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Structure, Spatial Distribution and Ecological Associations of *Uvariodendron angustifolium* (Annonaceae) in Ewè-Adakplamè Relict Forest, Benin: Implications for Conservation

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Abstract Uvariodendron *angustifolium* (Engl. & Diels) R. E. Fries is an aromatic, multipurpose Annonaceae species confined to the single relict forest island of Ewè-Adakplamè in southeastern Benin, where its threat level was previously estimated at 61%. Despite this well-documented vulnerability, no data were available on the demographic structure, spatial distribution and ecological relationships of its natural populations. This study aimed to fill this gap through a dendrometric inventory conducted in 45 one-hectare plots, complemented by relative neighbourhood density measurements and a co-occurrence analysis performed under R. The density of the adult population was 6.07 stems/ha, compared with 7.26 stems/ha for the regeneration stage. The diameter structure, fitted to a Weibull distribution (a = 1.99; b = 0.82; c = 2.04; skewness = 0.20), revealed a right-skewed distribution dominated by small-diameter individuals, with a near-absence of large stems attributable to repeated anthropogenic harvesting. The relative neighbourhood density analysis (Ω) showed an aggregated distribution within a 10 m radius around reference individuals, followed by a regular distribution between 10 and 30 m. Co-occurrence analysis with 42 heterospecific species revealed a marked predominance of random associations, with no significant negative association detected, indicating an absence of competitive exclusion within the surrounding woody community. These findings suggest that the survival of the species depends less on biotic interactions within its habitat than on the harvesting pressure exerted directly upon it.

Keywords: *Uvariodendron angustifolium, demographic structure, spatial distribution, ecological associations, conservation, Benin*

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1. Introduction

Biodiversity underpins the functioning of terrestrial ecosystems as a whole, whether through climate regulation, the maintenance of soil fertility, or the preservation of hydrological cycles on which human societies ultimately depend. The most recent scientific evidence nonetheless agrees on an alarming acceleration of its destruction. The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services already estimated that one million animal and plant species were threatened with extinction worldwide unless urgent measures were taken at both national and international levels [1], with invasive alien species standing among the main direct drivers of this extinction alongside overexploitation and habitat loss [2]. The African continent is no exception to this trend, experiencing continued losses of species and habitats [3,4], a situation that is widely shared among West African countries [5].

This regressive dynamic finds a particularly clear

illustration in the Dahomey Gap, a savanna corridor that currently separates the western Guinean forest block from the Lower Guinean Forest block and that is thought to have resulted from a drought episode at the end of the Holocene [6]. Within this mosaic of savannas and degraded formations, a few relict forest islands have nonetheless persisted and now function as true refuges for a Guineo-Congolian flora found nowhere else in the region [7]. The forest of Ewè-Adakplamè, located in the district of Kétou in southeastern Benin, is one of the most emblematic of these micro-refuges. Covering only 560 hectares, it harbours nearly 185 vascular plant species belonging to 54 families [8], and hosts rare or endemic species as well as phytogenetic resources of genuine cultural and socio-economic importance to the surrounding populations [9,10,11]. This forest remains nonetheless vulnerable, exposed to an ongoing intensification of human pressures such as deforestation, bushfires and resource overexploitation, in a context further compounded by climate change [11,12].

Among the botanical families best represented in these Guineo-Congolian forest relicts are the Annonaceae, a pantropical family of trees, shrubs and lianas ranking among the most diverse within the order Magnoliales, and playing a leading ecological role in structuring the understorey and shrub layer of African dense forests [13]. The genus *Uvariodendron*, recently revised taxonomically as part of a phylogenomic study of the tribe Monodoreae [13], comprises about fifteen African species, several of which have very restricted distribution ranges, making this group particularly sensitive to the effects of forest fragmentation. *Uvariodendron angustifolium* (Engl. & Diels) R. E. Fries strikingly illustrates this vulnerability. This species occurs as a shrub with marked cauliflory, its flowers and fruits arising directly on the trunk and main branches and giving off a characteristic lemon-like scent [10,14]. This olfactory feature is far from trivial, as it stems from the composition of its essential oils, dominated by geranial and neral, which confer on the plant a well-documented bioinsecticidal value against stored-product pests [15]; this in turn increases the harvesting pressure exerted on its natural populations and reinforces the urgency of ensuring sound conservation management. Locally, *U. angustifolium* is subject to multiple uses, documented through an ethnobotanical survey conducted among the surrounding populations from four sociocultural groups of the region [14]. This study identified seven categories of use, the most frequently cited relating to cultic (83.45%) and energy-related (58.98%) purposes, together with a significant influence of ethnicity, sex, age and education level on the knowledge held by local populations. It notably revealed a threat level of 61%, indicating that the species' natural populations are subject to considerable harvesting pressure within its only known habitat in Benin, since *U. angustifolium* is recorded there exclusively in the forest island of Ewè-Adakplamè.

This convergence of an extremely restricted distribution range, a high use value and pronounced anthropogenic pressure places *Uvariodendron angustifolium* among the priority species for conservation in the sub-region. Previous work on this species had, however, focused exclusively on the ethnobotanical dimension of the relationship between the species and local communities [14], without ever addressing the characteristics of its natural populations. To date, no data exist on the demographic structure of *U. angustifolium*, on how its individuals are distributed across the forest space, or on the nature of the relationships it maintains with the heterospecific species that make up its immediate environment. Yet these three dimensions are critical for assessing the regeneration capacity and resilience of a population confined to such a narrow habitat. The distribution of individuals by diameter class indeed provides insight into the renewal potential of a woody population [16], while spatial pattern analysis can reveal the ecological processes underlying the establishment and persistence of individuals, whether related to seed dispersal, intraspecific competition or microsite conditions [17]. As for interspecific associations, whether positive, negative or random, they offer a direct window into the facilitation, competition or neutral coexistence interactions that structure the surrounding plant community [18].

The present study seeks to fill this gap by characterising, for the first time, the population ecology of *Uvariodendron angustifolium* in its only known habitat, the forest of Ewè-Adakplamè. It pursues three specific objectives: to describe the species' demographic structure through its density and the distribution of individuals by diameter class, to analyse its spatial distribution pattern, and to characterise the nature of the ecological relationships it maintains with the heterospecific species coexisting in the same habitat. The results obtained should provide a concrete scientific basis for guiding conservation strategies for a species whose survival depends entirely on the preservation of a single forest island.

2. Material and Methods

2.1. Study Area

The study was conducted in West Africa, in southern Benin, within the community forest of Ewè-Adakplamè, the only known site where *Uvariodendron angustifolium* persists, a species whose threat level reaches 61% in this habitat [14]. This forest belongs to the Plateau phytogeographic district, characterised by dense-canopy semi-deciduous vegetation harbouring species such as *Mansonia altissima* (A. Chev.) A. Chev. (Sterculiaceae), *Nesogordonia kabingaensis* (K. Schum.) Capuron ex R. Germ. (Sterculiaceae) and *Uvariopsis tripetala* (Baker f.) G. E. Schatz (Annonaceae) [12]. It is located between 7°25'–7°30' N and 2°32'–2°35' E, in the district of Kétou, and is bordered by several surrounding villages, notably Adakplamè, Ewè, Gbèdji and Igbo-Owolo. The local climate is of the subequatorial type, marked by an alternation of two rainy seasons (March to July, then September to October) and two dry seasons (November to February, then August). Mean annual temperature is close to 28 °C, with heat peaks recorded during the dry season and minima occurring at the height of August. Annual rainfall ranges between 1,100 and 1,300 mm depending on locality [19,20]. Soils at Ewè-Adakplamè are predominantly ferralitic [21]. The local hydrographic

network is fed by both permanent and temporary streams belonging to the Ouémé watershed. Demographically, the peripheral zone of the forest shows a relatively high population density, ranging between 163 and 247 inhabitants per km² depending on locality [22]. The dominant ethnic groups, the Fon, Mahi, Holli and Nagot, derive their livelihoods mainly from agriculture, hunting, small-scale trade and the exploitation of forest resources [22,23], which partly explains the intensity of the anthropogenic pressures exerted on this relict forest island (Figure 1).

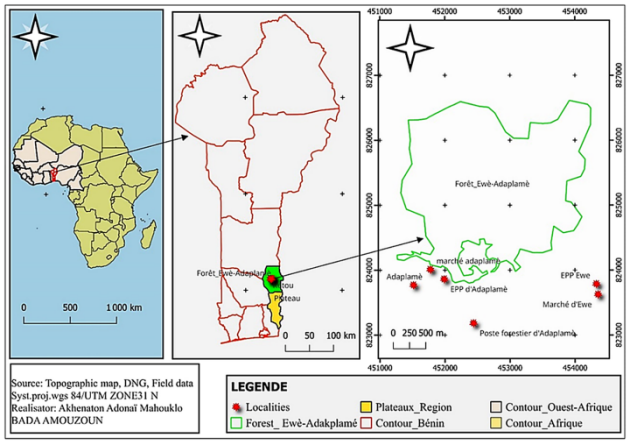

Figure 1. Geographical location of the study area (Ewè-Adakplamè Forest)

2.2. Data Collection

Data collection was carried out within 45 one-hectare plots, established using a stratified random sampling design intended to capture the ecological variability of the forest, taking into account vegetation homogeneity and the floristic representativeness of the different sectors. This design reproduces and adapts, for *Uvariodendron angustifolium*, the protocol already validated on a related Annonaceae species from the same study site, *Uvariopsis tripetala* [24]. Each georeferenced plot included, at its centre, a smaller subplot (50 m × 30 m) within which detailed floristic data were recorded.

Within each subplot, all woody individuals with a diameter at breast height (DBH) equal to or greater than 1.5 cm were recorded. This threshold was chosen because it corresponds to the diameter at which *Uvariodendron angustifolium* begins fruiting, allowing a reliable assessment of the dynamics of its adult population [25]. Each individual of the species was marked with a painted cross and fitted with a circular ring to facilitate subsequent re-measurement, following the standard forest monitoring protocol proposed by Chave et al. (2006) [26]. Specimens that were difficult to identify in the field were collected and subsequently identified at the National Herbarium of Benin (HNB). The precise GPS coordinates of each individual were also recorded to allow analysis of its spatial distribution.

The study of regeneration relied on 10 m × 10 m quadrats laid out diagonally within each 100 m × 100 m plot, following the method proposed by Bonou et al. (2009) [27] and Lokonon et al. (2013) [28]. This design allowed for a more refined estimation of seed production, regeneration density and the spatial structure of young individuals.

To characterise the fine-scale spatial distribution of *Uvariodendron angustifolium*, the number of neighbouring conspecific individuals was recorded around each reference individual (DBH ≥ 1.5 cm), within concentric distance bands of 0–10 m, 10–20 m and 20–30 m, following the approach of Condit et al. (2000) [29] and Kakpo et al. (2018) [30]. This information makes it possible to determine whether the species' spatial pattern is aggregated, random or regular, a key element for guiding conservation strategies.

2.3. Data Analysis

The structural analysis of the *Uvariodendron angustifolium* population focused primarily on density and diameter in order to assess its distribution and dynamics within the forest. Density was calculated using the following formula:

$$N = n / s \quad (1)$$

where N represents density expressed as the number of individuals per hectare, n the total number of *Uvariodendron angustifolium* stems counted per plot, and s the surface area of each plot.

The diameter structure of the adult populations was then fitted to a three-parameter Weibull distribution (a, b, c) using R software, whose probability density function is written as:

$$f(x) = \frac{c}{b}\left(\frac{x-a}{b}\right)^{c-1}\exp\left[-\left(\frac{x-a}{b}\right)^{c}\right] \quad (2)$$

where a denotes the location parameter corresponding to the minimum diameter observed, b the scale parameter related to diameter variability, and c the shape parameter indicating the overall form of the distribution. The asymmetry of this diameter distribution was further quantified using Pearson's skewness coefficient (SK), calculated as:

$$SK = \frac{\bar{x} - Mo}{s} \text{ or, equivalently, } SK = \frac{3(\bar{x} - Md)}{s} \quad (3)$$

where $\bar{x}$ corresponds to the mean , Mo to the mode, Md to the median, and s to the standard deviation. This index indicates whether the diameter distribution is symmetric or skewed, thereby helping to detect potential growth or recruitment constraints within the population.

The spatial distribution of the species was further characterised by calculating the relative neighbourhood density (Ω), following the approach proposed by Condit et al. (2000) [29]:

$$\Omega = \frac{Dx}{Ds} \quad (4)$$

where Dx represents the species-specific density calculated per concentric distance band (the ratio of the sum of individuals counted, Nx, to the surveyed area, As, within each band):

$$Dx = \frac{\sum Nx}{\sum As} \quad (5)$$

and Ds the overall density of individuals within the plot (the ratio of the total number of individuals, Ni, to the total plot area, Sp):

$$Ds = \frac{Ni}{Sp} \qquad (6)$$

Ω values close to 1 indicate a random distribution, values above 1 indicate individual aggregation, whereas values below 1 indicate a regular or overdispersed distribution, providing valuable insight into the ecological processes underlying the observed spatial structure.

Co-occurrence analysis between *Uvariodendron angustifolium* and the other woody species was performed using the *cooccur* package in R [31], based on presence/absence data recorded in each plot. This analysis made it possible to determine whether the spatial distribution of *Uvariodendron angustifolium* was positively or negatively associated with the presence of other species, thereby revealing potential ecological interactions or environmental constraints relevant to conservation planning.

3. Results

3.1. Structural Characteristics of *Uvariodendron angustifolium*

3.1.1. Density

The dendrometric inventory revealed a mean density of 6.07 stems/ha (± 2.96) for the adult stage of *Uvariodendron angustifolium* in the forest of Ewè-Adakplamè (Table 1). The regeneration stage, defined as individuals with a height below 1 m and a diameter below 1.5 cm, showed a density of 7.26 stems/ha (± 2.35), slightly higher than that of adult individuals.

Table 1. Density of *Uvariodendron angustifolium* in the forest of Ewè-Adakplamè

Stage	Mean (stems/ha)	Standard error
Adults	6.07	2.96
Regeneration (H < 1 m; DBH < 1.5 cm)	7.26	2.35

3.1.2. Diameter Class Distribution

Fitting the diameter structure of adult *Uvariodendron angustifolium* individuals to a three-parameter Weibull distribution yielded a location parameter a = 1.99 cm, a scale parameter b = 0.82 cm and a shape parameter c = 2.04, associated with a Pearson skewness coefficient of 0.20 (Figure 2). This distribution is right-skewed, or positively skewed, with a concentration of individuals in the small diameter classes and a progressive decrease towards the larger classes.

The diameter classes ranging from 2 to 3 cm, and from 4 to 5 cm, contained the highest densities per hectare, reflecting a population dominated by young, small-diameter individuals.

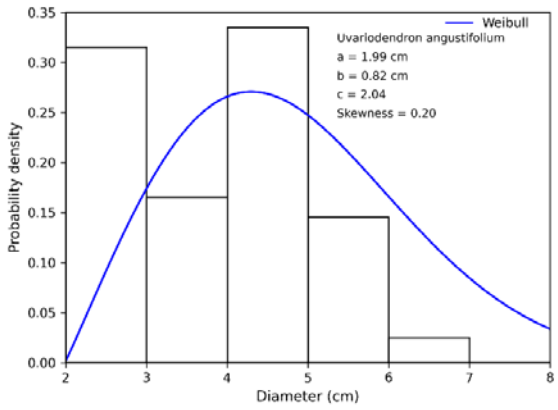

Figure 2. Diameter class structure of *Uvariodendron angustifolium* individuals in the forest of Ewè-Adakplamè

3.2. Spatial Distribution of *Uvariodendron angustifolium*

Analysis of the relative neighbourhood density (Ω) revealed a clear shift in the spatial distribution of *Uvariodendron angustifolium* depending on the distance considered around reference individuals (Table 2). Within the 0–10 m band, all individuals (100%) showed an Ω value above 1, indicating an aggregated distribution at this scale: *Uvariodendron angustifolium* individuals tended to cluster in close proximity to one another.

Beyond this 10 m radius, the spatial distribution was completely reversed. Within the 10–20 m and 20–30 m bands, all individuals (100% in each case) showed an Ω value below 1, corresponding to a regular, or overdispersed, distribution at these distances. At none of the three scales considered did any individual show an Ω value equal to 1, indicating that no purely random configuration was observed in this population.

Taken together, these results depict a spatial distribution structured in two stages: marked aggregation of individuals within a radius close to 10 m, followed by regular dispersion beyond this distance up to 30 m.

Table 2. Relative neighbourhood density (Ω) by distance band for *Uvariodendron angustifolium* in the forest of Ewè-Adakplamè

Ω values	Ω 0–10 m (%)	Ω 10–20 m (%)	Ω 20–30 m (%)
Ω > 1 (aggregated)	100	0	0
Ω = 1 (random)	0	0	0
Ω < 1 (regular)	0	100	100

3.3. Ecological Relationships between *Uvariodendron angustifolium* and Heterospecifics in the Ewè-Adakplamè Forest

Co-occurrence analysis between *Uvariodendron angustifolium* and the 42 heterospecific species recorded in its habitat revealed a clear predominance of random

associations over positive or negative ones (Table 3). Across all 42 species tested, no significant negative association was detected, indicating that no heterospecific species significantly avoided *Uvariodendron angustifolium* in space.

Forty of the 42 recorded species showed an exclusively random association with *Uvariodendron angustifolium*, with no significant positive or negative occurrence. Only two species, *Nesogordonia kabingaensis* (K. Schum.) Capuron ex R. Germ. and *Maerua duchesnei* (De Wild.) F. White, departed from this general pattern, showing a significant positive association in 4.76% of observed occurrences (1 positive occurrence out of 21), with the remaining occurrences also classified as random (95.24%, i.e. 20 occurrences).

In total, 42 significant random associations were thus recorded between *Uvariodendron angustifolium* and the heterospecific species of the Ewè-Adakplamè forest, compared with only 2 significant positive associations and no significant negative association.

Table 3. Nature of specific associations between *Uvariodendron angustifolium* and heterospecific species in the Ewè-Adakplamè forest

Species	Positive (%)	Negative (%)	Random (%)	Positive count	Negative count	Random count
Acacia polyacantha Willd.	0	0	100	0	0	1
Aidia genipiflora (DC.) Dandy	0	0	100	0	0	21
Albizia glaberrima (Schumach. & Thonn.) Benth.	0	0	100	0	0	21
Antiaris toxicaria (J.F.Gmel.) Lesch.	0	0	100	0	0	26
Carpolobia lutea G. Don	0	0	100	0	0	15
Ceiba pentandra (L.) Gaertn.	0	0	100	0	0	26
Celtis mildbraedii Engl.	0	0	100	0	0	1
Celtis prantlii Priemer ex Engl.	0	0	100	0	0	26
Celtis zenkeri Engl.	0	0	100	0	0	1
Chaetachme aristata Planch.	0	0	100	0	0	1
Cola millenii K. Schum.	0	0	100	0	0	26
Dalbergiella welwitschii (Baker) Baker f.	0	0	100	0	0	15
Dialium guineense Willd.	0	0	100	0	0	21
Dichapetalum madagascariense Poir.	0	0	100	0	0	21
Drypetes aframensis Hutch.	0	0	100	0	0	26
Drypetes floribunda (Müll.Arg.) Clapier	0	0	100	0	0	26
Drypetes gilgiana (Pax) Pax & K. Hoffm.	0	0	100	0	0	1
Englerophytum oblanceolatum (S. Moore) T.D. Penn.	0	0	100	0	0	26
Hildegardia barteri (Mast.) Kosterm.	0	0	100	0	0	1
Holarrhena floribunda (G. Don) Durand & Schinz	0	0	100	0	0	15
Hunteria umbellata (K. Schum.) Hallier f.	0	0	100	0	0	1
Hymenodictyon floribundum B.L. Rob.	0	0	100	0	0	1
Lannea nigritana (Scott-Elliot) Keay	0	0	100	0	0	1
Lasiodiscus mannii Hook. f.	0	0	100	0	0	15
Lecaniodiscus cupanioides Planch. ex Benth.	0	0	100	0	0	21
Majidea forsteri Radlk.	0	0	100	0	0	1
Maerua duchesnei (De Wild.) F. White	4.76	0	95.24	1	0	20
Mansonia altissima (A. Chev.) A. Chev.	0	0	100	0	0	26
Nesogordonia kabingaensis (K. Schum.) Capuron ex R. Germ.	4.76	0	95.24	1	0	20
Newbouldia laevis (P. Beauv.) Seem. ex Bureau	0	0	100	0	0	1
Pancovia bijuga Willd.	0	0	100	0	0	1
Pouchetia africana A. Rich. ex DC.	0	0	100	0	0	1
Pouteria alnifolia (Baker) Roberty	0	0	100	0	0	1
Rothmannia urcelliformis (Hiern) Bullock ex Robyns	0	0	100	0	0	26
Sterculia tragacantha Lindl.	0	0	100	0	0	26
Trichilia prieureana A. Juss.	0	0	100	0	0	26
Triplochiton scleroxylon K. Schum.	0	0	100	0	0	26
Uvariopsis tripetala (Baker f.) G. E. Schatz	0	0	100	0	0	26
Vitex micrantha Gürke	0	0	100	0	0	26
Warneckea memecyloides (Benth.) Jacq.-Fél.	0	0	100	0	0	1
Zanthoxylum leprieurii Guill. & Perr.	0	0	100	0	0	15
Zanthoxylum zanthoxyloides (Lam.) Zepernick & Timler	0	0	100	0	0	1

4. Discussion

4.1. Density and Demographic Structure

The density of 6.07 stems/ha recorded for adult *Uvariodendron angustifolium* individuals in the Ewè-Adakplamè forest confirms the rarity of this species even within its only known habitat in Benin. This value is markedly lower than that reported for the related Annonaceae species *Uvariopsis tripetala* in the same forest, where adult density reaches 12 stems/ha [24], even though both species share an identical habitat and a rigorously comparable sampling design. This discrepancy, observed at a constant site, reinforces the idea that the rarity of *U. angustifolium* does not solely reflect the restriction of its distribution range to a single forest island, but also points to a structural weakness inherent to the population itself, consistent with the 61% threat level already established for this species [14].

The diameter structure, with a Weibull shape parameter of 2.04, falls within the category of unimodal, right-skewed distributions described by Bin et al. (2012) [32] in numerous tropical tree species, where the relative conservation of intermediate diameter classes limits the expression of a reverse-J profile otherwise classically associated with massive and continuous recruitment. The pattern observed in *U. angustifolium*, with individuals concentrated in the 2–3 cm and 4–5 cm diameter classes, thus departs from the regeneration deficit pattern identified in *U. tripetala* at the same site, where the distribution had proven far more strongly contracted towards the larger diameter classes [24]. The fact that regeneration density slightly exceeds adult density is, in this respect, an encouraging indicator of a genuine regeneration potential in the species, although the low absolute numbers call for caution regarding overly optimistic conclusions about population persistence, insofar as the actual transition from the regeneration stage to the adult stage remains conditioned by survival rates that the present study did not measure [16,28].

The near-total absence of large-diameter individuals, for its part, has an explanation that extends beyond natural demographic processes alone. The young stems of *Uvariodendron angustifolium* are indeed subject to sustained harvesting for the making of sacred whips used during Oro cult ceremonies, a well-documented cultural practice in this area [14]. This pressure is compounded by multiple other uses relating to traditional human medicine, domestic energy, oral hygiene, food, magic and service wood, themselves aggravated by unregulated logging, recurrent fires and agricultural encroachment affecting the Ewè-Adakplamè forest [14]. This combination of harvesting pressures, which preferentially targets the most accessible and youngest stems, plausibly explains why the population fails to fully express its growth potential towards the larger diameter classes, despite initial recruitment that appears, for its part, to be maintained.

4.2. Spatial Distribution

The shift from an aggregated distribution within a 10 m radius to a regular distribution beyond this distance fits within a spatial pattern widely documented among tropical woody species, where short-distance aggregation generally reflects seed dispersal constraints, while the regularity observed at greater distances reflects the involvement of density-dependent regulation processes [17,29]. This type of transition between aggregation and overdispersion as a function of distance has been described in several tropical and subtropical tree species, notably in the subtropical forest of Gutianshan, where aggregation progressively decreases with individual developmental stage under the combined effect of self-thinning and Janzen-Connell-type mechanisms [33]. Such a shift in spatial pattern with distance is, moreover, not unique to this species, as Kakpo et al. (2018) [30] also demonstrated, using the same relative neighbourhood density index, different types of spatial distribution for a given species depending on the distance band examined.

The aggregation observed within the 0–10 m band around *Uvariodendron angustifolium* individuals could notably be explained by limited activity of seed dispersal agents, or by a predominantly gravity-driven dissemination mode, whereby fruits fall in the immediate vicinity of the mother plant before being buried in the soil where they germinate. The dispersal strategies adopted by a plant species are indeed closely linked to the nature of its dispersal agents [30]. The fruits of *Uvariodendron angustifolium* are reportedly consumed raw by several animal groups, notably birds, squirrels, monkeys and duikers, as well as by hunters who discard the seeds after consumption [14], which could explain the presence of individuals beyond the 10 m radius despite primary short-distance dispersal.

The Janzen-Connell hypothesis further offers a second, complementary interpretive framework to explain the regularity observed between 10 and 30 m. According to this model, mortality of seeds and young individuals intensifies in the immediate vicinity of conspecific adults owing to increased pressure from natural enemies or negative soil feedback, which favours the establishment of recruits at an intermediate distance from the parent tree and ultimately leads to a regularisation of the spatial distribution of adult individuals [34]. The aggregation observed within the 0–10 m band would thus correspond to a zone of primary seed dispersal still little affected by these regulatory mechanisms, whereas the regularity observed between 10 and 30 m would signal the cumulative imprint of intraspecific competition, secondary dispersal by fauna, and density-dependent mortality on the fate of individuals furthest from the parent trees.

4.3. Interspecific Relationships

The near-absence of deterministic associations, whether positive or negative, between *Uvariodendron angustifolium* and the 42 heterospecific species recorded in its habitat stands out as one of the most original findings of this study. Such a pattern, in which the vast majority of species tested show a predominantly random association, aligns with the predictions of the neutral theory of biodiversity, according to which species co-occurrence within a community may result primarily from stochastic processes of birth, death and dispersal rather

than from deterministic mechanisms of facilitation or competition [35]. This result contrasts with observations made in other tropical forest communities, where dominant species are instead involved in a disproportionate number of non-random spatial associations, leading to conclusions of departure from neutrality rather than confirmation of it [36].

The total absence of significant negative association deserves particular attention and finds a direct echo in the work of Calatayud et al. (2020) [37], who analysed spatial association networks across more than 300 terrestrial and aquatic ecological assemblages worldwide. These authors show that abundant species monopolise the vast majority of detected negative associations, whereas rare species are almost exclusively involved in positive or neutral associations, this general pattern partly explaining the persistence of rare species within competitive communities. The very low density of *Uvariodendron angustifolium* in the Ewè-Adakplamè forest fits well within this theoretical framework, since such a scarce species is unlikely to occupy a position dominant enough within the community to exert, or be subject to, measurable spatial exclusion from its neighbours.

This ecological interpretation must nonetheless be qualified in light of a statistical limitation inherent to co-occurrence analysis when applied to rare species. Cowans et al. (2025) [38] indeed demonstrated, through simulations of multispecies co-occurrence models, that the ability to detect significant interspecific interactions remains strongly dependent on sample size and on the detection probability of the focal species, with estimation bias becoming particularly pronounced when recorded abundance is low. Applied to the present case, this limitation suggests that the absence of detected negative association may reflect the combination of two non-mutually exclusive phenomena: a genuinely weak interspecific competition experienced by *Uvariodendron angustifolium* within this relatively closed forest environment, but also a statistical power constrained by the very rarity of the species, which limits the ability of the analysis to reveal real but rare negative associations.

The two marginal positive associations detected, involving *Nesogordonia kabingaensis* and *Maerua duchesnei*, remain too limited on their own to be interpreted as evidence of a genuine ecological facilitation relationship. They nonetheless fit within the same logic highlighted by Calatayud et al. (2020) [37], according to which the few significant associations involving low-abundance species tend to be positive rather than negative in nature, which could reflect a localised shared-microhabitat effect rather than an active facilitation interaction. These two relationships would benefit from being examined in light of complementary microsite data, notably edaphic and light-related, before being attributed with certainty to a specific ecological mechanism.

4.4. Implications for Conservation

Taken together, these results depict the profile of a species whose survival rests on a particularly fragile balance. The very low population density, combined with a distribution range restricted to a single forest tract of less than 600 hectares, places *Uvariodendron angustifolium* in a state of vulnerability comparable to that of other endemic or narrowly distributed woody species in Benin already identified as conservation priorities [12]. This situation also echoes the conclusions of a recent ethnobotanical study conducted in the neighbouring forests of Pobè and Dogo-Kétou, in the same southeastern region of Benin, which classified several heavily harvested woody species among conservation priorities, explicitly recommending the establishment of propagation programmes, whether traditional or assisted, for the most threatened species [39]. The demographic profile observed for *Uvariodendron angustifolium*, although marked by a slight excess of regeneration relative to adult numbers, is not sufficient to guarantee population persistence as long as survival rates between developmental stages remain unknown.

The spatial structuring evidenced, with short-distance aggregation followed by regularity beyond 10 m, calls for management measures that give priority to preserving the microhabitats where current regeneration hotspots are concentrated, rather than interventions uniformly distributed across the entire forest. The absence of negative association with other woody species further suggests that no selective management measure aimed at reducing interspecific competition is warranted at present, priority instead lying in the strict protection of existing population cores against anthropogenic harvesting, whose intensity has already been quantified through the 61% threat level established previously [14].

In this regard, the community-based status of the Ewè-Adakplamè forest, rooted in local cultural and cultic practices, represents both a challenge and a lever for the conservation of the species. Sacred and community forests of southern Benin have indeed demonstrated, in several comparable contexts, their capacity to effectively curb deforestation where the traditional authority governing them remains respected, though this effectiveness erodes as such traditional authority weakens under growing demographic and economic pressures. A management approach combining the formal recognition of the forest's protected status with the maintenance of traditional harvesting-regulation practices, in close consultation with customary authorities and Oro cult practitioners directly concerned with the use of the species, would thus offer a conservation pathway that is both culturally grounded and ecologically sound. Long-term demographic monitoring, coupled with restoration actions targeted at the zones of highest aggregation and, where appropriate, assisted propagation trials to strengthen adult numbers, appears to be the most appropriate approach for ensuring the long-term conservation of this species in its only known habitat.

5. Conclusion

This study provides the first quantitative data on the population ecology of *Uvariodendron angustifolium* in its habitat, the community forest of Ewè-Adakplamè, thereby filling a knowledge gap that had so far constrained any conservation action grounded in solid scientific evidence. Three major findings emerge from this work.

Demographically, the population is characterised by a particularly low density, lower than that of related species

coexisting in the same forest, yet it nonetheless displays a genuine regeneration potential, with the density of young individuals slightly exceeding that of adults. The near-absence of large-diameter individuals, more attributable to cultural and utilitarian harvesting than to a purely ecological constraint, nevertheless highlights that this regeneration potential alone is not sufficient to ensure population renewal as long as juvenile stems continue to be harvested before reaching full maturity.

Spatially, the species displays a two-scale distribution pattern, aggregated in the immediate vicinity of reproductive individuals and regular beyond ten metres, a pattern consistent with seed dispersal constraints and with the classic density-dependent regulation processes that structure tropical tree populations. This spatial organisation provides a concrete reference point for targeting conservation interventions towards genuinely active regeneration hotspots.

Regarding biotic interactions, the overwhelming predominance of random associations with the 42 heterospecific species recorded, together with the total absence of significant negative associations, indicates that *Uvariodendron angustifolium* is subject neither to competitive exclusion nor to marked dependence on any particular species within its forest environment. This finding, which fits within the broader framework of the neutral theory of biodiversity, suggests that the species' future depends less on its relationships with the surrounding floristic assemblage than on its ability to withstand the direct pressures exerted by human activities.

Taken together, these three components converge on a single conclusion: *Uvariodendron angustifolium* is not threatened by the internal ecological dynamics of its habitat, but by the intensity of the harvesting pressure exerted upon it within a narrow forest space itself at risk of disappearing. Its conservation cannot therefore rely on passive habitat protection alone, but must combine continuous demographic monitoring, targeted restoration of the most active population cores, and close involvement of local communities and customary authorities, who are both custodians of the uses that currently weigh on the species and potential guarantors of its future safeguard. In this respect, the forest of Ewè-Adakplamè represents not only the sole habitat of this rare species, but also a textbook case for the conservation of narrowly distributed endemic Annonaceae in West Africa, whose fate will largely depend on the ability to reconcile ecological imperatives with the sociocultural realities that have always shaped this type of forest heritage.

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The authors declare no conflicts of interest.

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The data that support the findings of this study are available from the corresponding author upon reasonable request.

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