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Temporal changes in the abundance of invasive plants in a tropical montane forest fragment of Costa Rica

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ABSTRACT

Introduction: Invasive plants can restructure forest understories by suppressing native regeneration, particularly in fragmented secondary forests. Understanding the population structure of potential invaders and their effects on native understory communities is essential for managing these ecosystems.

Objectives: To evaluate the population structure of two species with invasive potential, *Coffea arabica* and *Syzygium jambos*, and compare them with the increasingly abundant native species *Inga densiflora*, as well as quantify their effects on the abundance of understory plants in a 25 ha secondary montane forest fragment in Costa Rica's Central Valley over a period of 19 years.

Methods: All stems ≥ 30 cm tall were recorded across 70 plots of 4 m², totaling 809 individuals. The size distributions of the three focal species (*C. arabica*, *S. jambos*, and *I. densiflora*) were characterized, and model selection was based on the Akaike Information Criterion (AIC) to identify the best predictor of understory abundance. A negative binomial regression was selected to account for substantial overdispersion, using the abundance of each focal species and canopy cover as predictors. Sampling sufficiency was evaluated using cumulative abundance curves.

Results: Native understory species comprised 62.3 % of individuals, while *C. arabica*, *I. densiflora*, and *S. jambos* represented 9.0 %, 11.2 %, and 17.4 %, respectively. All three focal species exhibited populations dominated by seedlings and juveniles, with most individuals < 10 cm diameter and < 0.5 m height. Of the two invasive species, only *S. jambos* showed a significant effect on the understory community, exhibiting a modest but consistent negative association with understory plant abundance ($\beta = -0.046$, $p = 0.041$). Neither *C. arabica*, the native species *I. densiflora*, nor canopy cover had significant effects. Sampling curves stabilized after approximately 60 plots, indicating adequate sampling effort.

Conclusions: *S. jambos* was the most ecologically impactful of the three focal species, with the potential to suppress native recruitment as its population expands. These findings underscore the need for targeted management of *S. jambos* in fragmented secondary forests to prevent long-term degradation of understory diversity.

Key words: understory suppression; forest fragmentation; *Syzygium jambos*; secondary forests; invasion ecology.

RESUMEN

Cambios temporales en la abundancia de plantas invasoras en un fragmento de bosque tropical montano de Costa Rica.

Introducción: Las plantas invasoras pueden reestructurar el sotobosque al suprimir la regeneración nativa, particularmente en bosques secundarios fragmentados. Comprender la estructura poblacional de posibles



especies invasoras y sus efectos sobre las comunidades nativas del sotobosque es esencial para el manejo de estos ecosistemas.

Objetivo: Evaluar la estructura poblacional de dos especies con potencial invasor, *Coffea arabica* y *Syzygium jambos*, y compararlas con la especie nativa *Inga densiflora*, cuya abundancia ha aumentado, así como cuantificar sus efectos sobre la abundancia de plantas del sotobosque en un fragmento de bosque montano secundario de 25 ha en el Valle Central de Costa Rica durante un período de 19 años.

Métodos: Se registraron todos los individuos con una altura ≥ 30 cm en 70 parcelas de 4 m², para un total de 809 individuos. Se caracterizaron las distribuciones de tamaño de las tres especies focales (*C. arabica*, *S. jambos* e *I. densiflora*), y la selección de modelos se basó en el Criterio de Información de Akaike (AIC) para identificar el mejor predictor de la abundancia del sotobosque. Se seleccionó una regresión binomial negativa para considerar la marcada sobredispersión de los datos, utilizando como predictores la abundancia de cada especie focal y la cobertura del dosel. La suficiencia del muestreo se evaluó mediante curvas de acumulación de abundancia.

Resultados: Las especies nativas del sotobosque representaron el 62.3 % de los individuos, mientras que *C. arabica*, *I. densiflora* y *S. jambos* constituyeron el 9.0 %, 11.2 % y 17.4 %, respectivamente. Las tres especies focales mostraron poblaciones dominadas por plántulas y juveniles, con la mayoría de los individuos < 10 cm de diámetro y < de 0.5 m de altura. De las dos especies invasoras potenciales, solo *S. jambos* mostró un efecto significativo sobre la comunidad del sotobosque, presentando una asociación negativa, modesta pero consistente, con la abundancia de plantas del sotobosque ($\beta = -0.046$, $p = 0.041$). Ni *C. arabica*, ni la especie nativa *I. densiflora*, ni la cobertura del dosel tuvieron efectos significativos. Las curvas de muestreo se estabilizaron después de aproximadamente 60 parcelas, indicando un esfuerzo de muestreo adecuado.

Conclusiones: *S. jambos* fue la especie con mayor impacto ecológico entre las tres focales, con el potencial de suprimir la regeneración nativa conforme su población se expanda. Estos resultados resaltan la necesidad de un manejo dirigido de *S. jambos* en bosques secundarios fragmentados para prevenir la degradación a largo plazo de la diversidad del sotobosque.

Palabras clave: supresión del sotobosque; fragmentación del bosque; *Syzygium jambos*; bosques secundarios; ecología de invasiones.

INTRODUCTION

Invasive plants are opportunistic organisms capable of dominating a habitat and excluding the native flora (Blackburn et al., 2011; Hardy et al., 2025). The success of an invasive species, and the likelihood that an introduced plant becomes invasive, depends on both historical and biological factors (Gioria et al., 2023; Simberloff, 2015). Historical factors include the method and timing of introduction, habitat conditions at the time of establishment such as the presence of canopy gaps and trails (Joshi et al., 2015), and stochastic events including unintended introduction by humans (Simberloff, 2015). Biological factors involve the absence of effective natural controls such as herbivores, pathogens, or competitors, as well as the presence of functional traits in the invasive species favoring establishment, including, in the case of plants, shade tolerance, resistance to mechanical damage, and diverse

modes of sexual and vegetative reproduction (Bellard et al., 2016; Blackburn et al., 2011; Fine, 2002; Pyšek & Richardson, 2007). In addition, a broad spectrum of seed dispersers often facilitates their propagation across landscapes (Davies & Sheley, 2007).

Forest fragments provide favorable conditions for the establishment of invasive plants. These remnants represent only a limited subset of the original flora, often lacking the full range of ecological niches and environmental heterogeneity characteristic of continuous forests. If the reduced biotic and abiotic complexity of a fragment aligns with the ecological requirements of invasive species, a “perfect storm” may arise, promoting their proliferation. Such fragments often exist in a stationary phase of succession (Siqueira-Quirino et al., 2025), where canopy gaps and natural disturbances are rare, and native species colonization sources from nearby forests (i.e., seeds and dispersal agents) are limited. Under these conditions,

forest fragments are especially vulnerable to colonization and eventual dominance by invasive plants.

Many forest fragments of Costa Rica's Central Valley, particularly in the Western sector, originated from the abandonment of coffee farms and other agricultural lands (Avalos et al., 2006; Di Stefano et al., 1998). These secondary forests begin succession with a biased subset of the original vegetation, are strongly affected by edge effects, and are exposed to exotic species used in living fences or as shade trees in coffee plantations, which tend to persist in the regenerating forest, including coffee itself (*Coffea arabica*), which also persists in abandoned forests, becoming invasive in some cases (Joshi et al. 2009). Also, arbitrary decisions by farmers filter some species relative to others (Häger & Avalos, 2017). One such species is *Syzygium jambos* (Rosy Apple), introduced from South-east Asia as an ornamental living fence and fruit tree. *S. jambos* exhibits several traits typical of successful invaders, including shade tolerance (Fine, 2002), resistance to mechanical damage, vegetative propagation, and polyembryonic seeds that produce multiple propagules from a single fruit (Avalos et al., 2006; Di Stefano et al., 1998). Moreover, its fruits are consumed and dispersed by a wide array of birds and mammals. Rosy Apple has been erroneously favored as an option for reforestation since it establishes with relative ease under disturbed conditions and due to its capacity for vegetative propagation shows high survival (Avalos et al., 2021). However, this species is shade tolerant and sensitive to water stress and prospers only in areas where water is readily available (Brown, 2004).

The legume *Inga densiflora* is native to Costa Rica and is not recognized as invasive (Ley-López et al., 2016; Zamora & Pennington, 2001). It is commonly used as a shade tree in coffee plantations and valued for its fruits and firewood (Orozco-Cardona et al., 2013). When properly managed, it does not compete with coffee (Armbrecht et al., 2021). Nonetheless, its rising dominance in our study site, the Atenas Municipal Forest (AMF; Cambronero et al., in prep.), a regenerated forest fragment, suggests

that altered habitat conditions may be facilitating its dominance. Whether this trend reflects a shift toward this species eventually dominating the AMF remains an open question. *I. densiflora* is shade tolerant yet capable of persisting under open pasture conditions (Ley-López et al., 2016), and its seeds are dispersed by a broad array of frugivores; these traits could foster dominance within this forest fragment.

The objective of this study was to evaluate the population structure and abundance of *C. arabica* and *S. jambos* (two species with invasive potential) and the native species *I. densiflora*, as well as to quantify their effects on understory plant abundance in this forest fragment. I hypothesize that the humid conditions and high canopy cover of the AMF has favored an increase in the density of *S. jambos* since the study by Avalos et al., (2006), and that the combined density of these three focal species negatively affects the abundance of other understory plants. Temporal studies in tropical forest fragments are exceedingly rare, and this dataset provides a unique opportunity to compare changes in the abundance of two invasive species over a 19-year period. Understanding whether forest fragments maintain a dynamic equilibrium with respect to invasive plants is crucial for elucidating the population dynamics of invaders and their long-term effects on the native flora. Results of this study are relevant to improving the management of isolated forest fragments surrounded by agricultural lands.

MATERIALS AND METHODS

Site description: The study was conducted in September 2025 at the AMF, Alajuela, Costa Rica (9°58'26" N & 84°26'19" W; 1 300 m.a.s.l.). The area is characterized by a strong seasonality. During the rainy season (May–November), mean annual precipitation averages 3 000 mm. The dry season (December–April) is characterized by no precipitations to the point that some seasonal streams dry up (Cambronero et al., 2023). AMF is a 26.4 ha fragment of tropical premontane moist forest, that forms part of the Montes del Aguacate Biological Corridor.



This forest represents a late-successional stand that has regenerated for approximately 40 years after being used as a shaded coffee plantation (Avalos et al., 2006). Only 7.8 % of its perimeter is directly connected to other forest patches, while 56.5 % borders shaded coffee plantations. The remaining boundary borders Highway 3 (Avalos et al., 2006; Cambronero et al., 2023). AMF harbors about 119 tree species, with *I. densiflora* and *S. jambos* being some of the most abundant. This forest fragment harbors up to 19 species of medium- and large-sized mammals, including felids such as *Puma concolor*, *Herpailurus yagouaroundi*, and *Leopardus pardalis* (Cambronero et al., 2023).

Study species: *S. jambos* (rose apple) is native to Southeast Asia. It was introduced to Costa Rica by the late 19th century (Morales, 2020) and is now widely cultivated as an ornamental and shade tree in mid-elevation areas, often associated to coffee plantations. It has become an invasive species that reproduces readily in secondary and naturally regenerated forests, tolerating both open and shaded conditions. It has been used as a living fence to delimit the borders among coffee plantations, where it certainly can invade neighboring forest due to their shade tolerance capacity (Avalos et al., 2006). Its fruits are dispersed by a wide variety of seed dispersers, and because of its abundant regeneration, several authors recommend its eradication from protected areas. *C. arabica* L. (Rubiaceae) is native to the mountainous regions of the Southwestern highlands of Ethiopia, with natural populations also found in Southeastern Sudan (Boma Plateau) and Northern Kenya (Mount Marsabit). It is widely cultivated across many countries within the “Bean Belt” region between 25° N and 30° S latitude. *C. arabica* typically grows as a shrub or small tree, reaching 1.5 to 3 m in height, and prefers humid, montane environments at altitudes ranging from about 950 to 1 950 m.a.s.l. It thrives in tropical and subtropical climates with well-distributed rainfall and defined dry seasons. The species is generally grown as an understory shrub in its native forest habitats

but has also become naturalized in various parts of the world (Ovalle-Rivera et al., 2015). *I. densiflora* Benth. (Fabaceae) is distributed from Southeastern Mexico to Northern and Western South America. This species has great potential for forest restoration if managed correctly due to its fast growth, nitrogen fixing capacity, and plasticity to adapt to different light regimes (Ley-López et al., 2016).

Understory vegetation survey: Seventy 2×2 m plots were established along trails covering most of the AMF, spaced 10 m apart and positioned 2 m inward from the trail edge, alternating between the right and left sides. We kept the same plot size and shape of the Avalos et al. (2006) study. The plots were distributed across seven widely spaced areas within the AMF, with ten plots per area to capture the spatial heterogeneity of the site. Within each plot, the frequency of woody plants ≥ 30 cm in height was recorded in four categories: *S. jambos*, *C. arabica*, *I. densiflora*, and other understory species.

Description of population structure: Population structure was recorded by measuring the height of the three focal species, from the base of the stem to the highest apex. Stem diameter was measured at three-quarters of the total height for individuals < 1.5 m, and at 1.5 m above the ground for taller individuals. For plants classified as other understory species, only their frequency was recorded.

Measurement of canopy cover: Canopy cover was measured using a concave spherical densiometer model C (Forestry Suppliers), which provided a percentage estimate of canopy closure from the center of each plot facing North. The procedure followed Strickler (1959), which quantifies the proportion of canopy cover reflected in a concave mirror etched with a grid consisting of 24 squares, each divided into four equidistant points for a total of 96 points. The number of points not covered by foliage was counted, subtracted from the

total, and multiplied by 1.04 to estimate the percentage of forest canopy cover.

Evaluation of sampling effort and stability of abundance estimates: I used a permutation-based resampling procedure to evaluate the stability of cumulative abundance estimates for plant species across sampled plots. I randomized the order of plots 500 times and recalculated the cumulative mean abundance each time and generated a distribution of possible abundance trajectories that reflect variability due to sampling order and spatial heterogeneity. This corresponded to the precision and reliability of the abundance estimates to determine if the sampling effort was sufficient and if abundance estimates stabilize as more plots were added.

Then, I applied a permutation analysis to evaluate whether the number of sampled plots was sufficient to estimate the cumulative abundances of *C. arabica*, *S. jambos* and *I. densiflora*. If the cumulative means and their 95 % confidence intervals stabilized as sample size increased, this indicated that the number of plots was adequate to capture the frequency and distribution (and thus, the density) of these species in the AMF. In contrast, if there was wide uncertainty even at the maximum number of plots, it may indicate that a larger sample size was necessary to achieve representative estimates.

Statistical analysis and negative binomial regression: I used a negative binomial regression (library lme4 in R) to determine how the abundance of *C. arabica*, *S. jambos* and *I. densiflora* affected the abundance of other understory plants within the plots. The model included canopy cover as a fixed effect. I selected negative

binomial regression because the count data for other understory plants exhibited strong overdispersion (dispersion parameter = 4.57). All statistical analyses were conducted using R software (R Core Team, 2024).

RESULTS

Abundance and population structure: I found 809 plants ≥ 30 cm in 70 plots. Of these, 62.3 % were understory species other than the focal species, while 17.4 % were *S. jambos*, 11.2 % were *I. densiflora*, and 9.0 % were *C. arabica*. The population structure of the three focal species was dominated by seedlings since the vast majority had diameters below 10 cm (Fig. 1A), and heights below 0.5 m (Fig. 1B). Only a few individuals of *I. densiflora* reached the canopy (30 m).

After 60 plots, the average cumulative abundance values for the three focal species showed narrow uncertainty ribbons, indicating sufficient sampling effort for robust estimates of abundance (Fig. 2). The average number of *S. jambos* plants per plot (2.01 ± 3.73) was nearly double that of *I. densiflora* (1.30 ± 1.46) and *C. arabica* (1.04 ± 2.22).

Negative binomial regression: The negative binomial model was preferred to both the Poisson and zero-inflated alternatives based on the AICc criterion (Table 1) and was consistent with the observed overdispersion (4.57). The negative binomial model was chosen to explain the variation in the abundance of other understory plants using the categorical effects of *C. arabica*, *I. densiflora*, *S. jambos*, and canopy cover. The model showed that only *S. jambos* had a statistically significant effect on

Table 1

Summary of results comparing Negative Binomial, Zero-Inflated Negative Binomial, and Poisson models to account for the effects of *C. arabica*, *I. densiflora*, and *S. jambos*, and canopy cover, on the abundance of understory plants.

Model	logLik	AICc	Δ AICc	Weight
Negative Binomial	-194.97	403.3	0	0.775
Zero-inflated Negative Binomial	-194.97	405.7	2.47	0.225
Poisson	-215.85	442.6	39.36	0

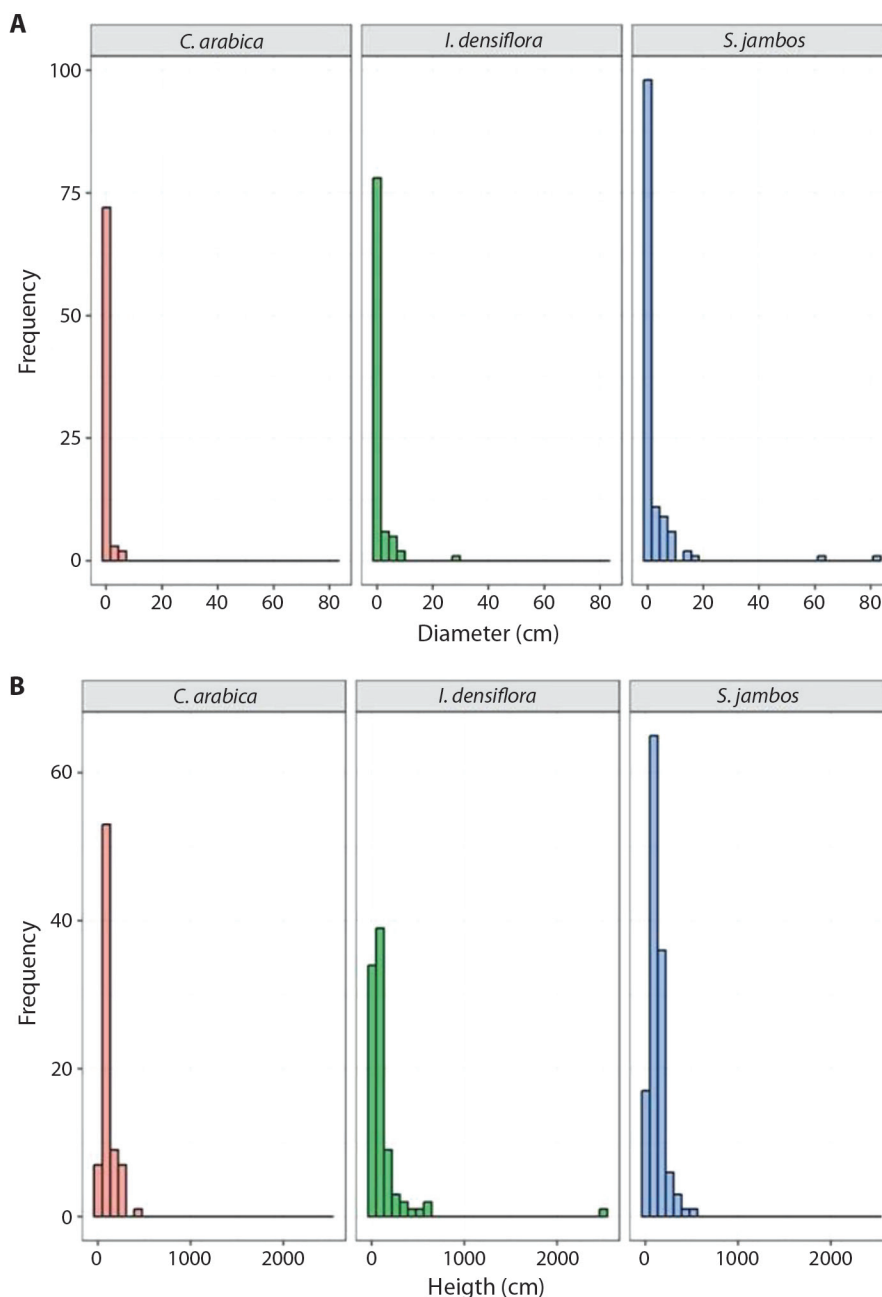


Fig. 1. (A) Diameter and (B) height distribution for *C. arabica*, *I. densiflora* and *S. jambos* at the AMF.

the abundance of other understory plants. The effect of *S. jambos* abundance was small but showed a negative impact on the abundance of understory plants ($\beta = -0.046$, $p = 0.041$,

Table 2). The increased abundance of *S. jambos* reduced slightly the density of co-occurring understory plants. In contrast, neither *C. arabica* nor *I. densiflora* showed significant

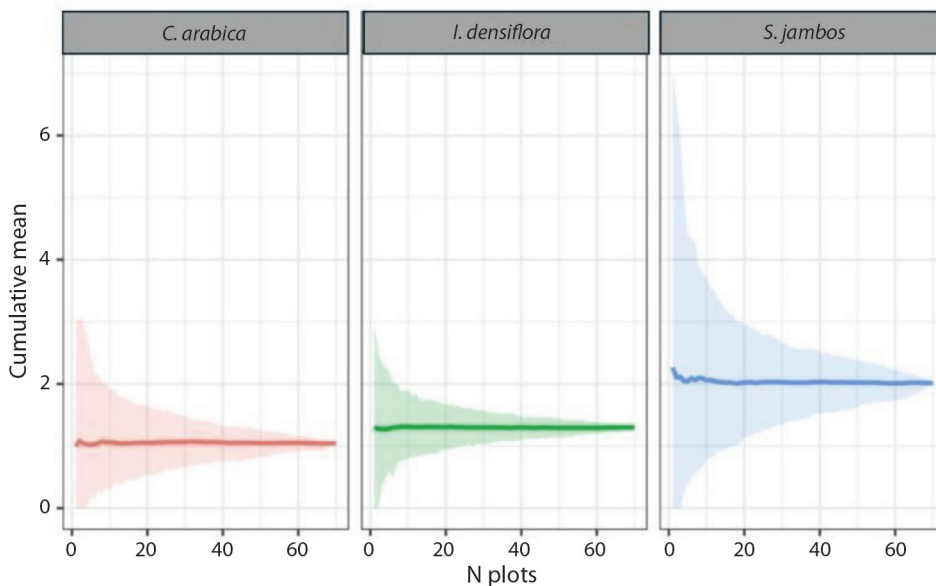


Fig. 2. Stability of cumulative abundance for *C. arabica*, *I. densiflora* and *S. jambos* vs. sampling effort (N plots of 4 m²) at the AMF. The ribbons around the means correspond to 95 % CI.

Table 2

Parameter estimates from the negative binomial model evaluating the effects of *S. jambos*, *C. arabica*, *I. densiflora*, and canopy cover on the abundance of other understory plants.

Predictor	Estimate	Std. Error	z-value	p-value
Intercept	2.83	0.88	3.20	0.0014
<i>S. jambos</i>	−0.046	0.022	−2.04	0.041
<i>C. arabica</i>	−0.013	0.034	−0.39	0.69
<i>I. densiflora</i>	−0.042	0.053	−0.78	0.42
Canopy cover	−0.0081	0.01	−0.81	0.41

effects on the frequency of other understory plants. Similarly, canopy cover did not show significant effects.

Variation in canopy cover: The AMF had a high value of canopy cover (mean = 89.05 ± 7.56 %). Half of the values were above 90 % of canopy cover. Although I observed some fallen trees and canopy gaps, the lowest canopy cover reached 70 % which is still high. Due to this narrow variation, canopy cover did not influence the abundance of understory plants.

DISCUSSION

Among the three focal species (*C. arabica*, *I. densiflora*, and *S. jambos*) only *S. jambos* had a significant, although small effect on the abundance of co-occurring understory plants, making my hypothesis partially correct since *S. jambos* did not increase its abundance since the Avalos et al. (2006) study, but still influenced the density of understory plants. This pattern is consistent with reports from other tropical forests where *S. jambos* forms



dense sapling banks that competitively displace native species through rapid growth and heavy shade production (Di Stefano et al., 1998). The lack of significant effects for *C. arabica* and *I. densiflora* suggests that these species, at the densities observed in our plots, may not yet exert strong competitive pressure on the broader understory community. These results showed a decrease in density of *S. jambos* over 19 years (17.42 % down from 51.1 %, Avalos et al., 2006) and are consistent with the value of 13.3 % out of 494 sampled plants reported by Cambronero et al., (in prep.).

S. jambos is native to the Indo-Malaysian Archipelago, was introduced first to the Americas through Jamaica in 1762 and later spread throughout the Neotropics as an ornamental and fruit tree. In Costa Rica's Central Valley, it likely escaped from coffee plantations where it was planted as a living fence. Its invasive success stems from traits such as shade tolerance, resistance to herbivory and mechanical damage, polyembryonic seeds, and wide dispersal by animals (Avalos et al., 2021; Di Stefano et al., 1998). Although farmers value it for soil stabilization and reforestation, its often aggressive spread and limited economic value make it a serious invasive species not suitable for reforestation efforts of native forests (Avalos et al., 2021). This species is sensitive to water stress, and the AMF provides an appropriate refuge since the area is a source of potable water for neighboring communities and thus maintains a relatively superficial water table. During periods of heavy rainfall, I have observed groundwater emerging naturally at the AMF, indicating a shallow water table. Di Stefano et al., (1998) observed slow growth, greater seedling concentration around the parent plants, and greater seedling mortality. In Puerto Rico, *S. jambos* can form monospecific forest stands and is considered to be a weed (Aide et al., 1996). Despite its long-term persistence in the AMF, the density of *S. jambos* appears to remain limited, suggesting that factors such as the disturbance regime, canopy gap dynamics, and competition with other species may contribute to keeping its populations in check.

The decline in abundance of *S. jambos* and *C. arabica* relative to the Avalos et al. (2006) study may be caused by the combination of several factors. Increasing canopy closure and the scarcity of canopy gaps likely limit the transition of seedlings into larger size classes, creating a demographic bottleneck despite continued recruitment. Avalos et al. (2006) already notes that *S. jambos* seedlings were common, but adults were rare, implying a strong limitation in progression to larger size classes. In addition, competition with native vegetation, density-dependent mortality, and reduced propagule pressure may contribute to constraining population expansion. These patterns are consistent with successional changes in mature secondary forests, where environmental conditions along the successional gradient determine the expansion of some invasive understory species (Dechoum et al., 2015). Consequently, the observed abundance decline does not necessarily indicate a lack of recruitment, but rather a limitation in recruitment success beyond the earliest life stages.

The case of *I. densiflora* is particularly relevant, being a native species. Its current representation in the community (11.24 % of plants sampled) remains relatively modest. Native species can, under certain circumstances, behave opportunistically and dominate a habitat if conditions strongly favor their establishment and expansion (Valéry et al., 2008). However, *I. densiflora* has generally been recommended as a suitable species for restoring disturbed forests (Ley-López et al., 2016) due to its physiological plasticity and high seedling survival. Legumes are also very successful in the first stages of regeneration due to their nitrogen fixing capacity and higher water use efficiency (Gei et al., 2018). Although its abundance has increased, the species still represents a small fraction of the community and shows no evidence of becoming a dominant component of the forest.

C. arabica persists mainly in regenerated forests after abandoned coffee plantations or in regenerating native forests adjacent to former coffee farms. Under deep shade conditions, *C.*

arabica's architecture changes relative to plants in a plantation: the internodes elongate, plants become taller, more slender and less branched, and reproductive output declines (pers. obs.). Although *C. arabica* can behave as an aggressive invasive species elsewhere (Joshi et al., 2009; Raymundo et al., 2018), in the AMF it appears capable of persisting but not proliferating and, therefore, it does not appear to impact understory natives.

The lack of significant effects of canopy cover on understory plant abundance contrasts with the expectation that light availability structures understory communities (Bohman, 2015). The canopy cover variation observed at the AMF might not capture the fine-scale light environment experienced by understory plants. Nonetheless, Avalos et al., (2006) reported a consistently high average canopy cover of 77 %. This stable canopy cover over the years further supports the notion that *S. jambos* and *C. arabica* are suppressed in the understory and unable to acquire sufficient resources to transition into reproductive stage.

The cumulative abundance curves demonstrate that our sampling effort was sufficient to characterize both invasive and non-invasive understory components reliably. The stabilization of estimates after approximately sixty 4 m² plots suggest adequate spatial coverage and lends confidence to our conclusions regarding species interactions and community patterns.

S. jambos is the most ecologically disruptive of the three species examined, with detectable negative impacts on native understory abundance even at relatively low densities. In contrast, *I. densiflora* and *C. arabica* appear to be less influential considering their current population structure. Given the strong representation of seedlings and juveniles across focal species, continued monitoring is essential to detect potential future shifts in competitive dynamics, particularly as these populations mature.

Recommendations and future research:

The AMF lacks a management plan. There is a lack of clarity regarding its role beyond being

an area of water generation for neighboring communities. However, it is a refuge for small to medium-sized communities of mammals (Cambronero et al., 2023) and very likely for other faunistic and floristic components. If a management plan is implemented, it should be multipurpose. The AMF also has potential as a recreational area and has an extensive system of trails. Enrichment planting of native trees could help the forest to maintain a high level of species diversity, increase its capacity to provide ecosystem services, become a reservoir of genetic diversity and a healthy recreational resource. To achieve these goals, it will be fundamental to continue the monitoring of invasive species.

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