# ARTICLE

# Flood disturbance and shade stress shape the population structure of açaí palm *Euterpe precatoria*, the most abundant Amazon species

Heloisa Dantas Brum and Alexandre F. Souza

**Abstract:** *Euterpe precatoria* Mart. is the most abundant plant species in the Amazon basin, and one of the main non-timber forest products on the continent. A thorough understanding of the ecology of this species is needed to support sustainable management initiatives. Resource availability, disturbance regime, and human management are some of the main factors influencing population structure. We described the species' life stages, evaluated its allometric relationships, and assessed the effects of habitat type (floodplain and upland) and proximity to human settlements on population size distribution in the Central Amazon near the Purus River. The height:diameter ratio increased from Seedlings to Juvenile 2, but decreased from Juvenile 2 to Reproductive 2, indicating changing height investment for any given diameter along these life stages. There was a marked habitat dependency in both the density and population size distribution, with populations in upland forests dominated by juveniles, whereas populations in the floodplains were dominated by reproductive palms. Proximity to human settlements was not related to population structure parameters. Our results suggest that the disturbance regime may have opposite meanings in várzea forests, where it limits recruitment under increased light levels, and in terra firme forests, where it may stimulate recruitment under limited light conditions.

*Key words:* várzea, terra firme, population structure, forest management, skewness, allometry.

**Résumé :** *Euterpe precatoria* Mart. est l'espèce végétale la plus abondante du bassin amazonien et constitue l'un des principaux produits forestiers non ligneux du continent. Une connaissance approfondie de l'écologie de cette espèce est nécessaire pour soutenir les initiatives de gestion durable. La disponibilité des ressources, le régime de perturbations et la gestion humaine se trouvent parmi les principaux facteurs qui influencent la structure de la population. Les auteurs ont décrit les étapes du cycle de vie de l'espèce, évalué ses relations allométriques et évalué les effets du type d'habitat (plaines inondables et hautes terres) et de la proximité d'établissements humains sur la distribution de la taille de la population en Amazonie centrale, à proximité du Rio Purus. Le rapport hauteur/ diamètre augmentait du stade semis au stade juvénile 2, mais il diminuait du stade juvénile 2 au stade reproducteur 2, témoignant de la variation de l'investissement quant à la hauteur pour un diamètre donné au cours de ces stades du cycle de vie. Une dépendance marquée à l'égard de l'habitat était observée quant à la distribution de la densité et de la taille de la population, les populations des forêts des hautes terres étant dominées par les juvéniles alors que les populations des plaines inondables étant dominées par les palmiers reproducteurs. La proximité d'établissements humains n'était pas liée aux paramètres de la structure de la population. Ces résultats suggèrent que le régime de perturbations peut avoir des conséquences opposées dans les forêts de *várzea*, où il limite le recrutement en fonction de niveaux accrus de luminosité, et dans les forêts de *terra firme*, où il peut stimuler le recrutement en fonction de niveaux limités de luminosité. [Traduit par la Rédaction]

*Mots-clés :* várzea, terra firme, structure de la population, gestion forestière, inclinaison, allométrie.

## Introduction

*Euterpe precatoria* Mart. is an iconic palm popularly known as açaí, asaí, palmiche, or manaca in South America (Henderson et al. 2019). It is the most abundant species in the Amazon basin, and is one of the few species that is hyper-dominant in four of the main five forest types in the region (ter Steege et al. 2013). It is also one of the main non-timber forest products from the continent

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(Stoian 2004). The species is traditionally used for the extraction of fruits, heart of palm, and timber by indigenous peoples (Anderson 1977; Albert and Le Tourneau 2007). It produces large quantities of dark, single-seeded fruits that, as in other *Euterpe* species, are dispersed by many birds and mammals (Leite et al. 2012). The fruit is commonly collected to produce a regional market product, a creamy beverage known as "açaí wine". The beverage is very nutritious and contains superior antioxidant and anti-inflammatory properties (Kang et al. 2012) that have been shown to have health benefits like memory protection when used as a dietary supplement (Carey et al. 2017). The consumption of *E. precatoria* fruit may be a sustainable alternative for this species in countries like Bolivia, where the traditional consumption of palm hearts leads to palms being killed for resource extraction (Rocha 2004; Velarde and Moraes 2008). Recently, the prices for *E. precatoria* products have increased dramatically due to the global commoditization of palm hearts and raw, processed, or lyophilized fruit pulp as a nutritional supplement increasingly consumed in Brazil, as well as exported to countries outside of South America (mainly Europe, Canada, and the USA) (Bussmann and Zambrana 2012). Market sales for the açaí berry (*E. oleracea* and *E. precatoria* combined) total USD $126.3 million/year in Brazil alone (Martinot et al. 2017). With increasing trade volumes, *E. precatoria* and many other exploited native species cannot meet demands in a sustainable manner (Mostacedo and Fredericksen 1999; Stoian 2004; Vallejo et al. 2016). A thorough understanding of the biology and ecology of this species is thus needed to support sustainable management decisions (Velarde and Moraes 2008).

One of the most easily measured population parameters in the field is population structure, which integrates a wealth of demographic information (Avalos et al. 2013; Peltzer et al. 2014). However, it may be a puzzling tool for natural population assessments, because the interpretation of population structure may be biased if arbitrary size classes are identified instead of ontogenetic life stages (Gatsuk et al. 1980; Souza et al. 2000, 2003; Caswell 2001). Furthermore, the patterns of relative abundance of the juveniles (and the adults they portray) are not a reliable proxy for future population growth and, therefore, for population persistence in any given habitat or set of environmental or human-imposed conditions (Johnson et al. 1994; Condit et al. 1998; Souza 2007; Virillo et al. 2011; Bin et al. 2012). Attempts to infer population persistence from static population structure and the abundance of juveniles relative to adults are, consequently, flawed if not measured over time; in fact, population size structures result from the realized growth, mortality, and fecundity rates across different size classes (Caswell 2001; Wright et al. 2003).

One of the effective uses of population structure is the comparison of size distributions across habitats with contrasting disturbance histories. Such comparisons have shown that species life-histories tend to produce patterns of population structure across similar habitats (Swaine et al. 1990; Poorter et al. 1996; Wright et al. 2003; Souza 2007; Souza et al. 2008, 2010). The analysis of repeat population structures can thus indicate a species' ecological strategy in contrasting environmental conditions. This approach uses the fast-growing resource acquiring vs. slow-growing stress-tolerant life history gradient repeatedly found worldwide (Grime and Pierce 2012; Reich 2014; Díaz et al. 2016). On one hand, left-skewed size distributions dominated by large individuals are characterized by chronic recruitment failure of gap-dependent species with large fecundities, high seedling mortality, and high sapling growth. On the other hand, right-skewed size distributions dominated by small individuals characterize shade-tolerant species with the opposite traits (Lorimer and Krug 1983; Swaine et al. 1990; Poorter et al. 1996; Wright et al. 2003; Souza 2007; Souza et al. 2008; Vlam et al. 2014).

Among the factors influencing population structure are resource availability, disturbance regime, and human management (Mostacedo and Fredericksen 1999; Souza 2004, 2007; Avalos et al. 2013; Peltzer et al. 2014). Habitat differentiation between várzea floodplains and upland terra firme in the Amazon basin are driven by contrasting light resources and disturbance levels. The Amazon basin harbors a great variety of floodplains covering nearly 500 000 km² (Junk et al. 2011*a*), including a variety of habitats such as seasonally inundated forests and swamps, with plant communities adapted to different flood regimes (Junk et al. 2012). These hydro-edaphic conditions exert strong control on plant species distributions, connecting floodplain floras even when rivers drain into distinct climatic regions (Wittmann and Junk 2003). Environmental variation linked to flood regimes affects the demographic parameters of neighboring populations, and may even be detected over short geographic distances (Otárola and Avalos 2014). The disturbance caused by seasonal flooding involves oxygen deprivation, sedimentation, and mechanical damage that frequently kills younger plants (Parolin 2009), and has triggered the evolution of metabolic pathways promoting either endurance or escape strategies (Parolin 2009; Voesenek and Bailey-Serres 2015). This could lead to the prevalence of larger plants in better lit and more productive floodplains, which would be favorable for adult growth and survivorship once the juvenile recruitment bottleneck is surpassed (Avalos et al. 2013; Otárola and Avalos 2014). Contrary to flooded forests, which present lower and more irregular canopies that allow more light penetration (Souza and Martins 2005; Sawada et al. 2015), the main limitation to plant growth and establishment in uplands is the deep shade cast by tall canopies (Kitajima and Poorter 2008; Avalos 2019), which severely reduce understory light levels (Svenning 2001,

2002; Myster 2016). *Euterpe precatoria* forms seedling banks in upland shaded understory (Peña-Claros and Zuidema 2000; Rocha 2004; Isaza et al. 2017), indicating a moderate degree of shade tolerance (Condit et al. 1998; Mostacedo and Fredericksen 1999) that allows it to wait for canopy openings (Avalos et al. 2013; Otárola and Avalos 2014).

Shady understory environments have prompted the evolution of ecological strategies distributed along a trade-off gradient from low growth/height shade stress tolerance to fast growth/height light acquisition (Grime 1977; Reich 2014; Forgiarini et al. 2015). Unflooded terra firme presents higher and more dense canopies than floodplain forests, where light is much more abundant (Myster 2016). In palms, the lack of secondary meristems precludes the exploitation of light through lateral growth, restricting plant responses to shading to increases in allometric height/diameter increments (Poorter et al. 2003; Niklas et al. 2006; Avalos and Otárola 2010). The height growth of *Euterpe precatoria* is supported by stilt roots, whose size scales with plant height rather than with topographic variation (Avalos and Otárola 2010). However, the effects of habitat variation between upland and floodplains on palm shape and allometry are scarcely known; even less studied are the effects of human management on the population ecology of *E. precatoria*. These effects are potentially sizable, since the species has been considered domesticated or semi-domesticated by indigenous people since pre-Columbian times (Clement et al. 2015; Levis et al. 2017). The intensive management of preferred species by indigenous and current local populations has taken place mainly along the floodplain margins of large rivers (McMichael et al. 2012), and is thus expected to influence the abundance of the species across different habitat types (Ticktin et al. 2012; Baldauf and Santos 2013). This would result from the negative effects of fruit or heart of palm harvesting on population recruitment (Mostacedo and Fredericksen 1999), and therefore the proximity to human settlements could decrease the number of juveniles.

Here we ask, what the effects are of habitats with contrasting light levels and disturbance regimes, i.e., várzea and terra firme, on the allometric relationships and population structure of *E. precatoria* in the Central Amazon? Specifically, we tested the following hypotheses: (1) there should be a significant interaction between plant shape as depicted in the height/diameter allometric relationship and habitat, with established palms presenting taller and more slender trunks in upland forests; (2) populations will present right-skewed size distributions in upland habitats where adult recruitment and productivity are light-limited, and in flood-prone várzea with a prevalence of larger palms, reduced size distribution skewness or even symmetrical size distributions are expected; (3) the density of seedlings and juveniles should be greater in uplands, whereas the density of adult trees should be greater in floodplains. In testing hypotheses 2 and 3, we controlled for a possible relationship between the distance from the nearest human settlement and the skewness of population size distribution (where more positive skewness reflects increased juvenile abundance). The outcomes of these tests can better inform management decisions by stakeholders and local users.

## Materials and methods

### Study area and species

*Euterpe precatoria* var. *precatoria* is a single-stemmed palm (but see Avalos and Schneider 2011) that may reach up to 20 m in height, with populations present from Central America to Bolivia (Stoian 2004). Individuals are obligate outcrossing monoecious, and present a long flowering period that provides easily accessed resources to thousands of insect flower visitors (Küchmeister et al. 1997). The species is large seeded (with ca. 11 cm diameter; Aguiar and Mendonça 2003) and germinates immediately after harvesting (Costa et al. 2018). The ability of *E. precatoria* to germinate in darkness, and its preference for relatively mild germination temperatures (20 °C), may favor its establishment in seasonally flooded habitats; its tolerance to only moderate desiccation allows germination in upland forests, but not in drier areas (Costa et al. 2018). As shown for other *Euterpe* species, germination is likely facilitated by frugivorous dispersal (Leite et al. 2012). Their seedlings tolerate shade and do not respond promptly to increased irradiance (Coelho et al. 2015). The species attains higher densities, sizes, and fruit productivity in floodplains than in unflooded uplands, where it shows signs of etiolation (Velarde and Moraes 2008).

The study was carried out in the Piagaçu–Purus Sustainable Development Reserve (SDR-PP), Amazonas State, located in the Purus–Madeira and Purus–Juruá interfluve in Brazil (Fig. 1). The reserve covers ca. 834 200 ha, and includes human habitation and the sustainable use and commercialization of natural resources. The climate is tropical Af (with no dry season), and annual rainfall ranges between 2000 and 2600 mm (Alvares et al. 2013). It harbors 65 riverine communities and more than 5000 people, who mainly live off of subsistence agriculture, fishing, hunting, and the extraction of non-timber forest products like açaí. The SDR-PP is located near by the municipalities of Coari and Codajás, which together account for 96% of the 50 000 tons of açaí produced in Amazonas state annually (IBGE 2018). In the study region açaí fruit are collected non-destructively by climbing, and heart of palm is not collected. Although the Purus river presents variations in volume of up to 10 m annually (ANA 2018), the flood-prone areas we studied are located in a high várzea, with seasonal flooding of up to 3 m for less than 50 days per year (Junk et al. 2011*a*).

**Fig. 1.** Lower Purus river area in Central Amazon, showing the location of riverine communities and the 10 blocks where individuals of *Euterpe precatoria* (açaí) were marked and measured. Landsat imagery courtesy of NASA Goddard Space Flight Center and U.S. Geological Survey. (Figure reproduced with the permission of V. Vasquez.)
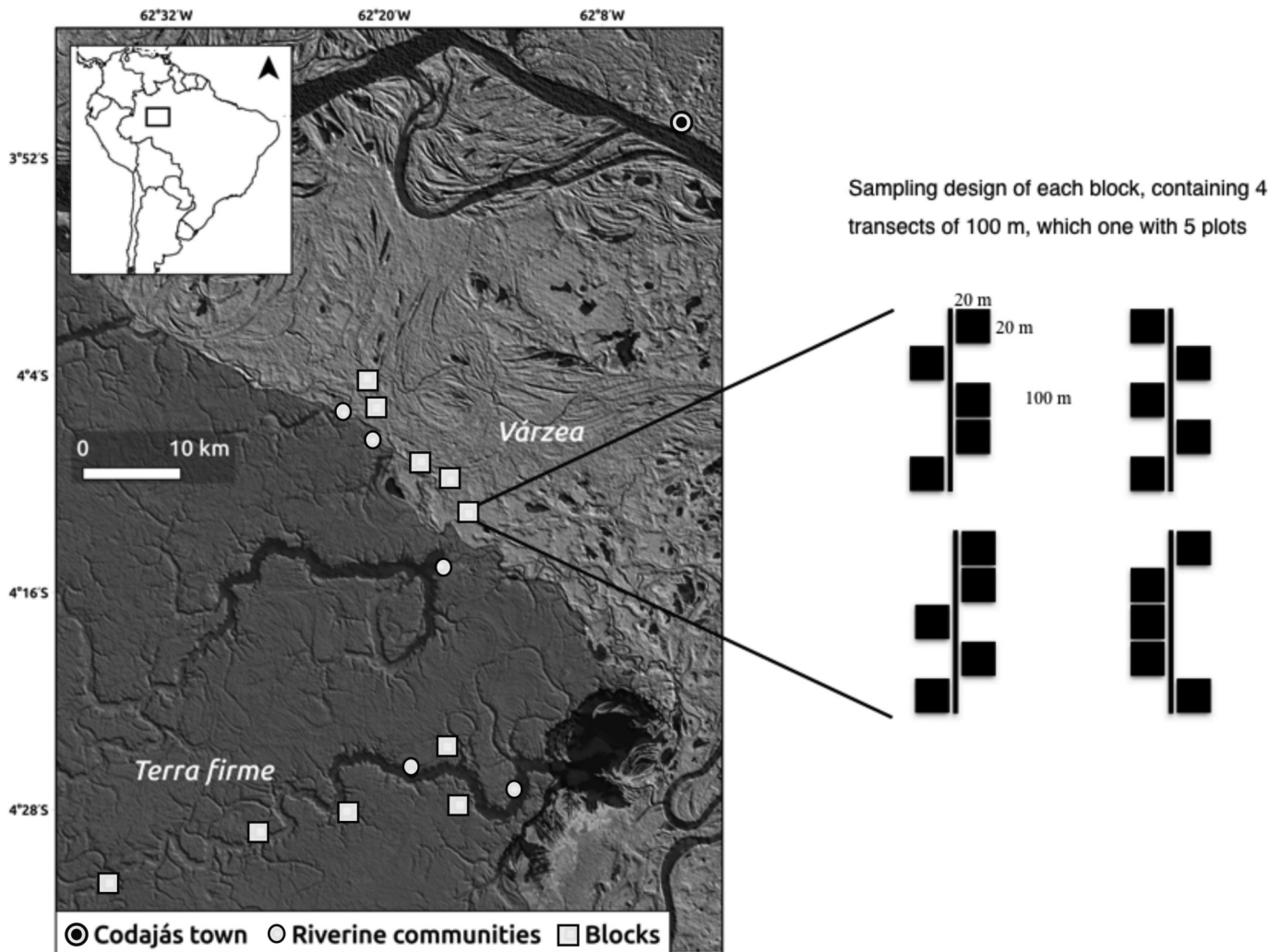


### Data collection

Sampling took place at sites selected after a participatory mapping effort with local residents. We asked members of the nearby communities about their extraction practices, and the sampling units were located in areas that they indicated were used for açaí fruit harvesting at differing intensities. Data was collected from 200 permanent plots (20 m × 20 m; total 8 ha) distributed in 10 blocks: five in the floodplain, and five in the upland (Fig. 1). In each block, plots were arranged in four transects 100 m long, each one subdivided into five plots, and stratified into two topographic positions. In each block, two transects were located in low-lying terrain, and thus, subjected to more frequent and long-lasting flooding; two were located in elevated terrain, resulting in less frequent and short-lasting flooding (with approximately one month of difference). Because the number of newly germinated seedlings was very large in the floodplain plots, we subsampled this life stage only through four 1 m × 1 m subplots located at the corners of each 20 m × 20 m plot.

Distance to the nearest human settlement was measured as the sum of linear distances actually traveled by land and water by the inhabitants of each settlement to reach the location of every transect, using a Garmin GPS map 62s and QGIS software (QGIS Development Team 2009). From February to March 2016, all individuals of *E. precatoria* were tagged and measured for diameter at soil level, total height, and number of leaves in all plots. When stilt roots or stem base enlargement were present, we measured the diameter from the first node above these structures. The diameter and height of individuals in early development without the aerial stem were measured at the base, which corresponds to the group of leaf sheaths. For seedlings, tags were tied to a wooden (in uplands) or metal (in floodplains) stick, to avoid damaging the plants. The presence and height of reproductive structures were also measured. We used the distance to the nearest human settlement as a proxy for the effects of human activities (Duvall 2007; Vandam et al. 2013; Sumarga 2017).

## Statistical analysis

*Euterpe precatoria* life stages were established based on macromorphological traits, which can provide classes that are more easily interpreted in terms of plant performance and development (Gatsuk et al. 1980). Further subdivisions within life stages were established based on breakpoints in the relationship between stem diameter and height. This was assessed through a LOESS regression between diameter and height after iterative adjustment of alpha (α) and lambda (λ) parameters (Jacoby 2000). All of the statistical analyses were performed in the open software R (R Core Team 2017). We opted to perform two complementary allometric analyses. The first was an ANCOVA, which evaluated the effects of life stages on the relationship between height and diameter, with all data pooled regardless of habitat. In a second ANCOVA, we focused on the effects of habitat type and life stage on the relationship between stem slenderness ratio and plant height. This analysis was restricted to Juvenile 2 and Reproductive 1 life stages, because these were the only stages that occurred in both habitat types. Slenderness ratios were the logarithm of the height:diameter quotient [log(H/D)] (Niklas et al. 2006). Low slenderness ratios indicate that very large self-loads are required to induce lateral elastic buckling, whereas high slenderness ratios indicate that smaller self-loads are required to produce global elastic buckling (Niklas et al. 2006).

We used the natural logarithm of height to quantify palm size, and the coefficient of skewness (g1, Zar 1996) to summarize the skewness of height distributions and, thus, population structure (Wright et al. 2003) at the transect (i.e., blocks of 5 plots, 20 m × 20 m) scale (*n* = 40). Values for g1 > 0 indicated right-skewed height distributions with a few tall and many short palms; g1 = 0 indicated symmetrical height distributions; and g1 < 0 indicated left-skewed height distributions with many tall and a few short palms (Zar 1996). Seedlings were excluded from population structure analyses because > 90% of them do not survive from one year to the next in the floodplains (H. Brum, personal observation). The few seedlings that survived from one year to the other in this habitat type depended on flood-free microhabitats, like small mounds of clay, or germinated in dry years with reduced flooding. This information comes from our demographic monitoring of the studied populations, and will integrate future analyses. The inclusion of seedlings in static population structure analyses, therefore, could distort the results and make comparisons with unflooded habitats misleading.

We used Generalized Linear Models (GLMs) to evaluate habitat (floodplain × upland) and human (distance to the nearest human settlement) effects on the skewness of population height distribution. Elevation was also included as a means to control for possible microtopographic effects on flooding duration. Following Zuur et al. (2009) and Plant (2012), different models were fitted to decide which model structure best described the error structures in the data. The second-order Akaike Information Criterion (AICc, used for small sample sizes) and ANOVA were used to compare models, and decide whether a random term was necessary. Models with a value for ΔAIC < 2 were regarded as equally plausible (Anderson and Burnham 2004). We fitted a GLM without a random term (i.e., containing fixed terms only), a Generalized Linear Mixed Model (GLMM) using blocks as a random intercept term, and a GLMM using both blocks and habitat types as random terms (Zuur et al. 2009). All of the models were fitted by maximizing the restricted log-likelihood using the functions 'gls' or 'lme' of the 'nlme' package (Pinheiro et al. 2017). The random effects in the GLMM accounted for the possible lack of independence of the skewness values estimated for the blocks. The 20 m × 20 m plot-level effects of habitat type and distance to human settlement on palm density were assessed through a GLMM using Poisson error, with blocks and transects as nested random terms (Zuur et al. 2009).

## Results

We marked and mapped 3613 individuals of açaí in different life stages in both floodplain and upland habitats. Observations of external macromorphological structures distinguished between two pre-reproductive stages: Seedlings and Juveniles. Seedlings were defined as individuals without the presence of an aerial stem and exhibiting fan-shaped leaves (Fig. 2). The minimum stem diameter found for reproductive palms was 10.0 cm, and Juveniles were palms with stem diameters smaller than this value at soil level (Fig. 2). Juveniles presented a marked discontinuity in the height:diameter relationship at ca. 1.5 m height (Fig. 3), and were subdivided into Juvenile 1 (height < 1.5 m) and Juvenile 2 (1.5 ≤ height < 10 m). The diameter:height relationship was non-linear (LOESS regression: α = 0.35, λ = 2; Fig. 3), with two marked slope changes. The first change was located at the transition between Juveniles 1 and 2, and the second among reproductive palms at ca. 23 cm diameter, a threshold from which higher diameter values were not accompanied by higher height values (Fig. 3). Reproductive palms were thus divided into Reproductive 1 (height ≥ 10 m and diameter < 23 cm) and Reproductive 2 (height ≥ 10 m and diameter ≥ 23 cm).

The dependency of the relationship between diameter and height on life stages was further confirmed through the significant interaction between life stage and diameter in the explanation of height in the first ANCOVA ($R^2$ = 0.97; $F$ = 53.35; df = 2, 1513; $P$ < 0.0001) (Fig. 4). The trend of the linear fit increased from Seedlings to Juvenile 1, and from these to Juvenile 2. The trend decreased from Juvenile 2 to Reproductive 1, and from these to Reproductive 2. This change indicated first increasing, and then decreasing height investment for any given

**Fig. 2.** Life stages of *Euterpe precatoria* (Arecaceae). (A) Fruit bunch. (B) Detail of fruit. (C) Detail of the seed with initial development of seedling. (D) Seedling. (E) Juvenile 1. (F) Reproductive stage. See text for a description of life-history stage characteristics. The bar next to each figure is a scale bar. (Figure reproduced with the permission of E.G. Oliveira.)
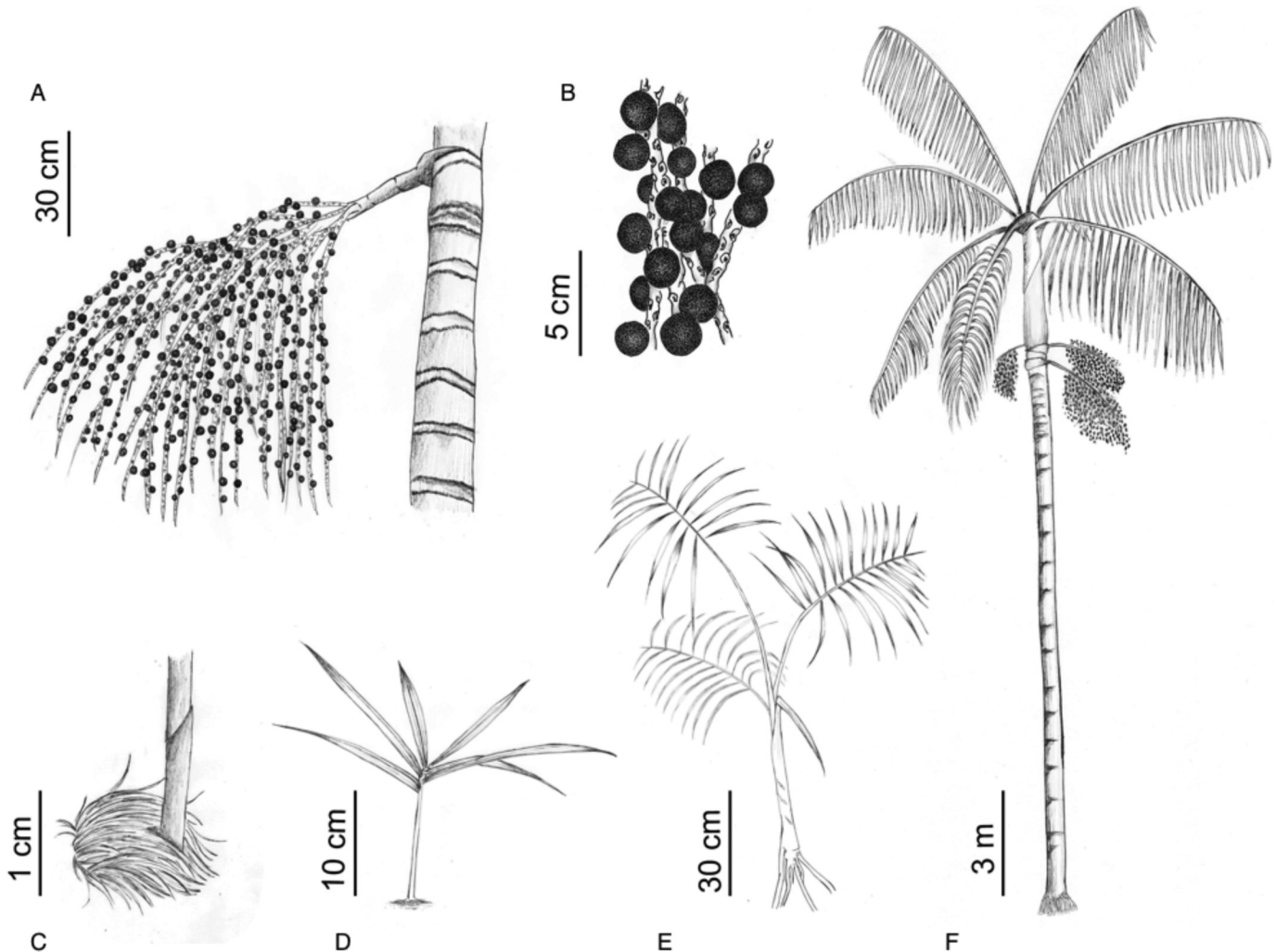
diameter along these life stages. A second ANCOVA tested for the effects of habitat type (upland × flooded forest) on the height:diameter relationship as depicted in the slenderness ratio; this time, excluding both Seedlings and Reproductive 2 palms because these two life stages were not detected in upland forests. The relationship between stem slenderness ratio and height was positive (Fig. 4), and was significantly affected by the interaction with life stage ($F = 40.63$; df = 1, 1033; $P < 0.0001$), with Reproductive having more slender stems than Juveniles (Fig. 4). Habitat type altered slenderness significantly ($F = 4.60$, df = 1, $P = 0.03$), which was higher on terra firme than on várzea (Fig. 4). The interaction of slenderness was not significant for life stages or height (Fig. 4).

Seedlings had the highest density among life stages, with average (±SD) 470.75 ± 486.21 plants·ha$^{-1}$ in the unflooded areas and 4025.0 ± 5086.31 plants·ha$^{-1}$ in the floodplains. Seedlings apart, overall palm density was greater in the unflooded forests (66.88 ± 129.38 plants·ha$^{-1}$)

than in the flooded forests (31.13 ± 79.65 plants·ha$^{-1}$). Palm density changed significantly with habitat as well as with life stage. The best GLMM model included the interaction between habitat and life stage, as well as blocks and transects as random terms (Table 1). This adds to the large standard deviation, and indicates that population density varied considerably at several spatial scales, possibly due to spatial heterogeneity in forest structure, light, and flooding regimes, as well as to dispersal limitation (Souza and Martins 2002; ter Steege et al. 2013). The habitat vs. life stage interaction indicates that the density of different stages varied between flooded and unflooded forests in different ways. For the várzea habitat, the model including elevation as a proxy for flood duration did not differ from the simpler model without this variable ($P = 0.51$, df = 1, $\Delta$AIC = 1.58), and was therefore discarded. Unflooded forests were dominated by juveniles, with Juvenile 1 and Juvenile 2 having the highest densities (Fig. 5). In contrast, flooded forests were dominated by Reproductive 1, which was the densest life

**Fig. 3.** Overall relationship between height and diameter of 3613 açaí palms (*Euterpe precatoria*) measured in upland and floodplain forests, Central Amazon. The fitted line is a LOESS regression.
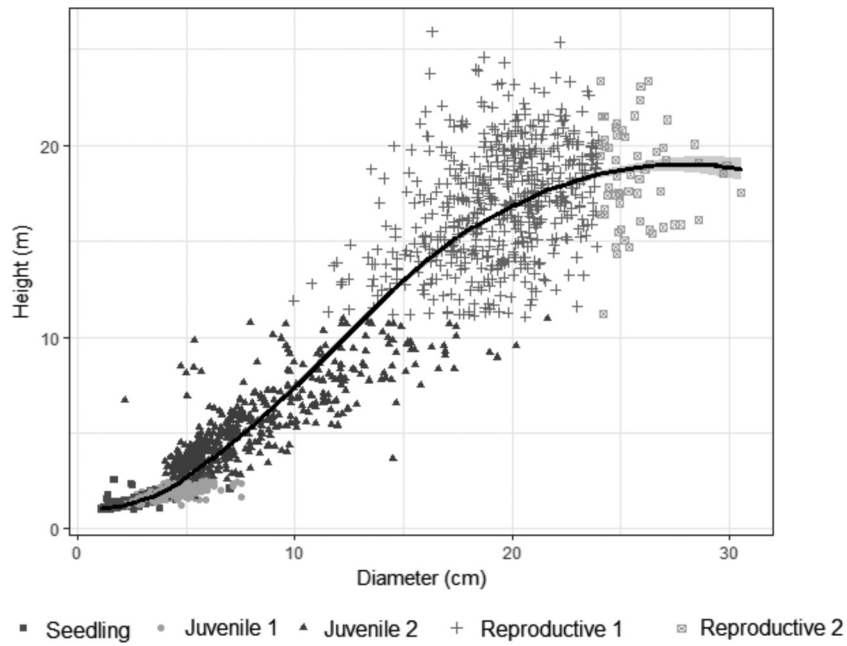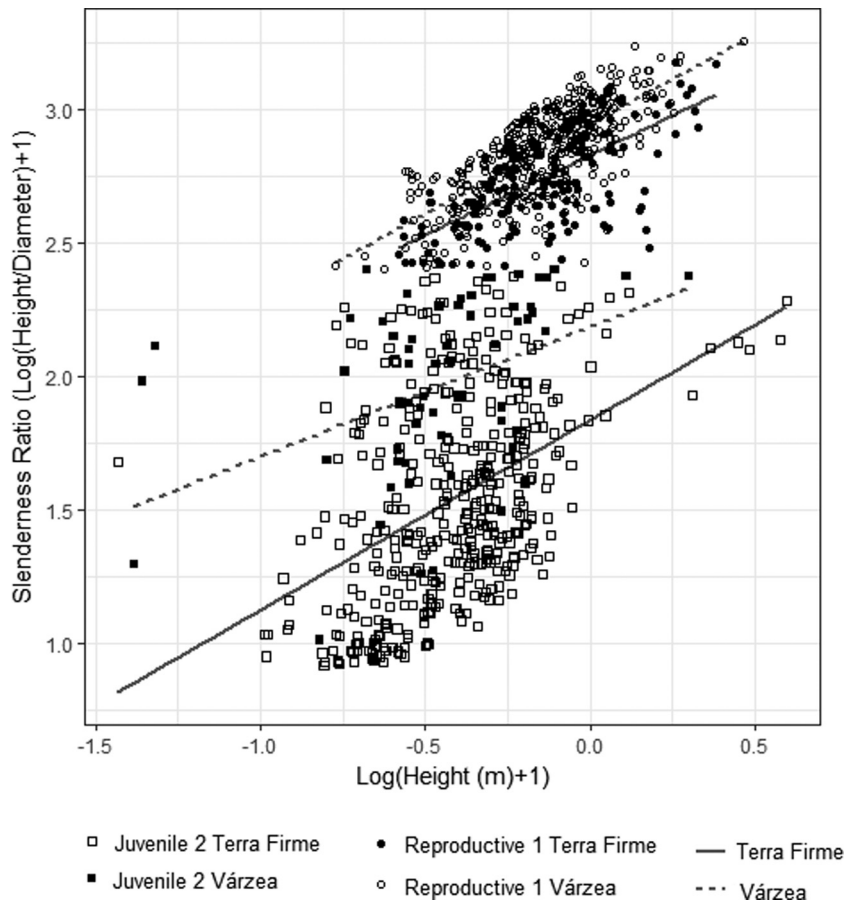


**Fig. 4.** Height:diameter relationship of *Euterpe precatoria* on a log scale with fitted linear model adjusted by life stage through ANCOVA.

**Table 1.** Models generated to test the factors affecting the density of individuals of the açaí population (*Euterpe precatoria*) in Central Amazonia.

| Model | Random factor | DF | AIC | ΔAIC |
|---|---|---|---|---|
| 1 | Habitat × Life stage | 13 | 3165.8 | 580.2 |
| 2 | **Habitat + Life stage** | 14 | 2585.6 | — |
| 3 | Habitat × Life stage | 8 | 3427.2 | 841.6 |

**Note:** The best model is presented in bold font.

stage. Reproductive 2 were scarce in flooded forests, and absent in unflooded ones. The population density of Reproductive 1 palms was larger in the high elevation várzea (5.44 ± 6.79 palms·400 m$^{-2}$) than in low elevation várzea forests (2.42 ± 2.54 palms·400 m$^{-2}$). Low várzea also had proportionally fewer Juvenile 2 and Reproductive 2 palms relative to the high várzea (Fig. 5).

Population structure, as measured using the symmetry of height distribution, did not show spatial structure. The AIC of the mixed model (GLMM) using blocks of plots to control for spatial effects on distribution symmetry was larger than the best model's AIC (Table 2). This indicates that the size structure of populations of *E. precatoria* did not present detectable spatial autocorrelation. The non-spatial GLM models including the effect of distance from the nearest human settlement were undistinguishable from the simplest model containing the effect of habitat alone, which also presented the lowest AIC. We can thus conclude that habitat effects sufficed to explain the variation in the symmetry of height distribution, and that human settlements did not have significant effects (Fig. 6A). Populations in unflooded forests presented right-skewed height distributions with positive symmetries, whereas populations in flooded forests showed uniform or negatively-skewed height distributions with negative symmetries (Fig. 6B). Population height distributions are given in Figs. 6C and 6D.

## Discussion

We identified natural life stages of *Euterpe precatoria*, the most abundant species in the Amazon basin (ter Steege et al. 2013). We registered changes in the allometric relationships of this species along its life trajectory, and also uncovered a marked habitat dependency in the density of different life stages. These changes were accompanied by variation in population structure in response to flood regimes, but not to nearness of human settlements. The patterns we uncovered have implications for our interpretation of widespread Amazon forest species distributed in habitats with contrasting disturbance regimes and resource levels like flooded várzeas and upland terra firme.

The interpretation of population phenomena is facilitated if biologically relevant classes of individuals are clearly identified, as through the identification of life stages instead of arbitrary size classes (Gatsuk et al. 1980; Caswell 2001). The macromorphological life stages of *E. precatoria* we identified fit known developmental phases

of palms (Tomlinson 1990; Souza et al. 2000, 2003). Similarly to *Euterpe edulis* (Carvalho et al. 1999), but differently from other palm species (Souza et al. 2000, 2003), *E. precatoria* seedlings did not produce entire leaves, but fan-shaped, pinnatisect leaf blades. The production of partitioned leaf blades by seedlings may reduce damage by herbivores, whose effects are particularly harmful in moist and shaded environments like the tropical forest understory (Carvalho et al. 1999; Baraza et al. 2004). Seedlings, which lacked an aerial stem, presented a very low height:diameter allometric relationship. This corresponded to the stem-building phase described for *E. precatoria* by Avalos and Otárola (2010). In this phase, intensive stem base growth takes place at the expense of height growth, and ensures plant establishment for future investments in height (Tomlinson 1990; Kimura and Simbolon 2002). The increasing allometric relationship from Seedlings to Reproductive 1 depicts increasing investment in height growth given an overbuilt stem base, that is further stabilized through adventitious roots. Tall palms are released from the biomechanical constraints considered in traditional allometric models because of enlarged stem bases, but also because they develop secondary thickening growth, and have additional support provided by stilt roots (Avalos and Otárola 2010). Finally, the height:diameter relationship is reduced in Reproductive 2 adults, for which larger diameter values corresponded to very small height increases. Forest canopy height is likely a key factor mediating *E. precatoria* allometric relationships throughout ontogeny.

### The treefall gap and flood disturbance regimes

Our first hypothesis was confirmed, as we found a significant interaction between palm shape through slenderness ratio and habitat. Palms had more slender trunks in várzea forests from the Juvenile 2 life stage. The mechanical stability of very slender columnar stems requires either tissues with high stiffness (elastic modulus E) or stems with low P, which is the maximum self-load that a column can support (Niklas et al. 2006). Throughout the Amazon basin, flooded forests form a variety of distinct ecosystems from neighboring upland forests (Junk et al. 2011*a*, 2012). However, a common factor linking different types of flooded forests is lower and more irregular forest canopies than upland forests, caused by flood-induced restricted tree growth (Souza and Martins 2005; Sawada et al. 2015). The increased slenderness we found in palms growing in the várzea forests suggests light-limited growth in terra firme forests, as well as a growth strategy that prioritizes the positioning of the crown in the canopy. This interpretation is supported by the finding that stem slenderness is positively correlated to adult stature (Poorter et al. 2003; Niklas et al. 2006) and light demand (Poorter et al. 2003), and higher slenderness allows várzea palms to rapidly reach the canopy with low construction and support costs (Poorter et al. 2003; Kitajima and Poorter 2008). It is pos-

**Fig. 5.** Average density of açaí (*Euterpe precatoria*) palms in unflooded terra firme and flooded várzea in Central Amazon. The error bars represent standard deviations. J1, Juvenile 1; J2, Juvenile 2; R1, Reproductive 1; R2, Reproductive 2.
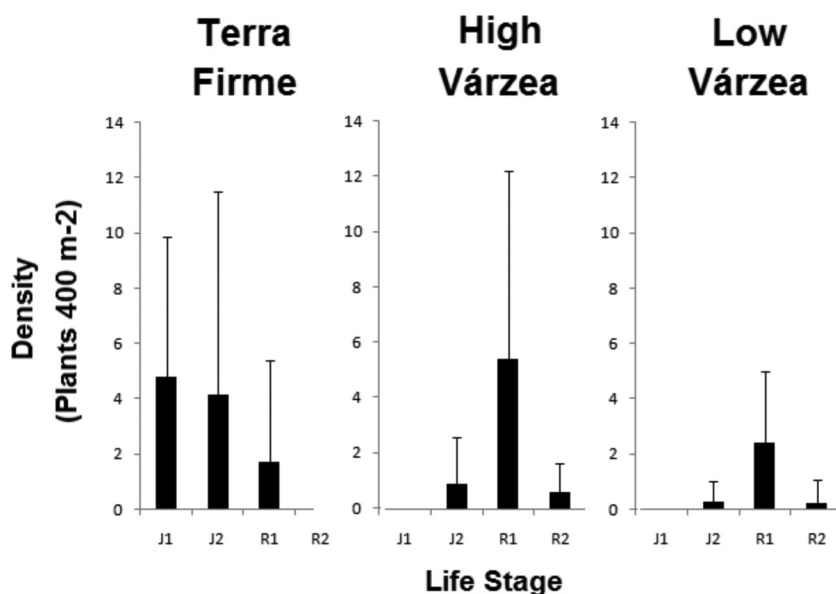


**Table 2.** Generalized linear models used to investigate the influence of habitat type (three levels: high and low várzea floodplain and unflooded terra firme) and distance to the nearest human settlement in explaining variation in the symmetry of *Euterpe precatoria* height distribution in Central Amazon.

| Model | Class | Fixed factors | Random factors | DF | AIC | ΔAIC |
|---|---|---|---|---|---|---|
| 1 | GLM | Habitat × Distance | — | 7 | 94.6 | — |
| 2 | GLMM | **Habitat × Distance** | Block | 8 | 96.57 | 1.97 |
| 3 | GLM | **Habitat + Distance** | — | 5 | 94.73 | 0.13 |
| 4 | GLM | **Habitat** | — | 4 | 94.63 | 0.03 |

**Note:** Model 2 controls for spatial autocorrelation through blocks of plots taken as a random factor. The models are presented in increasing order of AICc. The models presented in bold font are statistically equivalent plausible models (ΔAIC < 2).

sible that Reproductive 2 palms are shorter than Reproductive 1, owing to the fact that they are restricted to well-lit flooded forests, where the shorter and more open canopy reduces the need for further height growth. This agrees with the findings of Peña-Claros and Zuidema (2000), who reported that *E. precatoria* reached reproductive maturity at smaller sizes in Bolivia in the flooded forests than in upland forests. This indicates that increased light availability and reduced or no drought exposure in flooded forests sustain larger adult açaí populations (Stoian 2004), as found in other tropical forests in which increased adult palm density has been found in sites with increased canopy openings (Kahn 1987; Silva Matos et al. 1999; Souza and Martins 2006). The very high standard deviations associated with average palm density values indicates aggregated spatial distributions of individuals, which may track safe sites in flooded forests or canopy gaps in both flooded and unflooded areas (Souza and Martins 2002, 2006).

Agreeing with our second hypothesis, population size distributions in floodplain forests were significantly more left-skewed than in upland forests, indicating a prevalence of tall palms relative to small ones. Left-skewed population structures indicate chronic regener-

ation failure resulting from low survivorship and (or) growth among younger individuals (Condit et al. 1998; Caswell 2001). Flooding is known to produce oxygen deprivation, sedimentation, and mechanical damage, frequently killing younger plants (Parolin 2009; Voesenek and Bailey-Serres 2015). Given their abundance and prevalence in flood-prone várzeas, adult *E. precatoria* must possess physiological and (or) anatomical traits enabling them to withstand and grow under the deep seasonal flooding of Amazon floodplains, which may reach up to 10 m (Junk et al. 2011*b*). Our study area, however, can be regarded as a high várzea (sensu Ayres 1993), with flooding limited to no longer than three months and 2 m submersion (H. Brum, personal observation). This was the reason why elevation did not vary much between transects and the model including this variable was discarded. The effects of low várzea (with deeper and long-lasting floods) on *E. precatoria* population structure remain to be identified.

Juveniles were nearly absent from flooded forests, which were dominated by reproductive palms. Contrary to species whose seedlings may survive up to 300 days submerged (Parolin 2009), most of the dense aggregates of recently germinated seedlings we observed in the

**Fig. 6.** (A) The relationship between skewness and distance from the nearest community (each point represents one transect with five 20 m × 20 m plots) and (B) relationship between skewness and habitat. Skewness of the population of açai (*Euterpe precatoria*) in Central Amazon, in (C) terra firme, and (D) várzea. Pooled data from all of the transects were used to build the histograms.
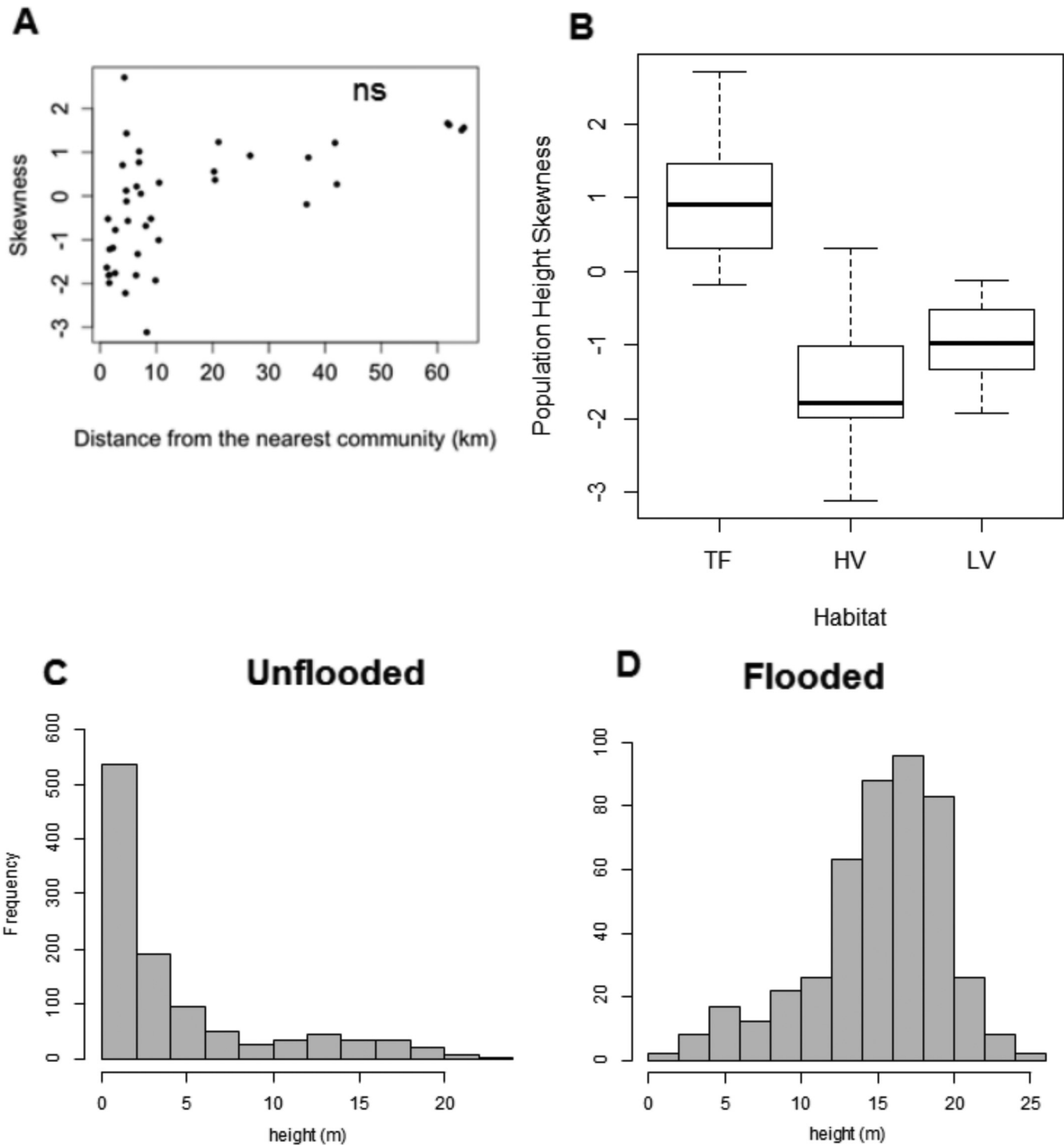
floodplains were quickly wiped out by the rising waters of the Purus river (H. Brum, personal observation). Seasonal flooding affects the dynamics of various plant species (Junk et al. 1989; Wittmann and Junk 2003; Wittmann et al. 2004), and is probably a key factor in the

population dynamics of *E. precatoria*. Inter-annual variation in the flood pulse is common, meaning that certain trees will not be flooded for one or two consecutive years if the water is atypically low (Parolin 2009). The establishment of new individuals in flood-prone habitats seems to

depend on the occurrence of a recruitment window in dry years in which flooding fails to eliminate young palms. Amazonian flood regimes have been changing, and extreme events are becoming more frequent (Marengo et al. 2013; Pinho et al. 2015). Long-term monitoring is needed to help us understand whether extreme flood years will offset the recruitment opportunities represented by more frequent low flood years, and what net effect this will have on *E. precatoria* recruitment.

The results for population density and height distribution indicated a different scenario for populations of upland terra firme forests. There, populations of *E. precatoria* probably suffer from light limitation due to competition with tall trees (Myster 2016). Seedling recruitment of *E. precatoria* is common in the shaded understory, where the species produces a persistent seedling bank (Rocha 2004). As we assumed in the introduction, *E. precatoria* must present a moderate degree of shade tolerance (Condit et al. 1998; Mostacedo and Fredericksen 1999) to withstand shade and wait for canopy openings (Avalos et al. 2013; Otárola and Avalos 2014). Reduced growth, as happens with young plants in the shade (Avalos 2019), is one of the factors that produces right-skewed population structures, because individuals accumulate in early life stages (Condit et al. 1998; Caswell 2001; Souza 2007). Our results thus indicate that *E. precatoria* suffers light limitation in upland forests, and that suppressed young individuals accumulate in the population until growth into the canopy and recruitment into the reproductive stage are both promoted by increases in light availability (Svenning 2001, 2002; Kitajima and Poorter 2008; Avalos 2019). This strategy corresponds to the cryptic pioneer strategy (Kitajima and Poorter 2008), because the species recruits under disturbed, high-light conditions, which if persistent, allow palms to grow faster and to attain maturity at an early age. However, if shaded during the first stages of regeneration, they could be suppressed and not reach maturity for decades (Kitajima and Poorter 2008; Avalos 2019). A result of such recruitment bottlenecks would be the low density of reproductive palms in upland forests relative to palms in the earlier life stages. Alternative explanations for the reduced densities of larger palms in upland forests could be water and nutrient competition with trees. Given the rainy climate prevailing in the study region, it is very unlikely that water competition between palms and trees are ecologically meaningful, but palm species have specific soil macronutrient requirements that may be altered by competition with trees (Cámara-Leret et al. 2017), and could possibly limit adult recruitment.

Different recruitment bottlenecks in upland and floodplain forests probably promote distinct *E. precatoria* population structures, but these do not inform population growth or viability in either of these two habitat types. This is because measures of population structure such as size distribution are not reliable proxies for future population growth and, therefore, of population persistence in any given habitat or set of environmental or human-imposed conditions (Johnson et al. 1994; Condit et al. 1998; Virillo et al. 2011; Bin et al. 2012). Otárola and Avalos (2014) suggest that source populations of *E. precatoria* in more open-canopy habitats with abundant adults could sustain sink populations in closed-canopy upland forests. Hypotheses such as this and the different disturbance regimes that we advanced above will have to wait for further study of the population dynamics of the species to understand its demographic patterns and long-term dependency on different kinds of disturbances to maintain viable populations.

Contrary to our expectations, the distance to the nearest human settlement, used as a proxy of management intensity (Ticktin et al. 2012; Baldauf and Santos 2013), had no effect on either population density or population structure. The populations we studied that were farther from human settlements are reachable by trails and by water. Therefore, one possible reason for the lack of effect on population structure by distance from human settlements could be that local people harvest and manage *E. precatoria* throughout the entire study area in a shifting way, as is common in Amazonia (Levis et al. 2017), and we were unable to sample populations outside their reach. Other possible explanations are that environmental effects overrun management differences, or that these were subtle enough to not produce detectable changes in population parameters. Because *E. precatoria* is regarded as a domesticated species (Clement et al. 2015; Levis et al. 2017), its distribution, abundance, and to some extent population structure could reflect unknown and unrecorded historical use by humans that blur current distance effects. Finally, the comparison of population size distributions across habitats with contrasting disturbance regimes allows the detection of functional groups of species with similar life histories (Swaine et al. 1990; Poorter et al. 1996; Wright et al. 2003; Souza 2007; Souza et al. 2008, 2010). Considering the resource acquiring vs. stress-tolerant life history gradient (Grime and Pierce 2012; Reich 2014; Díaz et al. 2016), the ecological strategy of *E. precatoria* could tentatively be understood as intermediate and small-gap specialist (Denslow 1980), because it produces large seeds, and seedlings that can germinate in the shade (Rocha 2004), but presents enough shade tolerance so as to produce Seedling and Juvenile banks, but needs increased light resource levels to attain maturity and sustain population growth (Avalos 2019), which is facilitated in open-canopy floodplains, given recruitment windows (Lorimer and Krug 1983; Swaine et al. 1990; Poorter et al. 1996; Wright et al. 2003; Vlam et al. 2014).

In conclusion, the population ecology of *E. precatoria*, the most abundant species in the Amazon basin, is mediated by the contrasting effects of their occupancy in

flood-prone várzeas and unflooded terra firme habitats. These dominant habitat types present opposite light levels and disturbance regimes that change population structure, abundance, and allometry. Future studies should gather data for population dynamics to assess the demographic mechanisms by which such patterns are produced. The effects of human activities on population processes of the species should be investigated in more detail to establish the degree to which it withstands frequent fruit removal and whether humans contribute with seedling establishment.

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