

RESEARCH ARTICLE

Increased clonal growth in heavily harvested ecosystems failed to rescue ayahuasca lianas from decline in the Peruvian Amazon rainforest

Michael A. Coe¹  | Orou G. Gaoue^{2,3,4} 

¹Department of Botany, University of Hawai'i at Mānoa, Honolulu, Hawaii, USA

²Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee, USA

³Faculty of Agronomy, University of Parakou, Parakou, Benin

⁴Department of Geography, Environmental Management and Energy Studies, University of Johannesburg, Johannesburg, South Africa

Correspondence

Michael A. Coe
Email: coem@hawaii.edu

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Abstract

1. Increasing harvest and overexploitation of wild plants for non-timber forest products can significantly affect population dynamics of harvested populations. While the most common approach to assess the effect of harvest and perturbation of vital rates is focused on the long-term population growth rate, most management strategies are planned and implemented over the short-term.
2. We developed an integral projection model to investigate the effects of harvest on the demography and the short- and long-term population dynamics of *Banisteriopsis caapi* in the Peruvian Amazon rainforest.
3. Harvest had no significant effect on the size-dependent growth of lianas, but survival rates increased with size. Harvest had a significant negative effect on size-dependent survival where larger lianas experienced greater mortality rates under high harvest pressure than smaller lianas. In the populations under high harvest pressure, survival of smaller lianas was greater than that of populations with low harvest pressure. Harvest had no significant effect on clonal or sexual reproduction, but fertility was size-dependent.
4. The long-term population growth rates of *B. caapi* populations under high harvest pressure were projected to decline at a rate of 1.3% whereas populations with low harvest pressure are expected to increase at 3.2%. However, before reaching equilibrium, over the short-term, all *B. caapi* populations were in decline by 26% (high harvested population) and (low harvested population) 20.4% per year.
5. Elasticity patterns were dominated by survival of larger lianas irrespective of harvest treatments. Life table response experiment analyses indicated that high harvest caused the 6% reduction in population growth rates by significantly reducing the survival of large lianas and increasing the survival-growth of smaller lianas including vegetative reproductive individuals.
6. *Synthesis and applications.* This study emphasizes how important it is for management strategies for *B. caapi* lianas experiencing anthropogenic harvest to prioritize the survival of larger size lianas and vegetative reproducing individuals, particularly in increased harvested systems often prone to multiple stressors. From an applied conservation perspective, our findings illustrate the importance

of both prospective and retrospective perturbation analyses in population growth rates in understanding the population dynamics of lianas in general in response to human-induced disturbance.

KEYWORDS

ayahuasca, *Banisteriopsis caapi*, integral projection model, liana, LTRE, non-timber forest products harvest, plant population dynamics, transient dynamics

1 | INTRODUCTION

Non-timber forest products (NTFP) harvesting contributes to local livelihoods and subsistence strategies of human societies worldwide (Shackleton, 2015; Ticktin, 2004). Despite the local importance of NTFP to rural communities around the world, globalization and an increased economic interest in these plants may result in overexploitation and potentially lead to negative effects on overall population fitness (Siddappa, 2015). For example, NTFP such as *Syngonanthus nitens* Ruthland, a perennial herb used in handicrafts in Brazil, may become less resilient to heavy and recurrent harvest when increased economic interest expands beyond that of traditional harvesters leading to contemporary harvesting methods that result in reduced population fitness (Schmidt & Ticktin, 2012). As such, the effects of NTFP overexploitation and increased harvest can significantly impact the physiology and vital rates of individual plants, alter demographic and genetic patterns of harvested plant populations, and change ecosystem- and community-level processes resulting in reduced yields and plant population decline (Ticktin, 2004). Therefore, a greater understanding of NTFP population dynamics and response to harvest is essential to informing sound management practices and defining sustainable harvest limits. High rates of harvest do not always negatively impact plant population fitness (Shackleton et al., 2015). These population-level effects of harvest are variable and depend on multiple factors including the life form and life history of the species, harvesting intensity, type of organs harvested, harvesting method, geographic and climatic region, other anthropogenic and environmental factors (Sampaio & Santos, 2015; Schmidt et al., 2011, 2015; Ticktin, 2004). Accordingly, over the last four decades, a growing number of studies have investigated the ecological effects of harvest on NTFP species across various life forms and geographic and climatic ranges (Gaoue, Horvitz, et al., 2011; Gaoue, Sack, et al., 2011; Gaoue & Ticktin, 2009; Hart-Fredeluces et al., 2021; Jansen et al., 2012; Mandle et al., 2015; Peres et al., 2003; Pinard, 1993; Schmidt et al., 2011; Schmidt & Ticktin, 2012; Ticktin, 2004; Ticktin & Nantel, 2004).

Plant demography studies to date, have primarily investigated the effect of harvest on the population dynamics of herbaceous species, trees, and shrubs with a limited number of studies specifically focused on lianas (Salguero-Gómez et al., 2015; Ticktin, 2004). Measuring lianas has proven challenging (Schnitzer, 2006; Schnitzer et al., 2005) and studies on their demography and population dynamics are rare (Nabe-Nielsen, 2004; Wong & Ticktin, 2015).

Estimating demographic parameters (e.g. population growth rate, elasticities and life table response experiments [LTRE]) has been valuable to inform restoration practices for some species of liana (Wong & Ticktin, 2015). However, more studies on the ecology of liana populations are needed to gain a better understanding of their response to harvest, the implications for ecosystem dynamics, and ideal management strategies for ecologically and culturally important liana populations. Lianas play important ecological roles in natural stand dynamics (Phillips et al., 2002; Schnitzer, 2006, 2015; Schnitzer et al., 2005, 2020), particularly on ecosystem level processes (Schnitzer, 2015) including altering biogeochemical cycling by accelerating leaf litter decomposition and enhancing nutrient turnover (Roeder et al., 2022). Beyond their ecological role, lianas are also economically important NTFP for the livelihoods of communities worldwide (Guadagnin & Gravato, 2013; Wong & Ticktin, 2015). Thus, research on liana population responses to chronic anthropogenic disturbance is critical to advance our understanding of the resilience of tropical socio-ecological ecosystems.

Matrix projection models (Caswell, 2001) are commonly used to investigate the effect of NTFP harvest on asymptotic population dynamics (see for e.g. Crone et al., 2011; Hart-Fredeluces et al., 2021; Schmidt et al., 2011). Demographic data including stasis, growth, regression and fertility are collected yearly on individual plants in populations and used to build a stage-structured matrix projection model, and to estimate population growth rates. The long-term population growth rate is used to infer whether the populations are expected to grow, decline or remain stable in the long-term based on current harvesting regimes. Developing matrix projection models may prove challenging, particularly for species where discrete life stage classes are less obvious or cryptic. As an alternative, developing integral projection models (IPM) relaxes the need to divide a species' life cycle into discrete classes, while using size as a continuous variable (Easterling et al., 2000). Further, assessing the environmental sustainability of NTFP harvest using only the asymptotic population growth rate may not be sufficient due to variability in the growth rate as a result of demographic and environmental stochasticity and the need to develop short term management plans for most species (Schmidt et al., 2011). As a result, complementary frameworks have been proposed including elasticity analysis and LTRE to account for prospective and retrospective responses of populations due to changes in vital rates driven by the effect of harvest (Caswell, 2000; Gaoue, Horvitz, et al., 2011, 2016; Pinard, 1993). Using IPM to infer the population growth rate response to perturbations in changes to

vital rates is a robust approach (Mandle et al., 2015) and has become widely used to advance our knowledge of population dynamics in response to harvest across a range of species (Easterling et al., 2000; Ellner & Rees, 2006; Mandle et al., 2015). However, because the demographic response to harvest of some important life forms such as lianas and herbs are seldom studied, our ability to develop a clear global mechanistic understanding of species response to harvest is limited (Schmidt et al., 2011).

Comparative demographic studies have shown that the relative contribution of vital rates to population fitness and persistence varies across life forms, life history and habitats (Adler et al., 2014; Enright et al., 1995; Franco & Silvertown, 2004; Silvertown et al., 1993). In general, the elasticity of the population growth rate to perturbation of survival tends to be the greatest for slow growing or long-lived life forms such as trees (Adler et al., 2014; Franco & Silvertown, 2004), whereas the relative contribution of clonality or vegetative reproduction to population fitness is greatest for fast-growing life forms such as perennial herbaceous species (Adler et al., 2014; Silvertown et al., 1993), perennial alpine species (Weppeler et al., 2006), terrestrial bromeliads (Ticktin & Nantel, 2004) and epiphytes (Mondragón et al., 2004). The role of clonality and its relative contribution to population fitness and persistence is expected to be an evolutionary response or life history trade-off between sexual and asexual reproduction driven by environmental stochasticity, disturbance (Silvertown, 2008), evolutionary history and genetic variance (Barrett, 2015; Hesse et al., 2008). In this context, clonality can serve as a mechanism for ecological and evolutionary rescue that allows certain plant species in decline to delay extinction and maintain genetic diversity in disturbed ecosystems (Franklin et al., 2021; Peniston et al., 2021; Silvertown, 2008). Although the importance of clonality or vegetative reproduction to population fitness of a few harvested species is well documented (see for e.g. Hart-Fredeluces et al., 2021; Orive et al., 2017; Ticktin et al., 2016), our understanding of the existence of this mechanism for the demographic persistence of liana populations is limited.

Several socio-economically important NTFP species found in Tropical South America including trees, lianas, shrubs and

herbaceous species are threatened by recurrent and heavy harvest (Baldauf et al., 2015; Peres et al., 2003; Sampaio & Santos, 2015; Schmidt et al., 2015). *Banisteriopsis caapi* (Spruce ex. Griseb) C. V. Morton is an economically and culturally important liana throughout the Amazon basin (Coe & McKenna, 2017; Luna, 1986; Luna & White, 2000; Figure 1). The stems and bark of *B. caapi* are harvested as the main source plant for *ayahuasca*, a psychoactive tea used in traditional Amazonian ethnomedicine that has in recent years become a pan-global phenomenon due to wide-spread use in the contemporary world (Morales-García et al., 2017; Tupper, 2009). Although traditional *B. caapi* harvesting methods by Indigenous people and local communities throughout the Amazon basin include selecting a few stems that are ≥ 1 in. (≥ 2.5 cm DBH) in diameter and up to several feet in length to produce modest amounts of ayahuasca, contemporary harvesters often select larger *B. caapi* lianas or harvest greater quantities of biomass beyond traditional harvesting limits to meet the supply and demand chains linked to the globalization and commodification of ayahuasca (Coe & Gaoe, 2023, unpublished data). Conservative estimates indicate that four million people worldwide have consumed ayahuasca in their lifetimes with only 10% of these people representing Indigenous communities. Furthermore, in 2019, approximately five and a half million servings of ayahuasca were consumed by nearly 820,000 people worldwide suggesting increased harvesting and intensity of *B. caapi* throughout the Amazon basin may be driven in part by the globalization of ayahuasca beyond traditional use by Indigenous people and local communities (Suárez Álvarez & Mazarrasa, 2023).

Though wild populations of *B. caapi* are found in the Amazon basin, they are thought to becoming rare at a local level (Coe & Gaoe, 2023, unpublished data). Further, increased use or harvest pressure on *B. caapi* populations are expected to force harvesters further into the Amazon rainforest which may be a result of population decline, overharvesting or deforestation due to the intensity and frequency of logging in the area. The impacts of harvest on wild *B. caapi* populations are expected to vary due to harvest frequency and intensity. While few studies have assessed the impacts of bark harvest on vital rates (Ticktin, 2004) of lianas, most studies to date



FIGURE 1 *Banisteriopsis caapi* Spruce ex. Griseb. (a) Axillary inflorescence, (b) samaroid schizocarps, (c) vegetative biomass and leaves, (d) mature stem often harvested for the production of ayahuasca and (e) mature liana growing into the canopy of the Peruvian Amazon rainforest.

have focused on assessing the environmental sustainability of harvest using long-term population growth rates. These approaches which are solely based on long-term projections, may underestimate the short-term effects of harvest (Gaoue, 2016). Elasticity analyses of short-term population dynamics are likely critical for the development of robust management plans (Bialic-Murphy et al., 2017; Gaoue, 2016), especially, for economically important plant species that are harvested under various harvest regimes. Furthermore, understanding the relative contribution of vital rates to differences in population growth rates prospectively and retrospectively will prove informative (Caswell, 2000). This study investigated the effects of differing levels of harvest intensity on *B. caapi* to better understand its population dynamics in the short- and long-term. We investigated the demography, elasticity patterns and LTRE of *B. caapi* in response to harvest under several harvest treatments.

2 | MATERIALS AND METHODS

2.1 | Study system

We investigated the demography of *Banisteriopsis caapi* Spruce ex. Griseb in a Shipibo-Konibo native community territory located in the Peruvian Amazon basin (Figure 1). Because of the increased globalization, commercialization, and economic interest of ayahuasca brew in the Amazon basin and in other countries around the world (Fotiou, 2016; Labate et al., 2016; Tupper, 2009; Winkelman, 2005), there is a growing concern of biopiracy of *B. caapi* lianas in the study area (Coe & Gaoue, 2023, unpublished data). Therefore, the details on the geolocation of the community and study system are left anonymous. Furthermore, the forest surrounding the study area has become locally known for being one of the primary locations where *B. caapi* is harvested and then sold in urban cities such as Iquitos where ayahuasca tourism has grown rapidly over the last several decades (Fotiou, 2016; Labate et al., 2016; Suárez Álvarez & Mazarrasa, 2023; Tupper, 2009). The forest surrounding the study area is often managed in part by the Shipibo-Konibo living in the area who establish small agricultural areas, locally known as *chakras*, and harvest NTFP for food, medicine, and rituals. The forest surrounding the study area is mixed successional with pioneer trees including *Cecropia sciadophylla* Mart. growing primarily along nearby riverbanks and old growth trees such as *Brosimum utile* (Kunth) Oken. and *Ficus insipida* Willd. located within the forest interior (Coe & Gaoue, 2023, unpublished data). The regional climate in the area is tropical humid (Köppen-Geiger classification) with a mean annual temperature of 26.4°C (Kottek et al., 2006). Annual rainfall in the area is approximately 1600mm (Casimiro et al., 2013). Field work was carried out with the oral consent of the *jefe* (local governing authority) and associated Indigenous committee of the Shipibo-Konibo community located within study area. No official permits were needed.

Banisteriopsis caapi (Malpighiaceae) is botanically described as a liana with brown bark and dark green ovate to lanceolate leaves up

to about 7 in. in length, 2–3 in. wide (Figure 1); The inflorescences are axillary, each with many small 5 petal flowers that are pink or rose-coloured; the fruit is a samaroid schizocarp composed of 2–3 samaras connected at the torus (Figure 1b); each samara has dorsal wings about 1.38 in. long (Gates, 1982; Schultes et al., 2001; Souto & Oliveira, 2012). Flowering generally occurs between December and August with samara production between March and August. It can also reproduce asexually or clonally where new ramets are generally formed when either mature shoots take root following host tree falls or anthropogenic harvests of mother plants.

2.2 | Demography of *B. caapi*

Populations of *B. caapi* are becoming more challenging to find in the Amazon basin due to increased logging, land-use changes, deforestation, and anthropogenic harvest driven by the globalization, commercialization, and commodification of ayahuasca brew. Access to known *B. caapi* population sites by Indigenous people and local communities is often hindered by increased distance travelled to locate it as a result of local harvest pressure, concerns of unauthorized harvest and biopiracy by outsiders driven by economic interests as a result of the globalization and commodification of ayahuasca brew, ayahuasca tourism, and the loss of botanical knowledge in proximity urban areas. Such challenges have limited our ability to thoroughly study the ecology of several important species and life-forms. In this study, we collected data on vital rates for two populations of *B. caapi* consisting of approximately 300 plants in total. In each population, we established three 4-ha permanent plots to assess the population dynamics of the lianas in response to harvest over a 2-year period (July 2017–2018). Both populations were harvested for woody stems during the census interval. Differences in harvesting intensity between the two populations were classified into two treatments based on several criteria including the accessibility of each site to harvesters and the total number of harvested lianas noted during the census interval. Treatment 1 was classified as a *B. caapi* liana population consisting of three plots that were less accessible to harvesters (farther into the jungle) and experienced low harvest pressure, whereas Treatment 2 was classified as a *B. caapi* liana population consisting of three plots that were more easily accessible to harvesters and initially experienced increased harvest pressure. Forty-one lianas were harvested at the beginning of the census period, whereas a total of 28 lianas were harvested during the census at $t + 1$. This resulted in an 31% total decrease in harvest intensity over the entire census period which significantly reduced the difference in harvest pressure between the treatments with an initial difference of nine harvested lianas between the treatments at time t and a difference of four lianas at $t + 1$.

We collected demographic data for each individual liana to estimate vital rates including growth, survival, and fertility. Each individual *B. caapi* liana was tagged with a numbered aluminium tag and GPS coordinates were taken to facilitate relocating these individuals during the re-monitoring of the population. Some tags were

removed the next year due to anthropogenic harvest. We used GPS coordinates to locate the stump or root system of harvested lianas and identify the individual liana and its previous tag number. For each individual liana, we used a precision calliper to measure its size as the diameter at breast height (DBH). Each point of measurement was marked to ensure the stem was measured in the same place from 1 year to the next.

For seedlings and clonal ramets, we measured basal diameter at the first point above the roots where the stem is cylindrical following Gerwing et al. (2006). Clonal ramets were defined as functionally independent ramets not connected to a mother liana. New seedlings were characteristic, upright without branching. Mother lianas were defined as the closest mature liana to a given seedling or clonal ramet. Given that reproducing lianas in the two populations were spatially distant, newly recruited free-standing individuals originating from seeds were identified with ease. Size measurements were used to estimate the growth function. We also noted if individuals were dead or alive at the next census to estimate survival from July 2017 to 2018. To measure fertility, we attempted to visually count the number of samaras (fruit that produce seeds) (Figure 1b) on each sexually reproducing liana. However, this was an impossible task given that the samaras were high up the canopy, small and hidden by foliage often invisible from the ground even with a binocular. Therefore, we estimated fertility directly using seedling or clonal spatial location relative to mother lianas. Because samaras tend to fall directly below each liana smoothed out by foliage, we assumed that our approach to measuring fertility was reasonable. We directly counted the number of seedlings and the number of ramets in genets produced nearest to a reproducing adult liana.

2.3 | Integral projection modelling

We used the demographic data to develop an integral projection model (IPM) (Easterling et al., 2000; Ellner & Rees, 2006; Rees & Ellner, 2009):

$$n(y, t + 1) = \int_{\Omega} K(y, x)n(x, t)dx, \quad (1)$$

where $n(y, t + 1)$ is the number of individuals of a given size y at time $(t + 1)$, $n(x, t)$ is the number of individuals in a given size x at time t , Ω represents the size range of the species over which the kernel function is integrated, and the kernel $K(y, x)$ is comprised of the size dependent survival-growth, $p(y, x)$, and the sexual fertility, $f(x, y)$ and asexual fertility $c(y, x)$ functions such that

$$n(y, t + 1) = \int_{\Omega} [p(y, x) + f(x, y) + c(y, x)]n(x, t)dx. \quad (2)$$

The survival-growth function $p(y, x)$ includes the size dependent probability of growing, $g(y, x)$, conditional on surviving, $s(x)$:

$$p(y, x) = s(x)g(y, x), \quad (3)$$

where the probability $p(y, x)$ that an individual will survive and grow to size y from size x the year prior is obtained by multiplying the size dependent probability an individual will survive $s(x)$ and the probability an individual will grow into a different size y from size x the year prior, $g(y, x)$. The size-dependent survival was estimated using a generalized linear mixed effect model with binomial errors and population as a random effect:

$$s(x) = \frac{\exp(a_s + b_s x)}{1 + \exp(a_s + b_s x)}, \quad (4)$$

where a_s and b_s are regression coefficients estimated using the *glmer* function in package *lme4* in R. The size-dependent growth function was estimated as a normal distribution with constant variance, mean μ and standard deviation σ :

$$g(y, x) \sim \text{Normal}(\mu, \sigma), \quad (5)$$

$$\mu = a_g + b_g x, \quad (6)$$

where a_g and b_g are regression coefficients, estimated using a general linear mixed effect model with population as a random effect in the same package with the function *lmer*. To account for the life history of *B. caapi*, the fertility function was expanded to include seed originated fertility $f(y, x)$ and clonal reproduction $c(y, x)$:

$$f(y, x) = s(x)f_f(x)f_n(x)p_{ge}f_d(y), \quad (7)$$

$$c(y, x) = s(x)c_f(x)c_n(x)c_d(y). \quad (8)$$

The seed-originated fertility $f(y, x)$ is obtained as the product of the probability that an individual will survive $s(x)$ to reproduce, the size-dependent probability of fruiting $f_f(x)$, the mean number of samaras produced given adult size $f_n(x)$, the probability of seeds germination and establishment p_{ge} , and the size distribution of new seedlings $f_d(y)$. The clonal fertility $c(y, x)$ is obtained as the product of the size-dependent probability of reproducing liana surviving $s(x)$, the probability that they produced clonal offspring $c_f(x)$, the number of clonal offspring produced given their size $c_n(x)$, and the size distribution of the new clonal offspring produced $c_d(y)$. In Equations 7 and 8, $s(x)$, $f_f(x)$ and $c_f(x)$ which are all size-dependent probabilities were estimated using Equation 4. However, $f_d(y)$ and $c_d(y)$ which are new offspring size distributions was estimated using Equation 5 and 6 with the mean and standard deviation were directly estimated from field data on seedling and clonal offspring. The size dependent number of seedlings, $f_n(x)$, and clones, $c_n(x)$, were modelled using generalized linear mixed effect models with Poisson errors and population as a random effect.

During the fieldwork, we were able to locate sexually reproductive lianas in the field, however, given logistical constraints with climbing well into the forest canopy, we did not have data for the direct average number fruits produced per reproductive individual. Therefore, based on the known reproductive ecology of *Banisteriopsis muricata* (Cav.) Cuatrec, a closely related species in the same botanical genus, we estimated an average liana fruit

production of 71 fruits produced by flowering individuals given that each fruit produces 2–3 samaras, and each reproductive plant produces 219 samaras (Zapata & Kalin Arroyo, 1978). We used this conservative estimate of size-independent fruit production for individuals that reach reproductive size. We then developed a conservative scenario of size-dependent fruit production between harvest treatments by varying the slope of the Poisson model for 0.1 (high harvest pressure) to 0.6 (low harvest pressure). The probability of seed germination and establishment p_{ge} was estimated as the ratio of new seedlings from field data and fruit production based on conservative estimates. Given demographic data collection for only one census period between July 2017–2018 our analysis of vital rates and elasticity patterns of the population growth rate are conservative representing the short-term projections and are interpreted as a representation of transient population dynamics.

2.4 | Analysis of vital rates, transient and asymptotic population growth rates

The numerical integration of the kernel K in Equation (1) across the size range produced a big square matrix for each population of *B. caapi*. The eigenvalues and elasticity analyses of the big matrices were conducted using the *popbio* package (Stubben & Milligan, 2007) in R (R Development Core Team, 2019). The dominant eigenvalue of each big matrix represents the long-term population growth rate, λ , and the subdominant eigenvalue of the big matrix represents the short-term or transient population growth rate, λ_1 . The dimension of the big matrix was selected by simulating the effect of varying the size of the matrix on λ and selecting the highest dimension that stabilizes λ .

We developed generalized linear mixed effect models (glmm) in R 3.4.3 (R Development Core Team, 2019) using the *lme4* package (Bates et al., 2015) to assess the effect of harvest and other covariates on vital rates (growth, survival, clonal and sexual reproduction). Random effects included plot number. Fixed-effect explanatory variables included the effect of harvest and size of *B. caapi* individuals. We log-transformed *B. caapi* size measurements to meet normality and homogeneity of variance assumptions. We also used generalized linear models with Poisson errors to assess the effects of harvest and size on the number of seedlings and clones produced. Our response variables for our *glmm* models were measurement data for growth, and binary data for survival and the probability of clonal and sexual reproduction. Our response variables for our *glm* models were count data. Therefore, we used *glmm* or *glm* with normal, binomial and Poisson error structures (Crawley, 2013). We used an information-theoretic approach following Gaoue, Sack, et al. (2011) to select the best fitting models that had greater explanatory power, where, for each response variable we estimated the Akaike information criterion (AIC) for each model, the difference in the AIC between each model (Δ AIC), and the model with the lowest Δ AIC. We

then, selected the models with the lowest Δ AIC < 2 (Gaoue, Sack, et al., 2011; Appendix A1).

2.5 | Elasticity analysis and LTRE

To assess the effect of perturbation on vital rates we conducted elasticity analysis following (Easterling et al., 2000):

$$e(x, y) = \frac{K(x, y)}{(\lambda)} \times \frac{v(x)w(y)}{(w, v)}, \quad (9)$$

where v and w are the left and right eigenvectors of λ and $K(x, y)$ represents the kernel derived from the IPM. In this approach, elasticity analysis estimates the proportional change in λ resulting in proportional changes in vital rates of individuals of a given size (Easterling et al., 2000).

To identify which vital rates contributed most to differences in population growth rates of *B. caapi* experiencing low or increased harvest pressure, we carried out LTRE (Caswell, 2000) using the following equation:

$$\lambda^t - \lambda^c = \sum (K^t - K^c)(\partial\lambda/\partial K^m), \quad (10)$$

where K^t is the kernel for *B. caapi* population experiencing increased harvest pressure with a dominant eigenvalue λ^t , K^c is our reference kernel for *B. caapi* population experiencing low harvest pressure with a dominant eigenvalue λ^c , $(\partial\lambda/\partial K)$ is the sensitivity of λ to perturbation of the mean kernel element evaluated by the midway kernel $K^m = (K^t + K^c)/2$. We designated the reference kernel (K^c) as the low harvesting treatment so that positive contributions from our LTRE represented differences in vital rates that contributed to the higher population growth rates of *B. caapi* populations experiencing increased harvest pressure.

3 | RESULTS

3.1 | Ayahuasca demographic responses to harvest

The size of *B. caapi* lianas in the populations that were measured at time $t+1$ were positively associated with their initial size measured at time t (Figure 2a). The size of individual lianas also had a significant effect on growth suggesting larger lianas within the population experienced greater growth rates ($\beta=0.908\pm 0.033$, $t=27.78$, $p<0.001$).

Survival of *B. caapi* lianas was greatest for individuals of intermediate sizes (Figure 2b). There was no significant effect of harvest on the growth for *B. caapi*. However, harvest had a significant effect on survival ($\beta=-2.396\pm 0.889$, $z=-2.695$, $p=0.007$). The population experiencing high harvest pressure had lower survival rates than the population experiencing low harvest pressure. There was a significant interactive effect of harvest and plant size on survival of *B. caapi* ($\beta=0.876\pm 0.319$, $z=2.741$, $p=0.006$) where survival of

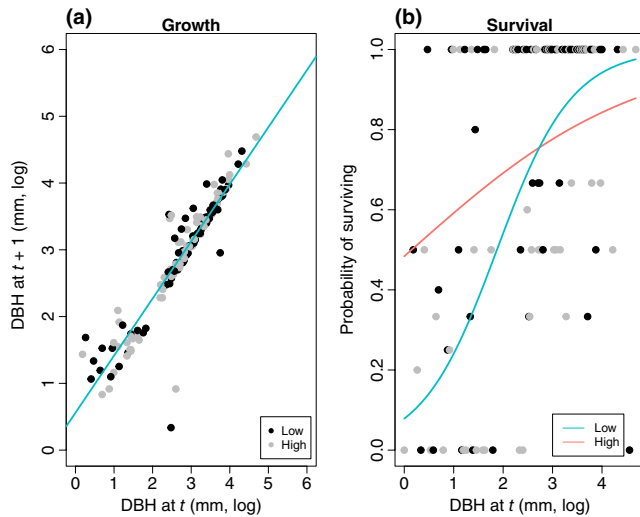


FIGURE 2 Demographic functions (vital rates) for *Banisteriopsis caapi* (a) growth (log scale) as a function of size (measured in mm) July 2017–July 2018, (b) the probability of survival to July 2018 as a function of size (log scale, previously measured in mm) in July 2017. The red line represents the regression coefficient for increased harvest whereas the blue line represents the regression coefficient for less harvest intensity. Black points represent size of lianas experiencing low harvest pressure and grey points represent size of lianas experiencing high harvest pressure.

smaller individuals is greater in the population experiencing high harvest pressure than the population experiencing low harvest pressure (Figure 2b). Furthermore, liana size had a significant effect on survival ($\beta=0.436\pm 0.204$, $z=2.132$, $p=0.033$) suggesting the probability of survival was size-dependent. Lianas that were >2.5 cm were more likely to experience mortality in increased harvested populations (Figure 2b).

In contrast, there was no significant effect of harvest on the probability of sexual and clonal reproduction. The size of *B. caapi* lianas had a significant effect on the probability of reproducing sexually ($\beta=1.680\pm 0.755$, $z=2.226$, $p=0.0026$; Figure 3a), where larger lianas produced the greatest number of seedlings. Similarly, larger lianas produced the greatest number of clones ($\beta=1.025\pm 0.429$, $z=2.390$, $p=0.017$; Figure 3b). Further, irrespective of plant size, harvest had a significant effect on the number of clones produced ($\beta=0.915\pm 0.428$, $z=2.138$, $p=0.032$).

3.2 | Population growth rates response to harvest

Over the long-term, the *B. caapi* population experiencing low harvest pressure was projected to increase by 3.2% per year ($\lambda=1.032$, 95% CI: 1.023–1.033), while the *B. caapi* population experiencing high harvest pressure was projected to decline ($\lambda=0.987$, 95% CI: 0.978–0.987) by 1.3% per year. However, short-term projections indicated all the *B. caapi* populations included in our study are projected to decline. Over the short-term, the population experiencing high harvest pressure was expected to decline faster at a rate of 26% ($\lambda_1=0.74$),

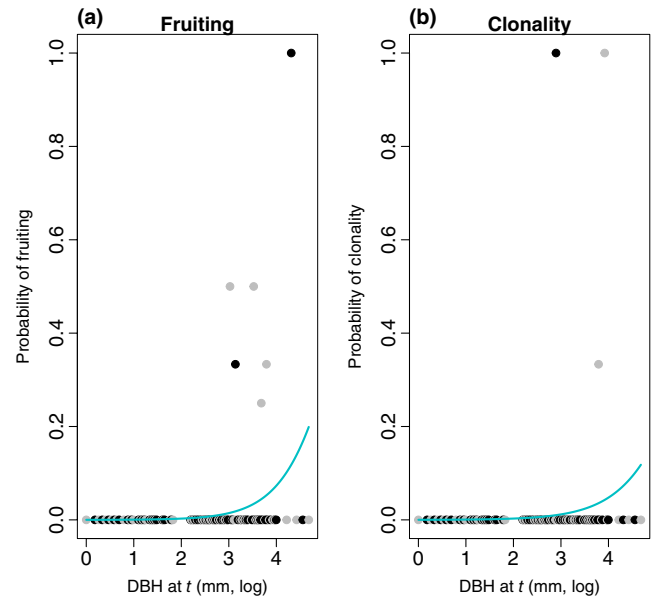


FIGURE 3 Size-dependent (a) seedling and (b) clone production for *Banisteriopsis caapi* (size on a log scale, previously measured in mm). Black points represent size of lianas experiencing low harvest pressure and grey points represent size of lianas experiencing high harvest pressure.

compared to the population experiencing low harvest pressure that were projected to decline at 20.4% ($\lambda_1=0.796$) per year.

Elasticity patterns for *B. caapi* indicate that survival of *B. caapi* lianas with greater DBH will have the greatest relative influence on the long-term population growth rate (Figure 4). Further, irrespective of harvest intensity, the elasticity analysis showed that the best approach to improve population growth rate is to ensure high survival-growth of lianas particularly those with size >4.5 cm DBH (Figure 4a,b). Harvesting tended to increase the range of sizes of lianas whose survival-growth has relative importance for the long-term persistence of the populations. Within the low harvested population, the population growth rate was most elastic to perturbation of the survival-growth of lianas >2.5 cm (Figure 4a). Within the high harvested population, this included lianas as small as 1.5 cm DBH (Figure 4b).

3.3 | Life table response to harvest

Increased harvesting of *B. caapi* lianas caused a 4.5% reduction in long-term population growth rate ($\lambda_L=1.032$ vs. $\lambda_H=0.987$) and a 5.6% reduction in population growth rate over the short term ($\lambda_{1L}=0.796$ vs. $\lambda_{1H}=0.740$). LTRE showed that such drastic reduction in population growth rate by increased harvesting is due to a significantly lower relative contribution of survival-growth of larger size, sexually reproductive *B. caapi* lianas in the population experiencing high harvest pressure (Figure 5). There was a greater relative contribution of survival-growth of smaller lianas (approx. 1–2 cm), including vegetative reproductive individuals, to the population growth

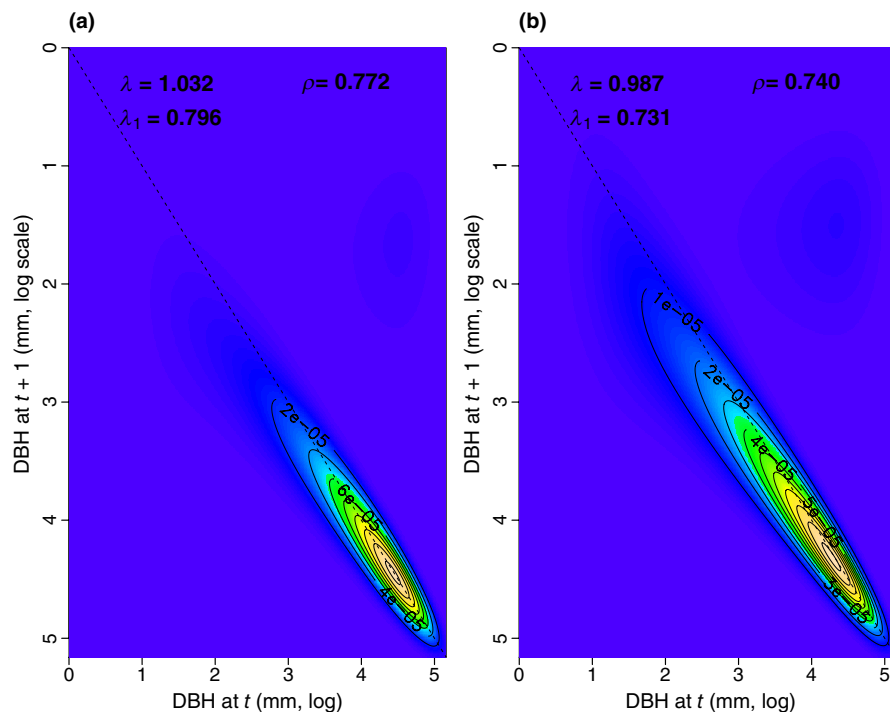


FIGURE 4 Elasticity contour plot for the *Banisteriopsis caapi* kernel. Elasticity patterns of the population growth rate are represented as follows where (a) elasticity patterns of *B. caapi* under low harvest pressure and (b) elasticity patterns of *B. caapi* under high harvest pressure. The dashed-line represents the survival intercept obtained from survival-growth functions and general linearized mixed effect models. Lighter colours (e.g. yellow) represent a greater relative contribution of vital rates to the population growth rate.

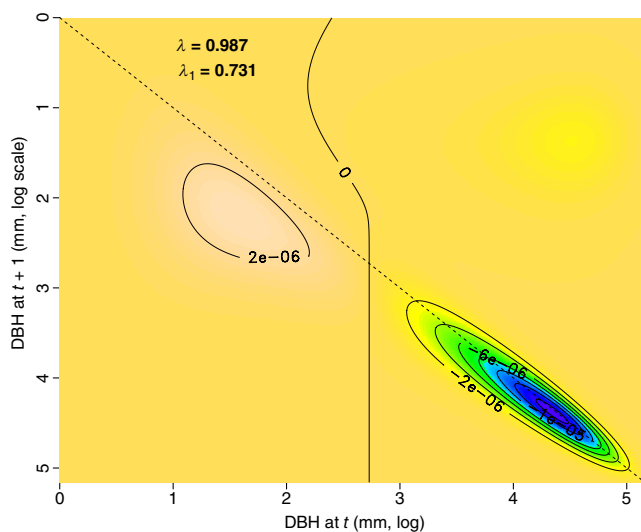


FIGURE 5 LTRE contributions of *Banisteriopsis caapi* lianas experiencing increased versus less harvest pressure. Darker colours represent life-history transitions that make greater contributions to higher λ values observed for the *B. caapi* population experiencing low harvest pressure. Lighter colours (e.g. yellow) represent life-history transitions that make greater contributions to higher λ values observed for the *B. caapi* population experiencing high harvest pressure. Values across the diagonal represent contributions from survival-growth, and those below the diagonal represent contributions from growth and clonal reproduction.

rate in the *B. caapi* population experiencing high harvest pressure (Figure 5). This indicates that the higher rate of clonal production in this population contributed to reducing the population decline but not enough to offset the reduced survival-growth of larger sizes of lianas in the population.

4 | DISCUSSION

Understanding the demographic response of *B. caapi*, to harvest is central to the sustainable management and the future of medical ecotourism in the Amazon basin. Our results indicate that small-to-intermediate size lianas had a greater probability of survival under the effect of harvest compared to large size lianas. Given that most harvested lianas in both *B. caapi* populations were of larger size (Coe & Gaoué, 2023, unpublished data), we expect the reduced rate of survival of larger lianas is a result of increased harvest pressure due the supply and demand chains linked to the globalization, commercialization, and widespread production of ayahuasca (Fotiou, 2016; Labate et al., 2016; Suárez Álvarez & Mazarrasa, 2023; Tupper, 2009). Although we found increased harvest intensity had a significant negative effect on the probability of *B. caapi* liana survival, there was no support for a significant negative effect of harvest of the *B. caapi* population experiencing low harvest pressure suggesting that some level of harvesting can be tolerated. In sites experiencing low harvest intensity 16 lianas were harvested at time t and only 12 harvested lianas at time $t+1$ suggesting that a certain level of harvest intensity can occur that allows the population to persist. This provides opportunities for conservation strategies through a use mechanism for such a sought-after species with important medicinal and cultural values.

We found intermediate to larger size lianas had a higher probability of reproducing clonally which may be an indirect effect of harvest as there were fewer seedlings ($n=18$) produced than clones ($n=54$) in response to harvest. Furthermore, the probability of fruiting was size-dependent where lianas >3 cm had a greater probability of reproducing sexually. At the same time, larger lianas experienced greater mortality rates with increasing harvest intensity in the *B.*

caapi populations with fewer seedlings produced than clones. These findings warrant further investigation. Thus, future research investigating if there is a trade-off in favour of clonal reproduction rather than seedling production in response to harvest is critical for advancing our understanding of the population dynamics of *B. caapi* in natural habitats. Although, empirical evidence for life-history trade-offs for certain life forms is well documented (see for example Enright et al., 1995; Silvertown et al., 1993), these demographic responses to harvest for liana populations are less understood. Therefore, advancing our understanding of these demographic patterns for liana populations is central to uncovering possible demographic processes underpinning life history strategies and genetic variability in liana populations experiencing recurrent harvest.

We highlighted the importance of elasticity analysis in determining vital rates that are likely critical for implementing management approaches of *B. caapi* and subsequently the sustainable development of ayahuasca. Our elasticity analysis showed that survival of larger *B. caapi* lianas is important for the persistence of the populations. This finding is supported by prior research (Franco & Silvertown, 2004) that demonstrated survival of adult individuals often have a greater relative importance to the contribution of the population growth rate particularly for long-lived species. Most of the empirical evidence for this theoretical framework come from studies of trees but rarely are lianas included (Franco & Silvertown, 2004; Silvertown et al., 1993). The few studies that have assessed elasticity values of liana population dynamics have also shown there is a greater relative importance of survival-growth of larger individuals to the population growth rate (de Campos Franci et al., 2016; Escalante et al., 2004; Kouassi et al., 2008; Nabe-Nielsen, 2004; Wong & Ticktin, 2015). These findings are informative in advancing our understanding of liana population dynamics in general, especially since studies on the population dynamics of a liana NTFP are scarce (Escalante et al., 2004; Kouassi et al., 2008; Wong & Ticktin, 2015). Thus, our study provides one of the rare population dynamics studies on a liana NTFP in response to anthropogenic harvest. Interestingly, the contribution of survival of larger *B. caapi* lianas to the short-term population growth rate were similar under both harvest treatments. This contrasts with previous studies suggesting that survival of young individuals contribute most to the short-term population dynamics of long-lived species (Enright et al., 1995; Koons et al., 2005). Such differences could be explained by low seedling recruitment in the liana populations and subsequent lack of change in the number of young individuals over time. It has been cautioned that long-term elasticity analysis may not always adequately describe the relative importance of vital rate life stage contributions to the short-term population growth rate (Bialic-Murphy et al., 2017; Haridas & Tuljapurkar, 2007). Thus, we suggest future research investigating both the short- and long-term elasticity patterns of *B. caapi* is critical to understanding the population dynamics of lianas and for the development of sound management plans for this culturally and economically important NTFP plant species.

Our results suggest that increased harvest pressure can significantly affect population dynamics of *B. caapi*. While the low harvested population of *B. caapi* lianas was projected to increase over

the long-term compared to the high harvested population which was shown to be in decline, both populations were projected to decline in the short-term. This highlights that long-term projections should be interpreted with caution, especially since there was an overall decrease in harvest pressure between the treatments over the census period and management plans are generally designed and implemented over the short-term (Bialic-Murphy et al., 2022; Fox & Gurevitch, 2000; Gaoue, 2016; Koons et al., 2005; Stott et al., 2011; Wong & Ticktin, 2015). We found greater survival-growth of larger size lianas in the low harvested *B. caapi* population which offset the 23.6% short-term to long-term difference in population growth rate. However, increased harvest by reducing the survival-growth of larger lianas led to a 25.6% reduction of the population growth rate from long- to short-term periods. Because these prospective and retrospective demographic patterns for the *B. caapi* populations under both harvesting treatments were similar, where changes in survival-growth of larger size lianas have the greatest impact on population growth rates, we suggest ecologically sustainable harvesting limits should include approaches towards selecting lianas that have less of an impact on population fitness while at the same time reducing the mortality of these harvested lianas.

4.1 | Implications for conservation

To date, we are unaware of any other study on the population dynamics of *B. caapi* or most lianas in response to harvest. Clearly, this area of research in population ecology is understudied and warrants considerable efforts to address growing environmental sustainability concerns in the Peruvian Amazon basin. Our research indicates that short-term population dynamics of *B. caapi* vary as a function of size in response to harvest where larger size lianas significantly contributed to vital rate functions both prospectively and retrospectively. Given that larger lianas were more likely to experience greater harvest pressure and mortality, approaches towards sustainable *B. caapi* harvest and ayahuasca production should consider novel management strategies to offset the reduction of survival-growth of larger *B. caapi* lianas with increasing harvest pressure and intensity.

Our finding that clonally reproductive individuals in the *B. caapi* population experiencing increased harvest pressure helped to reduce the overall rate of harvest-induced decline but failed to rescue the population warrants further investigation and consideration. In general, lianas are considered clonal species that periodically reproduce sexually, where trade-offs between reproductive strategies in favour of vegetative reproduction and overall population persistence are often driven by responses to disturbance (Ledo & Schnitzer, 2014) and environmental stochasticity (DeWalt et al., 2010; Schnitzer, 2005). Demography studies have shown that vegetative reproduction or clonality can drive population persistence, especially during unfavourable years (Mondragón et al., 2004) and variable ecoregions (e.g. old-growth vs. secondary forests; Ticktin & Nantel, 2004). Therefore, management strategies for *B. caapi* and lianas in general, should

ensure the survival of vegetatively reproducing individuals and new seedlings in increased harvested sites under variable environmental conditions. From an applied conservation perspective, our findings also illustrate the importance of both prospective and retrospective perturbation analyses in understanding the population dynamics of *B. caapi* lianas or lianas in general, in response to human-induced disturbance.

Finally, given that our study was done with a census interval of 2 years, long-term studies will greatly advance our understanding on the population dynamics of *B. caapi* in response to increasing harvest pressure over time. Further, it is critical that these studies include both transient and stochastic models rather than deterministic models to uncover population-level patterns in response to abiotic and biotic variability over both the short- and long-term. Additionally, rigorous studies of the reproductive ecology of *B. caapi* and potential life-history trade-offs and fitness in response to harvest pressure and intensity are critical to advancing our understanding of the population dynamics of this ecologically, economically, and culturally important liana along with the development of sustainable management and production of ayahuasca.

AUTHOR CONTRIBUTIONS

Michael A. Coe and Orou G. Gaoue conceived of the idea for the paper and outlined and structured its content. Michael A. Coe collected and analysed the data with contribution from Orou G. Gaoue. Michael A. Coe wrote the first draft of the manuscript with additional edits from Orou G. Gaoue. All authors read and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors report no conflict of interest.

DATA AVAILABILITY STATEMENT

The data generated and analysed for this study is available via the FIGSHARE repository, <https://doi.org/10.6084/m9.figshare.23811705> (Coe & Gaoue, 2023).

STATEMENT OF INCLUSION

Our study brings together collaborations between colleagues from several different countries, including Indigenous people and volunteers from an Indigenous-led NGO based in the country where the study was carried out. All collaborators were engaged early on with the research, study design and data collection processes to ensure that the diverse sets of perspectives were considered and to facilitate knowledge transfer.

ORCID

Michael A. Coe  <https://orcid.org/0000-0002-5550-4770>

Orou G. Gaoue  <https://orcid.org/0000-0002-0946-2741>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix A1. Tested models and the respective Δ AIC

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