dominated sites (forest/plantation) and the open sites.

Finally, to assess which forest structure and soil characteristics are associated with variation in microclimate conditions, we calculated the average of the following variables for each plot for each season: soil water content, standard deviation of soil water content at each sampling event, soil temperature, and daily soil temperature range for each season for each plot, yielding 12 observations per variable per season. We fit linear models using each of these as a response variables and each of the forest structure and soil texture variables (basal area, stem density, leaf area index, fine root mass, and percent soil clay) as predictor variables. For each predictor-response pair, we fit models with linear and log-transformed predictors and selected the model with the highest R^2.

All analyses were performed in R (R Core Team 2018). We used the lme4 package (Bates et al., 2015) to fit mixed effects models and the package emmeans to compare estimated marginal means (Lenth, 2021).

2.5.2. Puerto Rico dataset

Our ability to conduct statistical analyses was limited by the small number of plots and lower sampling intensity at the Puerto Rico site. Therefore, no statistical analyses were conducted on these data. Rather, we present the raw data and graphically and qualitatively compare the distribution of plot-level mean and standard deviation of soil water content measurements for each sampling event.

2.6. Simulation modeling

We carried out simulations of vegetation dynamics and microclimate with the Ecosystem Demography 2 (ED2) model. ED2 simulates complete surface water and energy budgets at sub-daily time scales (Longo et al., 2019 a,b), as well as the longer-term dynamics of plant growth, mortality, and recruitment (Medvigy et al., 2009). Vegetation is represented in terms of cohorts of plants. Each cohort is assigned a plant functional type (PFT), height, and stem number density. We employed five PFTs, including C4 grasses (Longo et al., 2019 a,b) and 4 tree PFTs (deciduous stem-succulent, deciduous, brevi-deciduous, and evergreen, described in detail in Xu et al., 2016). The model has previously performed well in simulating processes like tree growth, leaf area index, phenology, and litter production for a range of sites near the Horizontes field station (Medvigy et al., 2019; Xu et al., 2016). However, the model's predictions of soil water content had not previously been evaluated at these sites.

We used the model to carry out simulations of secondary succession in each of the Costa Rica plots. Simulations differed only in terms of their sand and clay fractions, which were set to the observed values. These fractions affected soil hydrology but not soil nutrients (for simplicity, we de-activated the model's nutrient parameterization in this study). In other respects, the simulations were the same. The initial stem density in each simulation was 1000 stems (or plants) ha^{-1}. Tree and grass PFTs were initialized with heights of 2 m and 0.5 m, respectively. Simulation duration was 50 years. Over the course of each simulation, PFT composition varied dynamically according to the model equations. Each simulated year was forced with 2018 meteorological data; thus, there was no interannual variability in weather.

We processed our model output to enable comparison with the observations from plots that differ in vegetation type. To compare with the O patches, we first selected the three simulations that were assigned sand and clay fractions corresponding to the O patches. We then extracted simulation year 2 because the simulated vegetation in this year corresponded reasonably well to the observed O state. And, like all years, the meteorology corresponded to the 2018 observations. We performed a similar simulation selection for the S, F, and P patches to ensure appropriate sand and clay fractions. However, we extracted different years in each case: year 6 for S, year 30 for F, and year 50 for P. No explicit management scheme was implemented for P.

3. Results

3.1. Soils, forest Structure, and throughfall

All plots that we sampled in both Costa Rica and Puerto Rico had relatively high clay concentrations, with an average clay concentration of 42% (range: 31 to 70%; Table 1). However, in Costa Rica, the clay concentrations were significantly lower in the O sites compared to other vegetation (Table 1). In general, for the sites in Costa Rica, forest biomass (i.e., basal area of woody stems and fine root mass), increased as expected across vegetation types according to the following order: open < shrub < forest < plantation (Table 1). However, there was variability among the plots within any given vegetation type and not all pairwise comparisons between types were significant (Table 1), especially for fine roots, which did not differ among vegetation types. O plots did not differ statistically from S plots in any metric of forest structure other than stem density, and P plots did not differ from F (Table 1). Mean LAI ranged from a low of 0.003 (i.e. essentially no canopy cover) in the O sites during the dry season to a high of 4.81 in F during the wet season and was consistently lower in O and S compared to F and P in both seasons (Table 1). While weekly throughfall varied over time from 0 to 142 mm (Figure S2), the cumulative amounts did not vary across vegetation types (Table 1). The three plots in Puerto Rico showed similar trends to Costa Rica (Table 1), with basal area increasing and canopy cover decreasing as follows: O < F < P.

3.2. Microclimate across vegetation types

3.2.1. Costa Rica

In Costa Rica, we collected 14,960 surface soil water content measurements, excluding the 20 points during a particular rainy event in October 2018 when soil water content values exceeded the capacity of our sensor. Soil water content ranged from a low of 0 to a high of 0.67 m^3 m^{-3}.

Soil temperature and soil water conditions varied among vegetation types, though these differences were not consistent across seasons or plots. During both the wet and dry seasons, O and S were warmest and experienced the largest daily temperature ranges, while P and F were up to 5°cooler on average, and experienced smaller daily temperature ranges (Fig. 2, Table 2). Relative to the open sites, soil temperatures in the forest site were on average 2.3 °C cooler during the wet season, and 5.1 °C cooler during the dry season (Table 3). Maximum temperature offsets were even more extreme, with forests an average of 5.6 °C cooler in the wet season and 11.9 °C cooler in the dry season. Temperature offsets were similar, but mostly smaller in magnitude in the plantation sites (Table 3).

During the dry season in Costa Rica, soil water content differed significantly among vegetation types, with O the driest at a mean of 0.009 m^3 m^{-3}, increasing to 0.092 m^3 m^{-3} at the forested plots. During the wet season, mean soil water content ranged from 0.23 to 0.27 m^3 m^{-3} and did not differ among vegetation types (Fig. 2; Table 2). However, the temporal variation of soil water content differed across vegetation types during the wet season, with open and shrub plots showing more frequent extreme high and low soil water content values (Figure S3). The standard deviation in soil water content did not differ among plots during the wet season, with all vegetation types displaying similar levels of spatial heterogeneity in soil water content (Fig. 2). During the dry season, O plots—which were very dry—showed significantly less spatial heterogeneity in soil water content, with S, F and P showing similar, higher levels of spatial heterogeneity.

3.2.2. Puerto Rico

We collected 1320 soil water content measurements over the 11 sampling events in Puerto Rico. In general, values of soil water content were higher at the plantation plot compared to O and F, especially during the months between June and September, when rainfall was very low (Fig. 3). Values of soil water content appeared similar at O and F (Fig. 3). Spatial heterogeneity in soil moisture content, as reflected in the standard deviations of measurement events, appeared similar among plots (Fig. 3).

3.3. Forest structure and soil influences on microclimate

Relationships between forest structure and soil water content differed between seasons for the Costa Rica data. None of the predictors we considered (basal area, LAI, fine root mass, or clay %) were associated with variation in average soil water content during the wet season (Fig. 4, Table S3). During the dry season, sites with higher basal area, stem density, and LAI (i.e., higher canopy cover) were wetter, as were sites with higher soil clay concentrations (i.e., higher soil water retention capacity). The standard deviation of soil water content was not significantly related to any of the variables we considered during either season (Fig. 4, Table S3).

In general, forest structure had cooling and buffering effects on soil temperatures (Fig. 4, Table S3). Plots with higher basal area and LAI were cooler during both the wet and dry seasons, but the cooling effects were stronger in the dry season. Similarly, sites with higher basal area, stem density, and LAI experienced narrower temperature ranges during wet and dry seasons. Neither fine root mass nor clay concentration had any impact on soil temperatures.

Table 1

Forest attributes in tropical dry forest plots of different vegetation types in Costa Rica (means plus standard deviations, N = 3 plots) and Puerto Rico (N = 1 plot per land use). For data from Costa Rica, significant differences among land uses were assessed with a one-way ANOVA followed by Tukey's HSD test for means separation. Values for vegetation type in Costa Rica within a column that share a letter do not different significantly.

	Basal area (m^2 ha^{-1})	Stem density (stems ha^{-1})	Fine root mass (Mg ha^{-1})	Wet season leaf area index	Dry season leaf area index	Canopy cover (%)- dry season	Clay concentration %	Cumulative throughfall from from 2018 to 08-08 to 2019–05-23 (mm)
Costa Rica								
open	0.02 (0.03)^a	11.1 (19.2)^a	0.90 (0.26)^a	0.04 (0.05)^a	0.003 (0.004)^a		35.5 (2.9)^a	428 (14.6)
shrub	5.5 (0.70)^{ab}	889 (126)^b	1.70 (0.71) ^{a}	0.88 (0.17)^a	0.05 (0.01)^a		41.5 (2.1)^{ab}	432 (20.8)
forest	17.6 (9.1)^{ab}	811 (302)^b	1.68 (0.56) ^{a}	4.81 (0.48)^b	2.08 (0.87)^b		45.2 (1.1)^b	395 (52.1)
plantation	22.2 (8.4)^b	1067 (500)^b	2.86 (1.57) ^{a}	4.70 (0.73)^b	1.51 (0.69)^{ab}		41.4 (2.9)^{ab}	419 (37.5)
Puerto Rico								
open	1.3					17.77	70.4	
forest	7.3					65.12	34.5	
plantation	24.5					69.08	32.1	

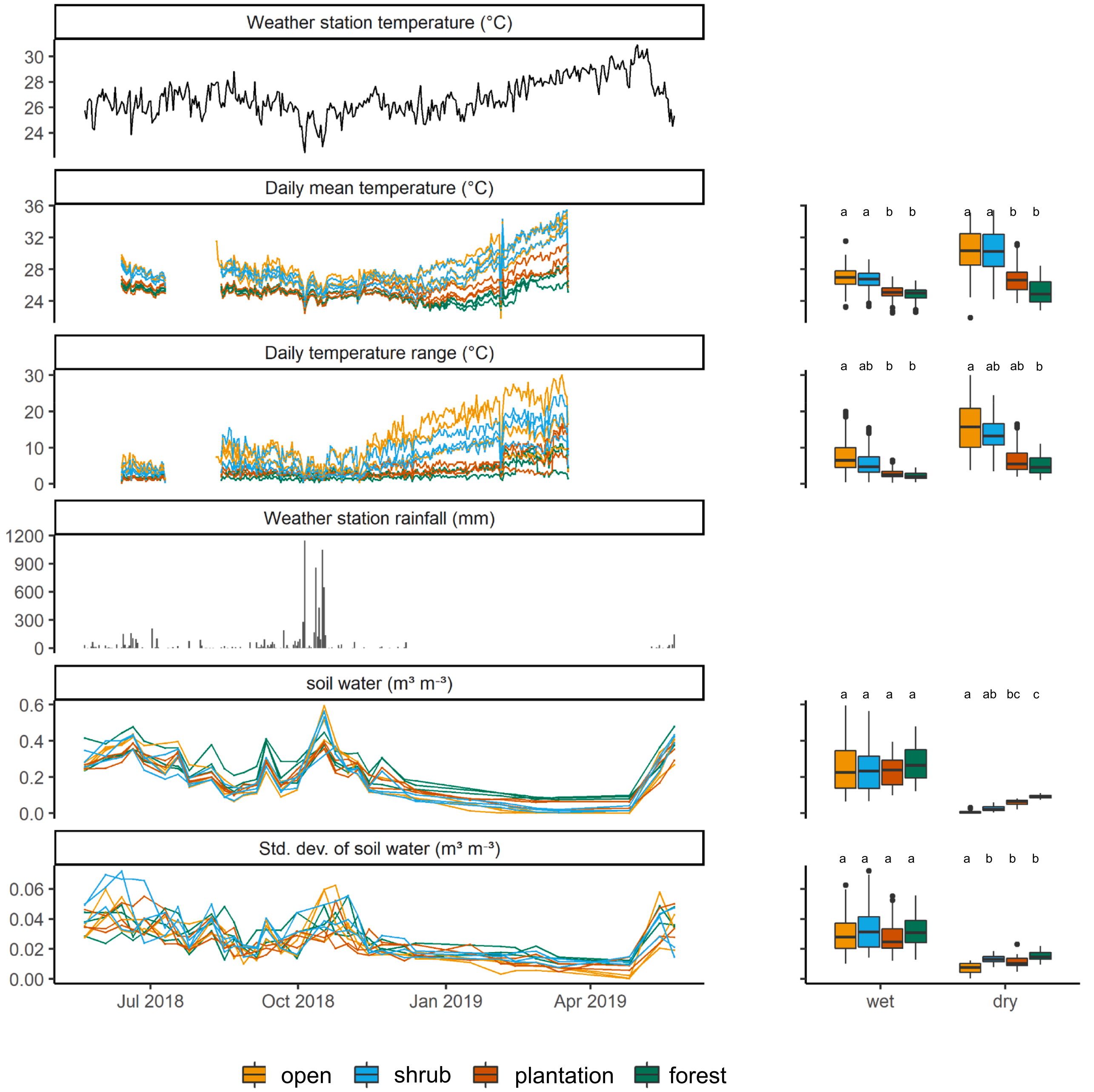

Fig. 2. Measured values of weather station temperature (a), daily mean temperature (b), daily temperature range (c), rainfall (d), soil water (e), and standard deviation of soil water at 20 measurement points (f) in 12 plots at the Costa Rica site. Boxplots show median and 2.5%, 25%, 75% and 97.5% quantiles of measurements by season across vegetation types. Boxes that share a letter did not differ significantly in a pairwise comparison of estimated marginal means.

3.4. Comparison of simulation model to observations

As in the observations (Table 1), simulated basal area, LAI, and PFT composition varied over successional time (Table S4, Figure S4). Simulated basal area and LAI were both much larger in F and P than in O and S, and variation was modest within a particular successional class. In terms of PFT composition, the grass PFT was present only in the O patches (Table S4). LAI of the most hydraulically conservative tree type increased over time and was greatest in P (Table S4).

We compared simulated soil temperature, throughfall, and soil water content to the observations. During the wet season, simulated and observed temperatures were correlated (Pearson's $r = 0.80$, $p = 0.002$) (Fig. 5a). However, model simulations overpredicted temperatures in the O plots. Simulated and observed temperatures were also correlated during the dry season (Pearson's $r = 0.84$, $p = 0.0006$), but 10 of the 12 plots were biased towards high values, i.e., simulated temperatures exceeded observed (overall mean bias of + 1.8 °C) (Fig. 5b). In terms of wet season soil water content, the model simulated a range of 0.21 to 0.29 m^3 m^{-3}, with the S plots having the lowest soil water content and the F plots the highest (Fig. 5c). This range across plots is comparable to the range of the observations (although we note again that the observed differences between vegetation types were not statistically significant). Also consistent with wet season observations, the model simulated more extremely dry days in O and S than in P or F (Figure S5). During the dry season, the model simulated very little variation in soil water content (Fig. 5d). Total throughfall was overestimated by the model (Fig. 5e). In both the simulation and observations, the F and P plots had less throughfall than the O and S plots (however, the observed differences

Table 2

Microclimate variables in tropical dry forest plots of different vegetation types in Costa Rica (estimated marginal means, with upper and lower confidence limits). Asterisks indicated that vegetation structure was a significant predictor for that variable (*** $p < 0.001$, ** $p < 0.01$). Values across vegetation types in a row that share a letter did not differ significantly in a pairwise comparison of estimated marginal means. Random effect indicates the plot-level standard deviation. Only random effects significantly different from 0 ($p < 0.05$) are shown. Test statistics and model p-values are presented in Table S2.

Variable	Open	Shrub	Plantation	Forest	Random effect (plot)
Mean soil water content ($m^3\ m^{-3}$)					
Wet season	0.246 (0.190, 0.302)^{a}	0.236 (0.179, 0.292)^{a}	0.234 (0.178, 0.290)^{a}	0.275 (0.219, 0.331)^{a}	n.s.
Dry season***	0.009 (0, 0.033)^{a}	0.027 (0.003, 0.052)^{ab}	0.058 (0.033, 0.082)^{bc}	0.092 (0.068, 11.67)^{c}	0.012
Soil water content standard deviation ($m^3\ m^{-3}$)					
Wet season	0.023 (0.022, 0.037)^{a}	0.034 (0.026, 0.041)^{a}	0.028 (0.020, 0.036)^{a}	0.031 (0.024, 0.039)^{a}	0.004
Dry season**	0.007 (0.004, 0.010)^{a}	0.013 (0.010, 0.016)^{b}	0.011 (0.008, 0.015)^{b}	0.016 (0.012, 0.019)^{b}	n.s.
Temperature (° C)					
Wet season***	27.0 (26.1, 27.9)^{a}	26.7 (25.8, 27.6)^{a}	25.2 (24.3, 26.2)^{b}	24.8 (23.9, 25.8)^{b}	0.49
Dry season***	30.3 (28.6, 32.0)^{a}	30.2 (28.5, 31.9)^{a}	26.8 (25.1, 28.5)^{b}	25.2 (23.5, 26.9)^{b}	0.89
Daily temperature range (° C)					
Wet season***	7.42 (4.5, 10.29)^{a}	5.6 (2.7, 8.47)^{ab}	2.9 (0.02, 5.77)^{b}	2.17 (-0.7, 5.04)^{b}	1.55
Dry season***	15.96 (9.06, 22.9)^{a}	13.88 (7.0, 20.8)^{ab}	6.45 (-0.45, 13.4)^{ab}	5.11 (-1.8, 12)^{b}	3.73

Table 3

Temperature offsets (°C) during the wet and dry seasons relative to the open sites.

		Wet season	Dry season
Minimum temperature	Forest	−0.3	−1.0
	Plantation	−0.3	0.1
Mean temperature	Forest	−2.1	−5.1
	Plantation	−1.9	−3.5
Maximum temperature	Forest	−5.6	−11.9
	Plantation	−5	−9.3

across plots were not statistically significant).

3.5. *Mechanisms determining simulated soil temperature and water*

To better understand variation of simulated soil temperature across vegetation types, we decomposed the simulated energy budget into net solar radiation absorbed by the ground (R_{solar}), net longwave radiation (R_{long}), sensible heat flux (H), and latent heat flux (LE). These energy fluxes were not measured in the field. The flux that varied most across vegetation types was R_{solar}. Increases in R_{solar} occurred in conjunction with increases in soil temperature (Fig. 6). Because of the relationship between vegetation type and LAI (Figure S4), increasing R_{solar} was also associated with decreasing LAI. There was also large variability in R_{long} across vegetation types. Due to radiative cooling, R_{long} varied inversely with soil temperature. Compared to the radiation fluxes, variations in H

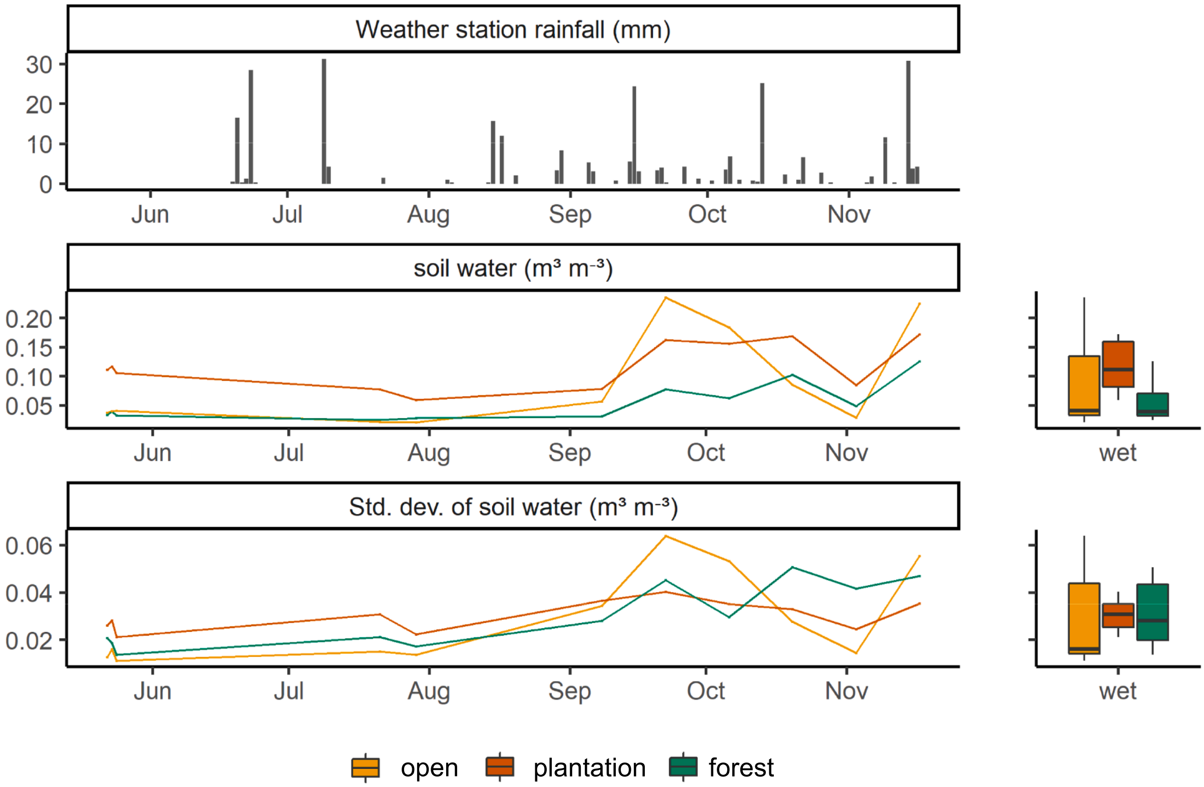

Fig. 3. Rainfall (a), volumetric soil water content (b) and standard deviation of soil water content (c) in 3 plots at the Puerto Rico site. Boxplots show median and 2.5%, 25%, 75% and 97.5% quantiles of measurements by season across vegetation types.

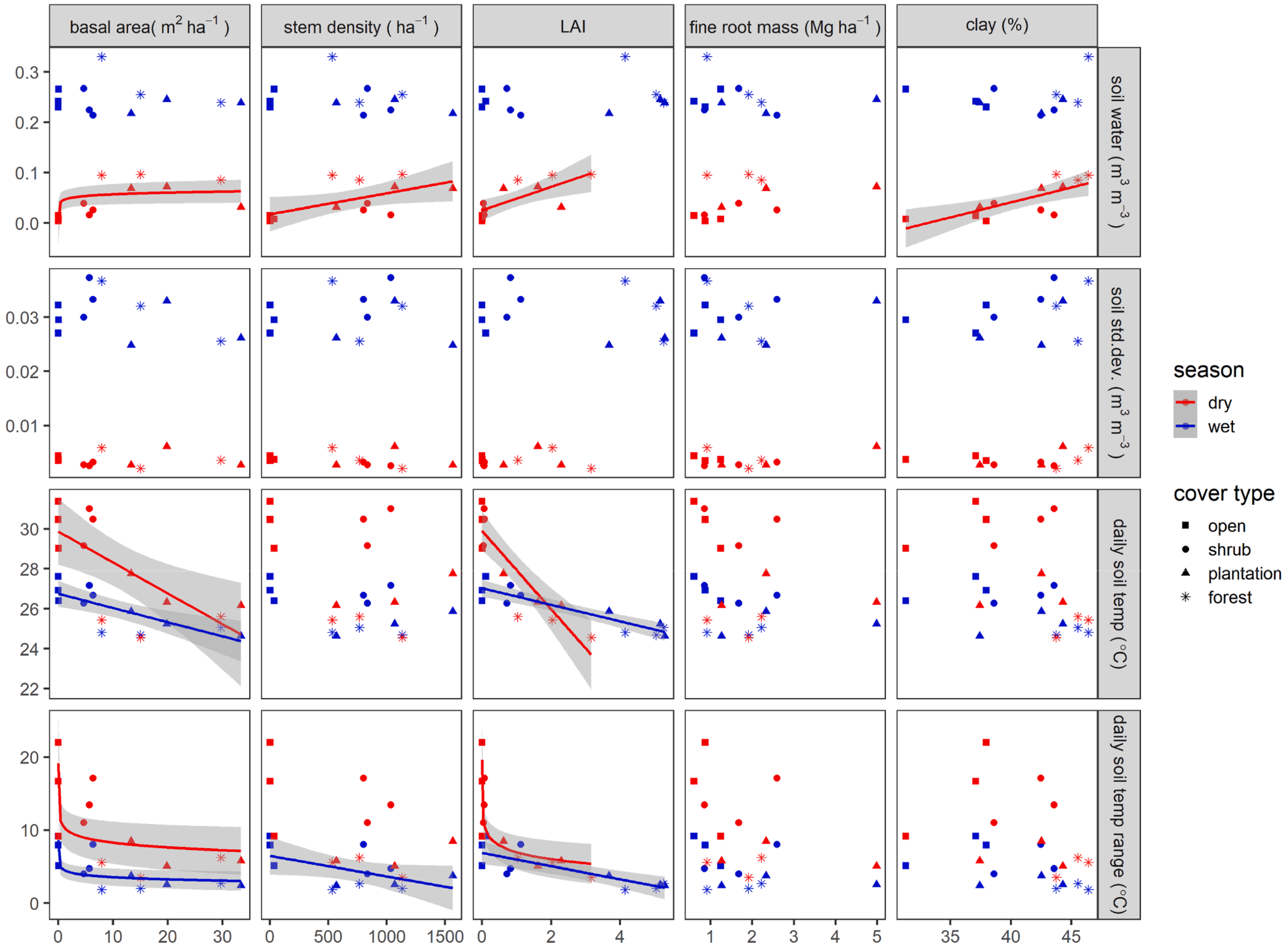

Fig. 4. Scatterplots illustrating the relationship between microclimate variables (y-axes, labeled in righthand panels) and environmental predictors (x-axes, labeled in top panels) at the Costa Rica site during the dry (blue points) and wet (red points) seasons in the four vegetation types (point shapes). Lines show predictions and 95% confidence intervals from linear models; only significant ($p < 0.05$) relationships are shown.

and *LE* across vegetation types were weak. *H* increased with increasing soil temperature, but there was no clear pattern in *LE*. Similar dynamics prevailed during the dry season (Figure S6).

Factors most strongly influencing the water budget of the top 10 cm soil included throughfall, evaporation, and leakage to deeper soil layers. Other water fluxes, including runoff and transpiration (derived from the top 10 cm) were both small (<0.2 mm day^{-1}). We found a strong negative relationship between soil water content and evaporation (Fig. 7). Surprisingly, soil water content was positively related to leakage and negatively related to throughfall (Fig. 7).

4. Discussion

Variation in microclimate is thought to be a key driver of tree demographics and species turnover in tropical dry forests (Uriarte et al., 2016), with important implications for restoration and natural regeneration. Yet, few measurements of microclimate across heterogeneous SDTF landscapes exist, limiting our ability to generalize microclimate patterns and successional processes in SDTF. Here, we showed average microclimate conditions under later successional vegetation are cooler and wetter than early successional stages, but differences in soil water content were present only during the dry season in a dry forest landscape in Costa Rica. During the wet season, although average soil water conditions did not differ, more open vegetation showed higher temporal dynamism with larger variation in observed soil water content values across measurement events. In other words, open sites had higher high values and lower low values during the wet season. Our results from Puerto Rico are broadly consistent with what we found in Costa Rica: the plantation had higher soil water content values during the rainless months, and the open site wetted up faster than more vegetated sites during the onset of the rains (Fig. 2). These findings are inconsistent with previous studies of SDTF microclimates, which found differences in soil water content along a successional gradient in Mexico only during the wet season, but not the dry season (Lebrija-Trejos et al., 2011). However, that study collected data only once during each season, in contrast to the weekly to monthly measurements that we made. Collectively, our data from Costa Rica and Puerto Rico imply that common assumptions about how microclimates influence successional processes in SDTF should be revisited. Below we discuss potential mechanisms that might explain our field data, differences between the modeling and empirical results, and the implications for secondary forest succession and restoration.

4.1. Mechanisms that account for seasonal patterns in microclimate across successional gradients

Our conceptual model describes the expected changes in biophysical properties and consequences for microclimatic variation over secondary forest succession (Fig. 1). Unsurprisingly, in both our study sites, basal area of woody vegetation and leaf area increased across vegetation types that represent a gradient of forest structure; while fine root mass also increased in nearly the same sequence, these results were not

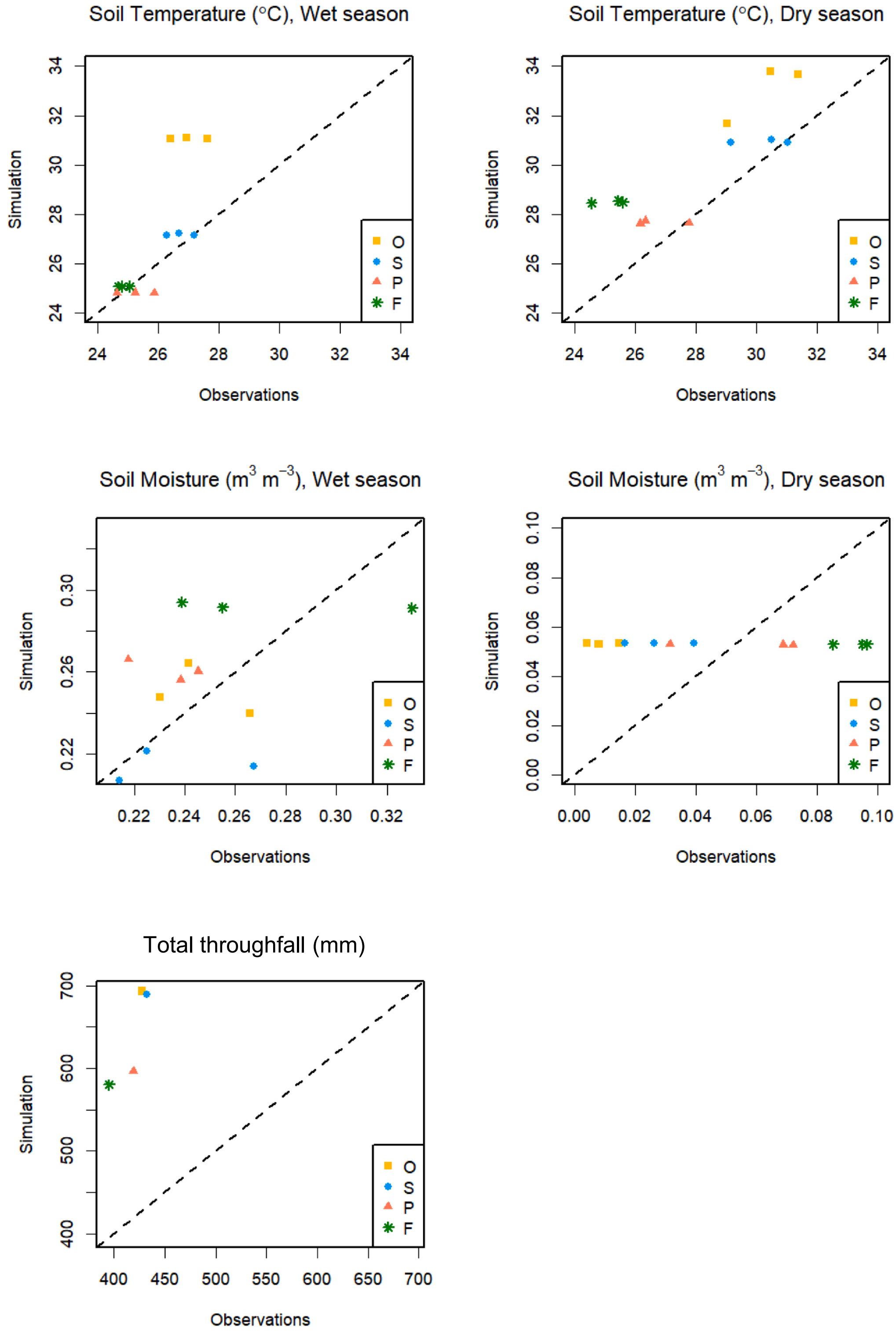

Fig. 5. Comparison of simulated and observed soil temperature and soil water. (a) Soil temperature, wet season. (b) Soil temperature, dry season. (c) Soil water, wet season. (d) Soil water, dry season. (e) Total throughfall, August-May. Dashed line indicates equality between simulation and observation.

significantly different. While the values of throughfall we measured were lower in F compared to the open vegetation (O and S) and P, cumulative values did not differ among vegetation types. Other studies have shown consistent reductions in throughfall along chronosequences (Calvo-Alvarado et al., 2018; Zimmermann et al., 2013), and it is possible that our single rainfall gauges per plot were not sufficient to quantify these patterns or their effects on soil moisture.

By contrast, there were clear and consistent effects of forest structure on soil temperature along the vegetation structure gradient. Global *meta*-analysis has shown that forest canopies buffer local climates, providing local cooling when temperatures are high and warming when temperatures are low (De Frenne et al., 2019). Our results are consistent with this global pattern though the magnitude of buffering we observe exceeds the mean values observed in their study (T_{max} offset ranges from

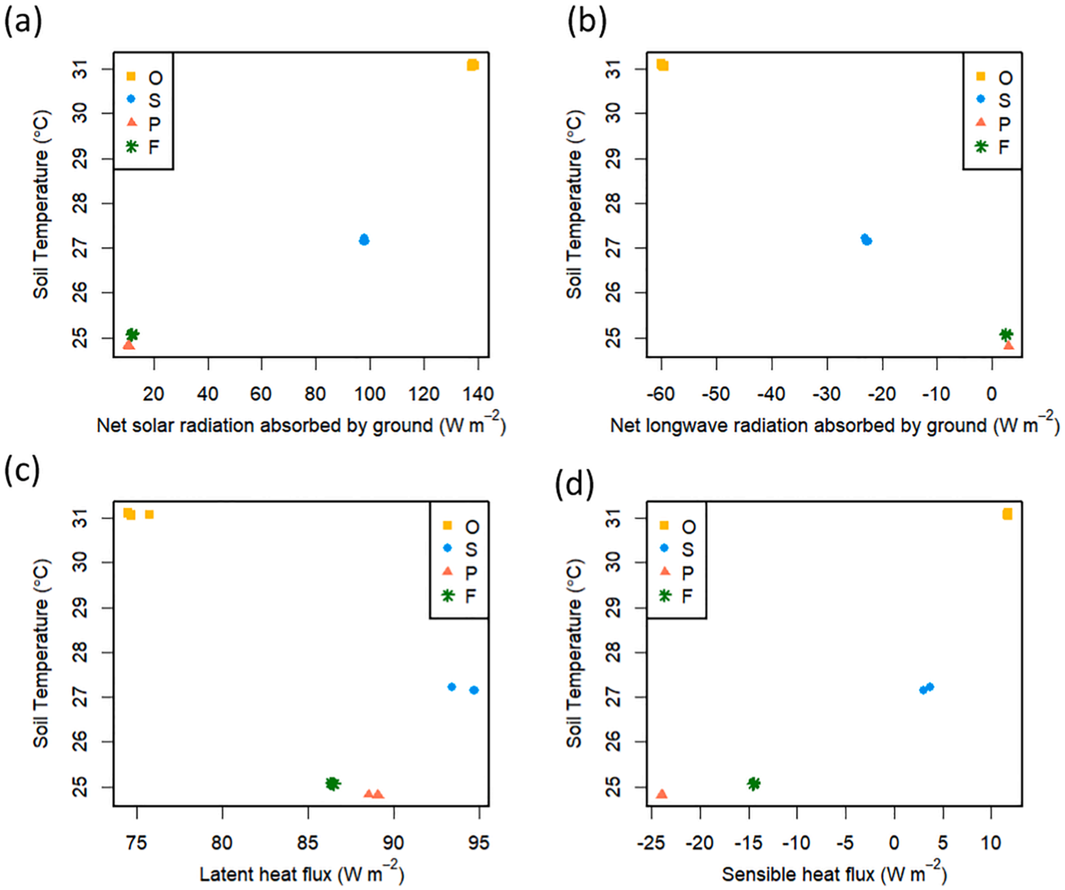

Fig. 6. Relationship between modeled soil temperature and energy fluxes (wet season).

−5.6 to −11.9 in our study, compared to −4.1 °C in De Frenne et al., T_{mean} offset from −2 to −5 compared to −1.7 in De Frenne et al.). Furthermore, we find evidence for a greater buffering effect of canopy during the dry season, when ambient temperatures are higher, in line with findings from an earlier study in Costa Rica dry forests (Janzen 1976). This result suggests that as temperatures warm in the future, the buffering effects of the forest canopy on temperature might become even more important. Recent results from European forests demonstrate that canopy buffering of microclimate can slow thermophilization of forest communities and explain lags between temperature shifts and changes in community composition (Zellweger et al., 2020). Our results suggest that this phenomenon may occur in tropical forests as well, with forest canopies providing refuge for species that might not persist if subjected to the regional climate. Moreover, the daily temperature range was consistently smaller for secondary forest compared to plantations in both seasons (Table 2, Fig. 2c), despite the higher basal area in plantations. This suggests that the buffering capacity of naturally regenerated forest, which is characterized by a more heterogenous tree community may be higher than even-aged tree plantations.

Forest canopies are also thought to influence micro-scale soil water conditions, with wetter conditions hypothesized under more developed or intact forest canopies (Pineda-García et al., 2013)). Here, we find mixed evidence for this phenomenon: soil water content was higher under later successional canopies, but only during the dry season at the Costa Rica site, which is consistent with previous studies in this region (Werden et al., 2020). Differences across forest structure during the dry season may be explained by seasonal variation in evaporation: most trees at our study site are drought-deciduous (Waring et al., 2019) and so transpiration fluxes are likely quite small during the dry season. Instead, higher levels of solar radiation penetration to the soil and ground evaporation in open sites may explain drier conditions there during the dry season. Some findings from temperate forests show wetter soil conditions under thicker canopies during dry periods due to lower ground evaporation (Isabelle et al., 2018). During the wet season, increased transpiration from forest canopies may balance out differences in solar radiation penetration and ground evaporation, diminishing differences across vegetation types (Fig. 1). Soil clay concentrations were correlated with soil moisture during the dry season (Fig. 4). However, it is difficult to isolate the role of soil particle-size distribution in explaining these results, because it also co-varied with vegetation type in the Costa Rica sites, with lower clay concentrations in the open sites.

Interestingly, the soil water content data from Puerto Rico were broadly consistent with the patterns from Costa Rica (Fig. 2, Fig. 3). Soil water content was higher in the plantation compared to the open and forest sites when there was no rain. The O site in Puerto Rico displayed similar “flashy” behavior as the Costa Rican sites, with lower values during the dry periods, reaching higher values more quickly than the forest and plantation sites once the rains started, even though the O site in Puerto Rico had higher clay concentrations than the other two forested vegetation types. Our results for both Costa Rica and Puerto Rico contrast with findings for a seasonally dry oak forest landscape in Mexico (Asbjornsen et al., 2004). That study tracked surface soil moisture (0 to 10 cm) every two weeks for two years in open sites, across forest edges and in forest interiors. Soil moisture was consistently lower in open and shrub dominated sites compared to edge or interior forests during both the wet and dry seasons (Asbjornsen et al., 2004). Given the important role of microclimatic conditions for many different ecological and hydrologic processes—from seedling dynamics to regional water balances (Maass & Burgos, 2011), and the increasing variability in tropical climates (Feng et al., 2013), there is a pressing need to establish observations across a range of climatic and environmental conditions to fully understand the drivers and consequences of microclimatic

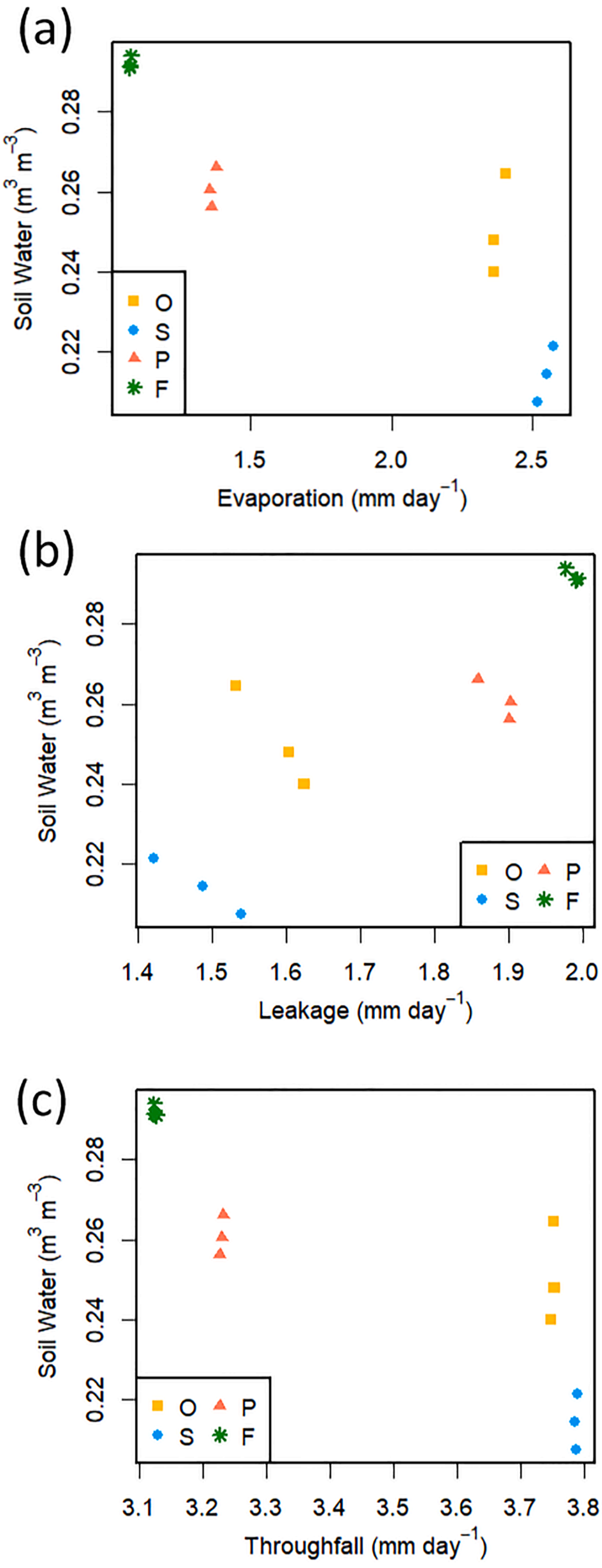

Fig. 7. Relationships between simulated soil water content (top 10 cm) and water fluxes during the wet season.

variation in tropical landscapes (De Frenne et al., 2021; Jucker et al., 2020).

4.2. Comparing field data to simulation results

The importance of simulated microclimate was recently underscored by Xu et al (2021), who emphasized the relevance of rainfall interception and throughfall dynamics for calculating canopy water content and vegetation optical depth. However, they did not evaluate the model's simulation of these quantities. Our simulation modeling exercise identified significant inconsistencies between field data and model results, highlighting areas for model improvement. Our analysis indicates that further work is needed to reduce model biases in microclimatic variables, especially for throughfall and dry season soil moisture dynamics. For example, adding a hydraulic lift parameterization may reduce the model's dry season soil water biases for the F and P patches (Neumann & Cardon, 2012). On the positive side, model simulations of wet season soil temperature and soil water content (Fig. 5a-b), and temporal variability in soil water content (Figure S4) were more consistent with observations. As physiological activity is higher during the wet season in SDTF (Lugo et al., 1978), the discrepancies between the model and observations may have limited impact on the ability for the model to accurately simulate vegetation dynamics (Xu et al., 2016).

Across vegetation types, there were stark differences in simulated energy and water fluxes. Low LAI in O and S patches lead to increased solar radiation absorbed by the ground, and higher soil temperatures. Other energy losses, like longwave emission and the sensible heat flux, partially compensate for this effect. Thus, we implicate accurate calculation of solar radiative transfer as essential for calculating soil temperatures. Because different models represent this radiative transfer differently (Fisher et al., 2018), model inter-comparison on this point would be informative.

In the model, soil water content (of the top 10 cm) was, somewhat surprisingly, principally determined by evaporation from the soil. Simulated F and P patches had relatively cool soil and moist air which suppressed evaporation, leading to higher soil water content during the dry season despite reduced throughfall and increased leakage. The dominance of evaporation is in contrast to temperate forests, where transpiration fluxes often dominate leading to wetter conditions in open sites (e.g. Keenan & Kimmins 1993, Kovacs et al., 2020, Ritter 2005). These mechanisms should be evaluated with field observations. In particular, many of the existing datasets (Asbjornsen et al., 2004; Lebrija-Trejos et al., 2011), including those reported here, only study surface soil water conditions, and cannot inform us about processes that occur throughout the soil profile, where seasonal water dynamics at lower depths in the profile may differ substantially from surface conditions (Reid et al., 2015).

4.3. Implications for secondary succession and restoration

In SDTF, soil moisture is thought to drive the major functional shifts over succession (Lebrija-Trejos et al., 2010), as well as affecting seed production, germination, and recruitment (Maass & Burgos, 2011). Over the course of succession, community trait values typically shift from those thought to confer resistance to water stress (e.g., high wood density) to values that represent less stress tolerance such as lower wood density (Poorter et al., 2019). These patterns suggest more severe moisture stress in more open, early successional SDTF environments, with alleviation of water stress occurring as the canopy closes. Our findings in two seasonally dry forests provide only limited support for this hypothesis. During the wet season, when most of the physiological activity takes place in these forests (Lugo et al., 1978), surface soil water content does not differ across vegetation types. It is possible that vapor pressure deficit (VPD), which we did not measure but is affected by temperature, differs more across SDTF vegetation types than soil moisture, and that VPD thus contributes more to environmental filtering of functional traits compared to soil moisture alone (e.g. Grossiord et al., 2020).

Microclimatic variation affects seed germination and seedling growth and mortality in tropical dry forests (Jaganathan & Liu, 2015; Maass & Burgos, 2011; Maza-Villalobos et al., 2013). Many studies have found that dry forest seedling mortality occurs mostly over the dry season (Gerhardt, 1993; Lieberman & Li, 1992; Werden et al., 2018). Beyond the well-established buffering effects of vegetation canopies on soil temperature mean and ranges, our most notable findings were that soil moisture is much higher under forest cover during the dry but not wet seasons in both Costa Rica and Puerto Rico. Whether this affects seedling survivorship during the dry season is not known but deserves further attention. Better understanding how general our findings are, and how they influence the demographic processes that underlie functional shifts across succession could help guide species selection and other management interventions to improve restoration success.

We note that we measured soil water content in only the top 5 cm of soil. While these measurements likely provide an adequate proxy for conditions experienced by seedlings, adult trees are well known to access deeper soil water, especially during the dry season (Oliveira et al., 2005, Stahl et al., 2013). Thus, our results may have limited applicability for understanding environmental filtering of adult trees during succession. This highlights the need not only for spatially extensive monitoring of microclimate, but also for intensive sampling to understand microclimate dynamics across vertical profiles.

In the context of other studies, our results show that we still lack general principles for predicting the relationships between vegetation structure and microclimate, particularly soil water content. Yet, new technologies that inexpensively and continuously monitor microclimate (e.g. Tomst TMS loggers, Wild et al., 2019) provide opportunities to collect spatially extensive and temporally detailed data on microclimates in restored and regenerating forests. These data will open the possibility for synthesis of microclimate patterns across sites. For restoration practitioners, this sort of information could guide species selection and management activities tailored to a particular site (e.g. Rose et al., 2020). Furthermore, improved representation of microclimate in dynamic vegetation models such as ED2 could open up new possibilities for the use of these models in management planning, for example to simulate ecological outcomes of different restoration actions. As the UN Decade of Restoration advances (Aronson et al., 2020), we highlight the importance of understanding microclimate for a more holistic understanding of the ecological processes that underlie restoration and regeneration.

CRediT authorship contribution statement

Naomi B. Schwartz: Conceptualization, Formal analysis, Visualization, Writing – original draft. **David Medvigy:** Methodology, Formal analysis, Writing – original draft. **Julian Tijerin:** Methodology, Visualization, Investigation, Data curation. **Daniel Pérez-Aviles:** Investigation. **David Rivera-Polanco:** Investigation. **Damaris Pereira:** Investigation. **German Vargas:** Data curation, Writing – review & editing. **Leland Werden:** Data curation, Writing – review & editing. **Dan Du:** Investigation. **Logan Arnold:** Formal analysis. **Jennifer S. Powers:** Conceptualization, Methodology, Writing – original draft, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

All data from this study have been deposited at: https://doi.org/10.5061/dryad.rbnzs7hcx

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120132.

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