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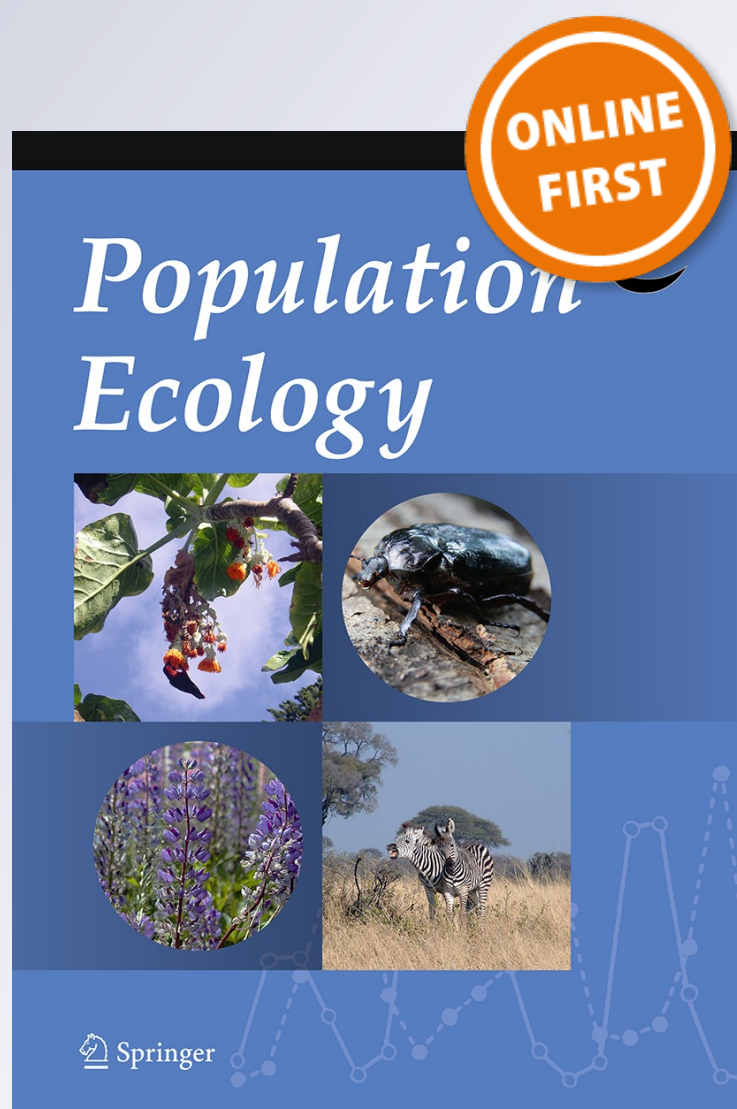
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ORIGINAL ARTICLE

Demography of *Oenocarpus bataua* and implications for sustainable harvest of its fruit in western Amazon

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Abstract *Oenocarpus bataua* is the seventh most abundant tree in the Amazon and one of the most used palms in the region. The main resource obtained from the species is the fruits that are harvested from wild populations for human consumption. Across its distribution area adults are most frequently felled to obtain the racemes, which may affect the palm's populations. In this paper we studied the demography of two populations of *Oenocarpus bataua* to assess the harvest potential of its fruits and the density variation in different habitats in the western Amazon to estimate fruit yields in different forest types. Non-inundated lands held the greatest densities with an average of 11 adults ha^{-1} (0–132 adults ha^{-1}). The population finite growth rate (λ) in Amacayacu, Colombia, was 0.9103 because of slow growth and low survival of stemless individuals and low recruitment. On the contrary, in Yasuní, Ecuador, we found a growing population with $\lambda = 1.0368$. According to our simulations, adult felling reduced transient population growth (λ_t) in both populations, especially when harvest was frequent even at low intensities. In Amacayacu a simulated harvest of 60 % year^{-1} of the fruits by climbing did not modify λ_t substantially, while in Yasuní, a regime of 80 % of annual harvest did not diminish λ_t below one and the initial number of adults. The results help to understand the demography of useful palms and to address sustainable management. For instance high yields can be obtained by shifting to non-destructive harvest techniques that can meet the increasing demand and maintain the populations.

Keywords Arecaceae · Geographic distribution · Integral projection models · NTFP · Population ecology · Wild foods

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Introduction

Palms are among the most useful plant families in Neotropical forests due their versatility and abundance (Balslev 2011). Seven species of palms are among the top

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20 hyper-dominant trees in the Amazon basin (ter Steege et al. 2013). One of them, *Oenocarpus bataua* Mart., is a solitary palm widely distributed in South America and ubiquitous in Amazonian forests (Kristiansen et al. 2009; Balslev et al. 2010, 2012). It grows in different environments, including a wide variety of hydric and edaphic conditions such as non-inundated or white sands forests (Svenning 2001). The species also usually ranks firsts among the most used wild palms for many Amerindian groups (Cámara-Leret et al. 2014). One of the reasons for its importance is the exceptional quality of its fruits that are rich in mono-saturated fats, antioxidants and proteins, from which beverages and oils are made (Montúfar et al. 2010). Given the fruits' outstanding quality, they are a fundamental part of the food security of Amazonian peoples (Balick 1986; Bates 1988), and at the same time a promising product in the cosmetic and food industry with growing market exposure (Brokamp et al. 2011; Isaza 2013). Apart from these properties, *O. bataua* satisfies a multitude of household needs, like construction materials, food, cordage, etc., especially in rural settings in northern South America (Balick 1986; Henderson et al. 1995). Because of these many uses, *O. bataua* provides important economic safety nets to its users since handicrafts, food, oil and other products can be sold at local and regional markets and generate cash incomes (Miranda et al. 2008; Brokamp et al. 2011).

Felling adult palms is the most common technique used to harvest fruits of *O. bataua* in the Amazon; this is a basic and destructive management practice (Bernal et al. 2011). It may cause reduced density or even local extinctions, especially in populations under constant destructive harvest (Vasquez and Gentry 1989; Miranda et al. 2009). A growing number of studies and management plans show that compared to felling the palm to harvest its fruits, non-destructive harvest methods (i.e., climbing) have much less negative effects on populations' dynamics (Miller 2002; Rocha 2004; Miranda et al. 2008). Already in some villages, adult palms are climbed when they are not too tall to cut racemes with ripe fruits (Miller 2002; Miranda et al. 2008). Nevertheless, the probable impacts of different management practices and regimes in populations of *O. bataua* are largely unknown to date.

From a biological viewpoint, sustainable management allows the indefinite persistence of the populations that provide a resource, and does not cause important reductions in the supply rate. Understanding the population dynamics that govern productive cycles provides important information for controlling effects of different management practices (Peters 1996; Ticktin 2004). Demographic studies provide such information (Caswell 2001). If recommendations of harvest are observation-based and concise, they may provide guidelines for ecologically sustainable management that can ensure the populations' conservation and continued market supply (Bernal 1998; Ticktin 2004). For example, the only matrix projection model (MPM) developed so far for *O. bataua* (Miranda et al. 2008), suggests that high changes in fecundity (removal of fruits) scarcely affects the populations' finite growth rate (λ), allowing a sustainable harvest. Moreover, because both resource supply and population dynamics may depend strongly on environmental conditions (Zuidema and Boot 2000; Vallejo et al. 2014), it is important to consider different environments when analyzing sustainability.

Population dynamics can be studied from a variety of perspectives and methods. Matrix projection models (MPM) have been the most commonly used tools to understand demographic patterns of plant species because their life cycles can be easily represented as matrices. They provide straightforward information about the populations' asymptotic growth rate (λ), estimating the contributions of different vital rates or stage classes to λ, and the expected population structure (frequency of individuals in each class), among other properties (Zuidema and Boot 2000). Recently, integral projection models (IPMs) have shown promising perspectives to understand plant dynamics (Merow et al. 2014). The advantage of the IPMs over MPMs is that information of every individual is used to construct functions known as kernels. Therefore, there is no need to use categories or classes and instead the individuals' variation is incorporated, providing smaller confidence intervals to estimate λ (Martorell et al. 2012).

Demographic models provide different indicators for assessing sustainability. The λ values inform us about the long-term persistence of the population if present conditions and management remain unchanged (Caswell 2001). However, management practices may affect environmental conditions in the long term, for instance if chronic adult felling or lack thereof alters the amount of light reaching the understory (Vallejo et al. 2014). Thus, the conclusions from demographic models may be valid only for a short time. The transient growth rate λ_t is an average of the growth rate up to a given time t in the future, and thus may be more realistic than λ (Groenendijk et al. 2012). Also, populations may be viable only if they have a certain minimum size below which endogamic depression, lack of reproductive partners or demographic stochasticity would lead them to extinction (Nazareno and dos Reis 2014). The time required to reach that threshold is known as time to quasi-extinction, and is yet another measure of sustainability. On the other hand, the amount of resource available, the third component related to sustainable management, depends on population size and thus on λ or λ_t, but also on population structure. For instance, if a harvest regime for *O. bataua* results in a stable population ($\lambda = 1$) that has very few adults, the amount of fruits

produced would be extremely small. Thus, we use the reduction in resource availability as a fourth measure of sustainability.

Here we present data for *O. bataua*'s density over a wide region in the western Amazon basin, covering four habitat types, and we perform a detailed demographic analysis of two of the populations using IPMs in different forest types. In particular we addressed the following questions: (1) How does the density of *O. bataua* vary across habitats differing in hydric and edaphic conditions in the western Amazon basin? (2) What are the vital-rates under different conditions? This part of the study was conducted under the two conditions in which *O. bataua* is most abundant, as they represent the largest portion of the available resource (3) What are the asymptotic growth rate (λ) and resource availability (considered to be proportional to the number of adults) under the two studied conditions? (4) Are current and alternative scenarios of fruit harvest sustainable in terms of population persistence and resource availability for both populations? The results presented here may help to define sustainable management practices for *O. bataua* fruit harvest and estimate fruit yields across different forest types in the Amazon and at the same time contribute to the understanding of population dynamics in tropical trees and the rationale of their sustainable use.

Materials and methods

Species and study area

Oenocarpus bataua is a single stemmed, monoecious palm, which grows to heights up to 25 m. Its infructescence has a stout peduncle and hanging rachillae with large, oily, black fruits (Galeano and Bernal 2010). It is widely distributed in lowland and premontane forests in South America, from Panama and Trinidad to northern Bolivia and central Brazil (Henderson et al. 1995). *Oenocarpus bataua* occurs in a wide variety of habitats with different edaphic and hydro-logical characteristics, including non-inundated and inundated forests, sandy soils and white sands (Table 1) (Kristiansen et al. 2009; Eiserhardt et al. 2011), sometimes in an aggregated pattern, forming mono-specific stands

(Peters et al. 1989) where the density depends on light conditions at micro-sites (Svenning 1999, 2001). Stands of *O. bataua* may have up to 104 adults ha^{-1} in flooded forests of northwestern Amazonas (Peters et al. 1989; Balslev et al. 2012), and up to 305 individuals ha^{-1} in *terra firme* forests in northern Amazon (Miller 2002; Balslev et al. 2010, 2012). In premontane forests of the Andes densities range from 31 to 551 adults ha^{-1} (Miranda et al. 2008; Balslev et al. 2010, 2012). *Oenocarpus bataua* produces fruits throughout the year, with asynchrony among individuals (Isaza 2013). The fleshy fruits are a well-known food for big fauna, like tapirs and agoutis, which in turn disperse the seeds (Bodmer 1991).

The Amazon basin covers 6.9 million km^2, and includes parts of Bolivia, Brazil, Colombia, Ecuador, Guyana, Peru, Surinam and Venezuela. The Amazon River drainage basin reaches up to 6500 m a.s.l. in the Andes and goes across a broad variety of forest types. It is a major hotspot of bio-diversity and the home of approximately of 40,000 plant species, 430 species of mammals and 1,300 of birds (Da Silva et al. 2005). In addition, 350 ethnic groups live in the basin, making it also a biocultural hotspot (OAS 2005). The main economic activity in the region is extractivism, especially of minerals, wood, game and non-timber-forest-products (OAS 2005).

We sampled *O. bataua* at four habitats defined in Table 1 to have a better understanding of its density and distribution on a large scale across the western Amazon basin in Colombia, Ecuador, Peru and Bolivia, from 4°03′N to 14°19′S during 1995–2009 (Fig. 1). For a detailed study of the population dynamics we selected, the two environments that can provide the largest amount of fruits: non-inundated and inundated forests (see results). We worked in the seasonally flooded forests or *varzeas* in the Tikuna community of San Martín de Amacayacu, Amazonas, Colombia (03°46′S, 70°18′W; 100 m a.s.l) because is an indigenous territory where *O. bataua* historically has been used for its fruits. We also worked in well drained or *terra firme* forests in the Yasuní National Park (YNP) (00°41′S, 76°23′W; 300 m a.s.l.), between Napo and Pastaza provinces in Amazonian Ecuador. That area is an ancestral territory of the Huaorani indigenous group, and *O. bataua* fruits are harvested for household consumption on an

Table 1 The habitat types sampled in the 266 transects (0.25 ha each transect) across western Amazon, with a description of each habitat and the number of transects sampled in each habitat

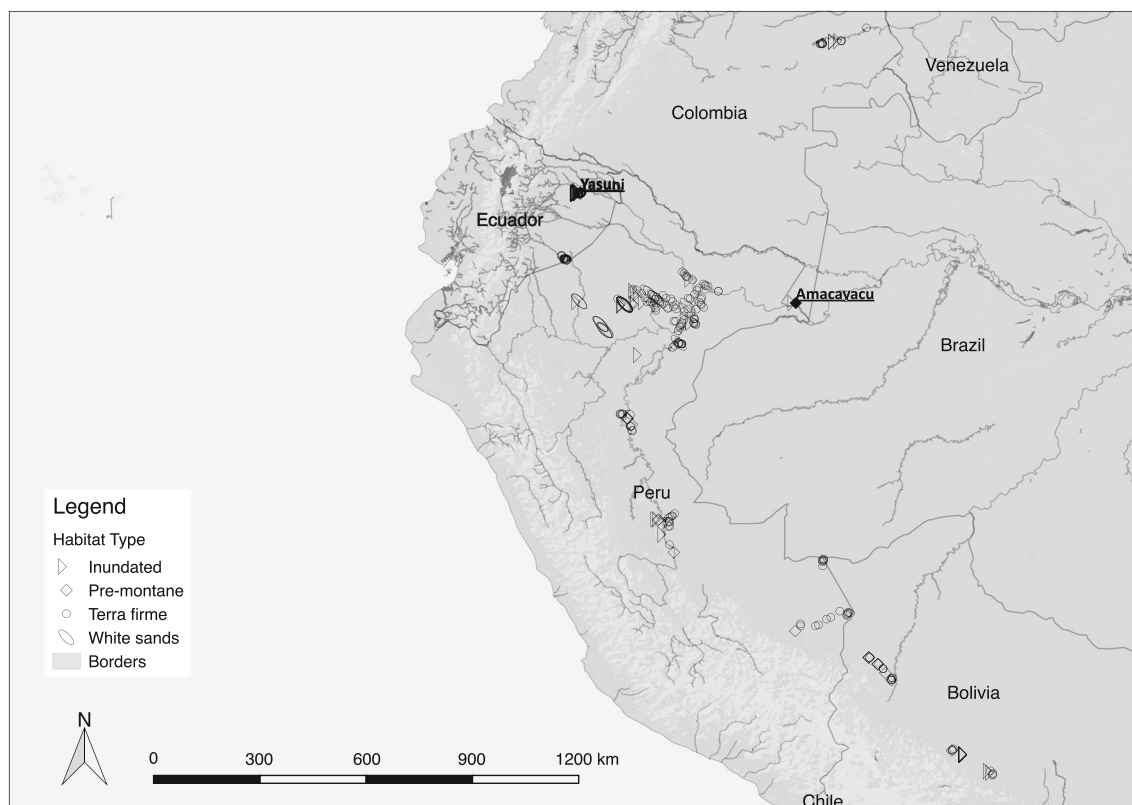| Habitat	Description	Number of transects
Inundated	Areas periodically inundated from rivers or permanently waterlogged	39
Non-Inundated	Never inundated. Variable terrain, areas of hills to flat terraces	180
Pre-montane forest	High-elevation pre-montane areas, in Andean foothills	19
White sands	Non-inundated, white-sand soils. Highly nutrient poor	28

Fig. 1 Map of the study area in the western Amazon basin and the locations of the 266 transects (total of 66 ha) in four types of habitat studied and two permanent plots

occasional basis. In Amacayacu the mean annual fruit productivity is around 18.5 kg individual^{-1} and 0.50 ton ha^{-1} year^{-1} in *varzea* forest (Isaza 2013), and 13.0–22.0 kg individual^{-1} or 0.70–1.43 ton ha^{-1} year^{-1} in *terra firme* forests (Miller 2002; Peralta et al. 2010).

Study design

Information on *O. bataua* density and distribution was obtained recording all *O. bataua* individuals with a standardized methodology (Balslev et al. 2010) using 266 transects of 5 × 500 m (0.25 ha), with a distance between transects of at least 500 m (very frequently much more than this). We placed transects in non-inundated, inundated, pre-montane and white sand soil habitats with tall, primary forests, avoiding any major disturbance in the different countries and regions to capture with sufficient accuracy the distribution of the species in each habitat. The potential productivity of fruits in transects was calculated using the fruit productivity range found in previous studies (Isaza 2013), ranging from 18.5–22.0 kg palm^{-1}.

Demographic data were sampled in permanent plots established in *O. bataua* dominated forests, with a distance between plots of a kilometer. In Amacayacu we established two 20 × 100 m plots in *varzea* forests. We performed four censuses 8 months apart from January 2011 until January 2013. The data of the 2 years were pooled to estimate the kernel of the integral projection model and to obtain annual values of the parameters. The population in Yasuní was followed over one year (2011–2012) to expand the results and give management recommendations for the species that relate to broader areas. In Yasuní, we established three 20 × 500 m plots in well-drained forests and seedlings were sampled in 40 randomly placed nested 5 × 5 m plots in each of the larger plots, giving a total of 120 small plots. In Amacayacu we followed 231 stemless individuals, 48 stemmed individuals, and 33 new seedlings recruited during the census. In Yasuní 632 stemless and 109 stemmed individuals were followed, and 44 new seedlings recruited into the population in one year. Due to the low density of adult individuals in Yasuní, 82 additional adults were followed in nearby areas to gather more information about their dynamics and reproduction.

In each plot all individuals were tagged, measured and counted in the first census. For stemless (comprising the seedling and juveniles categories used elsewhere) individuals we recorded: (1) the number of pinnae on the right side of the youngest leaf, (2) number of leaves produced. For

stemmed individuals (comprising the subadult and adult categories, used elsewhere) we recorded: (1) stem height, (2) leaf production, (3) reproductive status, and, if reproductive, (4) number of racemes. New seedlings were registered in the final census. The number of pinnae shows changes in the development of individuals and varies less than the leaf size due to environmental conditions (Bernal 1998). Height increase of stemmed individuals was calculated by multiplying the internode length by the number of leaves produced. Internode length was obtained counting the number of leaf scars every 1 m interval in 10 adults that had been felled in the two sites where demography was studied. The life span was calculated using size growth rates according to the life stage (pinnae number or stem height) and adding the time calculated for stemless and stemmed stages. To calculate the time spent in stemless stage we use the pinnae production rate in 2 years and calculated the time required to reach the maximum number of pinnae observed from the seedling stage (minimum number of number of pinnae observed). For stemmed individual we estimated the stem height increase based on leaf scars with the annual leaf production rate to know the amount of time spent to reach size y from size x (Pinard and Putz 1992; Bernal 1998).

Data analysis

To test if the density of adults and the total number of individuals differed across habitats we performed analysis of variance (ANOVA) followed by Tukey–Kramer tests, if the ANOVAs were significant.

Integral projection models (IPM) describe the dynamics of a population size structure in a discrete period of time (e.g., one year) (Easterling et al. 2000). The kernel $k(y, x)$ represents the transitions between individuals of every possible size, including births, where x is the size at time t, y is size at time $t + 1$. The model is given by the Eq. 1:

$$n(y, t+1) \int_X k(y,x)n(x,t)dx \tag{1}$$

The x variable can represent size, age or any other continuous variable that describes the demographic state of an individual, and X in the kernel integral is the range of possible sizes of x at time t and n is the distribution vector of the population. The kernel is also divided in three main functions which represent survival $[s(x)]$, growth $[g(y, x)]$ and fecundity $[f(y, x)]$ in the following equation:

$$k(y,x) = s(x)g(y,x) + f(y,x) \tag{2}$$

In general integral projection models, the kernel comprises functions over two or more domains, i.e., sets of values or variables that describe the demographic fate of individuals. Our model included two domains, **P** for stemless individuals, where the variable that describes individuals was the number of pinnae, and **Q** for stemmed plants described by stem length. We determined the functional expressions that defined the model parameters, i.e., the equations for the survival, flowering probabilities, etc. [see 'Electronic supplementary material' (ESM)] for each domain, by exploring different regression models and determining that fitted the data best. A similar procedure was followed to select the two functions that describe the transition from **P** to **Q**: The probability of transiting depending on the number of pinnae and the probability density function for the lengths of newly formed stems. We describe the functions that were selected according to the relevant domain, and the parameters estimated from the data in the ESM. All models included only significant terms.

From the kernels we obtained the asymptotic finite growth rate (λ) to establish the population growth tendencies ($\lambda < 1$ signifies a declining population, $\lambda = 1$ a stable population, and $\lambda > 1$ a growing population). To estimate the uncertainty in λ, we calculated confidence intervals from 1000 bootstrap replicates of the model randomly selecting with replacement different data points from the underlying raw data, building a new IPM model refitted from the new re-sampled data, and then calculating λ from the re-sampled IPM. The model was coded in R (R Core team 2014).

Elasticity analyses were obtained using two approaches: The first was to find the proportional change of λ to small perturbations in vital rates, i.e., any of the kernel parameters, θ. (Ellner and Rees 2006)

$$e_\theta = \frac{\partial \ln \lambda}{\partial \ln \theta} \tag{3}$$

Because logarithmic increments are equivalent to arithmetic scaled increments, the elasticity is proportional to the parameters evaluated. This approach allows finding the demographic parameters that have a greater impact on λ, and as a consequence, help to choose the most effective management strategies to maintain the populations' abundances under harvest.

The second method, described by Easterling et al. (2000) resembles MPM elasticity analysis, since both approaches use parallel mathematical equations (Caswell 2001). Nevertheless, given the continuous nature of the variables of the IPM, elasticity is evaluated as an integration of chosen kernel areas (Merow et al. 2014). This method allows us to evaluate the contribution of certain kernel regions to λ, where A and B are the lower and upper limits size widths corresponding to harvested sizes; and y and x are the size surface being perturbed in the kernel and e is the elasticity function.

$$\int\limits_{A}^{B}\int\limits_{A}^{B} e(y,x)dydx = 1 \qquad (4)$$

We carried out two sets of harvest scenarios for both populations. First, simulations of fruit harvest using climbing devices were performed to evaluate different extraction intensities (the fraction of fruits collected) and years between harvests by periodically reducing the production of fruits in the kernel. The second set of scenarios simulated harvest by means of felling adult palms. The procedure was similar to the previous one, but in this case a proportional reduction in the survival probabilities of adults accompanied the reduction in fruit production in the kernel. Because the kernel contains information about everything an individual of a given size is expected to do from time t to time $t + 1$, it is easy to envisage why felling affects both survival and fecundity: felling means killing the adult *and* collecting its fruits. If palms were felled after they reproduce, only survival would be modified and fecundity would remain unchanged. However, adults are felled just before they release their fruits, so their fecundity over the time interval is effectively zero. See ESM for details on how harvest simulations were performed.

To choose the frequency and intensity of harvest in the simulated scenarios, we used data from observed harvest regimes in different nearby areas of the Amazon. In Amacayacu the felling rate is 10 % of the adults every 4 years; in Yasuní 25 % year^{-1}; 40 % year^{-1} in Leticia, the biggest Amazonian city in Colombia. On the other hand, when adults were climbed we recorded a harvest rate of 40 % of the fruits year^{-1} legally in Chiriap (established in a management plan), a community nearby Yasuní; 70 % year^{-1} according to the Colombian law, and 80 % year^{-1} of legal and illegal harvest in Chiriap (Cevallos et al. 2013).

Because fruit production is expected to be proportional to the number of adults, to obtain an estimate of resource supply we estimated the number of adults in the two populations over a 100 year period for each harvest technique and regime from the first 100 iterations of the IPM starting with the observed size structures. Following our definition of sustainable management as one that does not reduce supply importantly, a harvest regime was considered sustainable if it did not face sensible reductions in the number of adults observed at both study sites. We set the quasi-extinction threshold to one adult individual, as it is the minimum number required to provide resource supply and regeneration, as a parameter to evaluate harvest sustainability. Likewise, we obtained the transient population growth rate (λ_t) after 100 year (λ_{100}) for each harvest scenario (Eq. 5),

$$\lambda_{100} = \sqrt[100]{\frac{n_{100}}{n_0}} \qquad (5)$$

where n_0 and n_{100} are the population size at the initial time and after 100 years, respectively, which also was used to assess the sustainability of harvest scenarios.

Results

Density and distribution on forest types

The density and distribution of *O. bataua* in the Amazon basin was variable and had a wide coverage, extending over different habitats (Fig. 2). We had at least 19 transects in each habitat type (Table 1). In the 266 transects (66 ha in total) we recorded a total of 43,725 individuals from seedlings to adults. Total density changed across habitats ($F_{3, 262} = 8.064$, $P < 0.0001$, Fig. 2), with forests of *terra firme* and terraces (non-inundated forests) showing the highest abundance followed by white sands (which did not
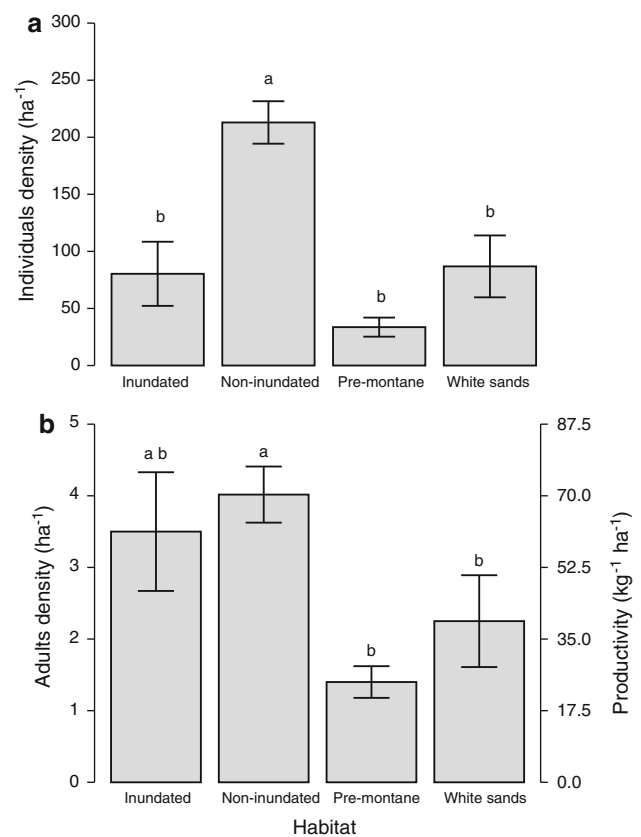

Fig. 2 *Oenocarpus bataua* mean density and standard error bars for **a** total of individuals and **b** adults and an estimation of fruit productivity in four types of habitat in western Amazon. Different letters above the bars indicate significant differences with an α (alpha) <0.05 calculated from Tukey–Kramer tests

differ from the remaining habitats). Adult density also depended on the habitat ($F_{3,\ 262} = 3.375$, $P = 0.0189$, Fig. 2), again with *terra firme* having the greatest density, followed by inundated forests, which did not differ from them statistically. Because adults are the ones producing the fruit, we chose these two habitats to conduct our demographic study.

Vital rate analysis

The annual rate of increase in the number of pinnae in Yasuní nearly doubled that in Amacayacu (with a slope of 1.052, SE = 0.131 vs. 0.519, SE = 0.0171, respectively). The survival of stemless individuals increased with the number of pinnae. The seedlings (individuals with bifid leaves) were the most vulnerable stage in the life cycle, having the lowest survival probabilities, with 60 % chance

to live in Amacayacu vs. 80 % in Yasuní. Size showed no significant effect on the survival of stemmed individuals ($P = 0.073$), because death events occurred throughout their size range, and—according to our observations—were due to disturbances to neighboring vegetation, wind throws and senescence, and not to related to harvest or size in the study plots. The flowering probabilities increased rapidly as the individuals became taller; in Amacayacu it reached 50 % when individuals were 6 m tall, while in Yasuní the same probability was reached when the stem was 6.5 m tall. Age estimations in both populations were similar but differed in the length of each stage. In the Amacayacu population, the life span was calculated to be 137 years, 80 of which were spent in stemless stage, and 57 in the stemmed stage. In Yasuní the age of fully developed individuals was estimated as 128 years; spending 50 years as a stemless individual and 78 years in the stemmed stage.
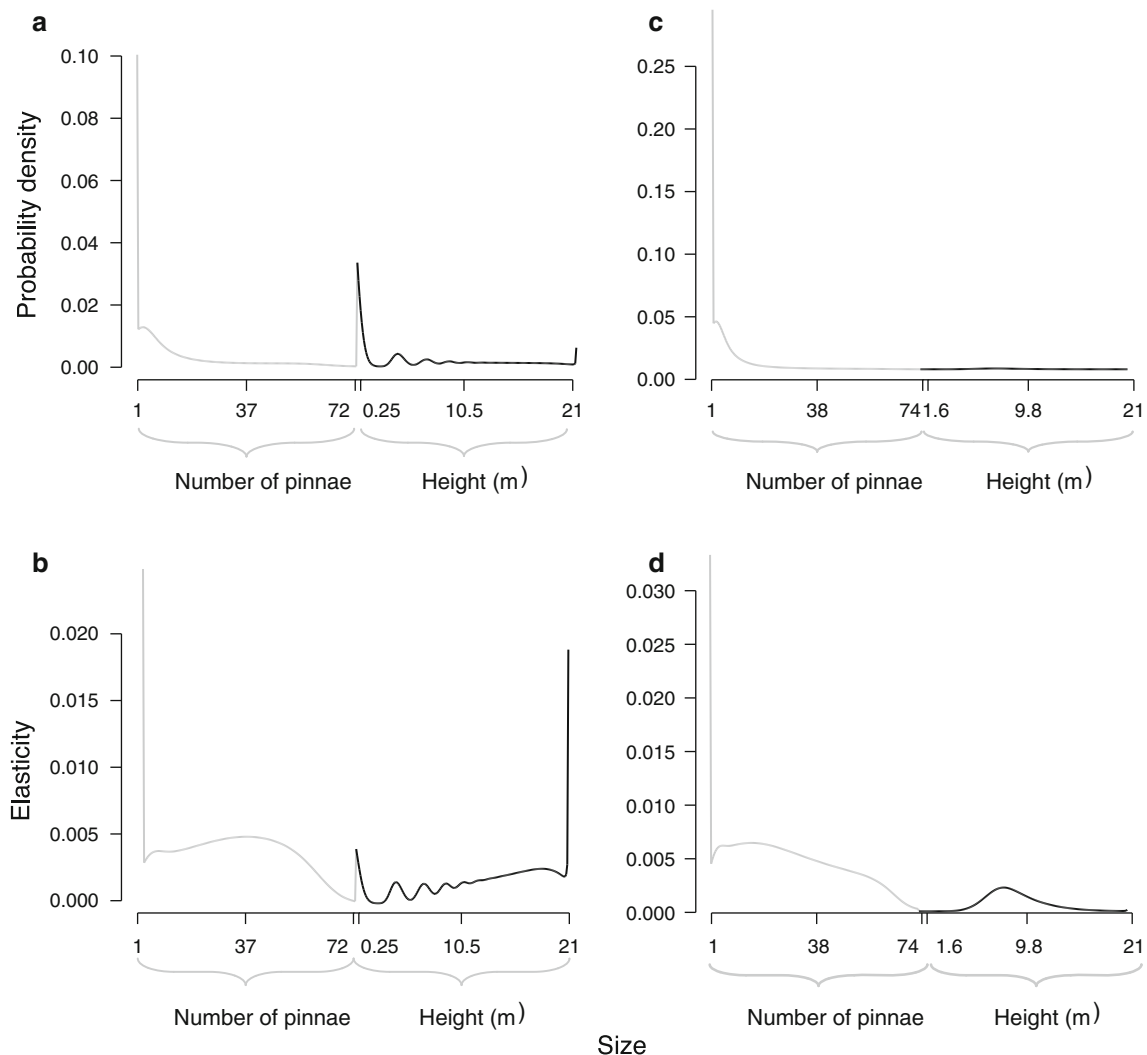

Fig. 3 Stable size structures of *Oenocarpus bataua* populations (**a**, **c**), and size-specific elasticities (**b**, **d**) in Amacayacu (**a**, **b**) and Yasuní (**c** and **d**). The elasticity of individuals in a size interval corresponds to the area under the elasticity functions shown. *Grey line* segment corresponds to stemless stage; black line segment to stemmed stage

Population dynamics parameters

The populations' stable stage distribution had an "inverted-J" shape with a greater frequency of seedlings (individuals with bifid leaves) and a sharp decrease in the subsequent size stages, more notably in immature stemmed individuals or subadults (Fig. 3a, c). The population in Amacayacu had a decreasing population growth rate, $\lambda = 0.9103$ [95 % CI (0.8804, 0.9623)]. The population of Yasuní had a slightly but not significantly increasing population, with $\lambda = 1.0368$ [95 % CI (0.9895, 1.0851)].

In Amacayacu, stemless individuals made the greatest contribution (0.6189 out of a total of one) to the total elasticity (Fig. 3b). The elasticity analysis of vital rates in that population showed that the parameters with a greater contribution to λ were related to the survival of stemless individuals and the probability to produce a stem (Fig. 4a). In Yasuní a similar pattern was observed in terms of plant sizes, with stemless individuals concentrating most of the elasticity (0.8492; Fig. 3d). The vital rates with greater elasticity were related to the growth of stemless individuals and the flowering function (Fig. 4b).

Harvest simulations

The multiple harvest regimes explored in Amacayacu diminished the already declining population size ($\lambda_t < 1$) expected in the absence of harvesting (Figs. 5a, b, 6a, b). In the fruit harvest simulations in Amacayacu, λ_{100} values differed little from the value with no harvest even when high intensities were modeled (80 % year^{-1}) (Fig. 5b), producing at most as one percent point of decrease than the no harvest situation. The same occurred in terms of number of adults (Fig. 5b) and the quasi-extinction time (Fig. 6b), (time at which the lines cross the horizontal line), which were not greatly modified even at high extraction quotas. In contrast, adult-plant felling caused an exacerbation of the declining tendency of λ_{100} and in the adults' number in comparison to the values of no harvest and the fruit harvest scenarios (Figs. 5a, b, 6a, b). Times to quasi-extinction were also reduced importantly. The reduction of λ_{100} was less severe with longer time intervals between harvest events, but still had lower growth rates than the fruit harvest simulations (Fig. 5a). Severe regimes, like that practiced in Leticia, where 40 % of adults were fell each year, will produce an almost two percent point reduction in λ_{100}, leaving no adults 20 year sooner than the no harvest scenario (Fig. 6a). The harvest scenario observed in Amacayacu in which 10 % every 4 years of the adults were removed, reduced λ_{100} in 0.3 percent point and adults will disappear 6 years earlier than if no harvest were performed (Figs. 5a, 6a).

Similarly, in Yasuní the simulations showed that harvesting the adults diminished λ_{100} and the quasi-extinction
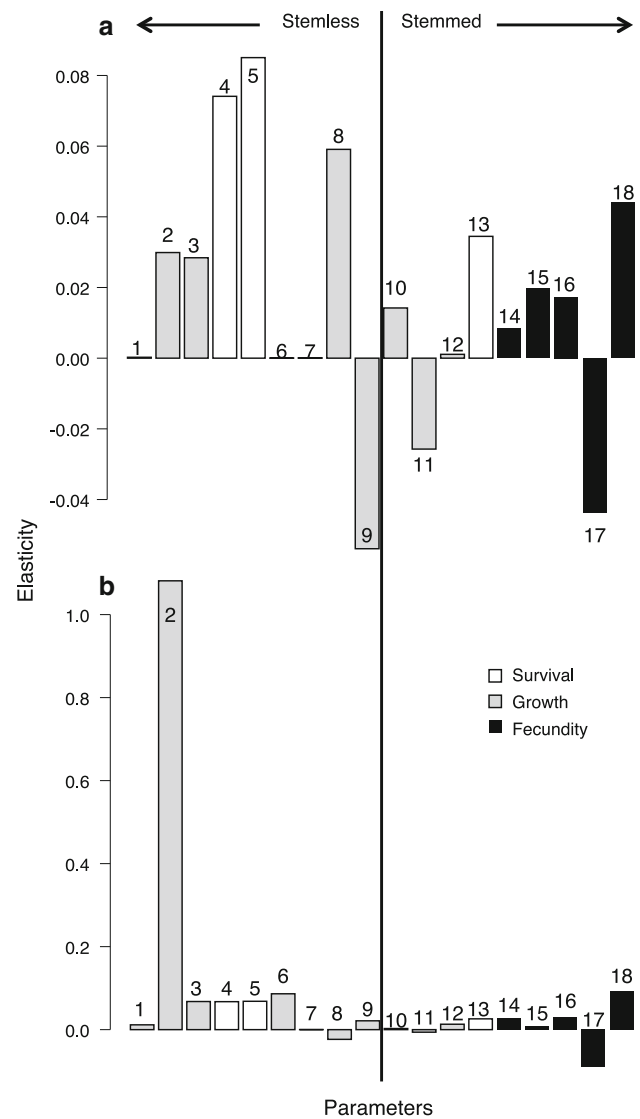

Fig. 4 Elasticity of the kernel parameters of *Oenocarpus bataua* that correspond to different stages (**P** domain is for stemless individuals—*left side* and **Q** domain for stemmed individuals—*right side*), and demographic processes (in the legend and above each bar 1 = intercept of **P** growth, 2 = slope of **P** growth, 3 = standard deviation of **P** growth, 4 = intercept of **P** survival, 5 = slope of **P** survival, 6 = mean stem length of individuals just developing a stem, 7 = standard deviation of the stem length of individuals just developing a stem, 8 = intercept of transition to **Q**, 9 = slope of transition to **Q**, 10 = intercept of **Q** growth, 11 = slope of **Q** growth, 12 = standard deviation of **Q** growth, 13 = mean of **Q** survival, 14 = intercept of reproduction probability, 15 = slope of reproduction probability, 16 = number of seedlings per raceme, 17 = intercept of number of racemes, 18 = slope of number of racemes. The panels correspond to each population: **a** Amacayacu, and **b** Yasuní

times more than only harvesting the fruits, and also that longer periods between harvests affected less the population growth, converging towards the no harvest trend (Fig. 5c, d). The harvest rate observed in Yasuní, of 25 % of adults year^{-1}, rapidly reduced the number of adults to
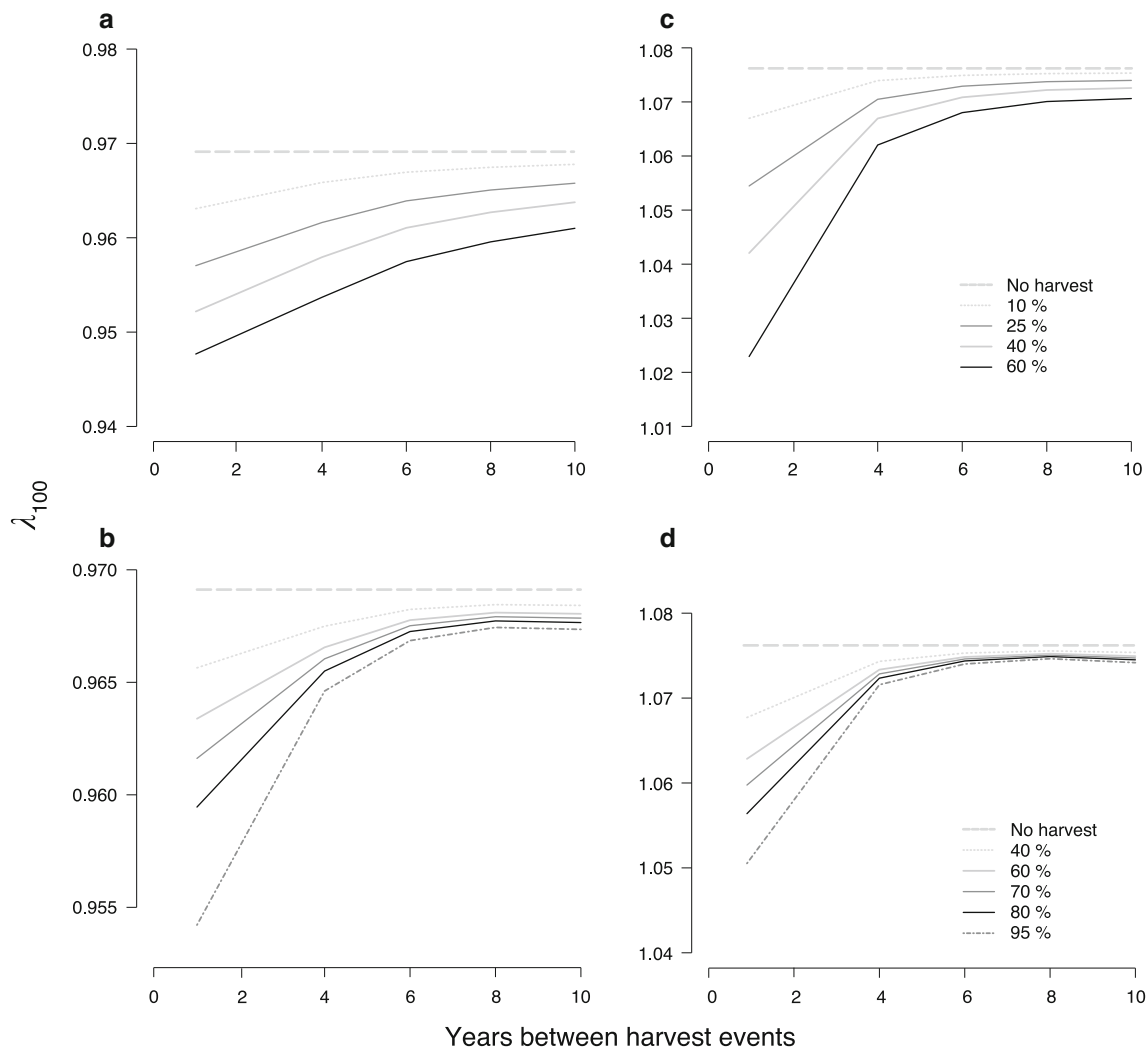
Fig. 5 Simulations of λ_{100} in two management scenarios with variable frequency and intensity of *Oenocarpus bataua* fruit harvest, **a** felling the adults in Amacayacu, and **c** in Yasuní; and cutting the racemes by climbing (**b**) in Amacayacu, and **d** in Yasuní. Legend in panel **c** corresponds to panels **a**, **c**, legend in panel **d**, corresponds to panels **b**, **d**

only one and the λ_{100} two percent point below the no harvest value (Figs. 5c, 6c). A mild scenario, removing 10 % of the adults every 4 year maintains the adults in the population (Fig. 6c). In comparison, the fruit harvest never reduced λ_{100} below one, nor the amount of adults under any scenario. Even intense annual harvest of 80 % of fruits reduced the population's λ_{100} by two percent points, but still maintain the adults abundance. Again, in Yasuní, longer harvesting cycles produced considerable increase in λ_{100} when fruit harvest was modeled (Fig. 5d). In addition to the outcomes of the harvest regimes, in Yasuní there was a reduction in the number of adults below one for about 25 years, independent of any harvest action (Fig. 5c, d); afterwards, the adults' density tended to recover, depending on the harvest regime.

Discussion

We present the first complete study that explores the population dynamics of *Oenocarpus bataua* to assess the harvest potential of its fruits. The population in Amacayacu, Colombia, had declining growth rates even with no harvest, probably as a result of slow growth and low survival in the stemless stage as well as low regeneration of the seedling stage. In Yasuní, Ecuador, we found a growing population with a high contribution from the stemless stage. Adult felling diminished λ_t in both populations, especially when harvest was done frequently even at small intensities; therefore harvesting by felling trees was in most scenarios unsustainable as observed in other demographic studies with palms. Harvesting fruits by climbing the palms
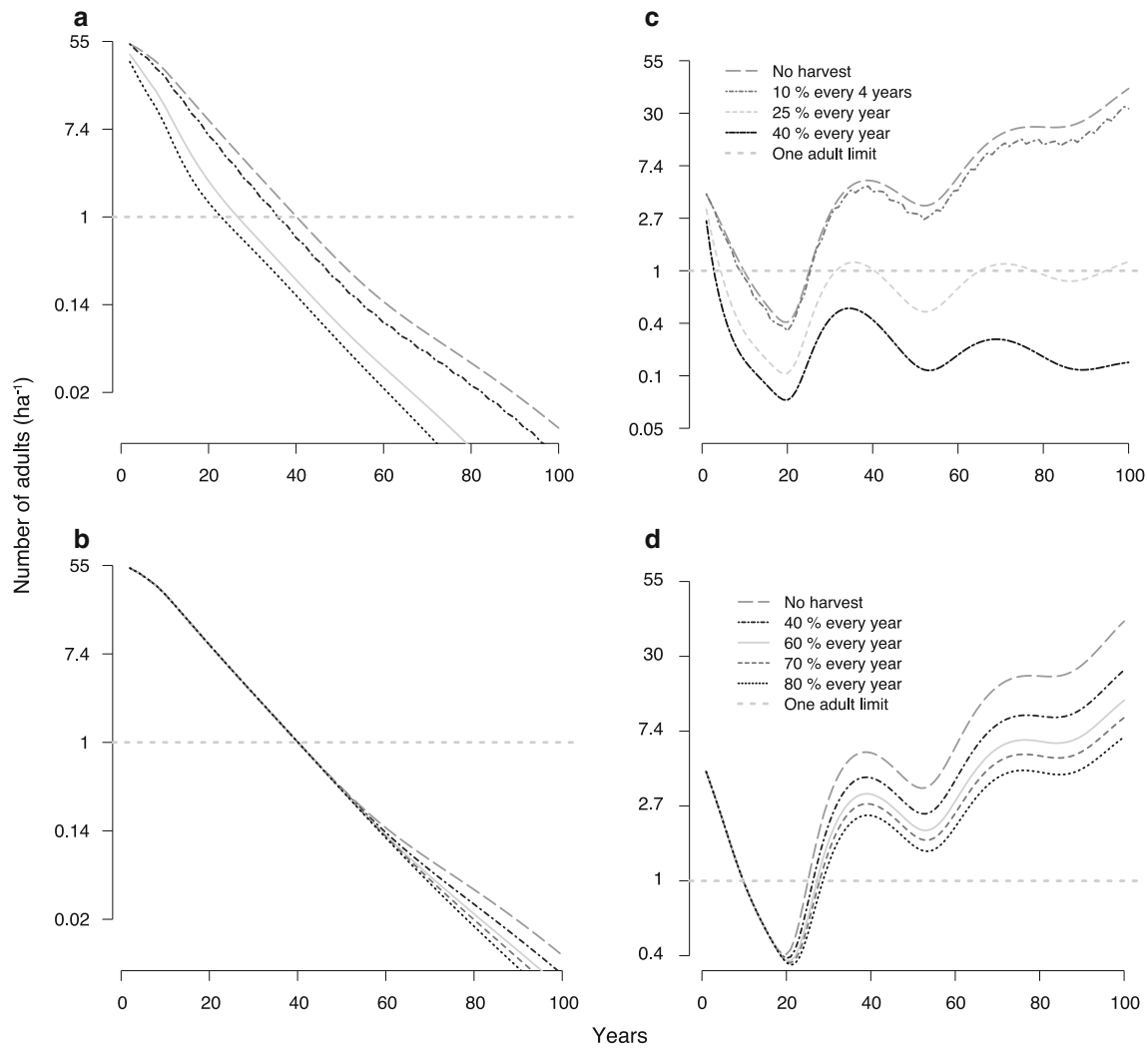
Fig. 6 Simulations in the number of adults in response to management scenarios observed for *Oenocarpus bataua* fruit harvest in 100 years, **a** felling the adults in Amacayacu, and **c** in Yasuní; and cutting the racemes by climbing **b** in Amacayacu, and **d** in Yasuní. The *horizontal grey broken line* represents the limit of a single adult left in the population. The *y*-axis is expressed in logarithmic scale. Legend in panel **c** corresponds to panels **a**, **c**, legend in panel **d** corresponds to panels **b**, **d**

did not reduce λ_t or the number of adults drastically, in the majority of the cases, in either population under any management scenario, also observed in other palm populations.

Density, distribution and fruit productivity

Oenocarpus bataua was abundant all over the Amazon habitat types sampled, as recorded elsewhere in the Amazon basin (Peters et al. 1989; ter Steege et al. 2013). *Oenocarpus bataua* is distributed over wide geographical ranges, covering different types of habitats in extraordinary densities, perhaps due to three characteristics: (1) It is a generalist species that can cope with different environments (Kristiansen et al. 2009; Balslev et al. 2010). (2) It has a great production of fruits and individuals when growing in suitable conditions (Balslev et al. 2010). (3) Its extensive use by pre-Columbian and current indigenous societies and consumption by large vertebrates may have extended its distribution (Bodmer 1991; ter Steege et al. 2013). Nevertheless, the species has a spatial aggregation at landscape scale, with diverse degrees of abundance, from scattered individuals to oligarchic forests, forming a patchy distribution (Svenning 2001; Eiserhardt et al. 2011), a variation also observed in the transects. This feature may be the consequence of the heterogeneity of the environmental and topographic conditions in the Amazon basin and local adaptations the species has to thrive in different habitats. Montúfar and Pintaud (2006) found ecological shifts in the local distribution of *O. bataua,* changing

gradually from being abundant in non-inundated forest in the west, to be equally abundant in flooded or non-inundated forests towards central Amazonia.

The mean productivity estimated from our sampled transects was low when compared with the productivity in oligarchic Amazonian forests with 0.70–3.40 ton ha^{-1} (Peters et al. 1989; Miller 2002; Miranda et al. 2008, 2009). Nevertheless, our transects with higher density could potentially produce 0.21–2.60 ton of fruits ha^{-1} year^{-1}, which falls within the estimates made in dense *O. bataua* stands. From these calculations and given the differences in adult-plant density we conclude that the commercial extraction of *O. bataua* would be more profitably performed in oligarchic forests, possibly in non-inundated habitats were the adults were more dense making the activity cost-energy efficient. Plots with low density are quite common and are likely to be only appropriate for local consumption and small markets.

Vital rates characteristics

The vital rates of *O. bataua* at our two study sites in Amacayacu and Yasuní had the same functional expressions and therefore they exhibit the same growth patterns, indicating that even if the two populations grow in different forest types at different rates, they share common life histories and growth strategies. The differences between populations were associated with the values of the parameters; for instance, the stemless individuals in Yasuní grew by 0.5 pinnae faster every year in small individuals (<6 pinnae) and 3 pinnae more in large individuals (>60 pinnae) than the same size individuals in Amacayacu (ESM). This difference is probably due to the effects of the drought of 2010 driven by the ENSO (El Niño-Southern Oscillation) (Marengo et al. 2011), which were apparently more prevalent in Amacayacu than in Yasuní according to climatic information (Lewis et al. 2011; Anderson-Teixeira et al. 2015), and supported with data that showed a significant increase of mortality of trees during this year in Amacayacu (Macía-Ruiz et al. 2011)

Population dynamics model

The population at Amacayacu was projected to decrease drastically over the next 100 years. Our estimates predicted that in about 46 years there would be only one adult per hectare in the population, a grim outlook for its maintenance and sustainability. On the other hand, in Yasuní λ was above one, which would allow a sustained fruit harvest if the management recommendations explored in the next section would be followed. The decline in Amacayacu is due to low survival and growth rates in the stemless stage and reduced seedling recruitment (Rojas et al. 2008).

Because even small variations in the stemless plants vital rates would affect λ importantly due to their high elasticity, reduction in these parameters may explain the decaying population in Amacayacu, as observed in other works (Zuidema and Boot 2000; Ferrer-Cervantes et al. 2012). Expansion and contraction growth cycles are common in plant populations, especially in slow growing species, which exhibit slow and intermittent size increments and spaced regeneration pulses (Ferrer-Cervantes et al. 2012) as a product of environmental conditions (Zuidema and Boot 2000). This suggested that the $\lambda < 1$ could be due to a contraction-growth cycle driven by the drought of 2010 (Marengo et al. 2011; Espinoza et al. 2013), but more demographic data of the species would have to be analyzed to prove this idea. Another factor that might have played a role in obtaining a $\lambda < 1$ in Amacayacu is the density dependence, since this population showed a high density of individuals in all of the stages, whereas in Yasuní it might not be operating given the low density of adults observed. The effect of the density dependence has been documented to affect the dynamics other palm populations (Löfgren 1995; Freckleton et al. 2003). In these studies it was shown that, the density of larger conspecific palms, usually adults, reduced the survival and transition of seedlings and small juveniles, imposing regulations in population growth and also may limit the harvesting possibilities (Freckleton et al. 2003).

Harvest scenarios

The data on which the demographic model is based represent a short period in relation to the life history of our study species. Therefore, the application of the results in different *O. bataua* populations should be done with caution because any population may differ in its growth behavior in relation to its environment and across time (Martínez-Ballesté et al. 2005). Nevertheless, the simulations provided a quantitative framework to guide the harvest of this important resource in the Amazon that has a potential to enter into global markets.

The majority of scenarios modeled confirmed that harvesting by felling the adults affected very negatively the populations' demography, diminishing their growth, the adults stocks, and the possibility of harvesting fruits sustainably in either population. The observed harvest rate of adults in Amacayacu (10 % every 4 years) was the only scenario in which the difference of the no harvest λ_{100} did not exceed one percent point and the number of adults over time did not change substantially in both sites, but fails to produce enough resources to meet the demand. The observed harvest rate of adults in Yasuní (25 % year^{-1}), kept just one adult in 100 year of simulations, while the no harvest projected a population with over 30 adults.

Numerous studies about harvest effects on palm dynamics reached the same conclusion; harvesting by felling adults produced negative impacts on palm populations (Zuidema and Boot 2000; Bernal et al. 2011). Further, we estimated that *O. bataua* fruits could be harvested in great proportions by climbing, since λ apparently was not largely affected by changes in the reproductive parameters (Miranda et al. 2008). Likewise, many palms exhibit demographic flexibility to reductions of fecundity (Bernal 1998; Rocha 2004). When climbed, a single adult supplied fruits for consumption and population regeneration for about 50 years, corresponding to the estimated duration of the mature stage estimated from yearly leaf production and leaf scars. This made possible a fruit production during adulthood of 462.5 kg individual^{-1} in Amacayacu and of 332.5 kg individual^{-1} in Yasuní (assuming supra-annual fruiting cycles) obtained by the product of average individual fruit productivity and the time of sexual maturity. In contrast, a felled adult produced a single time, on average 18.5 kg and 13.3 kg of fruits in Amacayacu and Yasuní, respectively; reducing the potential supply a single mature palm may yield. In a previous phase of the study, we found that climbing was more efficient (25 min to harvest a palm), effortless (according to harvesters the use of climbing devices is less strenuous than felling a palm with an axe or machete) and secure (when harvesters use safety equipment such as *estrobos* or triangles accidents rarely occur) than felling (60 min to harvest), which entailed gather the fallen fruits on dispersed areas and deal with the danger of vegetation falling or the intensive use of machete (Isaza 2013). Learning climbing techniques and access to equipment materials was the hindrance to adopt climbing in Amacayacu.

According to our simulations, the recommended harvest quota for Yasuní was 80 % every year, leaving 20 % of the fruits to nourish the fauna that depends on them and to allow the regeneration process (Bodmer 1991). This quantity allowed the harvest of 0.03 ton of fruits ha^{-1} year^{-1}, assuming that the current population density was preserved; this is a conservative figure as the population may be expected to grow according to our model. However, it should be noticed that in Yasuní we predict a decline in adults' density during the first 25 years, regardless of harvest, if the actual conditions persist. This deficit could be a consequence to the actual low adult density coupled with stochastic events, but given that the population is growing, we estimate new adults will replace and increase the present individuals. On the other hand, the model predicted that in Amacayacu after approximately 46 years, there would be no adults left in the population regardless of the harvesting practice, if the current λ is maintained. However, intense and frequent harvest cycles, especially of the adults, intensify the actual population

decline. Based on the simulations, the fact that the post-dispersal fruit predation rate was above 50 % (L.A. Núñez, personal communication), and our assumption that the Amacayacu population was experiencing a transitory contraction cycle, we suggest an annual harvest quota in Amacayacu should not be more than the 60 % of the fruits. This harvest regime, using the productivity data of the population represents 0.28 ton of fruits ha^{-1} year^{-1}.

The commercial harvesting potential for both populations was not very promising, given the low historic density of adults in Yasuní and the demographic restrictions in Amacayacu. Thus, it is suggested that these populations could be used to provide low commercial activity and subsistence needs, as has been the case until now. In spite of this, the Amacayacu population, with its high adult densities and proximity to local markets could be exploited if in upcoming years there is an increase in the survival and growth of juveniles and enhanced seedling recruitment, associated with expansion cycles where $\lambda > 1$, as observed in Yasuní.

The regulations for the harvest of non-timber forest products, such as *O. bataua* vary in different countries. In Colombia there is a harvest quota of no more than 70 % year^{-1} of the fruits, and Ecuador requires a management plan (República del Ecuador 2009; Corpoamazonia 2010; Cevallos et al. 2013). In Peru and Bolivia it is forbidden to cause the death of tree that provides fruit and the countries also require a management plan (República del Perú 2001; República de Bolivia 2006). In addition, in Bolivia no more than 90 % of the fruits can be harvested in rotating schemes. The harvest limit established in Colombia was higher than our estimated maximum quota in Amacayacu (60 % year^{-1}), and the one established in Bolivia was superior to the quota of both populations. According to our observations, the enforcement of rotation schemes is difficult to apply and monitor, especially in areas near urban markets, which likely end up in illegal harvest, as was the case in Chiriap. The establishment of equal harvesting quotas to all populations may lead to overharvesting in some of them, diminishing population growth rate and regeneration, which may play an important role in expansion periods. The present study underlines the importance of understanding the dynamics of populations in order to regulate or address management plans of wild products, since each population might differ in its behavior, which in turn affects the limits of the amounts to be extracted. In addition, the increasing interest of biocommerce initiatives to commercialize *O. bataua* fruits will possibly expand the markets (Brokamp et al. 2011) and will add more pressure on the resource; so in order to ensure a stable supply of fruits, there must be a permanent monitoring of the populations to adjust harvest quotas and set the limits to avoid over harvesting in periods with severe climatic fluctuations or with higher mortality rates.

References

Anderson-Teixeira KJ, Davies SJ, Bennett AC, Gonzalez-Akre EB, Muller-Landau HC, Joseph Wright S, Abu-Salim K, Almeyda-Zambrano AM, Alonso A, Baltzer JL, Basset Y, Bourg NA, Broadbent EN, Brockelman WY, Bunyavejchewin S, Burslem DFRP, Butt N, Cao M, Cardenas D, Chuyong GB, Clay K, Cordell S, Dattaraja H, Deng X, Detto M, Du X, Duque A, Erikson D, Ewango C, Fischer GA, Fletcher C, Foster RB, Giardina CP, Gilbert GS, Gunatilleke N, Gunatilleke S, Hao Z, Hargrove WW, Hart TB, Hau BCH, He F, Hoffman FM, Howe RW, Hubbell SP, Inmannarahari FM, Jansen PA, Jiang M, Johnson DJ, Kanzaki M, Kassim AR, Kenfack A, Kibet S, Kinnaird MF, Korte L, Kral K, Kumar J, Larson AJ, Li Y, Li X, Liu S, Lum SKY, Lutz JA, Ma K, Maddalena DM, Makana JR, Malhi Y, Marthews T, serudin RM, Mcmahon SM, McShea WJ, Memiaghe H, Mi X, Mizuno T, Morecroft M, Myers JA, Novotny V, De Oliveira AA, Ong PS, Orwig DA, Oserta R, Den Ouden J, Parker GG, Phillips RP, Sack L, Sainge MN, Sang W, Sri-Ngernyuang K, Sukumar R, Sun F, Sungpalee, Suresh HS, Tan S, Thomas SC, Thomas DW, Thompson J, Turner BL, Uriarte M, Valencia R, Vallejo MI, Vicentini A, Vraka T, Wang X, Wang X, Weiblen G, Wolf A, Yap S (2015) CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change. Glob Change Biol 21:528–549

Balick MJ (1986) Systematics and economic botany of the *Oenocarpus—Jessenia* (Palmae) complex. Advances in Economic Botany 3. The New York Botanical Gardener, New York

Balslev H (2011) Palm harvest impacts in north-western South America. Bot Rev 77:370–380

Balslev H, Eiserhardt W, Kristiansen T, Pedersen D, Grandez C (2010) Palms and palm communities in the upper Ucayali river valley—a little known region in the Amazon basin. Palms 54:57–72

Balslev H, Durán ZP, Pedersen D, Eiserhardt WL, Asturizaga AS, Paniagua-Zambrana N (2012) Subandean and adjacent lowland palm communities in Bolivia. Ecol Boliv 47:7–36

Bates DM (1988) Utilization pools: a framework for comparing and evaluating the economic importance of palms. Adv Econ Bot 6:56–64

Bernal R (1998) Demography of the vegetable ivory palm *Phytelephas seemannii* in Colombia and the impact of seed harvesting. J Appl Ecol 35:64–67

Bernal R, Torres MC, García N, Isaza C, Navarro J, Vallejo MI, Galeano G, Balslev H (2011) Palm management in South America. Bot Rev 77:607–646

Bodmer RE (1991) Strategies of seed dispersal and seed predation in Amazonian ungulates. Biotropica 23:255–261

Brokamp G, Valderrama N, Mittelbach M, Grandez CA, Barfod AS, Weigend M (2011) Trade in palm products in North-Western South America. Bot Rev 77:571–606

Cámara-Leret R, Paniagua-Zambrana N, Balslev H, Macía JM (2014) Ethnobotanical knowledge is vastly under-documented in north-western South America. Plos One 9:e85794

Caswell H (2001) Matrix population models—construction, analysis, and interpretation, 2nd edn. Sinauer Associates, Sunderland

Cevallos D, Valencia R, Montúfar R (2013) Ungurahua. In: Valencia R, Montúfar R, Navarrete H, Balslev H (eds) Palmas ecuatorianas: biología y uso sostenible. Herbario QCA de la Pontificia Universidad Católica del Ecuador, Quito, pp 209–224 (in Spanish)

Core Team R (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Corpoamazonia-Corporación para el Desarrollo Sostenible del Sur de la Amazonia (2010) Resolución 0727 del 19 de julio de 2010. Estatuto de Flora Silvestre—Aprovechamiento de productos forestales no maderables (PFNM); Corpoamazonia, Bogotá (in Spanish)

Da Silva JMC, Rylands AB, Da Fonseca GAB (2005) The Fate of the amazonian areas of endemism. Conserv Biol 19:689–694

Easterling MR, Ellner SP, Dixon PM (2000) Size-specific sensitivity: applying a new structured population model. Ecology 81:694–708

Eiserhardt WL, Svenning JC, Kissling WD, Balslev H (2011) Geographical ecology of the palms (Arecaceae): determinants of diversity and distributions across spatial scales. Ann Bot-London 108:1391–1416

Ellner SP, Rees M (2006) Integral projection models for species with complex demography. Am Nat 167:410–428

Espinoza JC, Ronchail J, Frappart F, Lavado W, Santini W, Guyot JL (2013) The major floods in the Amazonas river and tributaries (Western Amazon Basin) during the 1970–2012 period: a focus on the 2012 flood. J Hydrometeorol 14:1000–1008

Ferrer-Cervantes ME, Méndez-González ME, Quintana-Ascencio PF, Dorantes A, Dzib G, Durán R (2012) Population dynamics of the cactus *Mammillaria gaumeri*: an integral projection model approach. Popul Ecol 54:321–334

Freckleton RP, Matos DM, Bovi MLA, Watkinson ER (2003) Predicting the impacts of harvesting using structured population models: the importance of density-dependence and timing of harvest for a tropical palm tree. J App Ecol 40:846–858

Galeano G, Bernal R (2010) Palmas de Colombia. Guía de campo, 1st edn. Editorial Universidad Nacional de Colombia, Bogotá (in Spanish)

Groenendijk P, Eshete A, Sterck FJ, Zuidema PA, Bongers F (2012) Limitations to sustainable frankincense production: blocked regeneration, high adult mortality and declining populations. J Appl Ecol 49:164–173

Henderson A, Galeano G, Bernal R (1995) Field guide to the tropical palms of the Americas. Princeton University Press, Princeton

Isaza C (2013) Milpesos (*Oenocarpus bataua*). In: Bernal R, Galeano G (eds) Cosechar sin destruir. Aprovechamiento sostenible de palmas colombianas. Facultad de Ciencias-Instituto de Ciencias Naturales. Universidad Nacional de Colombia, Bogotá, pp 126–133 (in Spanish)

Kristiansen T, Svenning JC, Grández C, Salo J, Balslev H (2009) Commonness of Amazonian palm (Arecaceae) species: cross-scale links and potential determinants. Acta Oecol 35:554–562

Lewis SL, Brando PM, Phillips OL, van der Heijden GM, Nepstad D (2011) The 2010 amazon drought. Science 331:554

Löfgren A (1995) Distribution patterns and population structure of an economically important Amazon palm, *Jessenia bataua* (Mart.) Burret ssp. *bataua* in Bolivia. Växtekologi 2:1–20

Macía-Ruiz GC, Duque AJ, Cárdenas D, Maniguaje NL, Barreto JS (2011) Efectos de la sequía del 2010 en las tasas de mortalidad de árboles de un bosque de tierra firme en la Amazonia Colombiana. Revista Colombiana Amazónica 4(105):112 **(in Spanish with English abstract)**

Marengo JA, Tomasella J, Alves LM, Soares WR, Rodriguez DA (2011) The drought of 2010 in the context of historical droughts in the Amazon region. Geophys Res Lett 38(12)

Martínez-Ballesté A, Martorell C, Martínez-Ramos M, Caballero C (2005) Applying retrospective demographic models to assess sustainable use: the Maya management of Xa'an palms. Ecol Soc 10:17

Martorell C, Garcillán PP, Casillas F (2012) Ruderality in extreme-desert cacti? Population effects of chronic anthropogenic disturbance on *Echinocereus lindsayi*. Popul Ecol 54:335–346

Merow C, Dahlgren JP, Metcalf CJE, Childs DZ, Evans MEK, Jongejans E, Record S, Rees M, Salguero-Gómez R, McMahon SM (2014) Advancing population ecology with integral projection models: a practical guide. Methods Ecol Evol 5:99–110

Miller C (2002) Fruit production of the ungurahua palm (*Oenocarpus bataua* subsp. *bataua*, Arecaceae) in an indigenous managed reserve. Econ Bot 56:165–176

Miranda J, Zenteno F, Nina H, Mercado J (2008) El Majo (*Oenocarpus bataua*): una alternativa de biocomercio en Bolivia. Ediciones TRÓPICO, La Paz (in Spanish)

Miranda J, Moraes MR, Müller R (2009) Estructura poblacional, producción de frutos y uso tradicional de la palmera "majo" (*Oenocarpus bataua* Mart) en bosque montano (La Paz, Bolivia). Rev GAB 1:4–10 **(in Spanish with English abstract)**

Montúfar R, Pinatud JC (2006) Variation in species composition, abundance and microhabitat preferences among western Amazonian terra firme palm communities. Bot J Linn Soc 151:127–140

Montúfar R, Laffargue A, Pintaud JC, Hamon S, Avallone S, Dussert S (2010) *Oenocarpus bataua* Mart. (Arecaceae): rediscovering a source of high oleic vegetable oil from Amazonia. J Am Oil Chem Soc 87:167–172

Nazareno AG, dos Reis MS (2014) At risk of population decline? An ecological and genetic approach to the threatened palm species *Butia eriospatha* (Arecaceae) of Southern Brazil. J Hered 105:120–129

Organization of American States—OAS (2005) Amazon river basin: Integrated and sustainable management of transboundary water resources in the Amazon River Basin. Available via Water project series No. 8. https://www.oas.org/dsd/Events/english/Documents/OSDE_8Amazon.pdf. Accessed 28 Sep 2014

Peralta C, Tonore C, Miranda J (2010) Potencial natural y económico del majo (*Oenocarpus bataua*) en el norte amazónico y la región de Guanay (La Paz) en Bolivia. Technical paper. Universidad Autónoma de Beni, Bolivia (in Spanish)

Peters CM (1996) Sustainable harvest of non-timber plant resources in tropical moist forest: an ecological primer. Biodiversity Support Program, Washington DC

Peters CM, Balick MJ, Kahn F, Anderson AB (1989) Oligarchic forests of economic plants in Amazonia: utilization and conservation of an important tropical resource. Conserv Biol 3:341–349

Pinard MA, Putz FE (1992) Population matrix models and palm resource management. Bull Instr Fr études andines 21:637–649

República de Bolivia (2006) Norma Técnica para Aprovechamiento Comercial Sostenible de Recursos Forestales No Maderables en Bosques y Tierras Forestales Naturales. Resolución ministerial 22, Ministerio de Desarrollo Sostenible, La Paz (in Spanish)

República del Ecuador (2009) Texto Unificado de la Legislación Ambiental Secundaria en Ecuador (TULAS). Libro IV de la biodiversidad, Ministerio del Ambiente, Quito (in Spanish)

República del Perú (2001) Ley Forestal y de Fauna Silvestre. Decreto Supremo 014-2001-AG de agosto 4. Congreso de la República del Perú, Lima (in Spanish)

Rocha E (2004) Potencial ecológico para o manejo de frutos de açaizeiro (*Euterpe precatoria* Mart.) em áreas extrativistas no Acre, Brazil. Acta Amaz 34:237–250 **(in Portuguese with English abstract)**

Rojas RR, Correa A, Serna-Sánchez E (2008) Sombra de semillas, supervivencia de plántulas y distribución espacial de *Oenocarpus bataua* (Arecaceae) en un bosque de los Andes colombianos. Actualidades Biologicas 30:125–135 **(in Spanish with English abstract)**

Svenning JC (1999) Recruitment of tall arborescent palms in the Yasuní National Park, Amazonian Ecuador: are large treefall gaps important? J Trop Ecol 15:355–366

Svenning JC (2001) On the role of microenvironmental heterogeneity in the ecology and diversification of neotropical rain-forest palms (Arecaceae). Bot Rev 67:1–53

ter Steege N, Pitman NCA, Sabatier D, Baraloto C, Salomão RP, Guevara JE, Phillips OL, Castilho CV, Magnusson WE, Molino JF, Monteagudo A, Núñez-Vargas P, Montero JC, Feldpausch TR, Honorio Coronado E, Killeen TJ, Mostacedo B, Vásquez R, Assis RL, Terborgh J, Wittmann F, Andrade A, Laurance WF, Laurance SGW, Marimon BS, Marimon Jr BH, Guimarães-Vieira IC, Leão Amaral I, Brienen R, Castellanos H, Cárdenas López D, Duivenvoorden JF, Mogollón HF, de Almeida Matos DF, Dávila N, García-Villacorta R, Stevenson PR, Costa F, Emilio T, Levis C, Schietti J, Souza P, Alonso A, Dallmeier T, Duque Montoya AJ, Fernandez Piedade MT, Araujo-Murakami A, Arroyo L, Gribel R, Fine PVA, Peres CA, Toledo M, Aymard GA, Baker TR, Cerón C, Ángel J, Henkel TW, Maas P, Petronelli P, Stropp J, Zartman CE, Daly D, Neill D, Silveira M, Ríos Paredes M, Chave J, Lima Filho D de A, Møller Jørgensen P, Fuentes A, Schöngart J, Cornejo Valverde F, Di Fiore A, Jiménez EM, Peñuela Mora MC, Phillips JF, Rivas G, van Andel T, von Hildebrand P, Hoffman B, Zent EL, Malhi Y, Prieto A, Rudas A, Ruschell AR, Silva N, Vos V, Zent S, Oliveira AA, Cano Schutz A, Gonzales T, Nascimento MT, Ramírez-Angulo H, Sierra R, Tirado M, Umaña Medina MN, van der Heijden G, Vela CIA, Vilanova Torre E, Vriesendorp C, Wang O, Young KR, Baider C, Balslev H, Ferreira C, Mesones I, Torres-Lezama A, Urrego Giraldo LE, Zagt R, Alexiades MN, Hernández L, Huamantupa-Chuquimaco I, Milliken W, Palacios Cuenca W, Paulette D, Valderrama Sandoval E, Valenzuela-Gamarra L, Dexter KG, Feeley K, López-González G, Silman MR (2013) Hyperdominance in the Amazonian Tree Flora. Science 342:1243092

Ticktin T (2004) The ecological implications of harvesting non-timber forest products. J Appl Ecol 41:11–21

Vallejo MI, Galeano G, Bernal R, Zuidema PA (2014) The fate of populations of *Euterpe oleracea* harvested for palm heart in Colombia. Forest Ecol Manag 318:274–284

Vasquez R, Gentry AH (1989) Use and misuse of forest-harvested fruits in the Iquitos Area. Conserv Biol 3:350–361

Zuidema PA, Boot RGA (2000) Demographic constraints to sustainable palm heart extraction from a sub-canopy palm in Bolivia. In: Zuidema PA (ed) Demography of exploited tree species in the Bolivian Amazon. Scientific series 2, PROMAB, Riberalta, Bolivia, pp 54–79