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Functional diversity overrides community-weighted mean traits in linking land-use intensity to hydrological ecosystem services

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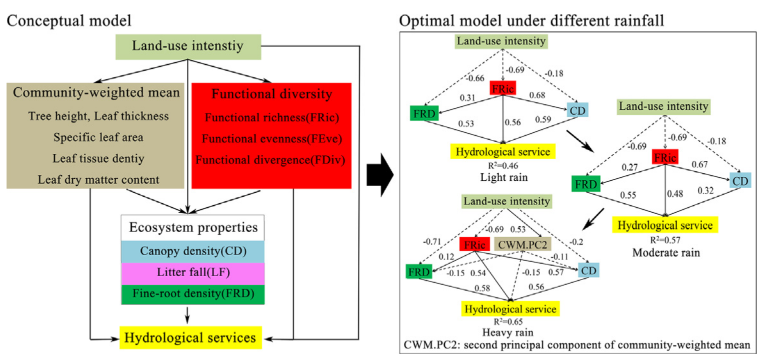
HIGHLIGHTS

- Impact pathways of land-use intensity on ecosystem service were quantified.
- Land-use intensity impacts hydrological services mainly by altering plant traits.
- Impacts primarily manifested by functional diversity not community-weighted mean.
- The mechanisms regulating this relationship varied by precipitation regimes.
- We move toward predicting hydrological service provisioning under climate change.

GRAPHICAL ABSTRACT



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ABSTRACT

Land-use intensification can importantly influence terrestrial ecosystem services by altering plant functional traits. Although we know that functional traits influence both ecosystem properties and services, we do not fully understand the mechanistic pathways governing these relationships nor how they will respond to global climate change. To identify the impact pathways of land-use intensity on hydrological services under changing precipitation regimes, we monitored hydrological services in 15 plots of different land-use types during 25 precipitation events (6 light, 8 moderate, and 11 heavy rains). Bayesian structural equation modeling was used to quantify the direct and indirect effects between land-use intensity, functional trait components (community weighted mean [CWM] and functional diversity [FD]), ecosystem properties (canopy density, litter fall and fine-root density), and hydrological services under different rainfall intensities. The impact of land-use intensity on hydrological service provisioning was regulated by plant functional traits regardless of intensity rainfall. Under light and moderate rain, FD significantly influenced hydrological services by altering canopy density and fine-root density, but we found no significant effect of CWMs. Under heavy rain, FD had significant, and greater, impacts on hydrological services than CWM of traits, although CWM of traits influenced hydrological services provision indirectly by altering canopy density and fine-root density. Land-use intensity indirectly affected hydrological services mainly by altering FD regardless of rainfall intensification, suggesting that the reduction of niche differentiation caused by land-use intensity is the main mechanism of hydrological services degradation. Our results suggested that the effect of land-use intensity on hydrological services are likely to change with

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increasing frequency of extreme precipitation events because of the different underlying mechanism at play and emphasize the importance of FD in maintaining hydrological services in respond to global environmental changes.

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1. Introduction

Land-use intensification is a primary driver of global environmental change and has been accelerating as a result of increasing anthropogenic activities, leading to severe degradation of ecosystem services that are essential for the well-being of humanity (Díaz et al., 2007; Allan et al., 2015; Chillo et al., 2018). Land-use intensity can not only affect the provisioning of ecosystem services directly (e.g., production (Allan et al., 2015), soil fertility (Gelaw et al., 2014)), but also influence ecosystem services indirectly (e.g., biomass (De Avila et al., 2018), soil retention (Zheng et al., 2008)) by altering plant functional traits (Ali et al., 2019; Chillo et al., 2017) or ecosystem properties (Zheng et al., 2008; Wen et al.,2017). While these relationships have been documented around the world (Díaz et al., 2007; Zheng et al., 2008; Allan et al., 2015), we still lack a mechanistic understanding of how ecosystem services respond to land-use intensity (Chillo et al., 2018). This crucially reduces our ability to predict how different land-use change scenarios will affect ecosystem service production, and therefore develop scientifically robust conservation plans (Lamarque et al., 2014).

There are three main hurdles in our search for the mechanisms underlying ecosystem services responses to land-use intensity. First, the role of different functional trait components in the relationship between land-use intensity and ecosystem services remains uncertain (Díaz et al., 2007; Mouillot et al., 2013; Chillo et al., 2018). The focus is on whether the traits of dominant species (denoted by community-weighted mean [CWM] of traits) or trait distribution among species (denoted by functional diversity [FD]) determine the quality and quantity of ecosystem service production (Lavorel, 2013; Cadotte, 2017). For example, the CWM of traits, rather than functional diversity, was found to be a more valuable predictor of the effects of land-use intensity on the rate of nutrient recycling (Finegan et al., 2015) and primary production (Conti and Díaz, 2013). However, other researchers have obtained conflicting results of FD offers greater explanatory power in fodder provision and carbon storage than CWM of traits (Cadotte et al., 2011; Lavorel, 2013; Mensah et al., 2016). It is clear, therefore, that further studies are needed to identify what components of plant functional traits are responsible for modulating the responses of ecosystem services to land-use intensity.

Second, the pathways that regulate the impact of land-use intensity and ecosystem services are understudied. Some studies have found that ecosystem properties are the most important mediators of the impact of land-use intensity on ecosystem services. For instance, high-intensity land use led to reduce soil retention by changing litter fall (Zheng et al., 2008) and canopy density (Salemi et al., 2013). Further, we know that ecosystem properties can also be affected by plant functional traits. For example, leaf dry matter content (Lamarque et al., 2014), as well as functional evenness (Lundholm et al., 2015), affect the production of litter fall. Most studies have focused on the path between three variables: land-use intensity, ecosystem properties, ecosystem services (Zheng et al., 2008; Salemi et al., 2013; Liu et al., 2017), or land-use intensity, functional traits, ecosystem services (Díaz et al., 2007; Allan et al., 2015). Few studies have explored the relationship among all four variables (land-use intensity, functional traits, ecosystem properties, ecosystem services) (Chillo et al., 2018), which obfuscates our search for underlying mechanisms.

Third, it is reasonable to expect that the mechanism of the impact of land-use intensity on key ecosystem services may vary with environmental conditions. For example, land-use intensity mat increase litter decomposition through indirect effects on plant traits(Chillo et al., 2018), however, a drought caused by climate change may reduce this effect, as it causes litter accumulation by altering functional traits toward more resource-conservative strategy (greater leaf dry matter content, lower leaf nitrogen concentrations) (Lamarque et al., 2014). Unfortunately, we know little about the mechanisms associated with other services, including hydrological services, key for plant growth and groundwater replenishment (Zheng et al., 2008). Hydrological services are clearly affected by both land-use and rainfall intensity at the local and global scale (Cao et al., 2008; Salemi et al., 2013) and are expected to be changed even further from baseline conditions, as global climate change continues (Donat et al., 2016; Schär et al., 2016). However, the mechanism of how land-use intensity impacts hydrological services is still unclear and therefore, so too is how they will respond to changes in rainfall frequency and magnitude. Given predicted shifts in rainfall regime with global climate change, revealing the internal mechanisms of the impact of land-use intensity on hydrological services under different rainfall will be crucial for generating scientifically-grounded, and sustainable land management strategies.

To try to tackle these challenges, we measured hydrological services in 15 land-use plots along the land-use intensity gradient for 25 rainfall events (including 6 light, 8 moderate, and 11 heavy) in Hainan Island, China. We also measured 5 plant functional traits(tree height, leaf thickness, specific leaf area, leaf dry mass content, and leaf tissue density) and 3 ecosystem properties (canopy density, litter fall, and fine-root density) that relate to hydrological services in each plot. We next built an informed Bayesian structural equation model (BSEM) based on current knowledge about the relationships among land-use intensity, functional traits, ecosystem properties and hydrological services (Díaz et al., 2007; Carreño-Rocabado et al., 2016; Chillo et al., 2018). We thoroughly examined the effects of different components of functional traits

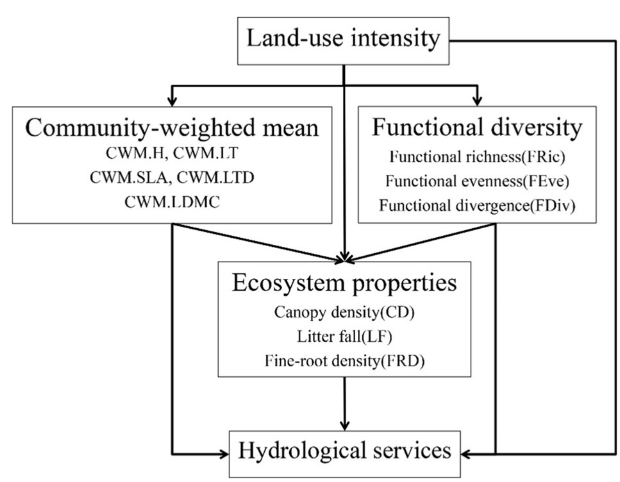

Fig. 1. Path diagram describing the hypothesized causal relationships linking land-use intensity to community-weighted mean of traits, functional diversity, ecosystem properties and hydrological services. Direct or indirect effects mean the factors impact hydrological services with or without intermediate pathways, respectively. CWM.H, community-weighted mean of tree height; CWM.LT, community-weighted mean of leaf thickness; CWM.SLA, community-weighted mean of specific leaf area; CWM.LDMC, community-weighted mean of leaf dry matter content; CWM.LTD, community-weighted mean of leaf tissue density.

(Fig. 1), including CWM of traits and FD. Our aim is to reveal the impact mechanisms of land-use intensity on hydrological ecosystem services. The specific objectives in this paper are to: (i) determine the factors, namely CWM of traits and FD, that contribute more to hydrological services following changes in land-use intensity; (ii) assess the relationships among with land-use intensity, functional traits, ecosystem properties and hydrological services; (iii) explore how the environment change (precipitation magnitude) affects these relationships.

2. Materials and methods

2.1. Study site

The study was conducted in the Hongmao Village, located in the south-eastern Baisha County, Hainan Island, China(19°4′ N, 109°31′ E) (Fig.2). The area has a tropical monsoon climate, with a mean annual temperature of 20–24 °C and mean annual precipitation of 1800–2900 mm. The rainy season is mainly from May to November. The main parent material of soil is granite and the predominant soil type is latosols (Yang et al., 2016). Prior to 2004 local residents had been destroying the forest using slash-and-burn techniques, and many natural forests were turned into artificial forests. After 2004, natural forests in this area were protected, but existing plantations were permitted as a mean to increase farm income. The main land use/land cover types of this region include mature forests, secondary forests, areca (*Areca catechu*) plantations, and monocultural rubber (*Hevea brasiliensis*) plantations. Occasionally, *Alpinia oxyphylla*, a medicinal plant, is intercropped with rubber to increase farm income. The area of above five forests accounted for 54.15%, 19.7%, 3.79%, 8.58%, and 6.99% of the study area, respectively.

The secondary forests and all plantations were transformed from mature forests. Most of the other vegetation including weeds in areca and rubber forests had been thoroughly removed by weeding. The dominant plant species of mature forests included *Castanopsis fissa*, *Lasianthus chinensis* Benth, *Camellia sinensis* var. *assamica*, *Dacrydium pierrei*, *Ternstroemia gymnanthera*, *Melastoma sanguineum* Sims, and *Syzygium chunianum*. The dominant plant species of secondary forests were *Wrightia pubescens*, *Psychotria rubra*, *Castanopsis jucunda* Hance, *Aporosa dioica*, *Glochidion sphaerogynum*, and *Lithocarpus corneus*.

2.2. Land-use intensity gradient

We established land-use intensity gradient based on the common land-use types and management intensity. We first selected locations within the five dominant land-use classes, including mature forests, secondary forests, areca forests, monocultural rubber plantations and rubber intercropped with *Alpinia oxyphylla* plantations. Within each land-use type, we selected three different management intensities based on field monitoring and surveys. Land-use intensity was assessed based on six parameters related to ecosystem properties, input and output of the production system in each plant community sample (Erb et al., 2013; Carreño-Rocabado et al., 2016). The six parameters included management intensity (biomass loss caused by the disturbance events), frequency of management practices (disturbance events), age of current system, magnitude of disturbance (percentage of undisturbed forest in a radius of 1 km), time since disturbance (time for natural regeneration), and standing biomass (indicate species richness). To reduce the dimensionality of our predictor variables, and control for potential collinearities, our final metric of land-use intensity was calculated by using principal component analysis (see details in Table S1).

2.3. Plant functional traits

We set up a 20 m × 5 m research plot in a representative area of each research site. The identity of all plants and community structure in each research plot (20 m × 5 m) were determined in August 2016. Dominant species in each plot were selected as those that together constituted at least 80% of the total community biomass (Conti and Díaz, 2013; Finegan et al., 2015).

Five important plant functional traits, including tree height (H), leaf thickness (LT), specific leaf area (SLA), leaf dry matter content (LDMC), and leaf tissue density (LTD) were measured in the field following the methodologies from Pérez-Harguindeguy et al. (2013). We chose these functional traits because they are sensitive to land-use intensity (Allan et al., 2015; Chillo et al., 2018), and profoundly affect ecosystem properties and processes associated with hydrological services (Lundholm et al., 2015; Finegan et al., 2015; Yin et al., 2018). Vegetation height is related to canopy density, litter fall and fine-root density (Lavorel, 2013; Conti and Díaz, 2013). Leaf specific leaf area and leaf tissue density directly affect water consumption through photosynthesis and transpiration (Yin et al., 2018), and indirect affect interception of rainfall by canopy density (Lundholm et al., 2015). Leaf thickness and

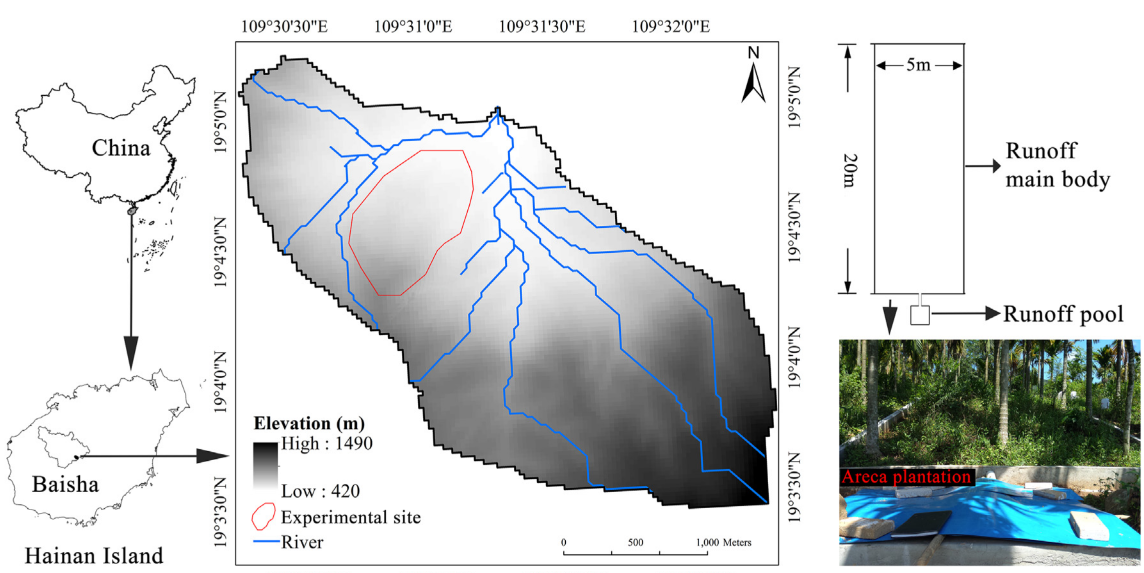

Fig. 2. Schematic of study area and runoff plot structure.

leaf dry matter content can affect rainfall interception via litter fall (Lohbeck et al., 2015; Liu et al., 2017). The functional traits values for all the species included in the study are presented in Table S2.

2.4. CWMs and FD

As recommended by empirical studies, CWM of traits were calculated as the mean trait value weighted by species' relative abundance in the community (Díaz et al., 2007; Shen et al., 2016; Häger and Avalos, 2017). We calculated the CWM for each of above functional traits (see details in Table S3) based on the methods of previous studies (Shen et al., 2016; Häger and Avalos, 2017), and then, CWM of studied traits was aggregated in PCA axes (Zhu et al., 2015) and results showed that all CWM of measured traits exhibited two principal components (see details in Table S4). CWM.PC1 mainly represented the variation in the community mean leaf dry mass content. CWM.PC2 mainly reflected the variation in leaf tissue density and specific leaf area.

Three complementary indices were used to measure FD (Villéger et al., 2008), including functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv), each of which is known to be closely related to land-use intensity(Díaz et al., 2007; Carreño-Rocabado et al., 2016), and influence ecosystem functions and services (Conti and Díaz, 2013; Zhu et al., 2015; Finegan et al., 2015). The differences among these three indices in determining ecosystem functions and services originate from their different emphases on community functional composition. FRic measures the dispersion of species in the functional traits space (Villéger et al., 2008; Schmera et al., 2009), while FEve quantifies how regularly the trait space is filled (Chillo et al., 2018). FDiv measures how the most abundant species diverge from the centroid of the community (Zhu et al., 2015). FRic and FDiv may be interpreted as the degree of niche differentiation in plant communities (Díaz et al., 2007; Finegan et al., 2015). The calculation methods of the three indices of FD were consistent with those from Villéger et al. (2008) and Carreño-Rocabado et al. (2012).

All CWM of traits and FD (see details in Table S3) were calculated using the FDiversity software (Casanoves et al., 2011; Zhang et al., 2017).

2.5. Ecosystem properties

We measured three ecosystem properties closely related to hydrological services: canopy density (CD), litter fall (LF), and fine-root density (FRD). These properties are thought to be related to land-use intensity (Allan et al., 2015; Chillo et al., 2018), and considered good proxies of ecosystem hydrological services. In this study, we try to use the relatively stable parameter to reflect the properties of different forest ecosystems. The ecosystem properties values for all the forest plots included in the study are presented in Table S3.

Canopy density was recorded every two months during sunny weather between September 2016 and August 2017 using a fish-eye camera to capture nine images of each runoff plot. The average canopy density was used for analysis.

Litter fall was estimated each month from September 2016 to August 2017 by collecting the litter from three 1 m × 1 m quadrats in each runoff plot (Zheng et al., 2008), and recording the dry weight after drying to constant weight in an oven at 65 °C. The total litter fall within one year in each forest ecosystem was used for calculation.

To examine fine roots, soil cores were collected from a spot 20 cm in diameter in each runoff plot by taking out soil cores, each 3.5 cm in diameter in August 2016. The spots were so distributed as to represent the upper, middle, and lower parts of each runoff plot, within which the spots were located at random. Three soil samples were collected from each spot. Thus, a total of 9 soil samples were obtained in each runoff plot, giving a volume of each soil sample (V) in each part. Each soil sample was passed through a 2 mm sieve and fine roots (smaller than 2 mm in diameter) were separated from the soil, washed, dried to constant weight at 65 °C, and weighed to determine the root mass (M). The fine roots in each forest ecosystem were measured once since the longevity of fine roots in the forest is about 1 year (Graefe et al., 2008; Yuan and Chen, 2010) and the length of fine roots in low altitude areas of tropical forests did not differ significantly between months (Graefe et al., 2008). Fine-root density (FRD) was calculated from the volume and the mass($FRD = M/V$)in the spot(Yu et al., 2016).

2.6. Hydrological service assessment

To measure the hydrological services, we constructed a standard 20 m × 5 m runoff plot to measure the surface runoff in each research plot. The standard runoff plots has been widely used to monitoring the hydrological services in forest ecosystems (Cao et al., 2008; Zheng et al., 2008; Nunes et al., 2011), including tropical rainforest(Verbist et al., 2010; Salemi et al., 2013) and plantations(Ferreira et al., 2016).

Each runoff plot was constructed with brick and measured a 20 cm tall and 12 cm wide. The interior of the wall had a coat of waterproof paint. The area enclosed was then back-filled with soil to achieve a uniform depth of 10 cm, leaving 10 cm of the wall exposed to delineate the main body of the runoff plot. A square runoff pool (1.2 m × 1.2 m × 1.2 m) was built on the downward slope below each runoff plot and connected to it by a polyvinyl pipe 20 cm in diameter (Fig. 2).

Surface runoff was monitored for each rainfall event between September 2016 and August 2017. If the runoff pool collected enough water, the quantity of runoff was determined by measuring the depth of the water in the pool; if the amount of water collected in the pool was too little to measure its depth accurately, the runoff was discharged into a bucket for measuring. Surface runoff was measured for 6 events of light rain, 8 of moderate rain, and 11 of heavy rain (see: 2.7 Precipitation magnitude classification).

Hydrological services were quantified basing on a runoff coefficient (RC) obtained by the following formula: $RC = runoff/rainfall$ (Muñoz-Villers and McDonnell, 2013).The runoff coefficient represents the water that flows away after the rainfall in the ecosystem, so that the opposite of the runoff coefficient (1-RC) indicates the water retained in the ecosystems. As a type of regulating services, hydrological services refer to the ability to retain water in ecosystems, as retain water can be used for plant growth and groundwater replenishment (Zheng et al., 2008; Muñoz-Villers and McDonnell, 2013). In this study, the characterization of hydrological services was represented using the quantity (1–RC). Thus, the greater the value of (1–RC), the greater the capability to provide hydrological service.

2.7. Precipitation magnitude classification

To identify the impacts of extreme precipitation on the relationships among plant functional traits, ecosystem properties, and hydrological services, we divided rainfall into three types based on the amount of total rainfall in 24 h in China's classification (Ma et al., 2015): light (<10 mm), moderate (10–25 mm), and heavy (>25 mm). We considered rainfall exceeding 3 mm at any one time a rainfall event, because field monitoring has shown that only rainfall >3 mm produces surface runoff. We deployed a HOBO U30-NRC weather station (Onset, Cape Cod, Massachusetts, USA) at each site to record meteorological data including rainfall (accurate to 0. 2 mm). From September 2016 to August 2017, a total of 103 rainfall events were recorded in the study area, divided into 46 events of light rain; 35, of moderate rain; and 22, of heavy rain, with heavy rains contributing >64% of the total rainfall (see details in Table S5).

2.8. Statistical analysis

We used Pearson correlation analysis to preliminarily investigate the relationships between land-use intensity, CWMs, FD, ecosystem properties and hydrological services in three types rainfall (light, moderate, and heavy rain), as well as the correlations between CWMs, FD, ecosystem properties and land-use intensity. Multi-model inference were conducted for hydrological services and predictor variables by starting from all 9 potential predictor variables under different rainfall types (Zhu et al., 2015), land-use intensity as a fixed variable, and 8 others as selection variables, resulting in a total of 255 possible models in each type of rainfall. The process of multi-model inference allowed us to account for multicollinearity between variables and to determine the most important variables (Zhu et al., 2015; Ali et al., 2017). Pearson correlation and multi-model inference analyses were completed with SAM 4.0 software.

From all subsets of analysis in multi-model inference, we selected the variables retained in the best-fit regression model with the lowest Akaike Information Criterion (Zhu et al., 2015; Ali et al., 2017) for the construction of Bayesian structural equation models (BSEMs). We used the BSEM because it is more robust to small sample sizes and provides more reliable formal model comparison statistics (Assaf et al., 2018). The BSEMs based on current knowledge of all predictor variables relationships (Fig.1) and were initiated by including all possible relationships. The least significant relationship was then removed stepwise until the fit of the model met requirements. We used several tests to assess the model fit of BSEMs, including the deviance information criterion (DIC) and the posterior predictive *P*-value (*PPp*). The model with the smallest DIC and a *PPp* approximately 0.50 indicates a plausible model, whereas *PPp* closer to 0 or 1 indicates that the model is not plausible (Dayer et al., 2016). The BSEMs were implemented using the AMOS 21.0 software.

3. Results

Land-use intensity was significantly correlated with functional traits, including the second principal component of CWMs (CWM.PC2), functional richness (FRic), functional divergence (FDiv), and ecosystem properties, including canopy density, litter fall and fine-root density (Table 1), meaning that land-use intensity has a significant impact on multiple ecosystem structures. Land-use intensity had significant effects on hydrological services regardless of rainfall intensity ($P < 0.05$, Table 1), as well as other variables except for the first principal component of CWMs (CWM.PC1) (Table 1), indicating multiple factors that jointly regulate hydrological services.

The best five regression models by multi-model inference for each rainfall types were presented and ranked according to the AICc

Table 1
Pearson correlation coefficients between land-use intensity, community-weighted mean of traits, functional diversity, ecosystem properties and hydrological service in different rainfall types.

Items		Land-use intensity	Hydrological services		
		LUI	Light rain	Moderate rain	Heavy rain
Land-use intensity	LUI	–	−0.472**	−0.620**	−0.615**
Community-weighted mean	CWM.PC1	−0.205	−0.14	−0.14	−0.1
	CWM.PC2	0.535*	−0.444**	−0.553**	−0.587**
Functional diversity	FRic	−0.697**	0.503**	0.650**	0.653**
	FEve	−0.012	−0.252*	−0.227*	−0.245*
	FDiv	−0.621**	0.419**	0.586**	0.544**
Ecosystem properties	CD	−0.653**	0.216*	0.435**	0.354**
	LF	−0.916**	0.563**	0.686**	0.703**
	FRD	−0.890**	0.585**	0.716**	0.716**

LUI, land-use intensity; CWM.PC1, the first principal component of community-weighted means; CWM.PC2, the second principal component of community-weighted means; FRic, functional richness; FEve, functional evenness; FDiv, functional divergence; FRD, fine-root density; CD, canopy density.
** $P < 0.01$.
* $P < 0.05$.

Table 2
Summary of the multiple regression models for the hydrological services in three rainfall types. Of all 255 models, the top five models are displayed and ranked according to their AICc values.

Rain types	Variables	R^2	AICc	△AICc	L(gi|x)	Weights
Light rain	3,6,8,9	0.472	583.465	0	1	0.13
	3,4,6,8,9	0.482	584.198	0.733	0.693	0.09
	2,3,6,8,9	0.474	585.491	2.026	0.363	0.047
	1,3,6,8,9	0.474	585.531	2.066	0.356	0.046
	3,5,6,8,9	0.473	585.659	2.193	0.334	0.043
Moderate rain	3,6,8,9	0.576	662.662	0	1	0.134
	3,4,6,8,9	0.581	663.444	0.783	0.676	0.091
	1,3,6,8,9	0.578	664.28	1.618	0.445	0.06
	3,5,6,8,9	0.577	664.628	1.966	0.374	0.05
	3,6,7,8,9	0.577	664.638	1.976	0.372	0.05
Heavy rain	2,3,6,8,9	0.657	1037.89	0	1	0.127
	2,3,4,6,8,9	0.659	1038.883	0.994	0.608	0.077
	3,6,8,9	0.65	1038.921	1.032	0.597	0.076
	3,4,6,8,9	0.655	1038.96	1.071	0.585	0.074
	1,2,3,6,8,9	0.659	1039.25	1.36	0.507	0.064

In the variables column, explanatory variables were: #1, the first principal component of community-weighted means; #2, the second principal component of community-weighted means; #3,functional richness; #4,functional evenness; #5,functional divergence; #6,canopy density; #7,litter fall; #8,fine-root density; #9, land-use intensity.

(Table 2). Most of these models exhibited high R-squared values, especially for moderate rainfall and heavy rainfall, which presented minimum R-squared values of >50%, indicating significant explanatory power for variations in hydrological services. Specifically, all displayed regression models included functional richness, canopy density, fine-root density (Table 2). For the optimal regression equation models (with high weights), the explanatory variables included functional richness, canopy density and litter fall under light and moderate rains, however, the variable of the second principal component of CWMs (CWM.PC2) was added in heavy rainfall (Table 2).

The final Bayesian structural equation models showed that functional traits and ecosystem properties could account for 46–65% of variation of hydrological services under land-use intensity, their ability to explain changes in hydrological services increases with rainfall intensity (Fig.3). In addition to the direct effect of functional richness, there was also an indirect effect on hydrological services through changes in canopy density and fine-root density, however, none of CWM of traits had a significant direct or indirect effect on hydrological services in light and moderate rainfall (Fig.3). In contrast, CWM.PC2 had a significant effect on hydrological services directly and indirectly by altering fine-root density and canopy density under heavy rain (Fig.3), but the impact intensity of the CWM.PC2 was less than the functional richness (Fig.4).

Land use intensity showed the strongest total effect among all factors regardless of rainfall intensity, followed by functional richness (Fig.4). Land-use intensity indirectly affects hydrological services mainly through direct impact on functional richness (Fig.3, Fig.4), although it also indirectly affects the hydrological services by altering canopy density and fine-root density (Fig.3). In contrast, there was no significantly direct impact between land-use intensity and hydrological services neglecting the type of rainfall (Fig.3).

4. Discussion

Land use change is one of the most important drivers of terrestrial ecosystem services degradation (Chillo et al., 2018; Zheng et al., 2019). Our study identifies, through a predictive Bayesian structural equation model parameterized with empirical data, direct and indirect effects of land-use intensity on hydrological services and attempts to tease out underlying mechanisms associated with plant functional ecology and key ecological properties at a community scale. This work differs from the previous in that it revealed that changes to the plant functional diversity were a key mechanism by which land-use intensity indirectly affected hydrological services.

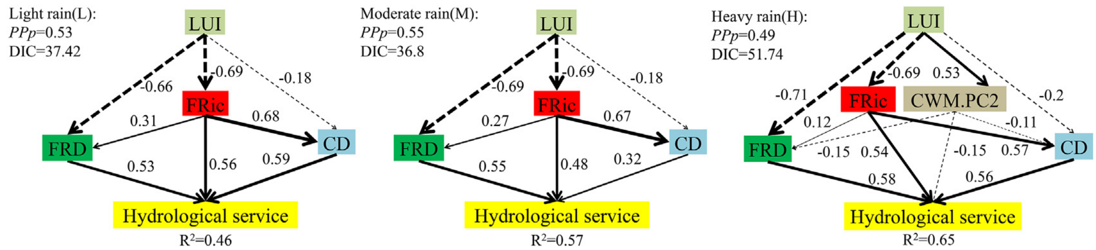

Fig. 3. Best-fitting Bayesian structural equation models examining direct and indirect relationships among land-use intensity, community-weighted mean, functional diversity, ecosystem properties and hydrological services in different rainfall types. LUI, Land-use intensity; CWM.PC2, the second principal component of community-weighted means; FRic, functional richness; FRD, fine-root density; CD, canopy density. Dashed arrows reflect negative relationship, solid arrows reflect positive relationships and standardized path coefficients are shown on the path. The thickness of the line indicated the strength of the standard regression coefficient. All lines shown represent significant relationships ($P < 0.05$).

The results highlighted that functional diversity is more important than CMW of the measured traits in regulating hydrological services, differs from previous research related to hydrological services (Zheng et al., 2008; Ferreira et al., 2016) and other ecosystem services, such as soil erosion(Zhu et al., 2015) and carbon storage (Häger and Avalos, 2017). In the present study, functional richness, as measured the niche space filled by the species within a community (Clark et al., 2012), and functional diversity may reflect some form of 'niche differences' (Carroll et al., 2011). A greater functional diversity, that is higher values and a wider range of functional traits, reflects not only the magnitude of niche differences but also differences in resource utilization either through space or time (Allan et al., 2015; Zhu et al., 2015), thereby leading to more pronounced effects on hydrological services.

We found that changes in functional diversity caused by land-use intensity can indirectly affect hydrological services though key ecosystem properties, including canopy density and fine-root growth. This diverges from existing research related to hydrological services which overlooked such indirect effects associated with functional diversity (Cao et al., 2008; Ferreira et al., 2016), although some studies have found this indirect effect in relation to soil fertility (Lundholm et al., 2015), productivity (Laforest-Lapointe et al., 2017) and forage availability (Chillo et al., 2018). We hypothesize that the mechanism of the indirect effect on hydrological services is that community with higher functional diversity promoted canopy density and fine-root growth by using light and soil nutrient resources more efficiently (Conti and Díaz, 2013). Specifically, higher canopy density is expected to intercept more rainfall and reduces the amount of precipitation reaching the ground (Thompson et al., 2016), thereby reducing the potential for runoff and erosion. Similarly, fine-root density is one of the most important root traits in a given ecosystem (Vannoppen et al., 2015), and is also known to facilitate percolation by making the soil more porous (Vannoppen et al., 2016), thereby improving hydrological services.

We observed that land-use intensity mainly affects hydrological services indirectly by altering functional diversity, although ecosystem properties also mediated indirect effects. This adds to our understanding of how the increase in land-use change led to the degradation of terrestrial ecosystem services. Previous studies have suggested that the change in ecosystem properties, such as canopy density (Salemi et al., 2013), litter fall (Zheng et al., 2008), and fine-root density (Vannoppen et al., 2015), were the main reasons for the decline of hydrological services caused by land-use change, but ignored the role of functional diversity. In fact, functional diversity can affect hydrological services through two different paths: directly and indirectly changing ecosystem properties, and the direct effects are greater than the indirect.

The results of this work are novel and differ from the previous work in that it revealed that environmental factors regulated the relationship among land-use intensity, functional traits, and hydrological services. This manifested in two ways. First, the functional trait-mediated implications of land-use intensity on hydrological services increased from 46% in light rain to 65% in heavy rain. Earlier research has pointed to a similar relationship, in which the extent of variation in carbon storage in tropical forests as explained by functional diversity increased after adding soil factors (Lamarque et al., 2014). Second, only functional richness hold a significant indirect effect on hydrological services in light and moderate rainfall. In addition to functional richness, in contrast, the CWM.PC2 also showed significant indirect effects in heavy rain. This demonstrates that rainfall magnitude or intensity plays an outsize role in regulating the intrinsic path of the impact of functional traits caused by land-use intensity on hydrological services. Considering the rising trends in the frequency and magnitude of heavy rain events due to global climate change (Donat et al., 2016; Schär et al., 2016), global climate change may frequently and profoundly change the internal pathway of land-use change impacts on hydrological services in the future. However, environmental factors did not change the most critical intrinsic pathways, as functional diversity was the most important factor in mediating the relationship between land-use intensity and hydrological services regardless of rainfall intensity. Overall, land-use intensity has a profound impact on the provision of hydrological services, and the increase of extreme precipitation could significantly and noncritical affect the internal mechanism of degradation of hydrological services caused by land-use intensity.

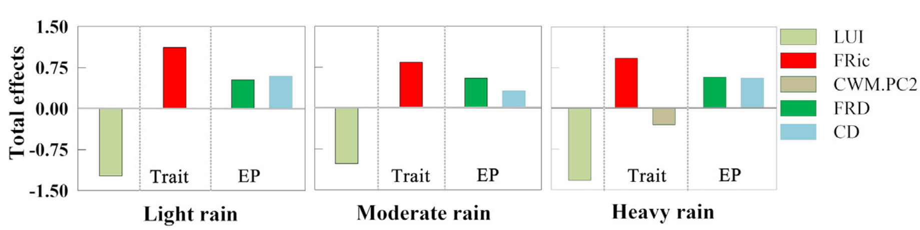

Fig. 4. The impact intensity of land-use intensity, functional traits and ecosystem properties on hydrological services in different rainfall types. Total effects were calculated by multiplying the path coefficient for the effect of land-use intensity (LUI) on functional traits/ecosystem properties with the path coefficient for functional traits on ecosystem properties and the effect of species functional traits/ecosystem properties on hydrological services. The best-fitting Bayesian structural equation models used to calculate the total effects. LUI, land-use intensity; FRic: functional richness; CWM.PC2, the second principal component of community-weighted means; FRD, fine root density; CD, canopy density; Trait, functional traits; EP, ecosystem properties. Higher column diagram mean large total effects.

The results obtained important for managers to make land use strategies in maintaining and improving ecosystem services, especially in the background of large areas of natural forests have been transformed into managed plantations in tropical regions (Muñoz-Villers and McDonnell, 2013; Wen et al., 2017). Sustainable management should aim at maintaining multiple categories of ecosystem services provision (Allan et al., 2015; Häger and Avalos, 2017), and the consideration of functional diversity helps in that way. Superficially we find that maintaining high functional diversity in land management increases the potential for hydrological services, as well as, potentially, other ecosystem services (e.g., soil fertility and carbon storage) (Cadotte, 2017; Chillo et al., 2018). Furthermore, functional diversity may also play an irreplaceable role in combating the impact of global climate change (e.g., extreme precipitation) on the supply of ecosystem services (Wright et al., 2015). Therefore, monitoring functional diversity may be a useful tool to design management strategies in face of continuing global environmental change.

5. Conclusions

By explicitly considering plant functional traits and ecosystem properties in relation to land-use intensity and ecosystem hydrological services, we found that land-use intensity has significant and indirect effects on hydrological services. The indirect effect on hydrological services, however, mainly comes from land-use intensity induced changes in functional diversity, not CWM of traits and ecosystem properties. We also revealed functional diversity caused by land-use intensity can indirect affect provision of hydrological services by changing ecosystem properties. However, its direct effects were greater than indirect effects, indicating the main mechanism of land-use intensity leading to hydrological service degradation is due to the reduction of the functional trait distribution among species. Interestingly, we discovered that precipitation intensity can regulate the relationships among land-use intensity, functional traits, ecosystem properties and hydrological services, although the most important role of functional diversity has not changed regardless of precipitation intensity. Therefore, functional diversity has the potential to serve as an important tool for sustaining hydrological services in response to key global environmental change, precipitation intensity.

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Author contributions

ZW designed the study, executed the experiments, collected and analyzed data, and produced a draft of the manuscript. Hua Z contributed to the design of the study and providing some input to various drafts of the manuscript. JS gave comments to various drafts of the manuscript and retouched the article, He Z participated in experiments as well as collected the data in the field. LL, and ZO provided comment on various drafts. All authors read and approved the final manuscript.

Date accessibility

More detail about the dataset is available upon reasonable request to the authors.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2019.05.160.

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