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Light preferences, population structure, and pre-dispersal fruit predation in the reverse-phenology tree *Bonellia nervosa* (Primulaceae)

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ABSTRACT

Introduction: *Bonellia nervosa* is a dry forest understory tree with reverse leafing phenology, as it produces leaves during the dry season and is deciduous during the wet season. Being a phreatophytic species, it relies on substantial root biomass to access groundwater and flush leaves during the dry season.

Objective: To assess the population structure of *B. nervosa* in Santa Rosa National Park, Costa Rica; analyze the relationship between stem diameter and plant height; and examine how canopy structure and light availability influence its local abundance. Also, to evaluate fruit maturity and pre-dispersal fruit predation during the late wet season to understand its reproductive success.

Methods: The study was conducted along the *Indio Desnudo* trail (6.16 ha). Hemispherical photographs were taken at each *B. nervosa* (n = 33) and at 10 random sites where the species was absent. Principal component analysis was used to consolidate seven light and canopy structural variables. The Chapman-Richards model was applied to examine the relationship between stem diameter and height. Fruit weight and seed count were analyzed and each fruit inspected for the presence of Tortricidae larvae.

Results: Adults dominated the population. An inflection point was identified at 70.6 cm in height, indicating a shift from relatively rapid to progressively slower growth. *Bonellia nervosa* sites had higher canopy openness (14.68 %) and transmitted more diffuse light (21.05 $\mu mol/m^2/s$) than sites where the species was absent (12.42 % and 18.22 $\mu mol/m^2/s$, respectively). Pre-dispersal fruit predation was low (16 % of fruits, n = 39) and by Tortricidae larvae.

Conclusions: Seedling scarcity creates a recruitment bottleneck. The dominance of adults, the low number of seedlings, and specific light preferences limit the plasticity and adaptive capacity of *B. nervosa* to environmental changes. Future research should focus on the physiological mechanisms underlying *B. nervosa*'s reverse leaf phenology and its resilience to climate change.

Keywords: phenological strategies; reverse phenology; pre-dispersal seed predation; tropical dry forests.

RESUMEN

Preferencias de luz, estructura poblacional y depredación predispersión de frutos en el árbol de fenología inversa *Bonellia nervosa* (Primulaceae)

Introducción: *Bonellia nervosa* es un árbol del sotobosque del bosque seco tropical con fenología foliar invertida al producir hojas durante la estación seca y ser caducifolio durante la estación lluviosa. Esta especie freatofítica depende de una biomasa radicular considerable para acceder al agua subterránea y desarrollar hojas durante la estación seca.

Objetivo: Evaluar la estructura poblacional de *B. nervosa* en el Parque Nacional Santa Rosa, Costa Rica; analizar la relación entre el diámetro del tallo y la altura de la planta; y examinar cómo la estructura del dosel y la disponibilidad de luz influyen en su abundancia local. También evaluar la madurez de los frutos y la depredación predispersión al final de la estación lluviosa para entender su éxito reproductivo.

Métodos: El estudio se realizó a lo largo del sendero Indio Desnudo (6.16 ha). Se tomaron fotografías hemisféricas de cada individuo de *B. nervosa* (n = 33) y en 10 sitios aleatorios donde la especie estaba ausente. Se utilizó análisis de componentes principales para consolidar variables relacionadas con la luz y la estructura del dosel. Se aplicó el modelo de Chapman-Richards para examinar la relación entre el diámetro del tallo y la altura. Se analizaron el peso de los frutos y el número de semillas, y se inspeccionó cada fruto para detectar la presencia de larvas de Tortricidae.

Resultados: La población estuvo dominada por adultos. Se identificó una transición de un crecimiento relativamente rápido a uno progresivamente más lento a los 70.6 cm de altura. Los sitios con *B. nervosa* presentaron mayor apertura del dosel (14.68 %) y mayor transmisión de luz difusa (21.05 μmol/m²/s) que los sitios donde la especie estaba ausente (12.42 % y 18.22 μmol/m²/s, respectivamente). La depredación predispersión fue baja (16 % de los frutos, n = 39) y causada por larvas de Tortricidae.

Conclusiones: La escasez de plántulas genera un cuello de botella en el reclutamiento. El dominio de los adultos, la escasez de plántulas y las preferencias específicas de luz restringen la plasticidad y capacidad de adaptación de *B. nervosa* a cambios ambientales. Las investigaciones futuras deben centrarse en los mecanismos fisiológicos que sustentan la fenología foliar invertida de *B. nervosa* y su resiliencia ante el cambio climático.

Palabras clave: estrategias fenológicas; fenología inversa; depredación predispersión; bosque tropical seco.

INTRODUCTION

Tropical dry forests rank among the most endangered terrestrial ecosystems (Buchadas et al., 2022; Miles et al., 2006; Murphy & Lugo, 1986; Sánchez-Azofeifa et al., 2013; Siyum, 2020), having been some of the first to be extensively altered by recent human activity (Buchadas et al., 2022; Janzen et al., 2016). As a result, old-growth, mature tropical dry forests are now rare, and most remaining areas are disturbed or undergoing regeneration (Duan et al., 2023; Griscom & Ashton, 2011; Quesada et al., 2009). These forests endure a pronounced seasonal drought (4-6 months) characterized by high temperatures and significant water deficits (Murphy & Lugo, 1995) and have evolved a distinctive phenology adapted to episodic growth (Frankie et al., 1974; Janzen, 1967). During the wet season, plants flush leaves and accumulate reserves for reproduction during the following dry period. As drought intensifies, most species shed their leaves, reproduce, and release seeds near the end of the dry period. With the onset of the rains, seedlings establish and store resources to withstand the prolonged drought of the dry season (Janzen, 1967). While these forests support a range of phenological strategies to cope with extreme seasonality (Giraldo & Holbrook, 2011; Lasky et al., 2016; Lópezaraiza-Mikel et al., 2013), one particularly distinctive adaptation is reverse phenology (Giraldo & Holbrook, 2011; Janzen, 1970).

Bonellia nervosa is a dry forest understory tree exhibiting reverse leaf phenology. Unlike most plants in this ecosystem, which are deciduous during the prolonged dry season and retain leaves in the wetter months (Frankie et al., 1974; Murphy & Lugo, 1986; Murphy & Lugo, 1995), *B. nervosa* produces a new crop of leaves only during the dry period and sheds them at the onset of the rains (Chaves &

Avalos, 2008; Janzen, 1970). This unusual phenological pattern requires a highly specialized resource-use strategy (Janzen & Wilson, 1974). In addition to concentrating leaf production at the beginning of the drought period, *B. nervosa* also flowers and initiates fruit development; fruit maturation and seed dispersal occur in the late rainy season (Chaves & Avalos, 2008). The plant must also accumulate reserves for fruit expansion and survival under the shaded conditions of the forest understory during the wetter months (Janzen & Wilson, 1974). This strategy requires *B. nervosa* to allocate a substantial portion of its biomass to root development (Chaves, 2002; Janzen, 1970), allowing it to access the water table and clearly defining it as a phreatophytic species. Similar leaf phenology and biomass allocation strategies have been observed in other phreatophytes, such as *Faidherbia albida* in the arid forests of the Sahel region in West Africa (Roupsard et al., 1999). A reverse leafing phenology allows *B. nervosa* to fix carbon during the dry season, maintaining a competitive advantage relative to deciduous plants. This strategy results in overall slow growth (and growth in pulses, Schwinning & Kelly, 2013), particularly during the seedling stage, as the plant must first develop a sufficiently large root system to tap the water table.

Bonellia nervosa establishes itself primarily in shaded microhabitats, where light acts as an environmental filter and plant abundance is modulated by seed dispersal and seed predation. In well-lit environments, the plant would incur higher maintenance costs and face competition from faster-growing species. Consequently, *B. nervosa* thrives as a deciduous understory tree under a closed canopy during the rainy season, developing a full crown of leaves in the dry season when the canopy opens (Chaves & Avalos, 2008). Consequently, it is less common in habitats with high light exposure—such as open savannas, pastures, forest edges, or very young secondary forests—or in areas with persistent, dense shade throughout the rainy season, especially in forests dominated by evergreen species with year-round canopies, such as old-growth, mature dry forests. This pattern suggests that *B. nervosa* performs best in intermediate shade or moderately shaded environments, such as old secondary forests (80-100 years), and is less frequent in habitats with intense sunlight (Janzen & Wilson, 1974) or dense shade, like riparian or mature, late-successional forests. These latter habitats have become rare in the tropical dry forest ecosystem due to widespread deforestation and cattle ranching (Stan et al., 2024).

The pattern of habitat selection of *B. nervosa* is congruent with our field observations and what is reported in the literature (i.e., Enquist & Sullivan, 2001; Janzen, 1970; Janzen & Wilson, 1974). Establishing under intermediate shade has important implications for its life history strategy and could influence its population structure and reproductive strategies (Avalos, 2019). *Bonellia nervosa* is found in secondary forests and dry areas on hilltops or cliffs providing competitive advantages at the soil level (Enquist & Sullivan, 2001). At Palo Verde National Park, we have observed it along the Guayacán trail, which is dominated by limestone outcrops. Under these conditions, *B. nervosa* does not establish itself in purely rocky areas but prefers flatter or slightly sloped terrain that can accumulate enough soil for the plant's roots to reach the water table. The phenological pattern of *B. nervosa* is unique, as no other species in Costa Rica's dry forests exhibits reverse phenology. This strategy comes with significant trade-offs, as *B. nervosa* is typically scarce and confined to habitats with intermediate shade such as old secondary forests. Reverse phenology likely puts this species at risk under climate change scenarios, where increased climatic variability could threaten the survival of early life stages during heat waves or fluctuating conditions of radiation and water availability.

The main objective of this study was to examine the population structure of *B. nervosa* in Santa Rosa National Park (SRNP). Specifically, we aimed to: (i) assess the abundance of adults, juveniles, and seedlings in an old secondary forest, (ii) evaluate the influence of canopy structure and light conditions on the occurrence of *B. nervosa* during the peak of the wet season when canopy cover is highest, and

(iii) analyze fruit maturity and the intensity of pre-dispersal fruit predation five months into the wet season. Given the slow and metabolically demanding process of accumulating root biomass and food reserves during early life stages, we expected the population to be dominated by adults, with relatively few seedlings. We hypothesized that population structure would be influenced by light availability, as well as the activities of seed dispersers and seed and seedling predators. Furthermore, we anticipated that *B. nervosa* would establish most successfully in moderately shaded environments, avoiding areas with either low canopy cover (high light) or dense shade.

Analyzing the population structure, habitat selection and predispersal fruit predation of this species is crucial to understanding the adaptive consequences of reverse phenology (Stan & Sanchez-Azofeifa, 2019). The rarity of the reverse leaf strategy may explain why it has been largely excluded from phenological analyses (Giraldo & Holbrook, 2011; Schwinning & Kelly, 2013). This stresses the need to develop effective conservation protocols that account for the phenological diversity of tropical dry forests to improve our understanding of their resilience in the face of climate change and habitat degradation (Miles et al., 2006; Siyum, 2020; Stan & Sanchez-Azofeifa, 2019).

MATERIALS AND METHODS

Site description: This study was conducted in SRNP, Guanacaste, Costa Rica (10°50’04” N & 85°36’45” W, 295 m.a.s.l) in September 2024, along the entire length of the *Indio Desnudo* trail. The forest in this area is classified as a tropical premontane forest (Holdridge & Grenke, 1971), with a canopy height of 25 m. It is dominated by representative dry tree forest species, including *Bursera simaruba*, *Enterolobium cyclocarpum*, *Manilkara chicle*, and *Calycophyllum candidissimum*. The average annual rainfall is 1 423 mm, with September and October being the wettest months. The mean annual temperature is 25.7 °C, and the relative humidity averages 81 % (SRNP Climatic Records). Established in 1974 to protect significant historical sites, SRNP also initiated an ongoing ecological restoration process (Griscom & Ashton, 2011). SRNP maintains transitional areas between tropical moist and tropical dry forests (Kalacska et al., 2004). It is estimated that the Indio Desnudo trail has undergone approximately 80 years of regeneration and is classified as a late secondary forest, since it contains three layers of vegetation with 50-90 % of the canopy being occupied by evergreen species. This follows the terminology of Cao et al. (2015), Castillo et al. (2011) and Kalacska et al. (2004).

Study species: *Bonellia nervosa* (C. Presl) B. Ståhl & Källersjö (Primulaceae, formerly classified as *Jacquinia pungens,* and then *J. nervosa* in the Theophrastaceae, Morales, 2003) has been described as an understory shrub abundant in deciduous and semi-deciduous forests throughout the Pacific coast of Mesoamerica, from Southern Jalisco, Mexico, to Northwestern Costa Rica (Ståhl, 1989; Ståhl & Källersjö, 2004). However, we have observed individuals reaching 4.86 m in height (this study) and up to 7 m (pers. obs.), indicating that *B. nervosa* should be considered a small understory tree. Mature individuals can attain not only these heights but also substantial stem diameters (20-30 cm). This species is associated with tropical dry forests, although Morales (2003) indicates it could reach moist forests. The overall structure of *B. nervosa* is xerophytic (Janzen, 1983) and drought-tolerant (Romero et al., 2023). Leaves are coriaceous, with the apex modified as a spine, and once with a complete crown, the plant seems like a cactus with very sharp spines pointing out (Janzen, 1970). The leaves are produced synchronously at the start of the dry season (Chaves & Avalos, 2008) but begin to senesce and drop two weeks after the beginning of the rainy season. Senescing leaves often can remain in the plant for more than five months into the rainy season (while finishing reallocation of resources). The species remains leafless–or if leaves remain, they are not functional–throughout the rainy season. The species is phreatophytic with a deep root system

(2 m tall individuals have roots reaching 3 m in depth; Janzen, 1970; Janzen, 1983), which taps the subsoil water allowing it to produce leaves during the dry season while most of the plant community is deciduous. Seventy-eight percent of the biomass of very young seedlings (8.5 cm tall, n = 15) goes into roots (Chaves, 2002). There is limited data on water relations. For instance, the range in predawn water potential spanned -2.62 MPa during mid-March, one of the widest ranges compared to the species examined by Oberbauer (1985) in Palo Verde. This indicates water stress during the peak of the dry season. The fruits are round berries (mean width = 2.6 ± 0.3 cm, mean length = 2.7 ± 0.2 cm, mean weight = 8.48 ± 2.76 g, n = 39), indehiscent and coriaceous, with the number of seeds proportional to fruit size, ranging from four to 24 (average 13 (5), n = 39).

Determination of population structure: We conducted thorough visual surveys for seedlings, juveniles, and adults of *B. nervosa* along the road from the Park Administration to the entrance of the *Indio Desnudo* trail near the Santa Rosa historical site, extending 30 m into the forest on both sides throughout the entire trail (our sample area was approximately 6.16 ha). We meticulously searched for seedlings (height < 0.6 m), juveniles (height > 0.6 and < 1.5 m), and adults (height > 1.5 m). For each plant, we measured height and stem diameter 10 cm above the ground and analyzed the allometry of the height and stem diameter relationship using the Chapman-Richards model (Domínguez-Calleros et al., 2017).

Relationship between canopy structure and the presence of *B. nervosa*: We took hemispherical photographs 1.5 m above the ground, directly above or next to individual plants, and at 10 random points along the *Indio Desnudo* trail where *B. nervosa* was absent. We used a Nikon Coolpix 5 000 camera with a fisheye lens, mounted on a tripod with the lens oriented vertically toward the canopy. The top of the image was aligned with the magnetic North as determined using a compass. Photographs were taken under overcast skies, near dusk, or after dawn, to minimize glare and prevent direct sunlight from obscuring parts of the image. We analyzed the photographs using Gap Light Analyzer (GLA, version 2.0; Frazer et al., 1999) and measured the percentage of visible sky (% sky area), canopy openness (% canopy openness), leaf area index (LAI, measured at zenith angles of 0°-LAI 4- to 60° and 0° to 75° -LAI 5-), and the percentage of direct, diffuse, and total light transmitted through the canopy.

Intensity of predispersal fruit predation: We inspected all *B. nervosa* plants for the presence of fruits and randomly selected 39 fruits. Using Scout Pro Ohaus Portable Electronic Balance, we weighed the fresh fruits and seeds and calculated the percentage of seed weight relative to the total fruit weight. We also recorded the number of fruits eaten by Tortricidae larvae and calculated the percentage of fruit damage. Additionally, we observed varying degrees of seed maturation; some fruits contained visibly unripe beige seeds, while others housed mature brown seeds.

Statistical analyses: We applied the Chapman-Richards nonlinear growth function (Domínguez-Calleros et al., 2017; Zhao-Gang & Feng-Ri, 2003) to model the relationship between height and diameter. This flexible sigmoidal model captures the trajectory of plant growth, characterized by an initial phase of rapid height increase followed by a gradual deceleration as the plant approaches its maximum size. The Chapman-Richards model is expressed as $H = a\ (1\text{-}b \times \exp\ (\text{-}k \times D))^{m}$, where H is height, D is diameter, and a, b, k, and m are parameters controlling the asymptote, growth rate, and curve shape. This approach allows for accurate estimation of inflection points, reflecting critical shifts in growth dynamics throughout plant´s ontogeny. The height-diameter allometric relationships provide insights into resource allocation strategies, responses to environmental changes, and transitions between life stages (i.e., inflection points), which often indicate shifts from vegetative to reproductive growth.

In addition, to explore the relationships among the seven light and canopy structure variables mentioned earlier, we conducted a principal component analysis (PCA). We selected the first two components, which accounted for 82.27 % of the variation, as response variables summarizing canopy structure. Subsequently, we performed a one-way ANOVA to compare these components between locations where *B. nervosa* was present and randomly selected points where it was absent. Additionally, we assessed the relationship between fruit weight and seed count using an ordinary least squares regression. We checked the adjustment to the assumptions of normality and equality of variances of parametric analyses. All statistical analyses were conducted using R software (R Core Team, 2024).

RESULTS

Population structure: We found 33 individuals ranging in height from 15 to 486 cm. Three individuals were under 50 cm, maintained functional leaves, and were classified as seedlings. The rest were classified as reproductive individuals since we found mature or rotten fruits still attached to the plant. These results support our expectation that seedlings will be rare, and that the population will be dominated by reproductive individuals (Fig. 1A). Stem diameter and height were significantly related (Fig. 1B). The inflection point was located at 1.1 cm in diameter and 70 cm in height (at this size, the model estimates the switch from fast to slower growth). The asymptotic maximum value of height was 437.74 cm.

Canopy structure: Sites with *B. nervosa* had significantly higher canopy openness (14.68 %) than random sites (12.42 %; $F_{1,41} = 7.49$, $p = 0.009$; Table 1, Fig. 2A), as well as greater transmitted diffuse light (21.05 vs. 18.22; $F_{1,41} = 9.11$, $p = 0.004$; Fig. 2B). However, these differences were modest in magnitude. Leaf Area Index (LAI4 and LAI5) was similar between groups, showing no significant differences.

The percentage of transmitted direct light and total transmitted light showed the strongest correlation (0.96), followed by transmitted diffuse light, canopy openness, and leaf area index (LAI) at zenith angles of 0°-60° (0.89, LAI 4, Table 2). Two principal components explained 82.27 % of the variation in canopy structure (Table 3). The first component (PC1, 50.61 % of the variation) was dominated by canopy openness and transmitted diffuse light. The second component (PC2, 31.66 %) was dominated by transmitted direct light.

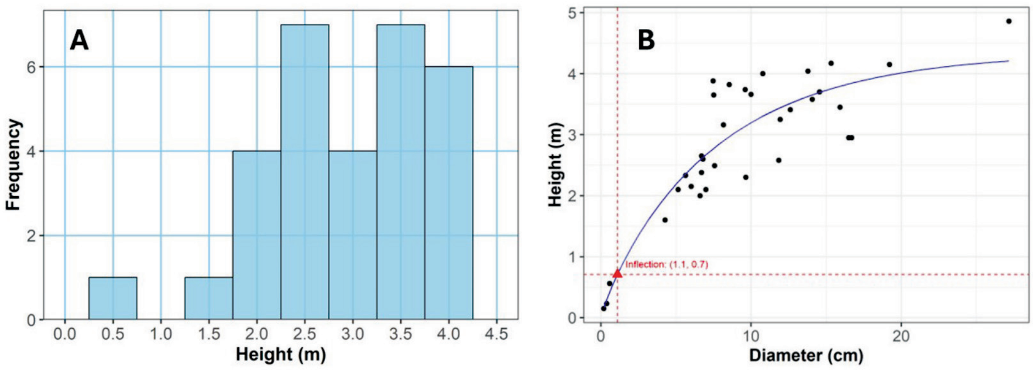

Fig. 1. A. Height distribution in the population of *Bonellia nervosa*. **B.** Chapman-Richards nonlinear growth model applied to the relationship between height and diameter ($R^2 = 0.78$, $F_{3,29} = 34.62$, $p < 0.001$) in 33 individuals of *B. nervosa*, SRNP, Costa Rica.

Table 1
Summary of canopy structure variables at the *Indio Desnudo* trail, SRNP, during the late wet season of 2024.

Site	N	Percentage sky area	Percentage canopy openness	LAI 4	LAI 5	Percentage t rans direct	Percentage trans diffuse
B. nervosa	33	99.88 (0.01)	14.68 (2.42)	2.11 (0.36)	2.10 (0.33)	25.84 (6.19)	21.05 (2.76)
Random	10	99.88 (0.01)	12.42 (1.82)	2.36 (0.42)	2.30 (0.36)	22.76 (2.88)	18.22 (1.92)

Values are means (± 1 SD) of 43 hemispherical photos taken at random sites and at sites occupied by *B. nervosa*.

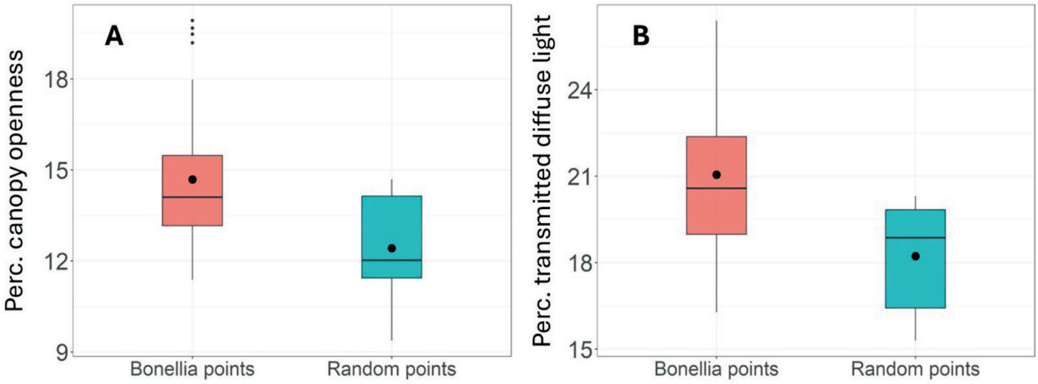

Fig. 2. Differences in light conditions between sites occupied by *Bonellia nervosa* and random sites in SRNP, Costa Rica. **A.** Percentage of canopy openness. **B.** Percentage of transmitted diffuse light.

Table 2
Correlation matrix of 7 canopy structure variables in the SRNP Forest in 2024 (n = 43 hemispherical photos).

	Percentage sky area	Percentage canopy openness	LAI 4	LAI 5	Percentage trans direct	Percentage trans diffuse
Percentage sky area	1					
Percentage canopy openness	0.17	1				
LAI 4	-0.15	-0.76	1			
LAI 5	-0.34	-0.71	**0.89**	1		
Percentage trans direct	-0.14	0.30	0.12	0.18	1	
Percentage trans diffuse	0.10	**0.89**	-0.50	-0.40	**0.59**	1
Percentage trans total	-0.06	**0.54**	-0.1	-0.009	**0.96**	**0.80**

Values represent Pearson correlation coefficients. Boldfaced values show significant correlations at p < 0.001. LAI = leaf area index at a zenith angle of 0°-60° -LAI 4-, and at 0°-75° -LAI 5-, Trans direct = transmitted direct light, Trans diffuse = transmitted diffuse light, Trans total = transmitted total light.

One-way ANOVA was used to test the hypothesis that *B. nervosa* prefers intermediate shade conditions and compared the sites where it was present relative to random sites where it was absent using these two components as response variables. PC1 scores (percentage canopy openness and percentage trans diffuse) were higher at *B. nervosa* sites (average = 0.42 ± 1.81) compared to random sites (average = -1.41 ± 1.38; $F_{1,41} = 8.68$, p = 0.005). There were no significant differences in PC2 scores (percentage of trans direct) between *B. nervosa* sites (average = 0.04 ± 1.61) and random sites (average = -0.12 ± 1.04; $F_{1,41} = 0.09$, p = 0.76; Fig. 2).

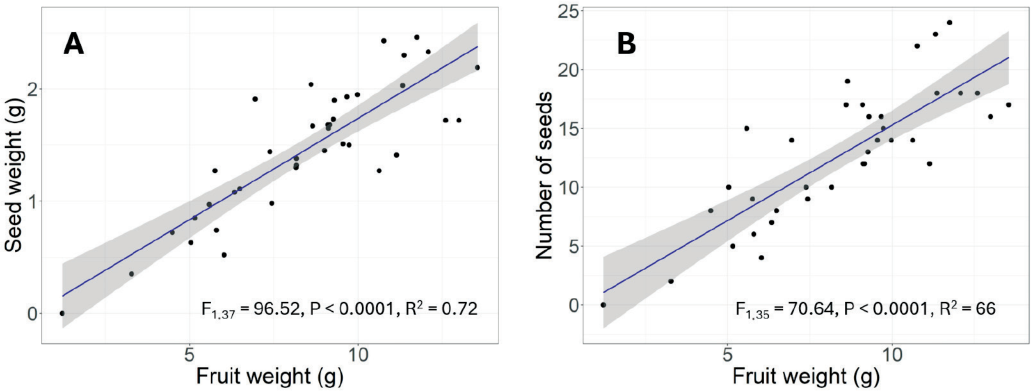

Fig. 3. A. Relationship between fruit weight and seed weight. **B.** Relationship between fruit weight and number of seeds in *B. nervosa*, SRNP, Costa Rica.

Table 3
Coefficients of the eigenvalues and eigenvectors of the PCA from seven variables obtained from the hemispherical photograph analysis in the *Indio Desnudo* trail, SRNP.

	Eigenvalue	Variation explained (%)
PC1	3.54	50.61
PC2	2.21	31.66
Cumulative variation		82.27
	PC1	**PC2**
Percentage sky area	0.109	-0.27
Percentage canopy openness	**0.50**	-0.11
LAI 4	-0.38	0.40
LAI 5	-0.35	0.46
Percentage trans direct	0.27	**0.54**
Percentage trans diffuse	**0.50**	0.14
Percentage trans total	0.38	0.46

Boldfaced values represent dominant loadings of the eigenvectors on each PC.

Predispersal fruit predation: There was a positive relationship between fruit weight, seed weight, and seed number (Fig. 3), indicating that larger fruits contain more and heavier seeds. Of the 39 fruits examined, six were infested by moth larvae from the Family Tortricidae (the only seed predator found), with one fruit having all its seeds consumed. The percentage of fruit predation was 15.38 %, although this likely fluctuated throughout fruit development since the last crop. Our observations were limited to fruits that remained until September, but many more were likely damaged earlier in the season.

DISCUSSION

The population structure, dominated by adults, suggests that seedlings are rare, likely due to multiple stressors. For instance, the high energy demand required to store reserves for surviving in the shade during the rainy season may increase seedling mortality. Additionally, seedlings are more susceptible to drought-induced mortality, including cavitation and hydraulic failure (Werden et al., 2023). Their small size further increases vulnerability to herbivory and pathogen damage, as they may be unable to regenerate tissue or compensate for losses effectively. In addition, seedlings are especially vulnerable to mechanical damage from falling branches. Competition with vines and other understory vegetation may further limit their survival. Our previous observations indicate that seedlings tend to aggregate around adult plants, consistent with the dispersion pattern typical of many tropical dry forest species (Hubbell, 1979), which may increase their exposure to herbivores and pathogens (Bhadouria et al., 2016). These combined pressures suggest that the seedling stage acts as a critical ecological filter influencing the habitat preferences of *B. nervosa*. Long-term, multi-season monitoring studies are necessary to accurately estimate seedling abundance and recruitment dynamics. A long-term population growth study, projected over several years, may be ambitious considering that *B. nervosa* appears to grow slowly. The Chapman-Richards model indicates an inflection point at approximately 70.6 cm in height, suggesting a transition from slow to even slower growth. We observed reproductive structures in an individual of 1.5 m in height, indicating that *B. nervosa* may begin reproducing at relatively small sizes and possibly early in its life cycle, which could shift resource allocation toward reproduction rather than growth and maintenance. Since leaves are produced only during the dry season, there may be minimal differences in leaf quality and function between seedlings and adults, although this hypothesis requires further investigation.

Bonellia nervosa is not an abundant species in the dry forests of SRNP. While it is capable of colonizing open areas such as forest edges (Janzen, 1970) and has occasionally been observed in pastures, it is more frequently found in old secondary forests within SRNP. Notably, it is absent from the park's only patch of primary forest, which remains evergreen during the dry season. This distribution suggests that *B. nervosa* prefers intermediate light conditions and avoids both the most open and the most shaded environments. This pattern was also supported by observations from A. Sánchez-Azofeifa, who did not find *B. nervosa* in forests younger than 50 years and found only three individuals in an 80-year-old plot, further indicating its affinity for late-successional stages (A. Sánchez-Azofeifa, personal communication, 2024). Our findings (five individuals/ha) are consistent with those of Glander and Nisbett (1996), who reported a very low density in Cañas, Costa Rica (0.06 individuals/ha). These observations suggest that *B. nervosa* may function as a late-successional species and a potential indicator of forest regeneration, especially in dry forest ecosystems where successional dynamics are slow and strongly shaped by water availability and disturbance regimes (Griscom & Ashton, 2011; Quesada et al., 2014). Its presence could therefore reflect structural and microclimatic conditions associated with more advanced stages of secondary succession.

A related species, *B. macrocarpa*, in Oaxaca, Mexico, was classified as a late-successional species by Romero et al. (2023). It typically occurs in tropical dry forests aged 50 to 70 years but has also been observed in early successional forests as young as two years old, but in low numbers. *Bonellia nervosa* employs a "long-lived pioneer" regeneration strategy, enabling it to associate with old secondary forests but limiting its abundance in early successional stages and primary tropical dry forests (Rüger et al., 2023).

Hemispherical photographs show that *B. nervosa* tends to occupy microsites with moderate canopy cover, suggesting a preference for intermediate light environments. The average canopy openness at sites where *B. nervosa* occurs was 14.16 %, with a LAI of 2.17. These values fall between those of cloud forests (Sylvester & Avalos, 2013) and mature lowland tropical rainforests, the latter typically exhibiting canopy openness below 10 % and LAI values approaching six (Bakar et al., 2023; Clark et al., 2008; Clark et al., 2021; Pfeifer et al., 2018). During the dry season, the mature forest patch at SRNP showed a canopy openness of 10.31 % and an LAI of 2.78 (pers. obs.). These values show that *B. nervosa* avoids dense shade and full exposure and is instead associated with intermediate light levels.

We consider our findings to be preliminary, highlighting the need for further research during the dry season, including a more through seedling census and a detailed comparison of leaf structure and function between seedlings and adults. The apparent restriction of *B. nervosa* to older secondary forests, and its absence from a broader range of habitats, suggests limited phenotypic plasticity in coping with environmental variation. This constraint may significantly affect the species' capacity to adapt to climate change. For instance, Sánchez et al. (2020) attempted to alter the species' leaf phenology through dry-season irrigation, but observed no significant changes, pointing to a potentially low level of genetic variation in response to water availability, although their results were inconclusive. The unique inverted phenology of *B. nervosa* underscores the need for further investigation into the physiological mechanisms determining its ecological strategy, particularly in the face of increasing climate variability (Schwinning & Kelly, 2013).

Bonellia nervosa shows a pulse in vegetative and reproductive growth during the dry season. The plant's energy reserves must support the production of a new canopy and the development of flowers and fruits. The fruits continue to expand and mature for at least five additional months during the rainy season, further depleting the plant's reserves. Additionally, the young leaves of *B. nervosa* are exposed to a relatively diverse array of herbivores during the dry season, which consume an average of 36.77 % of their area (Chaves & Avalos, 2007). While the fruit damage percentage observed in our study may seem low, the level of infestation by Tortricidae larvae should be monitored throughout the fruit's development. Adult moths likely lay their eggs in the immature ovaries, with the larvae developing as the fruit expands.

Chaves and Avalos (2008) reported that only 3 % of the flowers became fruits. This low reproductive success was associated with low levels of flower synchrony. *B. nervosa* is thought to be dispersed by rodents (Sumichrast's vesper rat, *Nyctomys sumichrasti*, Ceballos, 1990), as well as by the White-tailed deer, *Odocoileus virginianus*, Jara-Guerrero et al., 2018). During the 2024 dry season, white-faced monkeys (*Cebus imitator*) were also observed eating their ripe fruits in SRNP and in Taboga Forest Reserve, Guanacaste. Horses also have been seen eating *B. nervosa* fruits in SRNP (O. Chaves, personal communication, 2024). Possibly, there is no shortage of seed dispersers, but the species still shows low abundance.

Our study shows that *B. nervosa* has a population structure dominated by adults. Seedlings are scarce, likely because of the high energy demands for reserve accumulation, vulnerability to drought, and herbivory and mechanical damages. The species occurs in microsites with moderate canopy openness (~14 %), indicating a preference for intermediate light conditions and suggesting it functions as an indicator of late-successional forest stages. Its absence from very young and mature forests supports this interpretation. Although predispersal fruit predation was relatively low (~16 %), further monitoring is needed to assess fruit losses over the entire reproductive period. The species' slow growth, narrow habitat preferences, and distinctive reverse phenology point to limited phenotypic plasticity, justifying the need for long-term, multi-seasonal studies to better understand the recruitment dynamics and the resilience of this species to climate change.

Ethical statement: The authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgments section. A signed document has been filed in the journal archives.

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