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Value and benefit distribution of pollination services provided by bats in the production of cactus fruits in central Mexico

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ABSTRACT

Despite providing important ecosystem services in both natural and agricultural systems in the tropics, bats are often disregarded or considered pests; and research quantifying their importance as pollinators is scarce. We quantified the value and benefit distribution of bat pollination in the production of a major fruit crop in Mexico (pitayas, *Stenocereus queretaroensis*). We used exclusion experiments to quantify the effect of bat pollinators on crop yield and quality. We then used yield analysis to assess the market value of pollination services, combined with value chain analysis to assess the distribution of these economic benefits among actors. Bat pollination services to pitaya production are worth approximately US$2,500 per ha through increases in both fruit yield and size, with bats contributing around 40% of gross income across producers. Participation in the pitaya value chain provides a key seasonal source of cash income at a time of low agricultural activity, supporting livelihoods and household activities of the rural poor. However, the commercialisation of the pitaya has concentrated economic benefits with privileged groups who have access to land and markets. Our novel approach to valuing pollination services is transferable to other crops and pollinator species to demonstrate disaggregated socio-economic consequences of losing pollinators.

1. Introduction

Pollinators provide many benefits to humans, improving food production and security, and underpinning biodiversity and crucial ecosystem functions (Potts et al., 2016a). Nearly 90% of flowering plants are reliant on animals for pollination (Ollerton et al., 2011), with three quarters of leading global crops, particularly those that are richest in micronutrients, showing increases in production or quality when pollinated by animals (Eilers et al., 2011; Klein et al., 2007; Potts et al., 2016b). Bats pollinate many plants of high socio-economic value across the tropics (Kunz et al., 2011). However, bat populations are threatened in many parts of the world, with 80% of bat species requiring research or conservation attention (Frick et al., 2019), and the value of bats to the maintenance of ecosystems and human wellbeing is largely underestimated (Kingston, 2016).

The quantification of ecosystem service benefits in monetary terms is frequently used to support biodiversity and ecosystem conservation, though it is a complex and challenging issue, particularly where services are intangible and cannot be valued through existing markets (Adams, 2014; Hanley et al., 2015; Breeze et al., 2016). However, the economic valuation of pollination services, such as the direct contribution of pollinators to commercial crop production and quality, can be a useful mechanism to alert decision-makers to the consequences of losing pollinators (Hanley et al., 2015). Existing assessments of pollination services have either focused on the economic importance of insect pollinators, primarily honeybees (Gallai et al., 2009; Winfree et al., 2011; Hanley et al., 2015) or have established the role of bats as pollinators of tropical crop species, such as durian and fleshy fruits of columnar cacti (e.g. Ibarra-Cerdeña et al., 2005; Bumrungsri et al., 2009; Aziz et al., 2017). To our knowledge, none have directly valued the

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effects of bat pollinators on yield and quality of a commercial crop in economic terms (though see Sheherazade et al., 2019 for a rough estimation of the value of bat pollination to durian production in Indonesia).

One important issue is that, worldwide, ecosystem service benefits – including those of pollination services – are not distributed equitably between different social groups (Hassan et al., 2005). Rural and traditional populations in poor areas are often more dependent on ecosystem services for their livelihoods and will be disproportionately affected by declines in pollinator populations (Hassan et al., 2005; Kumar, 2012). Subsistence or smallholder farmers are less likely to have the economic power to switch to different crops if production fails, or to replace free wild pollinator-mediated services with bought services (Morton, 2007). At the same time, the ecosystem service benefits to different stakeholders depend on many socio-economic factors, such as market accessibility, land rights, and opportunity costs of labour and land (Shackleton et al., 2008). While access to ecosystem services can have an equalising impact on rural households, where there are constraints to access, some groups may be further marginalised (Kamanga et al., 2009). There is a considerable gap in the literature concerning the distribution of ecosystem service benefits across different stakeholders, particularly in Latin America; and a subsequent need for disaggregated analysis to identify constraints and improve access (Carpenter et al., 2006; Daw et al., 2011; Breeze et al., 2016; Laterra et al., 2019).

This paper uses the pollination by bats of an important cash crop in Mexico, the pitaya (*Stenocereus queretaroensis*) as a case study. Bats in the *Leptonycteris* genus are the principal pollinators of *S. queretaroensis*, enhancing both yield and quality of the pitaya crop (Tremlett et al., 2020). *Leptonycteris yerbabuenae*, the lesser long-nosed bat, and *L. nivalis*, the greater long-nosed bat, are species of nectar-feeding migratory bats distributed from Central America to the southern U.S.A. (Cole and Wilson, 2006). They are important pollinators of columnar cacti and agaves throughout their range, which play keystone ecological roles in arid ecosystems by providing structural resources, nutrients and water for a variety of animals (Frick et al., 2014).

The two main goals of this study are to a) quantify the value of pollination services to the pitaya sector in the most important production centre, and b) assess how these economic benefits are distributed between different actors throughout the pitaya commodity chain. Increased awareness of the economic importance of the contribution of bat pollination services may enable local communities and decision makers to take appropriate actions to ensure the protection of bat pollination services. A greater understanding of how these benefits are distributed intends to inform how future policies can enable more equitable access to, and participation in, the pitaya chain.

We use a direct yield analysis approach to estimate changes in both crop yield and quality between open pollinated and pollinator-excluded pitaya crops, and use current market prices to value these changes (Fig. 1). Yield analysis is particularly useful for assessing benefits of pollination services at a local level, directly capturing the benefits of pollination services to a crop and differences between cultivars (Breeze et al., 2016; Potts et al., 2016b). However, only benefits accruing directly to the producer are measured using this method. We therefore use value chain analysis to assess how the economic benefits are distributed among different actor groups, affecting livelihoods and wellbeing more widely (Bolwig et al., 2010; Schaafsma et al., 2014; Fig. 1).

A value chain describes the system and processes that occur along the chain of the production of a commodity and is often used to identify inequalities and constraints in the chain, particularly from the perspective of weaker actors (Kaplinsky and Morris, 2002; Meaton et al., 2015; M4P, 2008). Assessment of profits earned is a useful mechanism to identify barriers in the chain, as greater barriers to particular roles result in higher profits (Kaplinsky and Morris, 2002). However, it is also important to evaluate the returns to labour earned by different actors in the value chain. The poor must often work long hours to meet household needs, indicating 'time poverty' even where daily income is sufficient to provide wellbeing (Bardasi and Wodon, 2010). In this paper, we use

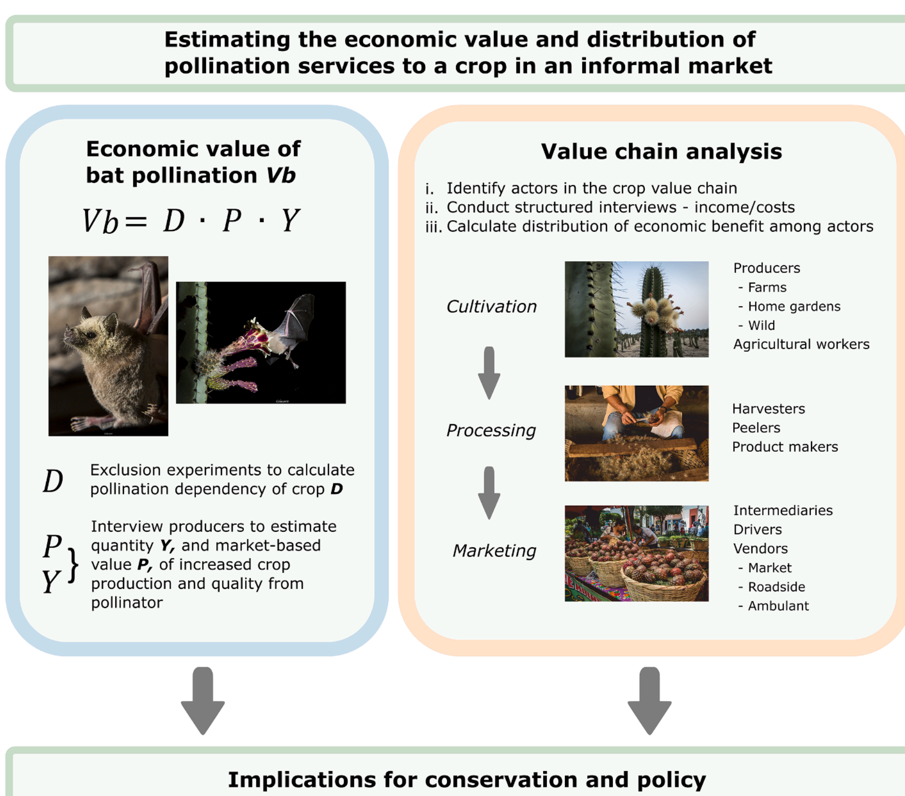

Fig. 1. Synthesis figure of the valuation approach.

interview data to assess how income is distributed among actors using distribution of profits and hourly wages as indicators of inequality. We then assess the constraints faced to access more profitable roles and suggest potential mechanisms to encourage fairer participation in the chain by actor groups.

2. Study system

2.1. Study site

In Mexico, 85% of all cultivated plant species are at least partly dependent on animal pollinators; this, combined with high poverty levels and population densities, means that pollination services are crucially important to a large component of the population (Ashworth et al., 2009). Most columnar cacti (Cactaceae) are highly dependent on bats for pollination, including all 22 members of the *Stenocereus* genus, which have been widely utilised for fruit production in Mexico since pre-Hispanic times (Casas et al., 1999; Kunz et al., 2011). However, pollinating bat species continue to be threatened in Mexico by land use and climate change, mining, and disturbance at roost sites (Zamora-Gutierrez et al., 2018; Frick et al., 2019).

Techaluta de Montenegro is one of the most important areas for the commercial production of the pitaya, the fruit of *Stenocereus queretaroensis,* a species of arborescent columnar cactus endemic to central-western Mexico (Ibarra-Cerdeña et al., 2005; Pimienta-Barrios and Nobel, 1994). Home garden cultivation of *S. queretaroensis* has occurred since the late 1800s, while intensive commercial production of pitayas began in the 1970s (Pimienta-Barrios, 1999). Low input requirements of water, fertilisers and pesticides result in a substantial financial return (Pimienta-Barrios, 1999). Additionally, the tolerance of *S. queretaroensis* to drought and poor soils, as well as the production of fruit in the dry season when other crops are scarce, make it a sustainable crop in the arid production area (Pimienta-Barrios and Nobel, 1994).

The municipality of Techaluta de Montenegro has an area of 79 km^2 (Mejía Rodríguez, 2012), nearly 40% of which is used for agriculture (INEGI, 2009). The main crops by registered volume (tonne) produced in Techaluta de Montenegro are alfalfa (13726 t), hay/pasture (4496 t), maize (3173 t), pitaya (719 t), avocado (700 t), sorghum (484 t) and squash (329 t) (SIAP, 2018). The pitaya generates the highest price per tonne of any crop grown in Techaluta de Montenegro, with a value of approximately Mex$19,200 / US$998 per tonne (SIAP, 2018). Registered pitaya production is expanding yearly, increasing by 71% between 2003 and 2018, from 420 t to 719 t (SIAP, 2018). This growth is driven by an increase in area under production (56 ha registered in 2003 to 86 ha in 2017; SIAP, 2018). Figures for both pitaya production and value are underestimates however, as much production is not officially registered with the government.

2.2. Pitaya value chain

The key stages in pitaya production are cultivation, processing (harvesting, peeling fruits, making products), marketing, and consumption. Pitaya production in Techaluta de Montenegro is dominated almost entirely by small commercial plantations and home gardens (Pimienta-Barrios, 1999). The value chain is short, due to the high perishability of the fruit (fruits must be eaten within one to two days of harvest) and subsequent localised market (Pimienta-Barrios, 1999). Most fruits are sold fresh, but a small but increasing proportion is used to make products. Producers largely sell fruits directly to the consumer, either at the roadside or at a market. Actors commonly have multiple functions in the value chain, and the use of intermediaries (defined here as an agent that buys fruit from producers to sell to vendors) is rare (see Supporting Information S1 for a more detailed overview of the stages in the pitaya chain).

3. Methods and data collection

We conducted our fieldwork in Techaluta de Montenegro (20.074°, −103.550°) during 2016 and 2017. Section 3.1 summarises the exclusion experiments we carried out to generate empirical data on changes in yield and fruit size between openly pollinated and pollinator-excluded pitaya crops. Next, we collected quantitative production and marketing data from 61 pitaya producers (Section 3.2). We combined these data to estimate the economic value of bat pollination to the pitaya sector in Techaluta de Montenegro (Section 3.3). Then, to assess the distribution of economic benefits resulting from bat pollination services, we analysed economic data collected through structured interviews with a sample of representatives from each actor group involved in pitaya production (Sections 3.2. and 3.4).

3.1. Effect of bat pollinators on pitaya crop yield and quality

We carried out exclusion experiments in 2016 to estimate crop yield under several pollination systems, whereby different flowers were exposed to certain pollinators using bags of different mesh sizes placed during the day or at night. This method has been used to determine effective pollinator taxa in many columnar cacti species in Latin America (e.g. Molina-Freaner et al., 2004; Ibarra-Cerdeña et al., 2005). Bags made from a very fine mesh excluded all pollinators, and bags made from 2 cm^2 mesh excluded vertebrate pollinators but allowed insects. Six different treatments allowed us to distinguish between diurnal vertebrate pollinators, diurnal insect pollinators, nocturnal vertebrate pollinators, and nocturnal insect pollinators; with open (all pollinators had access to the flower) and closed (no pollinators had access to the flower) pollination controls. We studied wild individuals of *Stenocereus queretaroensis* ($n = 30$), as well as three different cultivars chosen for their economic importance: Blanco ($n = 22$), Mamey ($n = 30$) and Tenamaxtle ($n = 27$). We placed each treatment on a separate flower on each cactus individual. We monitored flowers under each pollination treatment and recorded fruit set, then harvested fruits after a standardised number of days (52, 57, 54 and 52 days for Blanco, Mamey, Tenamaxtle and wild fruits, respectively) and weighed them. We used estimates from a binomial generalised linear mixed effects model to calculate the probable increase in fruit set with bats relative to diurnal pollinators for each cultivar and for wild cacti (for details, see Tremlett et al., 2020).

3.2. Data collection: Economic valuation and value chain analysis

We identified actor groups involved in the production of pitayas in Techaluta de Montenegro using semi-structured interviews with key informants, people previously identified to have expert or broad knowledge about the pitaya production sector (Newing, 2010). During the production season in 2017, we collected contact details of potential participants from each actor group by approaching actors at random in both the production area (Techaluta de Montenegro) and subsequent market areas (e.g. Guadalajara). We also used a snowball sampling technique whereby existing participants were asked to recommend other potential participants. Additionally, we randomly approached registered producers from a list of 189 provided by the municipality.

We then conducted structured interviews, using a standard set of pre-prepared interview questions (see Supporting Information S3). We asked participants for: characteristics of pitaya plantations and harvest; marketing and fruit prices; a detailed breakdown of financial costs and time spent on pitaya-related activities by both family members and employees; and details of socio-economic background. These topics were selected so we could fully determine aspects of income for each actor group (Kaplinsky and Morris, 2002; Sanogo, 2010; M4P, 2008). To validate responses, we asked each respondent several questions relating to total and monthly income, prices and profits. Interviews allowed accurate data collection while allowing participants privacy to discuss personal issues (Newing, 2010). We carried out pilot interviews in a neighbouring production town (Amacueca) in June 2017 to check and refine interview questions.

We carried out 124 interviews between July and August 2017. Interviews were conducted by trained volunteers and lasted between 40 minutes and 3 hours. Prior to starting the interview, we provided details of the project, data storage, and issues relating to anonymity and confidentiality, and obtained written consent from each participant. We had ethics approval from the University of Southampton ethics committee prior to carrying out data collection.

3.3. Economic valuation

To estimate the economic value of bat pollination V_b in pitaya production, we used a production value method (Winfree et al., 2011), which estimates the value of bat pollination assuming that there are no substitutes. This economic value is estimated using the following general model:

$$V_b = D \cdot P \cdot Y \quad (1)$$

where V_b is the economic value of bat pollination in pitaya fruit production, D is the crop's dependency on bat pollination (i.e. the fractional reduction in crop yield or quality in the absence of bat pollinators), P is crop price (expressed in Mex$ per fruit) and Y is crop yield (in fruits per producer).

Our exclusion experiments showed that bat pollination affects both fruit yield (Y), and fruit quality, in terms of size (Q). Thus, there are two separate elements to the crop's dependency on pollination: D_{yk} and D_{qkw}. We derived D_{yk} from the mixed effects model parameter estimates (see Section 3.1), indicating the difference between pitaya fruit set when bats were excluded (diurnal pollinators only) and fruit set with bats present, which varies across pitaya types (k). We derived D_{qkw} from empirical data collected on changes in fruit weights in the absence of bat pollinators in exclusion experiments (see Sections 3.1 and 3.3) and the subsequent impact on price, which varies across producers (w) and pitaya type (k). Hence, V_b has two additive components:

$$V_b = V_{yb} + V_{qb} \quad (2)$$

where V_{yb} is the value of the fruit yield attributed to bat pollination (Eq. (3)); and V_{qb} is the value of the fruit quality attributed to bat pollination (Eq. (4)).

To calculate the value of the fruit yield attributed to bat pollination for each producer, we multiplied the proportion of fruits produced of each pitaya type ($\frac{Y_{kw}}{Y_w}$) by the crop yield dependency specific to each pitaya type (D_{yk}). We then summed the change in fruit yield across pitaya types and multiplied this proportion by the gross revenues from selling pitaya fruits (V_w). To calculate V_{yb}, we then summed the value of the change in yield attributable to bats across all pitaya producers (W) in the study area, i.e.:

$$V_{yb} = \Sigma^W \left(V_w \cdot \left(\Sigma^K \left(D_{yk} \cdot \frac{Y_{kw}}{Y_w} \right) \right) \right) \quad (3)$$

Y_{kw} was inferred from total fruit production reported by the producer multiplied by the proportion of the cultivar/wild cacti under production.[1] The value of V_{ybw} therefore varies across producers, depending on each producer's total fruit production for each pitaya type (Y_{kw}), as well as their gross revenues from selling the fruits (V_w). We assumed an equal price for all fruits sold by each producer (i.e. the proportion of fruits sold per variety was taken as a proxy for the proportion of revenues per variety), as we did not have data on the number of fruits sold per producer in each price category or per cultivar. In reality, prices received by producers varied according to both fruit size and time of season; however, as producers sold the bulk of their fruits during the peak season for one price, and had fruit production dominated largely by one pitaya type (and therefore of a similar size), we deem this assumption defensible.

To calculate the value of the fruit quality attributable to bat pollination for each producer, we multiplied proportion of cacti produced of each pitaya type ($\frac{Y_{kw}}{Y_w}$) by the crop quality dependency specific to each pitaya type and producer (D_{qkw}). We then summed the change in fruit quality across pitaya types (K), and multiplied this proportion by the value remaining after subtracting the value of fruit yield attributable to bats from gross revenues from pitaya sales, $V_w - V_{ybw}$. To calculate V_{qb}, we then summed the value of the change in quality attributable to bats across all pitaya producers (W) in the study area, i.e.:

$$V_{qb} = \Sigma^W \left(\left(V_w - V_{ybw} \right) \cdot \left(\Sigma^K \left(D_{qkw} \cdot \frac{Y_{kw}}{Y_w} \right) \right) \right) \quad (4)$$

We assigned a null value for unstudied cultivars for both increase in fruit yield and size, which accounted for 13% of cacti under production overall.

To calculate D_{qkw}, we first collected data on the size of ten fruits in each of the small, medium and large size bands sold by the roadside in Techaluta de Montenegro in June 2018 to calibrate the weight ranges of fruits in different price categories. We then compared the proportion of fruits in small, medium and large size bands under the nocturnal and diurnal pollination treatments in our exclusion experiments for each pitaya type, and calculated the proportion of fruits that would drop to lower size bands for each pitaya type k in the absence of bat pollinators (Table 1). We assumed the most conservative size band changes by minimising the number of size bands dropped by fruits i.e. where a large fruit could have become either a medium fruit or a small fruit (as there were more fruits in both smaller band without bat pollinators), we chose a drop of one band rather than two.

The drop in size bands implies that the total value of pitaya fruits V would be lower in the absence of bat pollination because the fruits would be smaller, and producers would obtain lower prices per fruit. We weighted prices received by each producer at the beginning, middle and end of the season by the approximate volume sold in each time-band. Dependency values were therefore specific to each producer and depended on the weighted prices that each producer could negotiate at each size band: for example, a producer that received the same price for large and medium fruits would have a lower dependency value attributable to the decrease in fruit size in the absence of bat pollination than a producer that sold large fruits for a higher price than medium fruits. We calculated D_{qkw} by multiplying the percentage of fruits that would change size in the absence of bat pollination for each price-size category for each pitaya type S_{qk} by the difference in prices received by each producer. We then summed the differences across the price-size categories (see Supporting Information S2 for an example of this calculation):

Table 1
Percentage of fruits that moved between each size band in the absence of bat pollination for each cultivar and wild cacti, based on weights of fruits collected from exclusion experiments under nocturnal and diurnal pollination treatments.

	Large: no change	Large → medium	Large → small	Medium: no change	Medium → small	Small: no change
Blanco	0	9	24	2	9	56
Mamey	33	0	47	0	0	20
Tenamaxtle	6	25	62	0	7	0
Wild	0	0	16	0	21	63

[1] The inference was necessary because producers were unable to provide estimates of the total production or revenue per cultivar or the quantity sold per size (and thus price) category. For each producer, our dataset included: total quantity of fruits sold, gross revenues, number of cacti under production per cultivar, and average prices per fruit size (small, medium, large) and time in season (start, peak, end).

$$D_{qkw} = \Sigma^{Q}\left(S_{qk}\cdot\frac{P_{wq0}}{P_{wqb}}\right) \quad (5)$$

where $\frac{P_{wq0}}{P_{wqb}}$ is the fractional change in price received for each pitaya type for each producer, with P_{wq0} indicating the price received per fruit in the absence of bat pollination (for size band q_0), and P_{wqb} indicating the price received per fruit with bat pollination (for size band q_b). S_k is based on the information in Table 1, and is the percentage difference in the number of fruits moving between each size band q per variety k in the absence of bat pollination.

To assess the contribution of bat pollination to employment in the pitaya sector, we estimated total extra jobs J_b generated by bat pollination by multiplying the total number of employees E of each producer by the proportion of revenue attributable to bats $\frac{V_{bw}}{V_w}$. For example, we assumed that a decreased revenue of 35% would result in a workforce decrease of 35%. Thus:

$$J_b = \Sigma^{W}\left(\frac{V_{bw}}{V_w}\cdot E_w\right) \quad (6)$$

where J_b is total extra jobs generated by bat pollination, and E_W is the number of employees of each producer.

To estimate the total gross value of bat pollination services to the pitaya sector in Techaluta de Montenegro, we identified all likely *Stenocereus queretaroensis* plantations within the municipal boundaries of Techaluta de Montenegro, using satellite imagery (Google Earth, 2019). We marked the plantations as polygons and exported them to ArcGIS to calculate the area covered in hectares.

3.4. Value chain analysis

We used the data collected through interviews with different actors to understand the production, processing, marketing, and consumption stages of the pitaya value chain (Supporting Information S3). To better understand the distribution of economic benefit provided by bat pollination services, we assessed the proportion of income attributable to bats, profit, and hourly earnings across actors.

We first estimated the proportion of income attributable to bats for each actor. For all actors that produced fruits themselves we extracted values for the percentage of income attributable to bats from changes in both yield D_{yk} and quality D_{qkw}, from our individual level data collected through interview questions on production and marketing (section 3.3). A mixed model from the exclusion experiment detailed in section 3.1 provided an average estimate of D_y for individuals that did not produce fruits themselves. For actors whose income depended on the quantity but not quality of pitaya fruits, we assumed the proportion of their income attributable to bats was equivalent to D_y. This was assumed for waged workers (work availability depends on fruit volume, but we had no data on the specific volumes of fruits of each cultivar handled by their employers) and plantation owners that rented plantations to others (rent is calculated by number of fruits). For actors whose income depended on both quality and quantity of fruits (e.g. intermediaries and all types of vendors), but that did not produce fruits themselves, we calculated profit margins for small, medium and large fruits during peak production (as the bulk of fruits are sold during this time) by subtracting costs of buying fruits from prices received when selling fruits. We then inferred the overall volume of fruits of each cultivar in the market from the overall proportion of each cultivar under production across our sampled producers; and used data collected in section 3.3 on the proportion of fruits of each cultivar in each of the small, medium and large size categories (Table 1) to estimate the overall proportions of fruits in the market of each size category with and without bat pollination. We multiplied the proportion of fruits in each size category by the profit margin calculated for each actor, in scenarios of selling 100 fruits in both bat pollinator presence and absence, and took the difference between the two as the per cent increase in profit attributable to increased fruit quality with bat pollination. The proportion of income attributable to bats for product makers was assumed to be equivalent to D_y, as the prices of products did not vary according to the size of fruit used to make them.

We then calculated profit earned by each individual interviewed by subtracting direct costs incurred by pitaya-related activities (costs of renting pitaya plantations, agricultural inputs, salaries and compensations for employees or family members, marketing, transport, tools and equipment, loans, buying pitayas) from gross pitaya income (the sum of any income generated by selling pitaya fruits V, pitaya flowers, and/or pitaya products, as well as income generated by renting out pitaya plantations). Fixed costs e.g. of establishing pitaya plantations were not included in our calculations of costs and profits. For waged workers, costs (e.g. commuting, food, tools and equipment, maintenance) were subtracted from the hours worked in the season multiplied by the hourly wage received.

Finally, we calculated the profit attributable to bats by multiplying profit by the proportion of income estimated to be attributable to bat pollination services. Estimates of profit attributable to bats involved an assumption of constant variable costs per fruit (though we acknowledge that marketing and transport costs will probably not decrease linearly with decreased production).

To incorporate the number of dependents reliant on pitaya-generated income across actor groups, we calculated the per capita monthly income of actors by dividing monthly income by the number of people living in each household. To elucidate the trade-off between profits, working hours and reliance on unpaid labour by family members, we calculated the hourly wages of each actor group by dividing total profit by total hours worked unsalaried on pitaya-related activities by the respondent or family members,. except for waged workers where fixed hourly wages received are reported.

To understand the importance of pitaya-generated income, we collected data on whether respondents used it for direct household provisioning or were able to save or invest it for long-term benefit, for example by spending it on school fees. We also asked about other income generating activities throughout the year, and the proportion of yearly income generated by the pitaya. We evaluated constraints to access profitable roles in the pitaya chain by combining qualitative interview data with quantitative costs data.

We tested for differences between groups in profit, hourly wage and per capita monthly income with a Kruskal-Wallis test followed by non-parametric (Dunn) pairwise tests (using R packages 'FSA' and 'rcompanion'; Mangiafico, 2019; Ogle et al., 2019). We also calculated the Gini coefficient of inequality between groups in profit and hourly wage (using R package 'DescTools'; Signorell, 2019). Statistical analysis was done in R v. 3.5.3., using R packages 'dplyr', 'tidyr' and 'Rmisc' (Hope, 2019; R Core Team, 2019; Wickham and Henry, 2019; Wickham et al., 2019).

4. Results

4.1. Economic value of bat pollination service to pitaya production in Techaluta de Montenegro

Pollination by bats resulted in a greater probability of fruit set compared to other taxa in our exclusion experiment, increasing overall probable yield by 35% when averaged across cultivars and wild cacti (GLMM: $\chi^2 = 286.7$, $p < 0.0001$; Tremlett et al., 2020). However, the dependence on bats for fruit set varied between cultivars. Yield increased by 27% for Mamey (GLMM: $p < 0.001$) and 35% for wild individuals (GLMM: $p = 0.002$), but there was no effect of bat pollination on yield for Tenamaxtle (GLMM: $p = 0.65$) and Blanco (GLMM: $p = 0.60$) individuals. Crop dependency on bat pollination D_{yk} was therefore 0.27 for Mamey, 0.35 for wild, and zero for Blanco and Tenamaxtle individuals; and 0.35 when averaged across cultivars D_y. Neither the closed pollination nor pollination by nocturnal insects treatments resulted in fruit set.

Fruit weight decreased by 46% in the absence of bat pollination across all exclusion experiment fruits (excluding the two treatments that did not set fruit and could therefore not be included in analyses of crop quality). The dependence of the pitaya crop on bat pollinators for quality D_{qkw} varied with producer, as it depended on the price charged for fruits of different sizes, but the impact on price was highest for Mamey and Tenamaxtle cultivars, which dropped one or two price bands when bats were excluded (Table 1; Fig. 2a).

Of the 61 pitaya producers interviewed, 39 owned pitaya plantations, 40 rented pitaya plantations and 20 owned home gardens (some respondents produced fruit under more than one system). The total area under production for each producer ranged in size from 0.03 to 12 ha (mean = 2.58 ha), and fruit production Y_w ha^{-1} ranged from 4,200 fruits ha^{-1} per season to 633,300 (Table 2). The most commonly managed cultivars of *Stenocereus queretaroensis* were Mamey (63% of total cacti under production across producers interviewed), Tenamaxtle (7%) and Blanco (7%); as well as wild cacti (10%).

Bigger fruits command higher prices than smaller fruits (Fig. 2b). Vendors separate fruits into large, medium and small categories, with some adding categories at the extreme (tiny, jumbo). There is no minimum size for a pitaya fruit to enter the market. No other fruit characteristics (e.g. cultivar) affected fruit price at markets we visited. Weights of small fruits measured at markets in 2018 ranged between 21.7 and 42.1 g (n = 10), medium fruits between 56.3 and 69.5 g (n = 10), and large fruits between 68.1 and 90.6 g (n = 10). Fruit prices are highest at the beginning of the season (late May), when there is less fruit available and consumer demand is greatest (Fig. 2b). Prices are lowest during peak production (June).

Increased fruit yield resulting from bat pollination across the 61 producers interviewed had a mean total value (before costs) V_{ybw} of Mex $39,900 per producer (range: Mex$600 to 320,300 / US$32 to 16,700; Table 2). The mean value of increased fruit size resulting from bat pollination V_{qbw} was Mex$39,500 (range: Mex$0 to 298,400 / US$0 to 12,500; Table 2) per producer interviewed. Thus, by increasing fruit yield and size, bat pollination has a mean total market value V_{bw} of Mex $79,300 per producer, or Mex$48,400 (US$2,530) per ha (range: Mex $1700 to 246,400 / US$87 to 12,900; Table 2).

The percentage of gross crop value attributable to bat pollination ranged from 5% to 58% across interviewed producers, with bats contributing a mean 39% (±12 SD) of gross revenues from fruit sales per producer (Table 2), or 42% of total gross income summed across producers. Producers with a higher proportion of Mamey and wild cacti were more dependent on bats for total income, because fruit yield increased with bat pollination relative to diurnal pollination for Mamey and wild cacti, but not Tenamaxtle and Blanco. Additionally, producers that received higher prices for large Mamey and Tenamaxtle fruits than medium or small fruits benefited more from bat pollination, as fruits dropped one or two size-price bands in the absence of bat pollination.

We estimate that income attributable to bats for the 61 producers interviewed generated approximately 129 extra jobs further down the production chain (e.g. peelers, harvesters), though we acknowledge that job creation is not linearly associated with income. The number of paid workers employed by producers ranged from 0 to 33.

We classified 190 ha of pitaya plantations within the municipal boundaries of Techaluta de Montenegro from satellite images. This is likely to be an underestimation of the likely total area, as we could not distinguish spatially dispersed wild cacti and cacti grown in home gardens. Thus, we conservatively estimate the total gross value of bat pollination services to the pitaya in Techaluta de Montenegro to be approximately Mex$9,200,000, ranging between Mex$315,000 and Mex$46,800,000 (US$480,000: between US$16,500 and US $2,450,000).

4.2. Value chain analysis

4.2.1. Income and employment

Jobs generated by pitaya production are a chief source of employment in an area lacking many other opportunities and provide an important source of income and a strategy to diversify livelihoods (see Table S3 for a description of all actors and their roles). The pitaya was cited as the principal source of income by 49% of respondents, though only one household was completely reliant on the pitaya; all other households had multiple income streams. Participation in the pitaya chain is therefore a 'gap-filling activity' for most people: one that provides a seasonal income during the period of low agricultural activity, thus increasing its relative importance and compatibility with other livelihood activities (Marshall et al., 2006). The actor groups most heavily dependent on pitaya-generated income over the year, and therefore bat pollination services, were intermediaries and market vendors (an estimated 55% and 46% of yearly income respectively), with waged workers reporting between 15% (drivers) and 26% (harvesters) of yearly income coming from work with pitayas (Table 3).

However, the pitaya chain is characterised by informal, verbal contracts: just 33% of fruit sellers and 45% of waged workers had a contract arranged prior to the fruiting season, and all were verbal. Participation

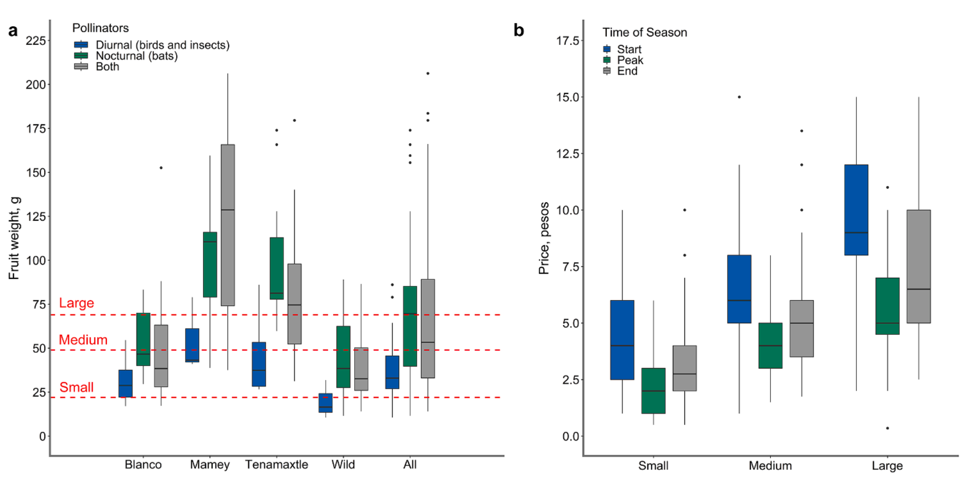

Fig. 2. a) Changes in fruit weight observed in exclusion experiments in 2016 between diurnal and nocturnal pollinators. Red dashed lines indicate lower weight boundaries of different price classes observed in markets in 2018 (small, medium and large); b) final prices (charged to the consumer) of fruits of different price classes (small, medium and large) at different times of the season in 2017: start = late May; peak = June; end = early July.

Table 2
Characteristics of pitaya production and value of bat pollination services across the 61 interviewed producers.

	Size of plantation, ha	Y_w ha^{-1}, # fruits	V_w, Mex$	Price of a small fruit[1], Mex$	Price of a medium fruit[1], Mex$	Price of a large fruit[1], Mex$
Mean ± SD	**2.58** ± 2.83	**51,547** ± 90,914	**187,895** ± 254,146	**2.0** ± 1.0	**3.5** ± 1.2	**5.0** ± 2.0
Range	0.03–12.00	4233–633,333	4,500–1,350,000	0.5–5.2	2.0–7.3	1.9–10.5
	Y_{bw}, # fruits	V_{ybw}, Mex$	V_{qbw}, Mex$	V_{bw}, Mex$	V_{bw} ha^{-1}, Mex$	% V attributable to bats
Mean ± SD	**12,447** ± 18,743	**39,861** ± 59,915	**39,460** ± 58,356	**79,321** ± 116,023	**48,405** ± 53,112	**39** ± 12
Range	335–94,920	610–320,355	0–298,399	610–618,754	1660–246,393	5–58

[1] Prices weighted by approximate volume sold at different times during the season (different prices are received by farmers at the beginning, middle and end of the season; see Fig. 2b). **Y_w** ha^{-1}: total number of fruits produced each year (yield) per hectare. **V_w**: gross revenues from fruit sales. **Y_{bw}**: total yield attributable to increase in fruit set with bat pollination relative to other taxa. **V_{ybw}**: total value of yield increase with bat pollination per producer. **V_{qbw}**: total value of size increase with bat pollination per producer. **V_{bw}**: total value of yield and size increase with bat pollination. **V_{bw}** ha^{-1}: value of bat pollination per hectare of pitaya plantation. **%V**: percentage of gross revenues from fruit sales attributable to increases in yield and size of pitayas due to bat pollination.

in the pitaya value chain thus precludes permanent, formal work with benefits such as health insurance and pensions that only accrue to workers in continuous employment, creating a lack of social security for most actors. Despite this, the lack of technical entry requirements, instant generation of cash at low times of the year, and higher wages relative to other low-skilled jobs, makes the pitaya sector an attractive employment option for resource-poor people. Working with pitayas offers a higher daily rate during the pitaya season than many other concurrent available job opportunities, such as agricultural day labouring (Mex$200 per day) or jobs tending plants in large greenhouses that grow berries for the export market (Mex$120 per day).

The discrepancy between the highest and lowest mean hourly wages of actors in the value chain (Gini coefficient = 0.67) indicates inequality in the distribution of both economic benefits and labour costs between actors. The low agricultural requirements of the cacti result in a low labour cost for landowners, particularly those that rent plantations to others for the production season. Actors that had multiple functions in the value chain, such as market vendors that both produced and sold fruit themselves, commonly worked very long hours of up to 22 hours a day. The mean hourly wage of plantation owners who rented plantations to others was 22.6 times higher than that of peelers and 5.4 times higher than that of market vendors (Mex$543, Mex$24 and Mex$101 per hour respectively; Table 3).

4.2.2. Costs

Wages and benefits are a major cost for all the different actors except intermediaries (Table S4). Transport costs (predominantly petrol) and rent are important costs for marketing actors. The costs incurred by intermediaries and market vendors are the highest, while plantation owners have among the lowest costs, thanks to the low agricultural inputs required (Table S4). A mean of Mex$1,260 per ha per year (US$66) was spent on compost, fertilisers, herbicides and pesticides combined. However, there is a high initial fixed cost of establishing pitaya plantations, representing a significant barrier to entry for other actors. Establishment costs are between approximately Mex$9,460–72,300 per ha (US$494–3,780 per ha), excluding the price of buying land, consisting of the costs of labour and buying cactus branches to plant. Furthermore, there is then a lag time before fruit production of up to 10 years. Access to formal credit is low: six percent of waged workers had access to credit and thirteen percent of non-waged workers. There was no significant difference between actor groups in per capita monthly income (Table 3), though those that earned the highest (plantation owners that rent their plantations out to other people, Mex$3,770 ± 1444 SE) had a per capita monthly income of nearly four times those who earned the lowest (peelers, Mex$1,000 ± 198 SE), indicating that access to land may be captured disproportionately by an already economically privileged group.

The majority of the income (84%) associated with pitayas accrues to the local community and is retained as cash income, supporting household activities (Table S5). Cash income generated from the pitaya was allocated to: household food (71% of respondents), rent and bills (54%), investment back into pitaya or other businesses (40%), savings (37%), household goods (36%), children's education (30%) and other uses including medical bills and paying debts (19%). Little pitaya-generated income is passed onto the government (7%) as few taxes are paid; most government revenue results from actors buying petrol from the state-owned distributor (Table S5). External agents, for example suppliers of packaging or agricultural inputs, accounted for the remaining 9% of pitaya-generated income (Table S5).

4.2.3. Profits

The distribution of profits between actors was unequal (Gini coefficient = 0.60). The highest profits (income minus direct costs) were gained by market vendors who both produced fruits and sold them directly to the consumer, achieving the highest final fruit prices (Table 3; Fig. S1). However, intermediaries, producers and plantation owners all earned a higher hourly wage (Table 3) indicating the high labour cost (long working hours) of market vendors. Additionally, many market areas have become saturated, with vendors citing too much competition from other sellers as a primary obstacle to making profit. The barriers to accessing the most profitable marketing situations are access to a vehicle and obtaining selling permits. Plantation owners that rented plantations to others achieved both the highest hourly wage and the second highest profit. As the plantations require little maintenance or input of resources, profit margins are good both for owners renting pitaya plantations out for the season for a fixed sum of money, and for those that harvest and sell the fruit themselves.

Producers that sold peeled fruits to other vendors could earn very high profits but there was substantial variation across respondents (Table 3). Profits earned by this group in our study are biased by one producer that had a very high production and took the fruits to Guadalajara to sell direct to market vendors; producers that sold to vendors or intermediaries in Techaluta earned much lower profits. The localised nature of the pitaya market results in a good level of market information throughout the chain and enables direct market access by most actors. This increases the power of producers to earn a fair price and results in intermediaries being uncommon, who frequently earn excessive profits in value chain assessments (Marshall et al., 2006). Nonetheless, the few intermediaries active in the pitaya chain earn a high profit due to the large number of fruits traded, despite earning the lowest profit margin on fruits (Table 4) and having the highest costs (Table S4).

A substantial part of pitaya-generated profit for all actor groups could be attributable to the impacts of bat pollination on crop yield and quality (Fig. 3a and b). Actors whose profits depended on the quality of fruits as well as quantity were more dependent on bat pollination services than actors who depended on quantity only, as profit margins per fruit decreased with fruit size (Table 4), and fruits were smaller in the absence of bat pollination. Intermediaries, and ambulant, roadside and market vendors had the largest mean percentage of profits attributable to bat pollination (62, 56, 47 and 46% of profits respectively; Fig. 3b). Actors with the highest value of profit attributable to bat pollination services however, were those that earned the most from working with

Table 3
Income indicators for different actor groups.

[1] Actor	Peelers*	Agricultur-al workers*	Ambulant sellers	Drivers*	Product makers	Harvesters*	Home garden owners	Roadside vendors	Plantation owners -do not rent out	Market vendors	Producers – sell fruit with spines	Producers – sell peeled fruit	Intermediaries	Plantation owners – rent out	**Kruskal – Wallis test** [3]
N	12	6	5	4	9	11	20	31	30	19	8	4	4	9	
Income indicators based on calculations in section 3.4:															
Wage/ Profit*, Mex$ ± SE	17,201 ^{ab} ± 3,856	7,500 ^{a} ± 2,869	45,156 ^{bcd} ± 6,214	10,369 ^{ab} ± 5,331	27,277 ^{abc} ± 7,048	12,126 ^{a} ± 1,413	49,751 ^{bc} ± 11,717	57,531 ^{c} ± 13,818	78,083 ^{cd} ± 18,504	125,590 ^{d} ± 24,979	17,505 ^{ab} ± 7,350	127,099 ^{bcd} ± 90,386	96,419 ^{cd} ± 47,984	102,409 ^{cd} ± 51,970	$\chi^2 = 64.2$, df = 13, $\boldsymbol{p < 0.0001}$
Hourly wage Mex$ ± SE	24 ^{b} ± 2	25 ^{ab} ± 0	31 ^{ab} ± 8	32 ^{abc} ± 9	35 ^{ab} ± 8	39 ^{abc} ± 7	47 ^{ab} ± 8	47 ^{b} ± 12	90 ^{ab} ± 25	101 ^{abc} ± 24	125 ^{abc} ± 55	165 ^{abc} ± 135	183 ^{ac} ± 61	543 ^{c} ± 234	$\chi^2 = 34.2$, df = 13, $\boldsymbol{p = 0.001}$
Income indicators based on answers to interview questions:															
Per capita monthly income Mex$ ± SE	1003 ± 198	1327 ± 217	1410 ± 370	1234 ± 115	2003 ± 653	1436 ± 228	1664 ± 382	1459 ± 220	2150 ± 409	2921 ± 871	1881 ± 189	1879 ± 221	2917 ± 896	3767 ± 1444	$\chi^2 = 11.0$, df = 13, $p = 0.61$
[2] **Per cent yearly income from pitaya**	23	23	23	15	33	26	35	36	45	46	32	35	55	37	

[1] The majority of respondents belonged to multiple actor groups, so individual data may be used for several groups (e.g. plantation owners that are also market vendors). Product makers here are those that did not also sell fruits (i.e. were solely product makers). Producers here are those that produce fruit but do not sell it directly to the consumer, but instead to another vendor or intermediary, either peeled or with spines. *Waged workers.

[2] Per cent of yearly income from the pitaya calculated from the average category rank that actors reported during interviews in answer to the question "What percentage of your average annual income comes from the pitaya?" (1 = 0–20%, 2 = 20–40%, 3 = 40–60%, 4 = 60–80% and 5 = 80–100%). The mid-point of each category range was used.

[3] Different letter superscripts indicate significant differences between mean incomes based on non-parametric (Dunn) pairwise tests at $p < 0.05$, using the Benjamini and Hochberg correction (using R packages 'FSA' and 'rcompanion' Mangiafico, 2019; Ogle et al., 2019).

Table 4
Profit margin (Mex$) per fruit of each size category during peak production (±SD) for actors buying fruit to sell rather than producing their own (cost of buying fruit subtracted from sale price received for fruit).

	Small (Mex$)	Medium (Mex$)	Large (Mex$)
Intermediaries	0.3 ± 0.3	0.6 ± 0.4	1.1 ± 0.8
Ambulant vendors	1.5 ± 0.4	2.3 ± 1.1	3.6 ± 1.2
Roadside vendors	1.3 ± 2.5	3.3 ± 1.8	4.3 ± 1.1
Market vendors	2.5 ± 0.0	4.1 ± 0.5	6.8 ± 2.5

pitayas: market vendors, producers and plantation owners (Fig. 3a; Table 3).

5. Discussion

Our study used an interdisciplinary approach to examine both the value of the direct impacts of bat pollination on crop yield and quality, as well as a disaggregated analysis of the distribution of the economic benefits among actors. We found the value of bat pollination services to be worth approximately US$480,000 in the municipality of Techaluta de Montenegro alone, highlighting the great importance of bat pollinators for the welfare of the rural production region, and the severe economic consequences should bat pollinator populations decline.

Leptonycteris yerbabuenae populations suffered severe declines in the 1980s, resulting from persecution and disturbance at roosts and loss of foraging habitats (Medellín, 2016). A conservation recovery programme has successfully used environmental education and roost protection schemes to increase population sizes, resulting in delisting of the species by both the Mexican and US governments (Trejo-Salazar et al., 2016; US Fish and Wildlife Service, 2018); though the species remains classified Near Threatened by the IUCN Red List (Medellín, 2016). However, it is vital that public awareness of the ecosystem services provided by bats continues, such as the contribution of bats to food security. This is particularly pertinent in the light of the recent Covid-19 pandemic that has widely negatively associated bats with the virus, driving new threats to bat populations (Fenton et al., 2020; Zhao, 2020). Our own recent engagement with inhabitants of the pitaya production area indicates growing concern about subsequent negative public perceptions of bat-pollinated fruits.

Economic valuations are one way of raising awareness of the unseen benefits of bats, with local context-specific research providing useful and relevant information to decision makers (Ninan and Inoue, 2013). The value of pitaya-generated income is significant in an area where 49% of people have an income insufficient to provide wellbeing (CONEVAL, 2010). Among individual pitaya farmers within our study region, we found considerable variation in dependence on bat pollination for income, highly impacted by the cultivars grown and the prices charged for fruits of different sizes. However at the community scale, our research showed pitaya production to be heavily dependent on bats, particularly that of the most economically important cultivar, with the spatial and genetic structure of pitaya plantations likely exacerbating the reliance on bat pollinators (Tremlett et al., 2020).

Our multi-faceted approach to estimate the value and distribution of pollination services may be useful for other animal-pollinated crops, particularly those in less formal markets where a lack of registered data on crop production or the value chain necessitates the collection of primary data. We found that pollinator-mediated changes in fruit quality had a high impact on the estimated value of pollination services, demonstrating the importance of conducting detailed field experiments to generate empirical data on the dependency of both crop quality and yield on different pollinators, as well as including multiple cultivars in study designs (Melathopoulos et al., 2015).

Additionally, we have shown that value chain analysis is a useful approach for the evaluation of the social distribution of economic benefits received from ecosystem services, allowing explicit analysis of inequities in income among actor groups and constraints to access roles (Gundimeda et al., 2018; Zhang et al., 2018). To our knowledge there has been no such attempt to disaggregate benefits from pollination services between actors for any crop (Suich et al., 2015). We found that access to the bat pollination service did not have an equalising impact, with some actors receiving a disproportionate share of economic benefit or labour costs, and the chain characterised by a lack of social security throughout. The change of the pitaya from a communally collected resource to an individually owned commodity may disadvantage poorer actors who lack the land or capital to establish plantations themselves or access profitable markets, despite an overall increase in economic wellbeing at the community level (Marshall et al., 2006; Kamanga et al., 2009). Laterra et al. (2019) found a lack of financial capital to be the most important source of inequality in access to ecosystem services across Latin America; inequality then increases over time as access to land gradually decreases with resource commercialisation. At the same time, the ease of entry to the pitaya chain (low technical entry requirements, a local market) may lead to excessive competition between

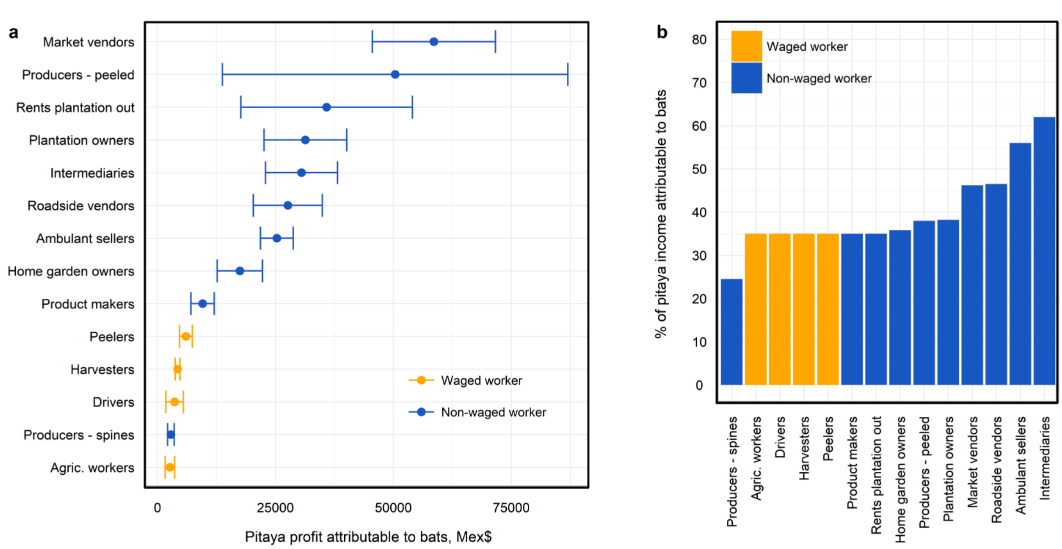

Fig. 3. a) The profit in Mex$ attributable to bats (±SE) across actor groups, calculated by multiplying profit by the proportion of income attributable to bats for each actor (for waged workers, 'profit' is wage received multiplied by hours worked, minus costs), and b) the mean percentage of pitaya-generated income estimated to be attributable to bats for each actor group.

small-scale producers and vendors in the production area, limiting profitability.

5.1. Conservation and policy implications

Communicating the economic benefits provided by bats helps to raise awareness among the public and policy makers of the importance of bat conservation actions (Cleveland et al., 2006; Boyles et al., 2011; Kunz et al., 2011). Community environmental education programmes can be an important tool to improve understanding of bats by generating more positive attitudes shaped by the benefits bats provide, rather than the damage they may cause (for example by vampire bats, *Desmodus rotundus*, which can transmit bovine paralytic rabies to livestock in Latin America) (López-del-Toro et al., 2009; Williams-Guillén et al., 2016).

Those actors who benefit the most from bat pollination services may be best placed to contribute to bat conservation practically (e.g. land owners) and economically (e.g. consumers). At a local practical level, protection of bat roosts and avoidance of persecution (many bats are killed under the mistaken assumption that they are vampires) will benefit bat populations, maintaining both the provision of pollination services and other bat-mediated ecosystem services such as seed dispersal and pest suppression (Kunz et al., 2011; Williams-Guillén et al., 2008). Additionally, to maintain the provision of bat ecosystem services in pitaya plantations, it is vital that the intensification of the pitaya sector does not result in increased use of pesticides and other agrochemicals. Pitaya production currently is largely small-scale and organic; however, production is expanding yearly, with attempts to export the fruits internationally. Pesticide exposure can have various lethal and sub-lethal effects on bats, including disruption of hormones and the immune system, reproductive failure, and changes to behaviour (Bayat et al., 2014). We found consumers of pitayas to have a higher monthly income and level of education than any of the actors involved in the production chain (Table S3), suggesting that they can afford to contribute to initiatives such as a 'bat-friendly' pitaya label (e.g. see Trejo-Salazar et al., 2016: bat-friendly tequila). Such initiatives could add a small surcharge to pitaya prices to feed into conservation efforts such as environmental education programmes or the installation of protection at roost sites.

Until now, there have been no direct economic valuations of bat pollination services provided to crops, though several studies have estimated the value of crop pest suppression by bats. Bat-mediated pest control has been valued between $0 (for coffee and cacao) and $183 (cotton) per ha, representing 0% and 12% of the total crop value respectively (Cleveland et al., 2006; Maas et al., 2013; Maine and Boyles, 2015; Puig-Montserrat et al., 2015; Taylor et al., 2018). The higher value of bat pollination (US$2,500 per ha) revealed by our study suggests that this may be a more effective economic argument for bat conservation in some areas.

This research also has important policy implications for equitable development. In order to ensure that benefits from bat pollination are distributed more fairly across actors, activities could be started at the community, government or NGO level, such as: selling fruits or products collectively; opening up new markets (with assistance to cope with any resulting extra certification or tax requirements) or improving access to existing markets; supporting new actors financially to establish plantations; supporting the introduction of a low-entry health insurance; and providing training and equipment to increase product-making capacity.

5.2. Limitations, uncertainties and knowledge gaps

Fruit set and fruit quality between pollination treatments may vary between years, impacted by fluctuations in climate and pollinator availability (Melathopoulos et al., 2015). Economic value will also fluctuate with changes in market prices, and institutional or external environmental factors (López-Hoffman et al., 2014). Nonetheless, our research has clearly demonstrated the economic importance of bats for the pollination of a highly valuable agricultural product.

Additionally, the production value method assumes that crop prices will be unaffected by decreased supply in the case of pollinator loss, and that farmers cannot compensate for reduced pollination supply by reducing input costs or employing substitutive pollination (Winfree et al., 2011). Techaluta de Montenegro contributes 40% of registered pitaya production in Jalisco (SIAP, 2018) and therefore price increases may be seen with decreased fruit supply. However, the pitaya is already a highly priced luxury fruit, and 67% of consumers interviewed in our study said that they would buy fewer pitayas if the price increased. Input costs are already low for pitaya producers and it is unlikely they could be reduced further without loss of employment. Furthermore, bats are wild pollinators that cannot be replaced by a managed service, e.g. from rented bee hives; and the cost of hand-pollination is likely to be prohibitive (Partap and Ya, 2012), though cost estimates are not available for this crop.

It was beyond the scope of this study to consider the distribution of benefits received by actors other than income. Poverty and wellbeing are complex and context dependent, now commonly described with multidimensional factors encompassing human and social deprivations as well as economic (Suich et al., 2015). For a better understanding of the impact of bat pollination services on wellbeing, the effect of pitaya-generated income on other objective elements of well-being (such as access to health services), and subjective elements (such as cultural importance or contribution to sense of identity) would need to be quantified.

6. Conclusion

The consequences of losing bat pollination services to pitaya production in Techaluta de Montenegro would be severe. By enhancing fruit production and fruit size, bat pollinators contributed around 40% of the total gross income of interviewed pitaya producers in the area, equivalent to US$2,500 per ha annually. This value reflects the high level of dependence of the pitaya crop on bat pollinators for both yield and quality; as well as the high prices achieved for pitayas. The reliance of local employment and income on pitaya production, and thus bat pollination services, is a strong argument for the conservation of bat populations in the production area. However, our value chain analysis showed that barriers to access the most profitable roles should be reduced to enable a fairer distribution of economic benefits among actors, which are currently disproportionately captured by groups already economically or socially advantaged. Our interdisciplinary approach combining exclusion experiments, plantation yield data and value chain analysis provides a novel basis for valuing the benefits of services by other animal pollinators and other crops, as well as the distribution of those services across actors.

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://doi.org/10.1016/j.ecoser.2020.101197.

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