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Can the Introduction of Modern Crop Varieties in their Centre of Origin Affect Local Ecological Knowledge? A Case Study of Papaya in the Yucatan Peninsula

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Abstract The effect on local ecological knowledge (LEK) of introducing modern crop varieties in their centre of origin has been generally overlooked. LEK of the reproductive ecology of cultivated and wild papaya was assessed in a Mayan community using questionnaires, in-depth interviews, and participant observation. Although the Maya have managed the wild variety of papaya for several centuries, there was more LEK of the recently introduced maradol variety. Most informants were unable to differentiate male and female plants, likely because the most common variety (maradol) in contemporary home gardens is typically hermaphroditic. Informants also mentioned that, in the past, sexual expression was manipulated. We conclude that the introduction of the maradol variety has contributed to the erosion of LEK of the reproductive ecology of papaya.

Keywords Crop wild relatives · In situ conservation · Local ecological knowledge (LEK) · Papaya · Maya · Yucatan Peninsula · Mexico

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Introduction

Future food supply is a major concern for societies around the world (Hopfenberg and Pimentel 2001). However, any increase in food production is strongly constrained by several factors, with particular threats from increasingly adverse environmental conditions, as well as the incidence of novel pests and pathogens promoted by climate change (Newbery *et al.* 2016). Due to the domestication bottleneck, modern crops frequently have reduced ability to respond to new environmental adversities (Doebley *et al.* 2006). Breeding modern crop varieties with their wild relatives (hereafter CWR) is an alternative approach for gaining resilience in the face of adverse environmental conditions because it develops genetically-based resistance to cope with environmental adversities by natural selection (Guarino and Lobell 2011).

The conservation of CWR has been recognized as crucial (Heywood 2015). However, CWR are threatened by human-driven environmental disturbances (Kell *et al.* 2012). Also, the base-line information on their biology needed to design conservation strategies is frequently limited, particularly in their centres of origin (Altieri *et al.* 1987). Given the value of CWR for future food security, ex situ and in situ conservation strategies have been implemented (Plucknett and Horne 1992). Because ex situ conservation removes plants from their socio-ecological context, it virtually halts evolutionary and domestication processes; therefore, more emphasis has been given to in situ conservation, which seeks to preserve the whole process of crop evolution, broadly defined by gene flow within and among the individuals and populations of cultivated and wild varieties of crops, as well as natural and artificial selection (Altieri and Merrick 1987). Also, in situ conservation may be the only feasible choice for plants producing recalcitrant seeds (Castañeda-Álvarez *et al.* 2016).

Thus, in situ conservation of CWR faces a big challenge because it requires conservation of habitat, species interactions, and the socio-cultural system involved in the management of these resources (Altieri *et al.* 1987).

Traditional agroecosystems may have the highest potential for achieving the goals of in situ conservation because most are frequently located in the crop centres of origin where CWR, landraces, and modern varieties co-occur (Altieri and Merrick 1987; Brush 1995). Also, traditional agroecosystems may maintain the evolutionary process and favour gene flow among wild and domesticated varieties because of their non-clean cultivation, their function as biological corridors, and traditional farming practices (Altieri and Merrick 1987; Galluzzi *et al.* 2010).

It has long been suspected that the socio-ecological system needed for effective in situ conservation of CWR can be severely affected by the conversion of subsistence to cash agriculture (Altieri *et al.* 1987). Particularly threatening is the introduction of modern crop varieties to centres of origin because modern cultivars can replace landraces or wild relatives (Altieri 2003; van de Wouw *et al.* 2010). This trend may be exacerbated by cultural changes in food preferences and a reduction in demand for local products associated with urbanization (van de Wouw *et al.* 2010). Also, natural hybridization between CWR and introduced modern crop varieties may produce undesirable effects on the yield of the latter (e.g., fewer and smaller fruit), so farmers may eliminate wild relatives from their land and the surroundings to prevent hybridization (Altieri and Merrick 1987; Moo-Aldana 2015). Displacement of CWR aside, LEK associated with the biology and management of wild varieties and landraces may be threatened by the introduction of modern crop varieties in crop centres of origin. Global plant conservation strategy, in addition to being aimed at conserving plant genetic resources, has also targeted LEK associated with phytogenetic resources (GSPC 2002), but LEK associated with CWR and how it is affected by the introduction of modern varieties have received little attention (Reyes-García *et al.* 2014).

In this study we looked at LEK of reproductive biology and pollination ecology of papaya (*Carica papaya*) in traditional agroecosystems in a Mayan community on the Yucatan Peninsula, which is within the centre of origin of this crop (Fuentes and Santamaría 2014). Our main goal was to assess whether the introduction of the maradol variety of papaya affected LEK of the reproductive biology and pollination ecology of papaya. The Maya have used the fruit of wild papaya since pre-Hispanic times (Colunga-García Marín and Zizumbo-Villareal 2004). However, since the early 1980s wild and modern papaya varieties (mainly maradol) co-occur in home gardens of the study area (Poot-Pool *et al.* 2012), which, together with extensive overlap in their reproductive phenology (both varieties produce flowers and fruit year round with a flowering peak from February to July), may promote competition for pollinators and inter-variety gene flow. We think that LEK of papaya's reproductive biology and pollination ecology is relevant for conservation and sustainable management of the species, especially for the wild variety because it is strictly dioecious (male and female plants occur in the same population), which means only female plants produce fruits and pollinators are absolutely needed for sexual reproduction. A study conducted in the 1980s, when introduction of the maradol variety had just begun in the Yucatan, revealed that the Maya recognized male and female sexual organs and plants in papaya and other species present in home gardens (Rico-Gray *et al.* 1988), which also suggests that LEK of reproductive biology was important to the Maya before maradol became the dominant papaya variety. Today, maradol papaya largely dominates home gardens in the study area and people show little interest in the wild variety. In contrast to wild papaya, most maradol plants are self-compatible hermaphrodites that do not need pollinators to set fruit (Brown *et al.* 2012). We thus predicted that the recent replacement of the wild variety by the maradol variety in the study area would negatively affect the LEK of the pollination ecology of papaya.

We compared LEK on the cultivation of papaya in adults of different ages; the expected result was that older people would have better knowledge of the topic than the young. Contextual retrospective information was gathered from key informants and participant observation to explore whether the introduction of the maradol variety was perceived to have a role in current use patterns of the two varieties of papaya and the LEK associated with them. Since the reproductive ecology of papaya is unknown in the study area, we simultaneously conducted some observations and experiments in order to learn about the breeding system, floral biology, and pollination ecology of both varieties. This information also helped us assess the accuracy of the information provided by the informants.

Materials and Methods

The Study System

The study was conducted in the locality of Pomuch in the municipality of Hecelchakán in the Mexican state of Campeche (20°08′13″ N, 90°10′26″ W). In 2010, about 8649 people lived in Pomuch: 4338 (49.8%) men and 4356 (50.1%) women, most of them of Mayan ancestry (≈75%) and *mestizos* (≈20%) (INEGI 2010). The main economic activities are related to agriculture and services (INEGI 2010). About one third (31.3%) of the population older than 15 years had not completed their elementary education in Pomuch (Sedesol 2010). Nearly 90% of the houses have a home garden, in which an average of 19 different plant species can be found per garden (Poot-Pool *et al.* 2012).

Papaya is common in home gardens and maradol is the only modern variety cultivated in the study area (Poot-Pool *et al*. 2012). In Pomuch, people do not plant wild papaya although it occurs naturally in home gardens, the surroundings, and in secondary forest. Wild papaya is locally called *ch'iich'puut* or *put*, which means 'bird papaya' in the Mayan language. This is probably because birds commonly feed on the fruit and disperse the seeds. Little, if anything, is known about the gene flow between domesticated papaya and its conspecific wild relatives in its centre of origin (Silva-Rosales *et al.* 2010). Wild papaya in the study area is strictly dioecious, while the maradol variety, in addition to having male and female plants, also has self-compatible hermaphrodites (Brown *et al.* 2012), and it is these most commonly seen in home gardens (Moo-Aldana 2015). It has been known since the last century that papaya can change sex (from male to female) following mechanical damage or when males are under strong environmental stress (Irons 1908; Freeman *et al.* 1980). There is no in-depth study on the pollination ecology of papaya in its centre of origin, but some studies conducted at other sites have reported that flies, bees (Marín-Acosta 1969), hawk moths (Renner and Feil 1993), and sunbirds (Dey *et al.* 2016) visit papaya flowers and may be effective pollinators. Apomixis (seed production in the absence of pollen) has been described for some modern varieties (Vegas *et al.* 2003), but there is no evidence of apomixis in the wild variety. Papaya seeds are recalcitrant, meaning that they are short-lived, cannot be dehydrated and survive, and this represents a big challenge for gene-banking (Walters *et al.* 2013).

Quantitative Assessment of LEK

From August to December 2014, LEK was scored quantitatively with a questionnaire in a probabilistic sample of 68 adults (>18 years old) who had resided in Pomuch for at least 10 years. The questionnaire was written in Spanish and read to the interviewees so that illiterate people could participate in the study. The majority of the people in Pomuch speak Spanish as their first or second language; monolingual Maya speakers were excluded from the survey, and represent a minority in this town (less than 10%). To choose the sample we used town blocks (204) as clusters and from these, we randomly selected 68 blocks. From each block, we selected the first house with a home garden on the southern face of the block; if the owner of the initially selected house refused to participate or was not available, the next house (clockwise) was chosen. Only one adult was interviewed per household to avoid pseudo-replication. Twenty-five men (36.7%) and 43 (63.2%) women answered the questionnaire. Men were 19–78 years old (mean age = 52.1 years old) and women were 21–70 years old (mean age: 45.7 years old). Most of the men (58%) had a job related to agriculture and most of women (83.7%) were housewives. Also, the majority of both the men (80%) and women (91%) were born in Pomuch.

The questionnaire consisted of 55 items written in appropriate and intelligible language. General and biographic information was recorded for all participants (name, age, gender, formal education level, place of birth, and length of residence in Pomuch). The first section had 15 questions covering generalities about papaya: if the informant was familiar with the plant, had consumed the fruit, had a papaya in their garden, and if they knew about management practices. The second section (21 questions) was about the sexual expression of papaya. We asked if the informant recognized sexual dimorphism, which plants produce the fruit, and whether plants that do not produce fruit were important. The third section (seven questions) was about flower visitors and pollination. We asked which visitors the informant had seen on the flowers of papaya plants, whether the flower visitors were perceived as beneficial or detrimental to the plant, and whether they were able to identify any floral reward (e.g., nectar). The last section (12 questions) was about the perceived relevance of the plant and its management practices. We asked about the utility of the plant, whether it was valuable in any sense, and whether informants believed that the wild and the maradol variety could breed. Throughout the questionnaire, we specified whether the information given was about the wild, maradol, or both varieties. Questions were open and closed, with open questions often used for those requiring a more extensive answer. Administering the questionnaire took less than two hours per person.

In-Depth Interviews of key Informants and Participant Observation

From September to December 2014, we conducted in-depth interviews with key informants who had some experience cultivating papaya. The sample was not probabilistic and was chosen using the snowball procedure. That is, first, with the help of local authorities (Comisario Ejidal), we identified an individual who worked on a papaya plantation and also grew papaya in his/her home garden. Later, this informant referred us to another person with similar characteristics and thus we proceeded iteratively until the information elicited became redundant (saturation point was reached with eight informants, five men and three women). Informant age was 52–72 years old for men (mean age = 62.2 years old) and 34–57 years old for women (mean age = 48.6 years old). The most frequent current occupation was related predominantly to agriculture (60%) for men and housework (67%) for women.

Interviews were conducted in the houses of the owners at a previously agreed time, and each lasted from 20 min to nearly two hours. The format was flexible and the topics were generalities about papaya, varieties and their differences, perceived relevance of the varieties, recent and past uses, the introduction of the maradol variety, sexual dimorphism, as well as current and past management practices. The interviewer made sure to specify which variety the information was about. The information was recorded in a field diary.

Simultaneously with the interviews, participant observation was conducted. Some informants showed the interviewer some papayas and management practices during the explanation. All relevant information was recorded in the field diary and photographs were taken, if allowed.

Reproductive Biology and Pollination Ecology

In a sample of 12 maradol plants (seven hermaphrodites, three females, and two males) and nine wild plants (five males and four females), we made some observations and did some experiments to obtain basic information regarding reproductive ecology. Sampling was not random because this part of the study was conducted in home gardens and only a limited number of the families allowed us to work in their gardens (n = 4). The sexual expression (i.e., male, female, hermaphrodite) of the plants selected does not reflect the frequency of papaya in the home gardens chosen because our aim was to have all possible sexual expressions per variety represented. On a number of flowers per plant (6–25) we observed flower visitors at intervals of 15 min on focal plants over two time intervals: from 09:00 to 12:00 h and from 17:00 to 20:00 h. On the same plants, but using different flowers and on different days, we measured nectar volume from 06:00 to 19:00 h at two-hour intervals using capillary tubes. Phenology at the flower level was also observed during the nectar survey. Specifically we recorded the time when flowers open (anthesis), when the stigma was visually receptive, when pollen was released and the time of corolla closure (senescence).

To assess apomixis and the potential for inter-variety hybridization, we conducted a hand pollination experiment. We selected 16 plants with pistillate/hermaphroditic flowers (five of the wild variety and 11 maradol), and tagged some floral buds that were about to open and later randomly assigned them to one of the following treatments: control (unmanipulated flowers, n = 7), apomixis (flowers were bagged until senescence, n = 17), and inter-variety cross pollination (wild papaya females were pollinated with pollen from maradol males and vice versa, n = 28). For the third treatment, the pollen from two males of a variety different from that of the pollen receptor was used. Pollen was placed on the stigma before midday until stigma saturation and the flowers remained bagged until corolla senescence. After three weeks, we recorded whether the experimental flowers had set fruit or aborted. The hermaphroditic flowers were emasculated before pollen dehiscence, except for the flowers of the control group.

Statistical Analyses

Each answer in the questionnaire was scored on a ratio scale: 0.2 to 3 points depending on the accuracy of the answer. The maximum possible score on the questionnaire was 32. We compared LEK scores between varieties with student's t test. Also, using an ANCOVA, we assessed whether age (a covariable on a log scale), gender (a two level factor), or their interaction were reliable predictors of the LEK score. An ANCOVA was run for each papaya variety (two models in total). The statistics were obtained from the minimal adequate models selected following the AIC criterion (the lower the AIC, the better; Crawley 2013). In both models, the minimal adequate models kept the effects of age and gender, but not the interaction term. Residuals were normally distributed and variances homogeneous.

The proportions of initiated fruit for each hand-pollination treatment were compared between varieties with a Chi square test. Species richness of flower visitors and diversity (Shannon's Index) were calculated per papaya variety and type of sexual expression.

All the analyses were run in R.14.0. (R Development Core Team 2011).

Results

Quantitative Assessment of LEK

The mean LEK score was statistically higher (t_{134} = 2.38, P = 0.02) for the maradol variety (6.91 ± 0.44; hereafter mean values ±1 standard error) than for the wild variety (5.37 ± 0.46). Men (8.08 ± 0.51) had a marginally higher mean LEK score about the maradol variety than women did (6.22 ± 0.3) ($F_{1, 67}$ = 3.19; P = 0.07). However, there was no difference between men and women in their LEK of the wild variety ($F_{1, 67}$ = 1.01; P = 0.32). Also, for the maradol variety, there was a positive

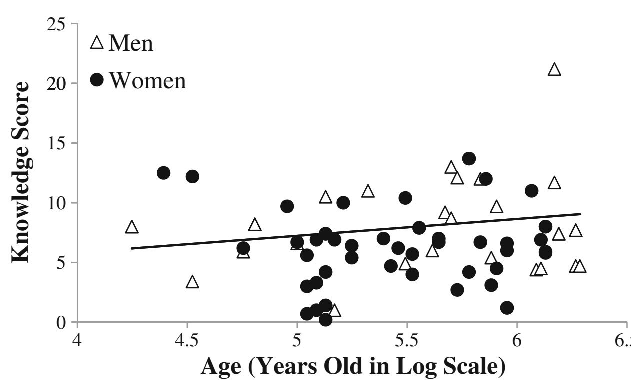

Fig. 1 Relationship between the score of LEKe about the reproductive ecology of maradol papaya and age (on a log scale) for men (*circles*) and women (*triangles*) from Pomuch, Mexico. The line shows the general trend for all data

and statistically significant ($F_{1, 67} = 3.19$; $P = 0.03$) relationship between LEK score and age of the informants (coefficient = 2.31 ± 1.24). For the wild variety, the slope of the relationship between LEK score and age was not statistically different from zero ($F_{1, 67} = 1.01$; $P = 0.32$) (Fig. 1).

In-Depth Interviews with key Informants and Participant Observation

Most of the informants (six) could not recognize male and female plants of either papaya variety. In fact, the informants used the terms "male" and "female" to refer to different fruit morphologies. According to some informants (three), the fruit of male plants have a convex apex whilst those of female plants have a concave apex. One informant also explained that a single plant could have both male and female fruit. Only two of the informants were able to identify male and female plants based on the morphology of the reproductive organs in both varieties of papaya. These two informants had received information or technical training about papaya cultivation from agronomists. In fact, one of them (aged 70) was an employee at a commercial papaya plantation.

None of the informants had personally induced a sex change in either variety of papaya; however, some (four) mentioned that more than four decades ago, their relatives used to cause some damage (transverse penetration of the main trunk or removal of the main apex, locally known as *capado de papaya* [papaya castration]) in order to increase the production or size of the fruit. They never invoked sex change as the underlying mechanism to explain changes in fruit production and were emphatic that this is not a current practice.

Some informants (four) mentioned that some insects as well as hummingbirds frequently visit the flowers of the wild and maradol varieties of papaya, and assumed that these visitors are seeking nectar. The activity of visitors on the papaya flowers was perceived by most of the informants (six) as relevant to apiculture but few informants (only two) made the connection between these visits and fruit set (i.e., pollination). Two informants mentioned that the wild and maradol varieties can breed, and pointed out that pollen might be transported on bees or the wind. One informant told us that some farmers clear wild papaya from an area of several meters around plantations to avoid between-variety pollen interchange, arguing that it produces undesired results in the quality of fruit, such as small size and circular shape.

During participant observation, we saw that the local inhabitants generally have no interest in the fruit of wild papaya. However, they did mention that in the past, wild papaya was not only tolerated, but also watered and weeded. Commonly, the fruit of wild papaya had been consumed and used to prepare some artisanal candies. Also, they pointed out that the entrance of modern varieties contributed to the loss of this traditional activity and the lack of interest in the fruit of the wild papaya. In contrast, the fruit of the maradol variety is currently highly appreciated, mainly because it fetches a good price in local markets where big, elongated fruit are especially prized. People plant the maradol variety, water and sometimes fertilize it. Although the locals do not care for wild papaya at all currently, they do occasionally tolerate it in home gardens; however, when the owners of the garden have maradol plants, they typically remove the wild variety arguing that the latter is useless and takes up space. Wild papaya also occurs in other traditional agroecosystems such as the *milpa* (traditional polyculture growing maize, pumpkin, and beans), where it is tolerated because some think that wild papaya helps reduce the attack of granivorous birds on maize. As in home gardens, no care is provided to wild papaya growing in the milpa. Some people said that papaya's landraces such as amarilla and mamey were grown in Pomuch more than a couple of decades ago; however, they were under the impression that the introduction of the maradol variety displaced these other varieties, which are no longer planted in Pomuch.

Reproductive Biology and Pollination Ecology

Flower anthesis of male and female plants took place at 07:00–08:00 h regardless of variety. In both varieties, male/hermaphrodite plants released the pollen, and the stigmas of the female/hermaphrodite plants showed symptoms of receptivity (brightness and turgidity) shortly after anthesis. Flower longevity in the wild variety (male and female flowers) was about 96 h, and in the maradol variety (male, female, and

Table 1 Percentage of flower visitors per variety (wild and maradol), and sexual expression (male, female or hermaphrodite) of papaya in Pomuch, Mexico. Frequency of visits is in parentheses. Total number of visits is given in the last line

	Wild		Maradol		
Visitor	Male	Female	Male	Female	Hermaphrodite
Apis mellifera	22.5 (9)	33.3 (1)	20 (1)	0 (0)	100 (1)
Trigona fulviventris	5 (2)	33.3 (1)	20 (1)	0 (0)	0 (0)
Trigona sp.	35 (14)	33.3 (1)	0 (0)	0 (0)	0 (0)
Cephalotrigona sp.	2.5 (1)	0 (0)	0 (0)	0 (0)	0 (0)
Diptera[1]	7.5 (3)	0 (0)	0 (0)	0 (0)	0 (0)
Diurnal Lepidoptera[1]	15 (6)	0 (0)	20 (1)	0 (0)	0 (0)
Sphingidae[2]	2.5 (1)	0 (0)	20 (1)	0 (0)	0 (0)
Vespidae[2]	0 (0)	0 (0)	20(1)	0 (0)	0 (0)
Amazilia rutila	10 (4)	0 (0)	0 (0)	0 (0)	0 (0)
Total	40	3	5	0	1

[1] Order

[2] Family

hermaphrodite flowers) was about 120 h. Only the males of both varieties produced nectar. Males of the maradol variety produced nectar only during the early morning (07:00–09:00 h). In contrast, males of the wild variety produced nectar twice a day (06:00–12:00 h and 17:00–19:00 h). Additionally, males of both varieties produced a sweet fragrance at night and in the early morning.

The flowers of both varieties were visited mainly by native and an exotic bee species (*Apis mellifera*), and by butterflies. The flowers of the wild variety were additionally visited by flies and a hummingbird species (Table 1). The assemblage of flower visitors in the wild variety was slightly more diverse (Shannon's index =1.8) than in the maradol variety (Shannon index = 1.5). In both varieties, male plants were more frequently visited than female/hermaphrodite plants (Table 1). Females of the maradol variety were not visited by any animal and only one exotic bee visited the hermaphrodites during the pollination survey (Table 1).

The fruit set of open-pollinated flowers was 100% and 75% for the wild and the maradol variety, respectively. However, these differences were not statistically significant (Table 2). The fruit set of inter-variety cross-pollinated flowers was statistically higher when the receptor of pollen was the wild variety (100%) than when it was the maradol variety (45%) (Table 2). Fruit set in the flowers bagged to test for apomixis was very low for the maradol (7%) and null for the wild variety; differences between varieties were not statistically significant (Table 2).

Discussion and Conclusions

The results of our study clearly suggest that, while recently introduced, the reproductive biology of the maradol variety of papaya is better known than the reproductive biology of the wild variety. This is interesting because it is known that wild papaya have been used by the Maya for several centuries (Colunga-García Marín and Zizumbo-Villareal 2004). The informants also mentioned during in-depth interviews and participant observation that wild papaya was cared for in situ and the fruit used to be consumed several years ago in Pomuch, but also emphasized that this is no longer the case. Nowadays papaya is a much appreciated fruit and consumed regularly in Pomuch; however, people consume the maradol variety almost exclusively. This evidence suggests that the maradol replaced the wild variety in the diet of people in Pomuch and this potentially contributed to eroding local ecological knowledge about the wild variety.

Table 2 Percentage of fruit set after two hand-pollination treatments (inter-variety cross-pollination and apomixes) and in open-pollinated flowers. Statistics shown are a comparison of the two papaya varieties: wild and maradol. Data are % of fruit set, sample sizes are in parentheses

	Fruit set (n)		
Variety	Open-pollination	Inter-variety cross pollination	Apomixis
Wild	100 (3)	100 (8)	0 (5)
Maradol	75 (4)	45 (20)	6.6 (12)
Statistics	$\chi^2_1 = 0.01$	$\chi^2_1 = 5.12^{**}$	$\chi^2_1 = 0.01$

$^{**}P < 0.01$

We predicted a positive association between the age of the informants and their LEK about the reproductive ecology of the papaya. This prediction was supported by data but, contrary to our expectations, this trend was only significant for the maradol variety. The maradol variety has been the dominant papaya variety for the last three decades in the study area; therefore, it is understandable that even the elderly have forgotten the peculiarities of the reproductive ecology of the wild variety and, as a result, only have distant memories of past uses and past management practices. Wild papaya is no longer managed in situ; instead, practices such as watering and weeding, common in the past for the wild variety, are currently reserved for the maradol variety. The lower degree of knowledge of young relative to older adults regarding the reproductive ecology of the maradol variety may be due to a relatively recent shift in the types of jobs held by the young on the Yucatan Peninsula (i.e., from mainly the primary sector to the tertiary sector; Eastmond *et al.* 2000). An increasing number of young adults in Pomuch commute daily or once a week to the main cities on the Yucatan Peninsula (Campeche City, about 20 km away, and Mérida, about 175 km away) to work or study in fields largely unrelated to agriculture (personal observation).

Everyday contact with the urban lifestyle also produces a change in the interest of the young who no longer see agriculture as a profitable activity (van de Wouw *et al.* 2010; Punch and Sugden 2013; Carpena-Mendéz 2015). Contact with the urban life style also results in changes in gastronomic preferences and eating habits, which is also known to affect the conservation of traditional crop varieties (Rijal 2010; van de Wouw *et al.* 2010). In Borneo, traditional varieties of taro (*Colocasia esculenta*) are tolerated along the margins of agricultural systems even though they are not commonly consumed. However, in contrast to our study area, in Borneo, taro has current relevance in rituals, language, and myths that seem to be associated with the conservation in situ of traditional varieties (Dove 1999).

According to our results, the reproductive ecology of the maradol and the wild variety are very similar in terms of their phenology and presumed pollinators. Differences in these properties are minuscule (maradol flowers live a few hours longer and are visited by a slightly less diverse assemblage of animals), and hardly perceived by the inhabitants of Pomuch. In contrast, the size of the fruit is a distinctive trait and is used by the informants to distinguish between the maradol and the wild variety. This is not surprising because the most important benefit obtained from papaya is the fruit. Because size is an important trait of the fruit, informants pay particular attention to the variables affecting it. It was quite interesting for us to find that some people associated small-sized fruit with pollen flow between the maradol variety and wild populations, which was not even reported in the literature (Silva-Rosales *et al.* 2010), but was experimentally confirmed in our inter-variety hand pollination experiment. Gene flow between modern and wild varieties is also worrisome because the breeding between genetically modified varieties and wild varieties is likely, and this may have catastrophic results including genetic introgression and the creation of weedy varieties. This, in turn, may have an even stronger impact on LEK because weedy or feral plants usually are less dependent on human management and pollinator activity for reproduction (Silva-Rosales *et al.* 2010; Brown *et al.* 2012).

It seems that LEK is broader when it is directly linked to productive activities and, therefore, has an impact on the family income. This notion is also supported by the fact that proper sexual expression was not identified by most of the informants and male sex change is no longer artificially induced. Male plants are very rare in the maradol variety in the home gardens of Pomuch relative to the wild variety (less than 1% and about 20% of the plants are males for the maradol and the wild variety, respectively; Moo-Aldana 2015). Instead, the most frequent sexual expression in this variety is hermaphroditism (≈85% of plants); thus, either identification or sex change induction has not been cost-effective in recent years. In contrast, the wild variety is strictly dioecious with evident sexual dimorphism (Brown *et al.* 2012; Fuentes and Santamaría 2014). People in the past likely realized that plants with a certain morphology do not produce fruit and discovered that these plants started setting fruit after some damage had been inflicted. Nowadays, with the introduction of the maradol variety, this practice is no longer needed owing to the dominance of hermaphrodites. The terms male and female are still being used but are completely unrelated to plant sexual expression.

Rico-Gray *et al.* (1988) realized that people in the neighbouring state of Yucatan (130 km away from the study area) were able to recognize the sexual expression of plants based on the morphology of their reproductive organs, which contrasts with our findings. That study was conducted in the early 1980s when the maradol variety was just being introduced. Potentially, differences in levels of LEK found between that study and this one result from the displacement of the wild varieties by the maradol variety. However, we recognize that we cannot ignore other potentially confounding effects such as geographic variation (i.e., the studies were conducted in different localities). The maradol variety dominates home gardens all over the Yucatan Peninsula, and consequently we did not have the opportunity to compare LEK in communities with and without it. This also justifies our retrospective approach (i.e., asking informants about past conditions).

The marginal trend of greater LEK of the reproductive ecology of papaya (for the maradol variety) observed in men contradicts the findings of previous studies that suggest that women generally have greater ethnobiological knowledge of plants in home gardens (e.g., de Almeida *et al.* 2012). That leads us to postulate that some papaya LEK is acquired by men working in commercial plantations (plantation owners preferentially hire men). In fact, one male interviewee explicitly stated that he used to work in a commercial plantation where he also received technical training. Therefore, it is possible that some LEK, particularly for men, on the reproductive ecology of the maradol papaya was recently acquired via formal education/training.

An important observation during fieldwork was the absence of papaya landraces that, according to the informants, used to be cultivated in home gardens in the study area. Landraces are the result of the traditional management of the wild variety, and are very important because they are adapted to local environments and usually are linked to local traditions (Brush 1995; Altieri 2003). Landraces are particularly valuable in traditional subsistence agriculture with no or little access to agrochemical inputs (Brush 1995). Landraces also usually co-occur with wild varieties, thus promoting gene flow between varieties and making landraces more resilient to environmental stochasticity (Brush 1995). The existence of landraces implies that people managed the wild variety and traditional management is, in some sense, traditional ecological knowledge put into practice. Because landraces have virtually disappeared in the study area, we assume that the LEK associated with managing papaya landraces is currently heavily eroded or has been completely lost.In conclusion, despite the fact that wild papaya had been managed for far longer, there was less ecological knowledge about its reproductive ecology in Pomuch than for the maradol variety. Understanding the reproductive ecology of papaya is very important for in situ conservation because it is a dioecious species and needs pollinators for sexual reproduction. Thus, to conserve wild papaya in situ we also have to conserve its pollinators. As suggested by our informants, it seems that the introduction of the maradol variety not only had a role in the displacement of the wild variety but also in the disappearance of papaya landraces. Important management practices have been virtually lost in this process (e.g., artificially induced sex change and in situ care of the wild variety), and the introduction of the maradol variety also seems to have played a role. The introduction of modern varieties to crop centres of origin represents a threat to the conservation of agrobiodiversity in situ and associated local ecological knowledge.

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Conflict of Interest Authors have declared that there is no conflict of interest.

References

Altieri M. A. (2003). The Sociocultural and Food Security Impacts of Genetic Pollution via Transgenic Crops of Traditional Varieties in Latin American Centers of Peasant Agriculture. Bulletin of Science, Technology and Society 23(5): 350–359.

Altieri M. A., Anderson M. K., and Merrick L. C. (1987). Peasant Agriculture and the Conservation of Crop and Wild Plant Resources. Conservation Biology 1(1): 49–58.

Altieri M. A., and Merrick L. C. (1987). In Situ Conservation of Crop Genetic Resources Through Maintenance of Traditional Farming Systems. Economic Botany 41(1): 86–96.

Brown J. E., Bauman J. M., Lawrie J. F., Rocha O. J., and Moore R. C. (2012). The Structure of Morphological and Genetic Diversity in Natural Populations of *Carica papaya* (Caricaceae) in Costa Rica. Biotropica 44(2): 179–188.

Brush S. B. (1995). In Situ Conservation of Landraces in Centers of Crop Diversity. Crop Science 35(2): 346–354.

Carpena-Mendéz F. (2015). Jóvenes Rurales, Memoria y Futuros Agrícolas en Latino América. Carta Económica Regional 27(115): 5–34.

Castañeda-Álvarez N. P., Khoury C. K., Achicanoy H. A., Bernau V., Dempewolf H., Eastwood R. J., Guarino L., Harker R. H., Jarvis A., Maxted N., Müller J. V., Ramirez-Villegas J., Sosa C. C., Struik P. C., Vincent H., and Toll J. (2016). Global Conservation Priorities for Crop Wild Relatives. Nature Plants 2: 1–6.

Colunga-García Marín, P., and Zizumbo-Villareal, D. (2004) Domestication of Plants in Maya Lowlands. Economic Botany 58(supplement): S101-S110.

Crawley R. (2013). The R book, John Wiley and Sons Ltd, Chichester.

de Almeida C. F. C. B. R., Ramos M. A., Silva R. R. V., de Melo J. G., Medeiros M. F. T., Araújo T. A. S., de Almeida A. L. S., de Amorim E. L. C., Alves R. R. N., and Albuquerque U. P. (2012). Intracultural Variation in the Knowledge of Medicinal Plants in an Urban-Rural Community in the Atlantic Forest from Northeastern Brazil. Evidence-Based Complementary and Alternative Medicine 2012(1): 1–15.

Development Core Team R. (2011). R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, Vienna.

Dey K., Mondal S., and Mandal S. (2016). Flower-Visitor Diversity with Reference to Pollen Dispersal and Pollination of *Carica papaya* L. International Journal of Advanced Research in Biological Sciences 3(2): 65–71.

Doebley J. F., Gaut B. S., and Smith B. D. (2006). The Molecular Genetics of Crop Domestication. Cell 127(7): 1309–1321.

Dove M. R. (1999). The agronomy of Memory and the Memory of Agronomy. In Nazarea V. (ed.), Ethnoecology: Situated knowledge/local lives, University of Arizona Press, Tucson, pp. 45–70.

Eastmond A., García A., and Cordova-y-Ordóñez J. (2000). Recent population and education trends on the Yucatan Peninsula. In Lutz W., Prieto L., and Sanderson W. C. (eds.), Population, Development, and environment on the Yucatan Peninsula: From ancient Maya to 2030, IIASA Research Report, Luxemburg, pp. 54–72.

Freeman D. C., Harper K. T., and Charnov E. L. (1980). Sex change in Plants: Old and New Observations and New Hypothesis. Oecologia 47(2): 222–232.

Fuentes G., and Santamaría M. J. (2014). Papaya (*Carica papaya* L.): Origin, domestication and production. In Ming R., and Moore P. H. (eds.), Genetics and Genomics of Papaya, Springer, New York, pp. 3–15.

Galluzzi G., Eyzaguirre P., and Negri V. (2010). Home gardens: Neglected hotspots of agrobiodiversity and cultural diversity. Biodiversity and Conservation 19(13): 3635–3654.

GSPC. (2002). Global strategy for plant conservation. Secretariat of the convention on biological diversity, United Nations Environment Program. www.cbd.int/gspc/strategy.shtml.

Guarino L., and Lobell D. B. (2011). A walk on the wild side. Nature Climate Change 1(8): 374–375.

Heywood V. H. (2015). In situ conservation of plant species – An unattainable goal? Israel Journal of Plant Sciences 62(1): 1–21.

Hopfenberg R., and Pimentel D. (2001). Human population numbers as a function of food supply. Environmental Development and Sustainability 3(1): 1–15.

INEGI. (2010). Censo de población y vivienda. INEGI, Mexico City. www.inegi.org.mx.

Irons M. J. (1908). Observations on Change of Sex in *Carica papaya*. Science 28(708): 125–126.

Kell, S.P., Maxted, N., and Bilz, M. (2012). European crop wild relative threat assessment: Knowledge gained and lessons learnt. In Maxted, N., Dulloo, M.E., Ford-Lloyd, B. V., Frese, L., Iriondo, J.M., Pinheiro de Carvalho, M.A.A. (eds.), Agrobiodiversity Conservation: Securing the Diversity of CROP WILd Relatives and Landraces. CABI International, Wallingford, pp. 218-242.

Marín-Acosta J. (1969). Insectos Relacionados Con La Lechosa. *Carica papaya* L. en Venezuela. Agronomia Tropical Maracay 19(4): 251–267.

Moo-Aldana R. D. (2015). Conocimiento Tradicional y Prácticas Sobre La Expresión Sexual y La Reproducción de La Papaya (*Carica papaya*) en Solares de Pomuch, Campeche. M.Sc, Thesis, Cinvestav.

Newbery F., Aiming Q., and Fitt B. D. L. (2016). Modelling Impacts of Climate Change on Arable Crop Diseases: Progress, Changes and Applications. Current Opinion in Plant Biology 32: 101–109.

Plucknett D. L., and Horne M. E. (1992). Conservation of Genetic Resources. Agriculture, Ecosystems and Environment 42(1–2): 75–92.

Poot-Pool W. S., Van Der Wal H., Flores-Guido S., Pat-Fernández J. M., and Esparza-Holguín L. (2012). Economic Stratification Differentiates Home Gardens in the Maya Village of Pomuch, Mexico. Economic Botany 66(3): 264–275.

Punch S., and Sugden F. (2013). Work, Education and Out-Migration among Children and Youth in Upland Asia: Changing Patterns of Labour and Ecological Knowledge in an Era of Globalisation. Local Environment 18(3): 255–270.

Renner S. S., and Feil J. P. (1993). Pollinators of Tropical Dioecious Angiosperms. American Journal of Botany 8(9): 1100–1107.

Reyes-García V., Aceituno-Mata L., Calvet-Mir L., Garnatje T., Gómez-Baggethun E., Lastra J. J., Ontillera R., Parada M., Rigat M., Valles J., Vila S., and Pardo-de-Santayana M. (2014). Resilience of Traditional Knowledge Systems: The Case of Agricultural Knowledge in Home Gardens of the Iberian Peninsula. Global Environmental Change 24: 223–231.

Rico-Gray V., García-Franco J. G., and Chemas A. (1988). Yucatecan Mayas Knowledge of Pollination and Breeding Systems. Journal of Ethnobiology 8(2): 203–204.

Rijal D. K. (2010). Role of Food Tradition in Conserving Crop Landraces on-Farm. Journal of Agriculture and Environment 11: 107–119.

Sedesol (2010) Campeche, Hecelchakán. Unidad de Micro-Regiones, Cédula de Información Municipal, México

Silva-Rosales L., González-de-León D., Guzmán-González S., and Chauvett M. (2010). Why there is no transgenic papaya in Mexico. Transgenic Plant Journal 4(1): 45–51.

van de Wouw M., Kik C., van Hintunm T., van Treuren R., and Visser B. (2010). Genetic Erosion in Crops: Concepts, Research Results and Challenges. Plant Genetic Resources 8(1): 1–15.

Vegas A., Trujillo G., Sandrea Y., and Mata J. (2003). Apomixis, Poliembrionía Somática y Cigótica in Vivo en Lechosa. Interciencia 28(12): 715–718.

Walters C., Berjak P., Pammenter N., Kennedy K., and Raven P. (2013). Preservation of Recalcitrant Seeds. Science 339(6122): 915–916.