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Evaluating ecosystem service trade-offs along a land-use intensification gradient in central Veracruz, Mexico

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A B S T R A C T

It is generally assumed that forests improve ecosystem service (ES) provisioning within landscapes. These assumptions drive policies (e.g. Payment for Ecosystem Services) that affect land-use without knowing if the desired services are achieved. Here we use a data-intensive approach to explore the synergies and tradeoffs between three regulating (hydrologic regulation, water quality, carbon storage) and one supporting ES (biodiversity). Using field-based measurements for ten ES indicators collected within eight land use/land cover (LULC) types we assess: (1) the relationship between ES indicators and LULC type and (2) the synergies and tradeoffs across ES indicators. For objective one, we found that primary forests promote more favorable hydrological services, including having greater base flow, flow regulation, and soil conductivity. For objective two, we observed synergies across many ES where management of one would improve provisioning for several other ES, specifically between low flow, carbon storage, and biodiversity. However, many ES parameters (e.g. water quality) had no relationship with other ES parameters. Our results underscore the value of site-specific research in addressing assumptions about the relationship between LULC and ES provisioning. More site-specific data is needed for more informed design of management strategies that can maximize ES benefits.

1. Introduction

The ecosystem services (ES) framework (Daily, 1997) has become a predominant strategy to ascribe human value to the benefits people receive from natural ecosystems and to help prioritize natural resource management actions. Applying the ES framework requires a clear understanding of how ES are produced by complex socio-ecological systems, as well as the benefits and demand for those ES by people (Carpenter et al., 2009; Bennett et al., 2015). While there are many strengths to the ES framework (e.g. interdisciplinarity, utility as a communication tool), a clear weakness stems from the lack of a scientific basis for linkages among ES (Schröter et al., 2014; Bull et al., 2016). In short, we are not confident of the synergies and tradeoffs across multiple ES when applied to a specific, unmeasured site (Kremen, 2005; Bennett et al., 2009). Synergies occur when the provisioning of two ES moves in the same direction; tradeoffs occur when one ES increases while another ES decreases (Bennett et al., 2009). Understanding the co-production of ES is important for the design of natural resource policies to avoid unintended declines in some ES and to maximize the overall impact of such policies. One general rule that has emerged across studies measuring multiple ES is that there are often clear tradeoffs between provisioning ES and cultural or regulating ES (Foley et al., 2005; Raudsepp-Hearne et al., 2010); however, less is known about the synergies and tradeoffs within each of these categories. A meta-analysis by Howe et al. (2014) found that tradeoffs existed between ES studied almost three times as often as synergies. For these reasons, there is increasing interest in bundling and streamlining policy implementation to avoid conflicting policies that cancel benefits

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Table 1
Table of ecosystem services considered in this study along with an explanation of the variable used.

Ecosystem Service	Measured Indicators	Explanation
Regulating service		
Hydrologic regulation	• Mean annual high flow • Mean annual low flow • Event flow regulation • Quick flow regulation • Soil Hydraulic Conductivity	The variables considered allow us to assess the availability of water for downstream users throughout the year and the ability of a catchment to regulate flow rates during high rainfall periods.
Water purification (water quality)	• High flow suspended solids • Base flow suspended solids • Coliform number • Nitrogen concentration	The variables considered consider contamination from human/biological contact (coliforms), fertilizer use (nitrogen), and disturbance and runoff (suspended solids).
Carbon storage	• Total carbon storage (above and below ground)	The total carbon storage is calculated from soil and vegetative carbon stored in the landscape.
Supporting service		
Biodiversity	• Shannon's biodiversity index	The Shannon index can assess the diversity of a community by considering both the number of species and the evenness of species across the community.

of ES provisioning (Plieninger et al., 2012; Simonit and Perrings, 2013).

Regulating ES – the benefits that flow from ES processes – are arguably some of the most important and vulnerable ES (MA, 2005). This category of ES includes life-sustaining processes such as water purification (measured by water quality), hydrologic regulation, and climate regulation. Concern over rapid land use/land cover (LULC) change and degradation of these ES has led to the emergence of a policy approach increasing in popularity: payments for ES (PES). PES policies aim to conserve the ES benefits that ecosystems provide by providing financial incentives to land owners to maintain or improve ES provisioning (Brouwer et al., 2011; Wunder, 2015). There are now several hundred PES programs in existence, many of them in the Global South and the majority focusing on protecting hydrologic ES (Salzman et al., 2018). Payment for hydrological services (PHS) programs have increased rapidly, especially in regions like Latin America, due to water's vital role in ensuring human well-being and the growing threats to the sustainability of reliable clean water with impending threats from climate change (Postel et al., 1996; Brauman et al., 2007; Buytaert et al., 2011; Goldman-Benner et al., 2012; Grima et al., 2016). While PES programs are sometimes framed to consider other services, PHS programs have come under criticism for a narrow focus on water, sometimes to the detriment of other ES (e.g., Lebel and Daniel, 2009; Daw et al., 2011; Goldman-Benner et al., 2012; Van Hecken et al., 2012).

Most studies that measure ES provisioning either map large landscapes or quantify site-specific ES, but rarely both. The majority of studies take a landscape-scale approach. The limitation to landscape-scale analyses is that they must effectively apply relationships between LULC types from spatially distributed data (e.g. remote-sensing products and digital elevation models), while quantification of ES provisioning is usually based on generalized and static assumptions (e.g. Naidoo and Ricketts, 2006; Nelson et al., 2009). These relationships typically use tree cover as a proxy for diverse ES and may not consider intrinsic properties of the specific sites or watersheds (Bennett et al., 2009). Most notably, Nelson et al. (2009) utilized InVEST models and found that there were few tradeoffs between biodiversity and other ES such as carbon sequestration and water quality. Raudsepp-Hearne et al. (2010) assessed how 12 different provisioning, regulating and cultural ES co-occurring across the landscape based on land cover data and census data. They found that certain ES were positively related while others exhibited tradeoffs. While the conclusions drawn from landscape approaches such as these are compelling, the relationships underpinning the analyses typically lack field validation of ES provisioning and, hence, may not accurately represent actual ES synergies and tradeoffs at scales that decisions are made about land use (Mokondoko et al., 2018).

Field-based measurements can more precisely quantify relationships across multiple ES (Kremen, 2005; Bennett et al., 2009). For example, the relationship between carbon storage and land cover is typically characterized as linear; trees store large quantities of above- and belowground carbon meaning greater tree cover fairly reliably leads to greater net carbon storage (Pan et al., 2011). However, the linkages between or within hydrological services, carbon, and biodiversity are often more nuanced. For example, greater forest cover generally leads to lower annual stream flow, but with more stable baseflows and dry season (low) flows (Bosch and Hewlett, 1982; Bruijnzeel et al., 2006; Muñoz-Villers and McDonnell, 2012). Forests also tend to maintain relatively low annual runoff, and high soil hydraulic conductivity, soil water storage capacity, and recharge, thereby resulting in increased stream water quality (Ilstedt et al., 2007; Zimmermann and Elsenbeer, 2008). Additionally, site-specific field measurements can highlight complex relationships across LULC types. For example, Muñoz-Villers et al. (2012) found that a 20-year-old naturally-regenerating forest in the mountains of Veracruz, Mexico provided similar streamflow patterns as a primary forest. Despite this result, additional factors that can influence streamflow patterns (e.g. slope, soil conditions, and topography), can vary dramatically across landscapes, further reinforcing the need for data from locations where decisions are made.

A site-specific approach can thus help quantify the complexities between different ES and the consequences of LULC change for ES synergies and tradeoffs. Using a suite of field-collected data allows us to consider how ES vary even within a single category (e.g. seasonal flow vs. total annual flow). There is increasing recognition of the need to combine site-specific, field-based ES measurements with landscape-scale analyses to inform policy decisions (Rieb et al., 2017); however, there remains a lack of field-based data for informing these relationships (Tallis et al., 2008; Naidoo et al., 2008; Bennett et al., 2009). This is particularly important in areas investing heavily in PHS or other PES programs that may be basing these efforts on misguided assumptions about ES provisioning; e.g. greater forest cover always results in greater ES provisioning.

We explore the synergies and tradeoffs between three regulating (hydrologic regulation, water quality, carbon storage) and one supporting ES (biodiversity) in the tropical montane forests of central Veracruz, Mexico (Table 1). We use ten ES indicators instead of one value per ES that allow us to explore the nuanced complexities within ES that are important for decision making. For example, if a certain LULC had high nitrogen concentrations but low coliforms (both water quality) then a land manager might modify land management differently than if the inverse were true. This knowledge would not be captured if the water quality was distilled into a single metric. Using field-based measurements for these ten ES indicators collected within eight LULC types we assess: (1) the relationship between ES indicators and LULC type and (2) the synergies and tradeoffs across ES indicators by LULC. Due to active and well-studied PHS programs that have been operating since 2003 in the study area (see Muñoz-Pina et al., 2008; Martínez et al., 2009; Scullion et al., 2011; Nava-López et al., 2018; Mokondoko et al., 2018; Jones et al., 2019; von Thaden et al., 2019), Veracruz provides an ideal study site to examine relationships between LULC and ES as well as the synergies and tradeoffs across ES. Accurately quantifying ES synergies and tradeoffs provides a critical foundation for improving decision-making processes in ways that optimize benefits within complex socio-ecological systems.

2. Methods

2.1. Study area

The study area is located in the upper Antigua watershed in central Veracruz on the eastern slopes of the Cofre de Perote volcano (4,282 m a.s.l; 19.491 N, −97.150 W). The Pixquiac river (in the upper Antigua) provides 38% of the water for Xalapa, Veracruz, the capital city and a popular area for regional tourism (Pare and Gerez, 2012). The vegetation within the region is predominantly tropical montane cloud forest (TMCF) as it lies within a distinct fog belt that occurs predominantly in the dry season (November-April). The climate within the Pixquiac watershed varies significantly based on elevation, with an average annual temperature of 9.5 ∘C and mean annual precipitation of 1708 mm at 3102 m elevation, 15.4 ∘C and 2804 mm at 2100 m elevation, and 19.3 ∘C and 1755 mm at 1188 m elevation (Holwerda et al., 2010; CICESE, 2019). The region is considered a biodiversity hotspot by the World Wildlife Fund (Gillespie et al., 2012) because of its unique location at the convergence of the Trans-Mexican volcanic belt, the Gulf of Mexico coastal Plain, and the Mexican Central Plateau. It is also considered a priority watershed in Mexico due to marked degradation of hydrologic dynamics (Cotler et al., 2010).

The landscape in the study area comprises a complex patchwork of managed and natural vegetation types (Fig. 1 and Table 2) that include forests, pastures, row-crop agriculture (e.g. sugarcane, maize, potato), and coffee. The expansion of the urban populations of Xalapa and Coatepec have displaced agriculture resulting in new areas within the watershed being utilized for agriculture. Estimates suggest that 77% of the watershed has been converted from its original forest cover to alternative agricultural land uses Muñoz-Villers and López-Blanco, 2008). The remaining landscape exists as forest patches, many in young, isolated, or degraded forms (Douglas et al., 2007). The predominant agriculture within the cloud-affected zone is shade-grown coffee; covering 17.4% of the Pixquiac watershed it is the primary crop providing income for many land owners (Table 2; von Thaden et al., 2019). Due to complex land use histories and land-tenure arrangements, coffee farms range from small collective land holdings to large corporate plantations. Sugarcane represents the dominant land use at lower elevations with flatter topography while smaller extensions of other crops (e.g. maize and potatoes) occur mainly at higher altitudes. While some lands are managed under private ownership, many (∼25%) exist under communal land tenure *(Ejido)* systems, with individual parcels and commonly managed land that are typically forest (Ponette-Gonzalez and Fry, 2014; Registro Agrario Nacional (RAN), 2017).

Due to the combination of extensive deforestation and declining water availability for downstream users in the city of Coatepec, particularly base flow in the dry season, the first PHS program in Mexico was launched in the Gavilanes watershed in 2003, with a national PHS program starting the following year (Nava-López et al., 2018). A second PHS program was started in 2007 in an adjacent watershed (Pixquiac) to help insure water availability for the state capital of Xalapa. These PHS programs focus on forest conservation with the stated goal of protecting downstream water supplies. Mexico has separate PES programs that focus on forest conservation for carbon and biodiversity ES, and REDD + has recently begun operating within the country, but is not yet present in the study area. Assessments of the PHS programs in our study area have suggested modest success at maintaining forest coverage and mixed success at optimizing ES due to a poor job of targeting areas important for ES in the region (e.g. Ponette-Gonzalez and Fry, 2014; Mokondoko et al., 2018; Asbjornsen et al., 2017; Von Thaden et al., 2019).

2.2. Biophysical data collection

To consider the relationship between ES and LULC, we quantified a suite of indicators (Table 1) that signify the health of hydrology, carbon, and biodiversity in first-order catchments that were dominated by a singular LULC type (50–100 ha; Table 2, Fig. 1, Table S1) that comprised the main LULC types in the study area. Actual coverage of the primary LULC ranged from 47% to greater than 90% meaning that all catchments were a mixture of LULC which introduces variability to our study. Water quality and hydrologic regulation indicators were sampled at the outlet of first order catchments while the remaining indicators were measured within replicated plots in the core catchments and other plots of the same land use in the region. To examine tradeoffs between hydrologic, carbon, and biodiversity services, an extensive plot network was established that included eight targeted LULC types (i.e., Table 2, Table S1). These included three forest stages (primary, mature secondary, and young secondary forests), two management types of shade coffee farms (high and low intensity), two management types of pastures (high and low intensity), and sugarcane (See Table S1 for watershed and plot locations). Following widely held assumptions about LULC-ES relationships (e.g. Nelson et al., 2009) we expected that (1) LULC types with greater tree cover (forests and coffee) would have higher ES provisioning (as measured by various ES indicators) and (2) that clear positive relationships would exist between hydrologic regulation, water quality, carbon, and biodiversity leading to obvious benefits of certain LULC types that promote these benefits (forests) over others.

A LULC classification for the study region was generated using SPOT imagery from the dry season in 2014. For more information on LULC mapping and validation see Von Thaden et al. (2019). Images were classified using Trimble eCognition® Developer 9.0 with an object-based approach and the Random Forest (RF) classifier. For LULC classification of the primary sites and validation samples for mapping, forests were categorized into general age classes through visual assessment of sites and conversations with owners about land use history. Primary forest was any that was determined to be over 50 years old, mature secondary forest any that was determined to be between 20 and 50 years old, and young secondary forest was any that was less than 20 years old. Previous work has demonstrated that stand age affects species composition and hydraulic regulation (Williams-Linera, 2002; Muñoz-Villers and McDonnell, 2013). Forests, pastures, and coffee farms were subdivided to test if the ES provided by each land use varied with forest stage (forests) or two levels of management intensity (pastures and coffee). Management intensities for pastures were defined by the density of cattle and the use of pesticides or fertilizer. Intensity in coffee farms was defined by the density of coffee plants, shade trees, and the use of fertilizers. All information was obtained through assessment of field sites and conversations with land managers.

2.2.1. Hydrologic regulation

Within each catchment, streamflow and rainfall measurements were collected from 2015 to 2019. This 4-year data set provided sufficient data for consideration of flow response across rainfall events and seasons. For streamflow, one V-notch weir was installed at each catchment outlet and water level was logged every 1.5 minutes using a Solinist Water level sensor (model 3001) paired with a barometric pressure recorder (model 3001). By calibrating the stream height to the weir, we calculated streamflow (L s^{-1}) using the experimental stage-discharge relationship (ASTM, 2001), calibrated with field-derived rating curves generated via volumetric-and salt dilutions measurements of discharge (Moore, 2005). Rainfall was measured at one point within each

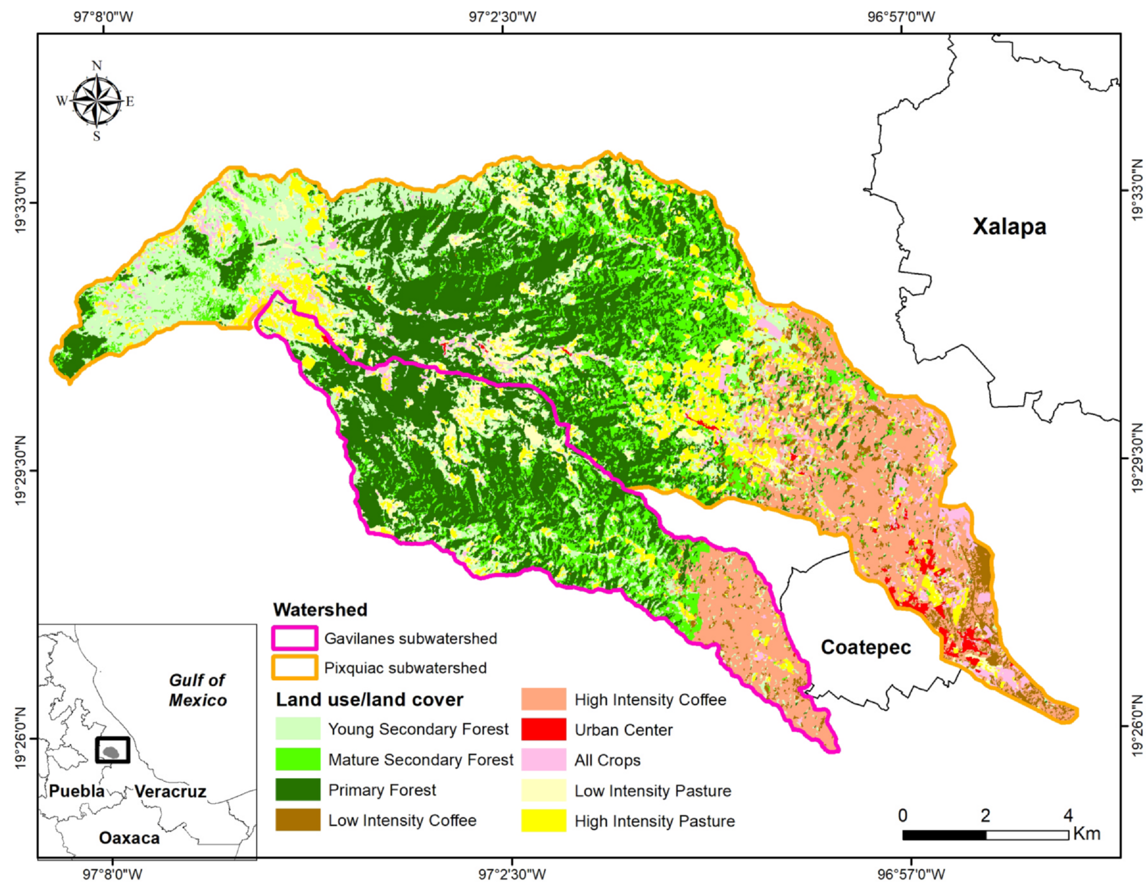

Fig. 1. Classified map of land cover/land use within the Pixquiac watershed in Veracruz, Mexico. The map includes the eight land uses analyzed in the study as well as urban locations. The classification came from 2014 SPOT imagery using at least 100 reference points and run in Trimple eCognition Developer 9.0 (adapted from Von Thaden et al., 2019).

Table 2
Summary of coverage of each land use/land cover type in this study across the Pixquiac watershed in Veracruz, Mexico. Values were all derived through a land use classification analysis (Von Thaden et al. 2019) conducted using 2014 SPOT imagery.

Land Use/Land Cover	2014 SPOT Classification (ha)	Percentage of Watershed
Young Secondary Forest	2054.60	19.4
Mature Secondary Forest	1466.58	13.8
Primary Forest	3065.20	28.9
Low Intensity Coffee	1462.72	13.8
High Intensity Coffee	379.23	3.6
Low Intensity Pasture	617.69	5.8
High Intensity Pasture	913.94	8.6
All Crops	538.44	5.1
Urban Center	114.86	1.1

catchment using a tipping bucket rain gauge. Two different setups were used, some catchments used a Campbell Scientific rain gauge (TE525MM, resolution 0.1 mm; Logan, UT, USA) connected to a data logger (CR1000) logging every 10 minutes while others used a Davis Instruments rain gauge (Model 6465, resolution 0.2 mm; Hayward, CA, USA) logging every 15 minutes. Measurements of rainfall ran from February 2015 to February 2019 while weir measurements began in July 2016 and ended in February 2019.

These measurements were used to calculate various hydrologic indicators at the daily and storm-event scale. Specifically, we focused on four indicators that are representative of the hydrologic "health" of a catchment. These indicators were the mean annual high flow, mean annual low flow, the quick flow regulation, and event flow regulation. It is important to consider multiple indicators of hydrologic regulation because the same LULC can lead to diverging responses that should be captured to assess the relationship between LULC and ES. Mean annual high flow was calculated as the mean flow rate of the highest 5% of flows recorded while the mean annual low flow was the mean of the lowest 5% of flows. Quick flow regulation was calculated as the stream flow rate during these periods divided by the event rainfall. The event flow regulation is a similar calculation except it considers the stream flow over the entire rainfall event divided by the event rainfall. Both indicators indicate how the streamflow within a catchment varies in response to discrete rainfall events. For further detail on hydrological modeling and additional analysis see López-Ramírez et al. (2020).

It should be noted that this suite of indicators reveals significant information about catchment hydrology but does come with some limitations. The mean annual high flow and mean annual low flow cannot account for differences in rainfall, geology, or groundwater storage across each catchment. Because of these concerns, we included event flow regulation and quick flow regulation that are standardized by the amount of rainfall in that event within that catchment. This approach reduces variation in the response as a function of rainfall. While we feel it is important to acknowledge these limitations, these data are highly robust, providing a solid foundation on which to analyze ES tradeoffs.

Soil hydraulic conductivity is a measure of the ability of a soil to transmit water and is therefore an ES indicator when studying hydrological services (e.g. Zimmermann et al., 2006). We measured field-saturated hydraulic conductivity (K_s) using a Guelph Permeameter (Soilmoisture Equipment Corp.). To minimize the confounding effects of soil type (e.g., parent material geochemistry and age) on K_s, we concentrated our sampling effort on sites within the Antigua watershed. We revisited the same forest, coffee, and pasture sites where we had conducted vegetation and carbon inventories. To expand our spatial coverage, we opportunistically sampled additional sites within each land-use type where landowners granted us access (n = 47). Soils across sites were dominated by clay- to silt-sized particles (i.e., low sand contents in all sites), with silt becoming increasingly abundant with elevation. The most common texture under forest and pasture was silty clay, whereas soils in coffee and sugarcane sites tended to exhibit higher clay contents (N. Looker, unpublished data). We augured a borehole to a depth of 25 cm at each of three points (separated by 5 m) in a line perpendicular to the local slope. The steady-state flow rate for each of two applied pressure heads (5 and 10 cm, verified by measuring the depth of ponding at the bottom of the borehole) was calculated from the change in water level in the permeameter reservoir. A single-headed approach was used (Elrick and Reynolds, 1992) by averaging K_s for the two heads applied to each borehole, and then estimating the geometric mean K_s for each site. Considering that K_s has previously been shown to vary by orders of magnitude within individual sites (Reynolds et al., 1992), the geometric mean summarizes the central tendency of infiltration capacity more robustly than does the arithmetic mean.

2.2.2. Water quality

For each stream, water quality was monitored near the outlet of each catchment. From May 2015 to June 2017, monthly samples of stream water were collected during baseflow conditions and taken back to the laboratory at the Instituto de Ecologia (INECOL, Xalapa, Veracruz, Mexico) for processing (26 total baseflow samples per catchment). Periodic sampling of storm water quality was conducted using towers with bottles at different heights installed in each stream. As water level rose, each bottle was fit with an s-shaped piping that only allowed water into the bottle. Between 8 and 28 storm events were captured for each catchment. Bottles were collected immediately following storm events and also processed at the laboratory.

All water samples were analyzed for nitrate, suspended solids, and coliforms. Nitrate, suspended solids, and coliform bacteria provide a good set of criteria to evaluate ES related to water quality. Numerous water quality indexes have been developed and most include these three parameters (Tyagi et al., 2013). Each ES indicator is driven by a different mechanism and thus each provides the land manager with unique information about the watershed. Nitrate is a good indicator of land use impacts related to agriculture and fertilization, suspended solids is a function of the amount of runoff and erosion occurring in the watershed, and coliform bacteria represent the influence of human and animal waste on water quality. We quantified nitrate levels using the brucine sulfate technique. The brucine sulfate technique uses spectrophotometry to quantify the reaction between nitrate ions and brucine sulfite. Total suspended solids were calculated using the gravimetric method, with samples filtered through 0.45 μm pore size polyamide membranes and the total mass of solids divided by the volume of water. Total coliforms were quantified using Coliscan Easygel (Micrology Labs Goshen, IN, USA) which requires counts of coliform colonies on petri dishes incubated with the water sample.

2.2.3. Carbon storage

Carbon was quantified from 65 plots sampled; 32 plots were within the 8 first-order catchments with 33 additional replicate plots sampled throughout the larger Pixquiac region. In each forest and coffee site, four 400 m^2 plot (diameter of 22.56 m) were established and GPS coordinates recorded (See Table S1 for plot locations). A correction factor for slope and horizontal distance was used to maintain the total projected ground area constant. Within each plot, for all individuals > 5 cm diameter at breast height (DBH), we determined GPS coordinates, DBH, estimated tree height, crown diameter, and species identity. Within each 2-m radius subplot, shrub and herbaceous layers were sampled. Woody individuals < 5 cm DBH and > 25 cm tall were identified to species level, and percent cover, and number of plants were recorded. For the herbaceous layer, percent cover of each species of herbs, grass and ferns was estimated visually by two researchers independently (see Vizcaino-Bravo et al., 2020). The individuals were identified in the field; herbarium specimens of unidentified individuals were collected for identification at the herbarium (XAL) at the Instituto de Ecología (INECOL). Fewer than 5% of species were distinguished as morphospecies.

To quantify aboveground carbon in pastures, only subplots were used due to the absence of trees within the pastures. Samples were dried and weighed for dry biomass and carbon quantified as 50% of the dry biomass (Brown and Lugo, 1982). To quantify crop carbon, we chose to measure a sugarcane crop. Our estimates likely represents an upper bound value on aboveground carbon storage from crop fields as the other predominant crops in the region (maize and potato) would be expected to store lower amounts of carbon. Further, of the crop coverage within the watershed, the majority of the area is devoted to sugarcane with the other crops often consisting of small plots maintained by a single landowner for subsistence use. To do this, we harvested all sugarcane biomass in 1 m^2 plots, oven dried it, and obtained the dry mass.

Within each plot soil organic carbon was sampled at three locations down to 1 m depth. Each of these sampling points was 7.3 m from the plot center and spaced at 120 degree angles. A half-round soil corer was driven into the ground with a hammer and soil samples separated from depths of 0–5, 5–15, 15–30, 30–60, and 60–100 cm. In the laboratory at INECOL, soil depth intervals were analyzed for carbon content using the dry combustion method (LECO elemental analyzer, Michigan, USA; Nelson and Sommers, 1996) and bulk density using the clod method (Blake and Hartge, 1986). Additional plot-based sampling was conducted in the same locations as the soil hydraulic conductivity measurements. After comparing the bulk density values, we obtained from the soil cores using the clod method with previously published values for soils in the region (e.g., Campos et al., 2007; Marin-Castro et al., 2016) and our own unpublished data from related work, we determined that bulk density was overestimated for the depth intervals due to compaction in sample collection. Consequently, we employed a Monte Carlo approach to estimate soil organic carbon storage and differences among LULC types by resampling the carbon content data from the soil cores and bulk density values we obtained with the ring method in a companion study in the Pixquiac watershed. The depth distribution of carbon content (% carbon by mass) was randomly paired with a topsoil (0–5 cm) bulk density and subsoil bulk densities values (5–100 cm). For each of the randomized pairings of carbon and bulk density, total carbon storage in the mineral soil (i.e., ignoring litter) was estimated by multiplying the mass of each soil layer (bulk density × layer thickness) by carbon concentration and summing across all layers. For each iteration, carbon storage was averaged by land-use type. The randomized pairing of carbon concentration and bulk density values and estimation of carbon storage by land-use type was repeated 1000 times.

These data were collated to produce estimates of total aboveground, coarse and fine root, total plant, soil, and total plot carbon. Aboveground biomass (AGB) was estimated from tree diameter and height using the following allometric equation for moist tropical forests from Chave et al. (2005):

$$AGB = 0.0509 * \rho D^2 H \tag{1}$$

where ρ is wood density, D is tree diameter, and H is tree height. A region-specific average of 0.64 was used for wood density (Berry unpublished data). Allometric equations from Cairns et al. (1997) were used to quantify root biomass (RB) where

$$RB = e^{(-1.0587+(0.8836*\,ln(AGB))} \tag{2}$$

Where AGB is above ground biomass calculated from Eq. (1). For both above- and belowground biomass, plant carbon was considered as 50% of the biomass (Brown and Lugo, 1982). To incorporate coffee plant biomass, we used the following allometric equation from Hairiah et al. (2001):

$$Biomass = N * (0.2811\ D^{2.0635}) \tag{3}$$

Where D is the diameter of the main stem and N is the total number of coffee plants in the plot.

2.2.4. Biodiversity

Vegetative biodiversity was calculated for each site using the Shannon Diversity Index for trees, shrubs, and herbaceous species as $H' = -\Sigma p_i \ln p_i$ where

$$H' = -\sum_{i=1}^{s} p_i \ln p_i \tag{4}$$

where p_i is the proportion of the ith species at each site, S is the number of species in each site. The Shannon Diversity Index is unitless and considers both species richness (total number of species) and evenness (how frequent each species is within the area). Because of sampling strategy, our study does not consider diversity of other taxonomic groups but acknowledges that the results may vary depending on the group (See Vizcaino-Bravo et al., 2020 for additional analysis and commentary on biodiversity in the region). Generally, floral diversity is positively correlated with faunal diversity across taxonomic groups and serves as a good proxy for overall diversity (Castagneyrol and Jactel, 2012).

2.2.5. Analysis

To compare the potential value of each ES, we assessed them using standardized scores (SS) of associated indicators that consider both the mean and standard deviation of the population. Specifically, we calculated the number of standard deviations difference between the mean of any given land use and the mean for primary forests (z-score; Zar, 1999). Since primary forests are what mostly receive ES payments in the region, all land uses were considered relative to primary forests. Thus, for each indicator of interest, if an SS is negative, then it has lower ES provisioning for that indicator than primary forests. In cases where an SS is positive then the ES provisioning is greater than primary forests. The SS value for each ES was also summed together within each LULC to obtain a total ES indicator score.

To determine whether ES provisioning changes across LULC types we conducted a one-way analysis of variance (ANOVA) and compared means using Tukey's honestly significant difference (HSD). This method was used for mean annual high flow, mean annual low flow, carbon storage, biodiversity, and all water quality parameters as response indicators. Event flow regulation and quick flow regulation were analyzed using the Dunn test and means compared using the Kruskal-Wallis test. For soil conductivity, the Tukey correction for multiple comparisons was applied to tests of significance. Satterthwaite approximation was used to obtain degrees of freedom. Linear regressions were used to explore tradeoffs in ES indicators. This was chosen over multivariate alternatives due to different ES indicators being collected at different scales (hydrology at the catchment scale; carbon, biodiversity, and soil conductivity at the plot scale) necessitating analysis of the LULC means only. While Lee and Lautenbach (2016) suggests that this could change the relationship between ES indicators, we are confident that our regressions reflect true relationships since data were collected in the same locations. All data analysis was conducted in R (version 3.4.2) or JMP (version 13.2, SAS Institute, North Carolina, USA).

3. Results

3.1. Hydrologic regulation

There were strong differences in mean annual high and low flows across LULC types (Fig. 2a, mean annual high flow $F_{7,44} = 35.1$, $p < 0.001$; Fig. 2b, mean annual low flow $F_{7,4897} = 173648$, $p < 0.001$). High flows were greatest in catchments dominated by primary forests and intensive pasture while the lowest values were in sugarcane. Low flows were greatest in primary forests and mature secondary forests while the lowest low flows were in low intensity coffee and sugarcane. These results highlight the strong variation in flow regulation based on predominant land use alone. Both quick flow regulation and event flow regulation exhibited some apparent differences but due to strong variance in these responses there were no significant differences across LULC (Fig. 2c and d).

Soil hydraulic conductivity was greatest in primary forests and mature secondary forests (Fig. 2e) but was only significant using pairwise means from intensive pasture. Young secondary forests and low intensity coffee sites had similar values (~9 cm h^{-1}), while all remaining land uses (intensive coffee, low and high intensity pastures, and sugarcane) had hydraulic conductivity values that were similarly low (2.5–5.7 cm h^{-1}).

3.2. Water quality

Stream water quality presented varying results depending on the indicator analyzed (Fig. 3). Suspended solids during high flow periods were typically at least 10 times greater than during base flow periods across all land uses (Fig. 3a and b). Suspended solids during baseflow periods showed a significant effect of land use, but not always in ways predicted ($F_{8,439} = 3.31$, $p < 0.001$). The highest values were in low intensity coffee and sugarcane (0.057 ± 0.016 and 0.037 ± 0.003 g L^{-1}, respectively), which were significantly greater than mature secondary forests, high intensity coffee, and both pasture systems. There were no significant differences in high flow suspended solids across land uses ($F_{7,108} = 1.23$, $p = 0.29$), suggesting that runoff was high enough in all land uses to minimize any differences in suspended solids seen in the base flow suspended solids. Coliforms were greatest in sugarcane and low intensity coffee (Fig. 3c, 21024 ± 878 and 20140 ± 996 # 100 mL^{-1}, respectively) which were 32–72% greater than all other land uses except for intensive pasture ($F_{7,406} = 7.75$, $p < 0.001$). Nitrogen concentration was generally low (< 0.3 mg L^{-1}) in all land uses except for both coffee sites, which had values over 1.0 mg L^{-1} (Fig. 3d, $F7_{,192} = 49.2$, $p < 0.001$).

3.3. Carbon storage

Total carbon storage was greatest in the primary forest with an average of 332 ± 45 Mg ha^{-1} when both above and below ground carbon were considered (Fig. 4). This value was nearly double that of both secondary forests (mature secondary: 171 ± 18 Mg ha^{-1}; young secondary 171 ± 17 Mg ha^{-1}) and significantly greater than all other land cover types ($F_{7,57} = 18.61$, $p < 0.001$). Both secondary forest ages had similar total carbon suggesting rapid recovery of carbon stores by young regenerating secondary forests. Total carbon was lower but also similar for coffee and sugarcane, while pastures had the lowest values. Coffee carbon storage was 77 ± 19 Mg ha^{-1} for high intensity coffee and 99 ± 12 Mg ha^{-1} for low intensity coffee. The sugarcane value reported (87 ± 17 Mg ha^{-1}) considered total carbon storage for mature crops when sugarcane is fully grown. Thus, for much of the year, when the crop is still growing, carbon storage would be much lower. These calculations also do not consider the carbon liberated when fields are burned immediately prior to harvest.

3.4. Biodiversity

Biodiversity scores were similar across all forest types (Fig. 4) suggesting that even the young secondary forests can harbor similar levels of biodiversity as primary forests ($F_{7,43} = 59.5$, $p < 0.001$). Despite similar scores, the analysis done by Vizcaino-Bravo et al. (2020) in these sites finds that the species composition was different across forest

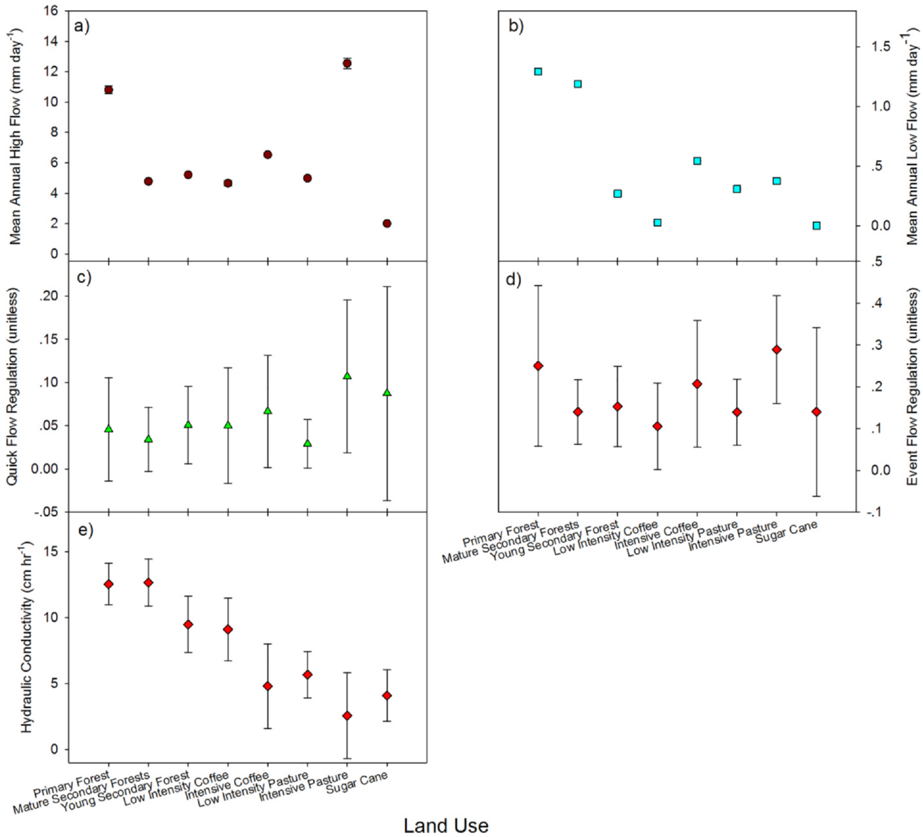

Fig. 2. Ecosystem hydrologic parameters used to analyze ecosystem service tradeoffs across land cover/land use. The figure shows (a) mean annual high flow, (b) mean annual low flow, (c) quick flow regulation, (d) event flow regulation, and (e) soil hydraulic conductivity across eight land uses in Veracruz, Mexico. Points represent averages and error bars are standard deviation. For (a) and (b), error is small and thus error bars are not visible.

sites. Low intensity coffee had the next highest diversity score which was significantly greater than intensive pasture and sugarcane.

3.5. Integrated analysis of ecosystem services

All forest types had greater net ES provisioning than the remaining land uses when comparing standardized scores (SS; Table 3, Fig. 5). Mature secondary forests had similar net SS as primary forests. Surprisingly, both coffee intensities had very low net SS (−10.89 and −9.53), closer in value to high intensity pastures (−10.70) and sugarcane (−10.55) than to primary forests. The difference was driven particularly by the low values for carbon, biodiversity, nitrogen concentration at base flow, and soil hydraulic conductivity (Fig. 5). Also notable was the net SS of the low intensity pasture (−7.01), which was higher than high intensity pasture and sugarcane and can be explained by positive water quality values. Sugarcane had low SS for carbon,

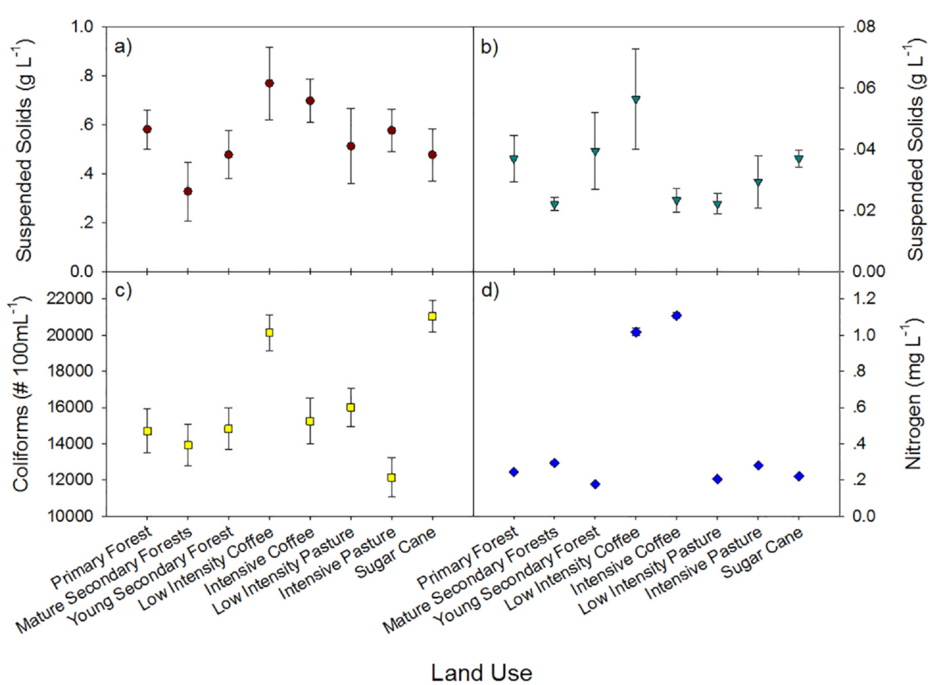

Fig. 3. Ecosystem water quality parameters used to analyze ecosystem service tradeoffs across land cover/landuse. The figure shows (a) suspended solids in peak flows, (b) suspended solids in base flows, (c) coliform concentration, and (d) nitrogen concentration across eight land uses in Veracruz, Mexico. Points represent averages and error bars are standard error.

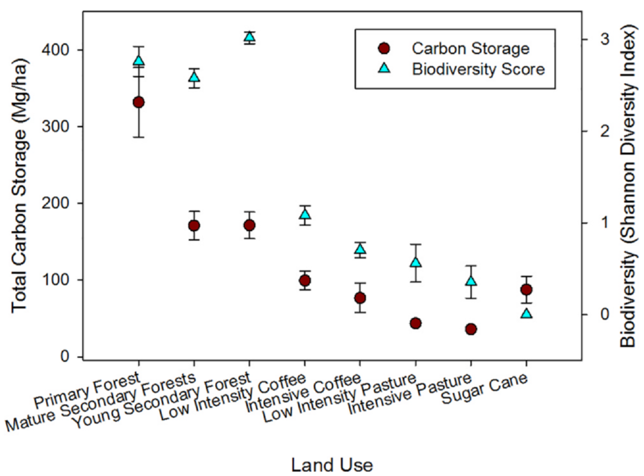

Fig. 4. Total carbon storage (circles) and biodiversity (triangles) values across the eight land cover/land use categories in Veracruz, Mexico. Points represent averages and error bars are standard error.

biodiversity, and stream flow indicators but had nutrient values similar to primary forests.

3.6. Tradeoffs among ecosystem services across land uses

Linear regressions between ES revealed several expected synergies and tradeoffs among services as well as some unexpected results (Fig. 6). There were consistent positive relationships between carbon storage, mean annual low flow, and soil hydraulic conductivity. (Fig. 6a and e). This suggests that greater vegetation increases soil conductivity which, in turn, regulates mean annual low flow, carbon storage, and to an extent, biodiversity (Fig. 6c and e). As expected, there was also a significant positive relationship between carbon storage and biodiversity (Fig. 6c). Surprisingly, there were no significant relationships between water quality indicators and most other ES measured. The only exception was a negative relationship between coliforms and mean annual high flow (Fig. 6b). Additionally, there was no relationship between stream flow regulation parameters (event regulation or quick flow regulation) and any other ES indicator measured (carbon, biodiversity, or water quality). Finally, event flow regulation had a negative relationship with mean annual high flow (Fig. 6d) and quick flow regulation had a positive relationship with soil conductivity (Fig. 6f). These findings are explored further in the discussion.

4. Discussion

There has been a persistent call by the ES community for more studies that empirically assess relationships between ES and LULC types in poorly studied regions of the world (Tallis et al., 2008; Bennett et al., 2009). This is due to the fact that the study of ES has shifted to larger landscape-scales but often relies on simplified assumptions about ES provisioning across these LULC types. We find that collecting site-specific data reveals interactions, or lack thereof, between ES that would not have been known by relying on assumed positive relationships between tree cover and ES provisioning. For example, when all ES were aggregated together, primary and mature secondary forests had greater ES provisioning than other land uses in our study area, but other tree-based land uses such as shade-grown coffee did not exhibit high ES provision (Net Standardized Score, Table 3). We also find that many measures of water quality and hydraulic regulation did not exhibit synergies with carbon and biodiversity ES. The lack of a relationship between these indicators may lead to a lack of improved ES provisioning or unintended consequences as a result of LULC change in the region. Below we explore some of these unexpected outcomes from our analysis.

4.1. Ecosystem service provisioning across land use

We find that conversion of primary forests to all other land uses in the study would result in net decreases in ES provisioning, with the exception of mature secondary forests, which have similar net ES provisioning as primary forests when averaged across all ES measured (Objective 1). Greater mature secondary forest ES was driven predominantly by similar hydraulic regulation, water quality, and biodiversity SS as those of primary forest. Further, even young secondary forests still exhibit good ES provisioning relative to other land uses. Increased vegetation could enhance soil properties that promote infiltration and lead to greater hydrologic regulation and water quality. The net suite of benefits from forests of all ages is particularly encouraging for conservation efforts suggesting that reestablishment of previously managed lands to forests can provide similar benefits to hydrologic outputs and biodiversity, even as young secondary forest (< 20 years old in our study). Thus, targeting PHS programs to promote and protect natural regeneration of ecosystems should improve ES provisioning in relatively short periods of time.

In contrast to a number of other studies (e.g. Jose, 2009; De Beenhouwer et al., 2013; Jha et al., 2014) we find that the shade-grown coffee farms of the region have relatively poor ES provisioning across all metrics. Water quality, base flow, soil hydraulic conductivity, carbon, and biodiversity all had ES values substantially lower than all three forests ages. While there are some calls for coffee agroforestry systems to be incorporated into PHS programs because they have closed canopies (albeit less dense), this study reinforces that canopy cover does not necessarily lead to similar ecosystem services as mature forests (Manson et al., 2008; Lewis et al., 2019). Managers of traditional coffee plantations used fewer fertilizers and pesticides (Pers. Comm. Gomez Aguilar) and supported higher densities of understory vegetation cover, which we expected would yield more favorable ES, but this was not the case. Traditional coffee sites still support high levels of human activity and rarely incorporate riparian buffers which could further diminish hydrological ES (Martínez et al., 2009).

Table 3

Summary of the standardized score values of hydrologic regulation parameters (blue), water quality parameters (brown), and carbon/diversity tradeoffs (green). These values are used for Figs. 5 and 6 and derived as the standardized difference from the primary forest. Thus, primary forests net as zero on this scale and a positive or negative value signifies greater or lesser ecosystem service provision by that land use relative to primary forests.

Land Cover/Land Use	Mean Annual High Flow	Mean Annual Low Flow	Quick Flow Regulation	Event Flow Regulation	Soil Conductivity	High Flow Suspended Solids	Base Flow Suspended Solids	Coliforms	Nitrogen Concentration	Total Carbon Storage	Biodiversity	Net Standardized Score
Primary Forest	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**0.00**
Mature Sec. Forest	1.72	-0.21	0.44	-1.72	0.03	0.59	0.41	0.09	-0.11	-1.30	-0.16	**-0.22**
Young Sec. Forest	1.60	-2.09	-0.18	-1.52	-0.79	0.25	-0.07	-0.02	0.15	-1.34	0.22	**-3.79**
Low Intensity Coffee	1.76	-2.58	-0.16	-2.26	-0.89	-0.44	-0.54	-0.65	-1.70	-1.97	-1.46	**-10.89**
High Intensity Coffee	1.22	-1.52	-0.78	-0.68	-2.00	-0.27	0.38	-0.07	-1.90	-2.12	-1.79	**-9.53**
Low Intensity Pasture	1.66	-2.00	0.62	-1.73	-1.77	0.16	0.41	-0.16	0.09	-2.41	-1.88	**-7.01**
High Intensity Pasture	-0.50	-1.87	-2.29	0.61	-2.58	0.01	0.21	0.31	-0.08	-2.46	-2.06	**-10.70**
Sugar Cane	2.52	-2.63	-1.55	-1.72	-2.18	0.24	0.00	-0.76	0.05	-2.12	-2.40	**-10.55**

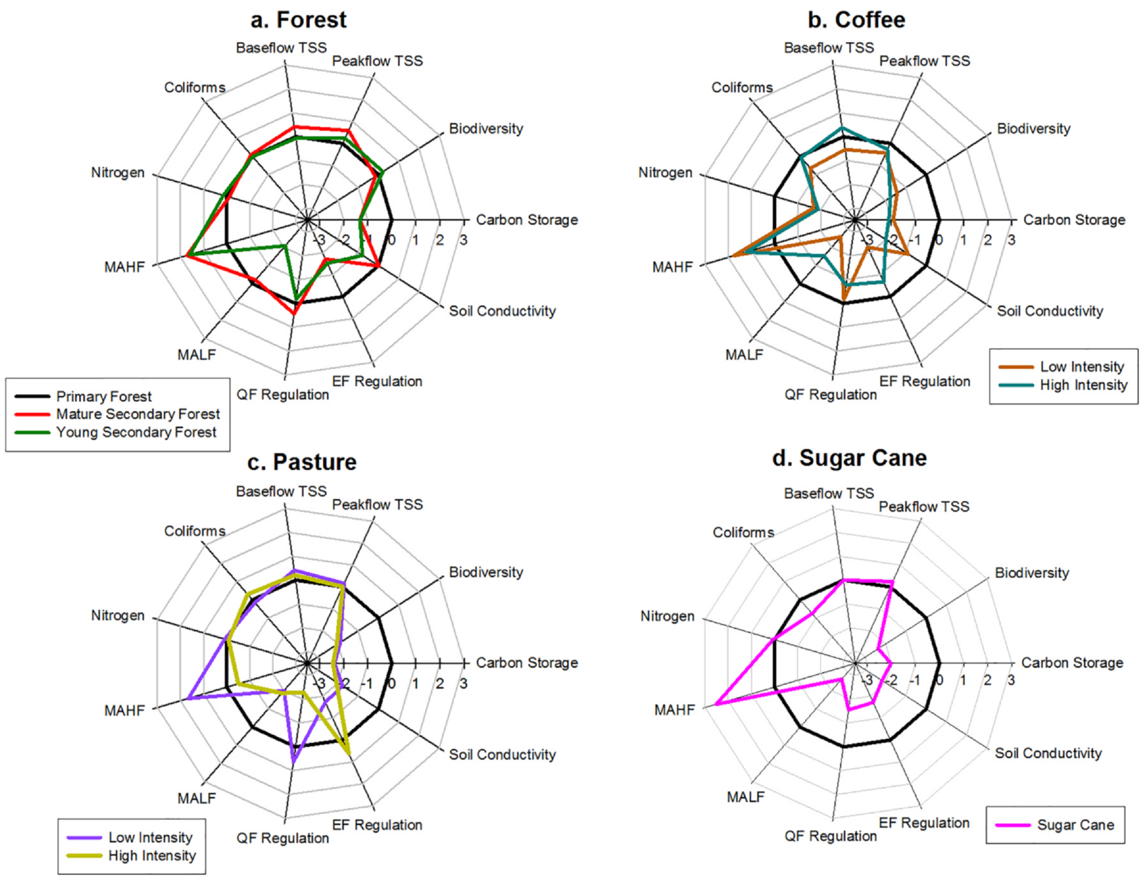

Fig. 5. Radar plots of the standardized scores of each land cover/land use across the ecosystem services in this study. In each, the black line represents the mean value of the primary forest plots which was used as a reference value. Where the study line is inside of the black line, the net effect of conversion to that land use would be negative. Where the study line is outside the black line represents a net improvement for that service if converted from primary forest. Total radar plots are grouped by (a) forest, (b) coffee, (c) pasture, and (d) sugarcane. Abbreviations are used for total suspended solids (TSS), event flow (EF) regulation, quick flow (QF) regulation, mean annual low flow (MALF), and mean annual high flow (MAHF).

Several studies have found greater ES provisioning from traditional (low intensity, extensive) shade coffee plantations compared to more intensively managed shade coffee plantations, including carbon storage (De Beenhouwer et al., 2016; Guillemot et al., 2018), water quality (Quintero et al., 2009; Jesus-Crespo et al., 2016), infiltration rates (Meylan et al., 2017), and biodiversity (López-Gómez et al., 2008; Guillemot et al., 2018). Moreover, these studies have even suggested that traditional shade coffee systems maintain similar carbon stocks (Tadesse et al., 2014; De Beenhouwer et al., 2016; Guillemot et al., 2018) and hydrologic regulation services (Marin-Castro et al., 2016) as the mature forests that they replaced. We find that ES provisioning of coffee is lower than forests and not affected by management intensity, supporting one other study to date (Cerda et al., 2017). Low ES provisioning relative to forests is likely due to high human activity in both high and low intensity coffee sites. While we did not quantify the degree of human activity or machinery use, both catchments had many paths and dirt roads bisecting the watershed. Community members were also routinely seen within the catchments while conducting this research. Increases in human activity can also influence stream water quality and runoff (Wei et al., 2007; Zhang et al., 2012). Overall, our results suggest that, no matter the management strategy, coffee farms in the region ultimately lead to reduced ES provisioning and should not be considered as a clear alternative for PHS programs.

4.2. Tradeoffs and synergies across ecosystem services

There were strong synergies between carbon storage, biodiversity, mean annual low flow, and soil hydraulic functioning whereby provisioning for one allowed for greater provisioning of the others (Objective 2). However, there were no statistical relationships (positive or negative) between water quality parameters and the remaining ES (with the exception of a negative relationship between coliforms and mean annual high flow). The meta-analysis of Lee and Lautenbach (2016) also finds no relationship or an undecided relationship between water quality and eleven of the sixteen other ES measured. There were also unexplained negative relationships between event flow regulation and mean annual high flow. This suggests that the assumed synergies and tradeoffs that often underpin landscape-scale ES assessments (Naidoo and Ricketts, 2006; Nelson et al., 2009) were not found (i.e., decreasing water quality with LULC changes). However, we do not conclude that there are not synergies and tradeoffs between ES as have been demonstrated in other studies (e.g. Lee and Lautenbach, 2016 and associated references). Instead, site-specific heterogeneity and unknown factors that cannot be captured in landscape-scale relationships lead to predicted synergies or tradeoffs not applying to a specific location where land-use and management decisions are made. There are several unobserved factors that could drive each ES in different directions. For example, use of streams by communities can vary across land uses and affect water quality (Yillia et al., 2008). The lack of tradeoffs could also be explained by the complexity of land uses within each catchment. The heterogeneity of land use within each catchment could have had a disproportionate influence on the ES measured despite being dominated by a certain LULC type. Additionally, the location of the dominant cover relative to streams could affect how each ES alters hydrologic and water quality ES indicators. No matter the mechanism for our results, the lack of clear relationships demonstrates that

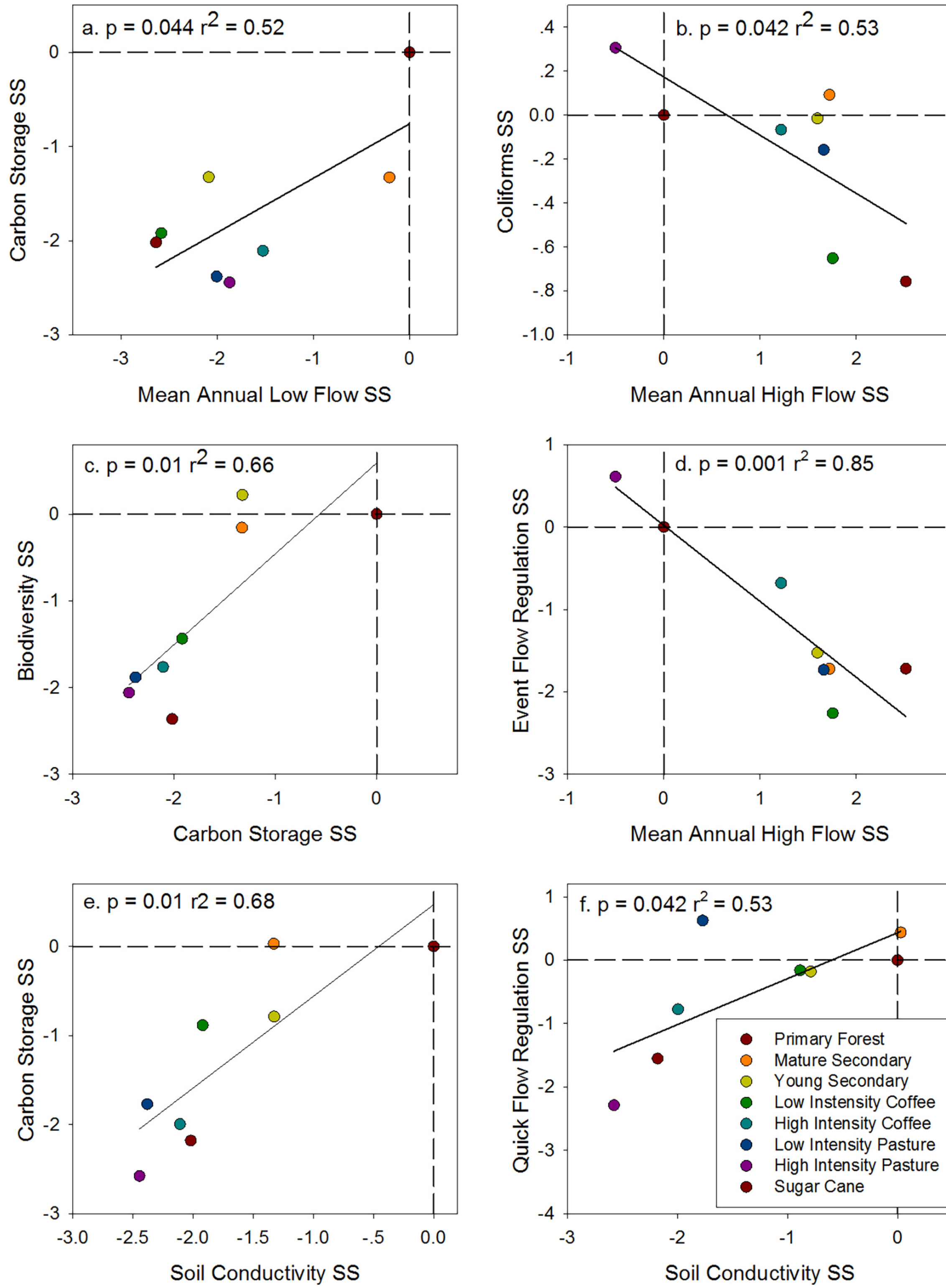

Fig. 6. Linear regression relationships between ecosystem service benefits provided by each land cover/land use. Each figure represents the land use aggregated relationship between the standardized scores (SS) derived for each parameter. Where relationships are significant, the line is included on the figure and the r^2 relationship is noted. Positive values represent ecosystem service provisioning greater than primary forests while negative values represent lower ecosystem service provisioning than primary forests.

determining ES provisioning simply on land use may not lead to accurate results.

There is a current debate about whether there are "tradeoffs" (i.e. negative relationships), "synergies" (i.e. positive relationships), or no relationship amongst various ES (e.g. Rodríguez et al., 2006; Lele et al., 2013; McShane et al., 2011; Howe et al., 2014). In our study, we find that across diverse land uses, there is no consistent set of synergies in ES provisioning across LULC types, particularly with water quality or hydrologic regulation and the other measured ES. This was somewhat surprising as the meta-analysis of Pretty et al. (2006) found that improving agricultural practices improved water quality, carbon sequestration, and water balance all simultaneously, although it should be noted that the scale of that study was much larger than the current one. That study analyzed case studies from countries around the world while this study takes a very focused look at the empirical ES data within a specific region. Our comparison across eight different land uses does not reveal synergies between water quality and carbon parameters. Instead, we find very strong and positive relationships between carbon storage, biodiversity, and soil hydraulic properties. Evidence from this analysis highlights that tradeoffs and synergies between ES can not necessarily be predicted by generalized relationships, stressing the importance of having an empirical, region-specific data set on which to base policy and management decisions.

4.3. Limitations

The data presented in this study are important for decision makers but there are still limitations to how our data should be interpreted. The relationship between LULC and ES provisioning is often confounded by heterogeneity in LULC, geology, and topography of sites (van Dijk et al., 2011). While we sought catchments dominated by one land use, the percent coverage of that land use within the catchment may affect linking ES provisioning to LULC. The percent coverage by the dominant land use varied from ~50% to greater than 90% (López-Ramírez et al., 2020). In addition, the position of the dominant land use relative to streams, as well as the composition and distribution of other land uses are in the catchment, will also influence catchment hydrology. Further, each catchment has varying areas, slopes, soils, and geologies that influence water flows as well. All of these parameters will increase variation in the relationship between LULC and ES provisioning. Additionally, this study only quantified hydrological metrics in one catchment per land use types which limits our ability to interpret how these relationships might hold across other landscapes. We accounted for these differences by using hydrological metrics that controlled for precipitation of the site.

While these concerns may seem like a limitation, they ultimately reflect the reality of highly heterogeneous LULC within complex montane landscapes. Few catchments are dominated by a single LULC and thus this complexity needs to be further addressed to improve our understanding of ES provisioning in montane regions. Despite these caveats, the long-term data set and replication of plot level data reveal a site specific ground-level analysis that is invaluable to our understanding of ES provisioning.

4.4. Policy implications and conclusions

Understanding tradeoffs and synergies has important implications for designing effective PHS policies, and other natural resource management actions, that seek solutions that optimize a particular ES or create an optimal balance among several ES. Decisions related to the design of PHS policies typically rely on the assumed benefits of forest cover to hydraulic regulation or water quality. However, the preservation of forest over other managed land use types will not always lead to greater water quality or hydraulic regulation. For example, this study finds improved water quality in pastures as well as forests demonstrating that LULC is not the only factor driving water quality. In addition, this study also demonstrates a weak or no relationship between water quality and other ES provisioning. Thus, maximizing “hydrological services” within a PHS program may inhibit the ability to enhance provisioning of other services important to certain beneficiaries.

The ultimate goal of PHS programs is to maximize ecosystem services within a region but it is simply impractical to return all land to primary forest. The shade-grown coffee farms of the region provide great potential to promote ES provisioning relative to other managed LULC and there have been proposals to incorporate them into PHS programs. We suggest that to be considered in PHS, there should first be an active approach to promoting better management practices that enhance ES provisioning. This could include promoting soil stability, modifying fertilization and pesticide treatments, reducing human use of streams, and promoting tree species with greater carbon storage. If this occurs, then we would expect improved ES provisioning as has been seen in other studies (Quintero et al., 2009; De Beenhouwer et al., 2016; Jesus-Crespo et al., 2016; Guillemot et al., 2018) which could lead to incorporation into PHS as in other countries (e.g. Costa Rica LeCoq et al., 2011). Changes to management practice could be combined with community based monitoring of ES to educate and encourage more sustainable practices (Danielsen et al., 2009; Shirk et al., 2012). This approach would allow land managers to maintain their productive activities while also enhancing ES provisioning.

It is admittedly labor-intensive to collect thorough, site-specific data sets to assess ES provisioning. Even within this study, which collected data across many sites through multiple years, there are still limitations to the conclusions we can draw. Landscapes exhibit incredible heterogeneity in LULC history, geology, and topography, yet, land managers have to make decisions about ES management using landscape-scale approaches that allow for ES quantification over large regions. Both types of assessments can provide value as the former is more accurate for site-specific policy decisions while the latter allows for conclusions at larger spatial scales; combining these two approaches can result in more robust assessments (Rieb et al., 2017). Our results demonstrate that, broadly, ES provisioning is positively related to the extent of primary forests and thus landscape-scale analyses in similar regions that are based on assumptions about tree cover-ES provisioning are supported. However, when ES assessments strive to quantify the effects of LULC changes on specific ES and the associated synergies and tradeoffs across ES, then care should be taken. It is critical to note that this complexity would not be captured if each broad ES were distilled into a single value. Inherently, each ES indicator is valuable in the right context and how and when to bundle services needs to be methodically analyzed. Future research should further explore the optimal “balance” between allocating funds towards site-specific assessments and landscape ES quantification that will consider regional complexity and minimize error in the conclusions. This may involve creative ways to incorporate site data from remote locations, such as citizen science or complementary high-resolution remote sensing of key areas. As more studies reveal patterns around synergies or tradeoffs between services, a clearer picture of these complex relationships can be established which will allow for more informed design of conservation policies and land use management strategies that can maximize ES benefits for the well-being of individuals and communities.

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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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://

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