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Spread of invasive ginger *Zingiber spectabile* (Zingiberaceae) in successional and old-growth tropical forest

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ABSTRACT

Introduction: *Zingiber spectabile*, a shade-tolerant ornamental ginger native to Southeast Asia, is invading tropical wet forest understories in Central America. This shade-tolerant species is of concern, yet no ecological impact or management assessment exists.

Objective: To examine the invasion patterns of *Z. spectabile* in primary and secondary forests, reproductive capacity, effects on understory vegetation, and the effectiveness of control efforts.

Methods: Field trials were conducted in 30-year-old secondary forest and in primary forest remnants in Southern Costa Rica that were invaded by *Z. spectabile*, which was introduced to the region in the early 1990s. Control efforts consisted of aboveground biomass removal and herbicide application to rhizomes.

Results: Both primary and secondary forests showed substantial invasion, but stem and inflorescence densities and aboveground biomass were three-fold higher in secondary forests, suggesting that secondary forests are more susceptible to invasion. *Z. spectabile* exhibited high reproductive capacity via prolific nodal sprouting (all cut stems producing 5.8 ± 0.3 rooted sprouts); inflorescences produced 64.3 ± 7.9 seeds each, yielding approximately 104 717 to 312 314 seeds/ha across invaded sites. Seed germination rates were similarly high in primary (58 %) and secondary (47 %) forests but lower in pasture (3 %). With one year of control efforts, *Z. spectabile* reinvaded, regaining over 35 % of aboveground biomass. During the first year following control, native herbaceous plant density increased by 61.5 % in secondary forest; there were no significant responses of woody seedlings or saplings in either forest type.

Conclusions: These findings suggest that *Z. spectabile* invasion affects some components of understory plant communities, especially in secondary forests, and underscores the need for longer-term studies of invasion impacts and understory responses to control. Given the labor-intensive nature of biomass removal and the limited effectiveness of herbicides, improved and scalable management strategies are urgently needed.

Key words: non-native plant invasion; forest degradation; Costa Rica; tropical forest succession; ginger; forest fragmentation.

RESUMEN

Expansión del jengibre invasor *Zingiber spectabile* (Zingiberaceae) en bosques tropicales en sucesión y primarios

Introducción: *Zingiber spectabile*, un jengibre ornamental tolerante a la sombra y nativo del sudeste Asiático está invadiendo el sotobosque de bosques tropicales húmedos en Centroamérica. Esta especie es preocupante, pero no existen evaluaciones de impacto ecológico ni de manejo.

Objetivo: Examinar los patrones de invasión de *Z. spectabile* en bosques primarios y secundarios, su capacidad reproductiva, los efectos sobre la vegetación del sotobosque y la eficacia de los esfuerzos de control.

Métodos: Los ensayos de campo se realizaron en bosque secundario de 30 años y en remanentes de bosque primario en el sur de Costa Rica que estaban invadidos por *Z. spectabile*, introducida en la región a inicios de la década de 1990. Los esfuerzos de control consistieron en la remoción de biomasa aérea y la aplicación de herbicida a los rizomas.

Resultados: Tanto el bosque primario como el secundario mostraron una invasión sustancial, pero las densidades de tallos e inflorescencias y la biomasa aérea fueron más de tres veces mayores en el bosque secundario, lo que sugiere mayor susceptibilidad a la invasión. *Z. spectabile* mostró alta capacidad reproductiva mediante abundante brotación nodal (todos los tallos cortados produjeron 5.8 ± 0.3 brotes enraizados); las inflorescencias produjeron 64.3 ± 7.9 semillas cada una, generando aproximadamente entre 104 717 y 312 314 semillas/ha en los sitios invadidos. Las tasas de germinación fueron similares en bosque primario (58 %) y secundario (47 %), pero menores en potrero (3 %). Después de un año de control, *Z. spectabile* reinvadió, recuperando más del 35 % de la biomasa aérea. Durante el primer año posterior al control, la densidad de hierbas nativas aumentó 61.5 % en bosque secundario, sin respuestas significativas de plántulas leñosas en ninguno de los dos tipos de bosque.

Conclusiones: Estos resultados indican que la invasión de *Z. spectabile* afecta algunos componentes de las comunidades del sotobosque, especialmente en bosques secundarios, y resaltan la necesidad de estudios a más largo plazo sobre los impactos de la invasión y las respuestas al control. Dada la naturaleza laboriosa de la remoción de biomasa y la eficacia limitada de los herbicidas, se requieren estrategias de manejo mejoradas y escalables.

Palabras clave: invasión de plantas no nativas; degradación forestal; Costa Rica; sucesión de bosques tropicales; jengibre; fragmentación forestal.

INTRODUCTION

The global spread of nonnative invasive plant species is accelerating due to climate change, land-use shifts, international trade, and biodiversity loss, all of which degrade habitats and increase their susceptibility to invasion (Bradley et al., 2010; Hoang & Kanemoto, 2021; Seebens et al., 2021). These challenges are especially acute in developing regions, where data are sparse and capacity for monitoring and management remains limited (Pires-Adelino et al., 2021; Rojas-Sandoval et al., 2023). Tropical forests in Latin America are particularly understudied compared to temperate and island systems, where invasive species inventories and management receive more attention and resources (Chong et al., 2021; Pyšek et al., 2020). This disparity has reinforced the perception that tropical forests are more resistant to invasion due to high species diversity and structural complexity (Chong et al., 2021; Lonsdale, 1999). However, recent assessments in Central America have documented a striking diversity of nonnative invasive plant species now spreading across all major habitat types (Avalos et al., 2021; Chacón-Madrigal et al., 2022; López, 2012). Over 80 % of these species were intentionally introduced, primarily for horticulture, forestry, and agriculture (Pagad et al., 2018; Galán et al., 2021; Rojas-Sandoval & Ackerman, 2021). Of particular concern is the near-total lack of information on ecological impacts and management strategies for most species now established across this region (Chacón-Madrigal et al., 2022; Chacón-Madrigal & Rojas-Rojas, 2021).

To date, the nonnative plant species of greatest concern for both forest restoration and forestry activities in Central America have

been African pasture grasses and ruderal forbs (Padmanaba & Corlett, 2014; Rojas-Sandoval et al., 2023). These light-demanding species rarely establish in forest understories, and forest recovery—through natural succession or assisted restoration—generally assumed to results in their suppression via increasing canopy cover (Cava et al., 2018; Holl et al., 2000). However, this strategy is ineffective against shade-tolerant exotic species, which are increasingly invading closed-canopy forests worldwide (Martin et al., 2009). The presence of shade-tolerant exotic species represents a growing management challenge, particularly in the understudied but highly biodiverse forests of Central America. Given the lack of targeted research and context-specific strategies, the ecological consequences of these species may go unnoticed until impacts on regeneration, species composition, and forest resilience are well underway (Constantz et al., 2025).

Among the shade-tolerant species that have been flagged as being of particular concern in Central America is *Zingiber spectabile* (Griff.), also called beehive ginger, shampoo ginger, or maraca (Avalos et al., 2021; Chacón-Madrigal & Rojas-Rojas, 2021). No ecological impact or management assessment for this species currently exists. Native to Malaysia, *Z. spectabile* is a perennial herb widely cultivated for its spectacular inflorescence, hardiness, and popularity in cut flower arrangements and landscape (Nery et al., 2015; Palupi et al., 2019). Widespread introduction via the horticulture industry coupled with minimal biosecurity protocols for ornamental plants provides a broad pathway for invasions (Rojas-Sandoval & Ackerman 2021). Though existing studies of its reproductive biology focus on its ornamental use (Nery et al., 2015; Ferreira-Rezende et al., 2021), the species exhibits traits common among highly invasive plants (Lowe et al., 2000), including prolific clonal and sexual reproduction and attractiveness to generalist pollinators and seed dispersers (Arumugam et al., 2021) (Fig. 1A, Fig. 1B, Fig. 1C, Fig. 1D). It has rapidly colonized the understory of both successional and primary tropical wet forests, spreading from botanical gardens and agricultural stations in Costa Rica (Chacón-Madrigal, 2009; Organization for Tropical Studies, 2012), as well as in forested areas of El Salvador and Honduras (Chacón-Madrigal et al., 2022) (Fig. 1A).

The spread of *Z. spectabile* is especially concerning given the well-documented impacts of related shade-tolerant ginger species in other tropical regions. For example, *Hedychium gardnerianum* (kahili ginger) has been shown to dominate understories, suppress native species, and inhibit regeneration in Hawaii (Minden et al., 2010), New Zealand (Byrne, 1992), Cuba (Oviedo-Prieto et al., 2012), and Zimbabwe (Chikowore et al., 2023). *Z. spectabile* may exert similar effects through competition with native herbaceous plants and young woody seedlings which are critical to forest succession. These risks are especially important given that herbaceous plants comprise up to 40 % of vascular species in tropical forests (Costa et al., 2005) and understory communities are key to regeneration and other ecosystem functions (Deng et al., 2023). Because both herbaceous plants and woody seedlings and saplings are most vulnerable to stress during early development (Deng et al., 2023; Ribbens et al., 1994), invasive species in the understory may significantly affect forest resilience and patterns of succession. This is of particular concern given that regrowing forests make up a third of the Neotropical forest area (Chazdon et al., 2016).

This paper provides the first baseline information on the invasion patterns, reproductive traits, and potential ecological impacts of *Z. spectabile* in successional and old-growth forests within a typical fragmented landscape in Costa Rica. Specifically, we conducted field experiments to: (1) compare invasion levels between secondary and old-growth forests, (2) measure *Z. spectabile* reproductive capacity in situ, and (3) assess how invasion affects germination, survival, and growth of native tree seedlings. Current management strategies rely on annual cutting of above-ground biomass and/or manually excavating and deeply burying all plant biomass-approaches considered prohibitively labor-intensive and costly by local

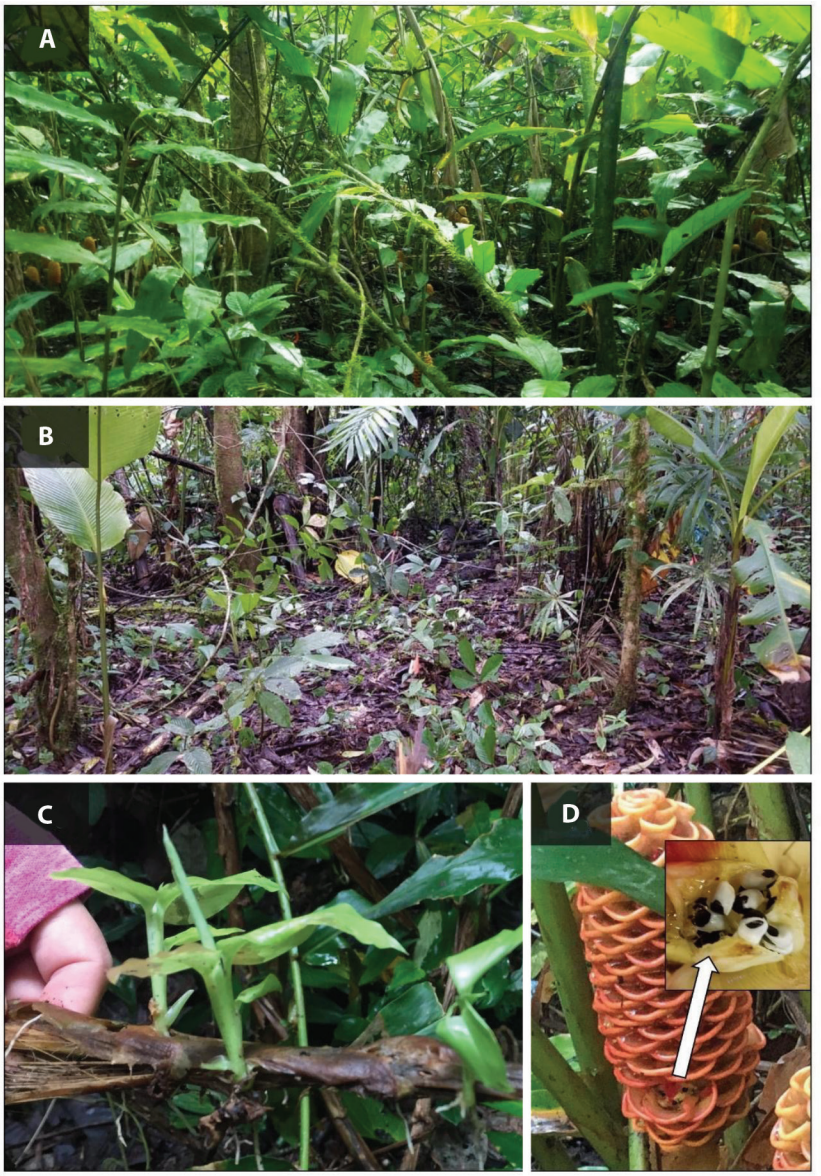

Fig. 1. A. Heavily invaded secondary forest experimental plot with understory dominated by *Z. spectabile*. **B.** Experimental plot following removal of above-ground biomass of *Z. spectabile* and application of herbicide to rhizomes. **C.** Clonal sprouting from cut stem placed on forest floor. **D.** Mature inflorescence with seeds visible in basal bracts (expanded view in inset photo). Photo credit CJ Pardo Dewald.

land managers (R. Quirós, D. Cole, and O. Vargas, pers. comm.). We therefore tested an alternative control method, involving aboveground biomass removal followed by a standard chemical treatment for rhizomatous plants, to (4) evaluate its effectiveness, and (5) measure understory vegetation responses to this management approach.

MATERIALS AND METHODS

Study sites and introduction of *Z. spectabile*: The study was conducted at two conservation focused research sites, Loma Linda Field Station (LLFS) (8°44'08.2" N & 82°55'24.8" W), and Las Cruces Biological Station (LCBS), 8°47'7" N & 82°57'32" W) in Coto Brus county, Southern Costa Rica. The LLFS study site includes a ~ 30 ha primary forest and immediately adjacent ~ 16 ha secondary forest (30-year-old), while LCBS protects ~ 200 ha of old-growth forest along with other areas under various stages of recovery. These forests are typical of fragmented landscapes in Central America and are surrounded by a mosaic of mixed-use agricultural land (Zahawi et al., 2015). The region hosts tropical premontane rain forest (Holdridge et al., 1971), from 1 100-1 340 m.a.s.l., with 3 500–4 000 mm annual rainfall.

Study sites were selected based on known introduction histories and ongoing spread (Organization for Tropical Studies, 2012). *Z. spectabile* was introduced in the early 1990s as an ornamental plant, supplied by the founders of the Wilson Botanical Garden, which is located immediately adjacent to the forest reserve of LCBS. *Z. spectabile* was introduced at about the same time (early 1990s) at LLFS, where it was planted along the edges of primary and secondary forests (D. Cole pers comm). It was first observed growing in remnant forests at LLFS and LCBS in the early 2000s (R. Quiros and D. Cole pers comm) and has since been noted to have invaded forests across several adjoining counties in Southern Costa Rica (Organization for Tropical Studies, 2012).

Species overview: *Z. spectabile* is a perennial herbaceous plant species that spreads through underground rhizomes, from which it produces tall, upright pseudostems (tightly packed overlapping leaf bases) that can reach 1-4.5 m length. Nodes along the pseudostems where leaf sheaths originate provide growth zones that can bear new shoots and adventitious roots. The inflorescence is a cylindrical spike up to 30 cm long, composed of overlapping waxy bracts. *Z. spectabile* exhibits nocturnal anthesis, with flowers opening at night and lasting approximately 24 hours (Palupi et al., 2019). Following successful pollination, *Z. spectabile* produces capsule-shaped fruits containing seeds that ripen over several months (Ferreira-Rezende et al., 2021) (Fig. 1A, Fig. 1C, Fig. 1D). Existing studies (Arumugam et al., 2021) and local observations show that the flowers and fruits are visited by a wide variety of generalist insects and birds.

Patterns of invasion and reproduction: In June 2017, we conducted a preliminary survey at LLFS to assess patterns of *Z. spectabile* invasion and reproduction. Because the species was introduced simultaneously along the edges of both primary and secondary forests, which are immediately adjacent to each other, we were able to directly compare invasion levels between forest types. We established 14 paired 100 m^2 circular plots along transects in each forest type (n = 7 per type) to minimize potential environmental variation between sites. As it is not possible to distinguish individual plants from their aboveground foliage in heavily invaded areas, we used leaf-bearing pseudostems (hereafter referred to as stems) as the unit of *Z. spectabile* density. Within each plot, we counted all stems ≥ 1 m tall as well as all inflorescences.

To evaluate vegetative reproduction via sprouting from nodal segments—which can occur after manual stem cutting, a common management practice in the region—we collected 20 fully developed stems 1.0-1.5 m in length (mean 14.5 nodes per stem, range 10-18) from separate plant clusters and placed them randomly on the forest floor within a 20 × 20 m area with intermediate canopy cover (65-80 %). We recorded all occurrences of nodal sprouting every two weeks for a six-month period, after which all stems had stopped sprouting and were nearly completely decomposed.

To assess sexual reproduction via seeds, we collected 10 mature inflorescences from 10 randomly selected individuals and counted all visible mature and immature seeds. To evaluate

the potential for seed germination across different habitat types, we placed a total of 300 mature seeds in batches of 10 in 10 separate seed depots spaced evenly along 100 m transects in each of three habitats: secondary forest, primary forest, and nearby pasture that was recently fallowed and dominated by nonnative pasture grasses, primarily *Urochloa brizantha* (A.Rich.) R.Webster (n = 10 depots per habitat). Seed depots were covered with 2.5 mm wire mesh to prevent removal by insects or rodents (average seed size is approximately 6 × 3.5 mm). We monitored seed survival and germination twice monthly for six months, recording seeds as germinated or dead (i.e., visibly damaged or decomposed).

Effects of invasion on tree seedling germination, survival, and growth: To evaluate the effects of *Z. spectabile* invasion on native tree seedling establishment, we conducted a one-year experiment beginning in May 2022. Five 20 × 20 m blocks were established in closed-canopy primary forest at both LLFS and LCBS, for a total of 10 blocks. Blocks were spaced at least 60 m apart. Within each block, three 3 × 3 m plots were designated to represent different invasion conditions: (1) no *Z. spectabile* present ("not invaded"), (2) *Z. spectabile* present ("invaded"), and (3) *Z. spectabile* present with all aboveground biomass manually removed ("removal"). Invaded and removal plots were established in areas with as similar levels of *Z. spectabile* stem density as possible (9.8 to 15.3 mean stems m^{-2}). In removal plots, no herbicides were used: all aboveground biomass was clipped and removed at the start of the study, and regrowth was cleared periodically. Non-invaded plots were located in areas without *Z. spectabile* when possible, although in several cases, it was necessary to remove a few *Z. spectabile* stems at the start of the study.

We used four late-successional native tree species differing in seed size: *Otoba novogranatensis* Moldenke, *Pseudolmedia glabrata* (Liebm.) C.C. Berg, *Lacistema aggregatum* (P.J. Bergius) Rusby, and *Erythroxylum macrophyllum* Cav. Species were selected based on (i) sufficient seed availability at the start of the study, (ii) their common dispersal into forest restoration sites, and (iii) their regional abundance. Seeds were collected from at least three parent trees per species and tested for viability using a float test. Depending on seed availability, 16-24 seeds per species were sown in each plot in a grid pattern. Germination and seedling survival were monitored bimonthly, and final seedling height was measured after one year.

Effects of management intervention on *Z. spectabile* and understory vegetation: Beginning in June 2019, we conducted a one-year study to assess understory vegetation responses to *Z. spectabile* management in the primary and secondary forests at LLFS. We established 24 8 × 8 m (64 m^2) experimental plots, with 12 plots in each forest type. Plots were randomly located throughout each forest and placed at least 10 m from treefall gaps, waterways, or forest edges. To evaluate potential initial differences that could influence understory vegetation, we measured percentage canopy openness (measured using a hemispherical camera positioned 1 m above ground level, at consistent times of day and under similar cloud conditions) and soil moisture (% volumetric water content (VWC), measured with a Field Scout (TDR) 150 soil moisture meter) at four evenly spaced points within each plot and the basal area of trees (i.e., the combined cross-sectional area of all stems > 5 cm DBH).

To quantify levels of *Z. spectabile* invasion, we recorded the number of individual stems in each plot, categorizing them into two size classes: small stems (0.25-1 m length) and large stems (> 1 m length). We also counted all *Z. spectabile* sedlings, defined as recently established, individual plants with a maximum stem length < 25 cm. Based on preliminary surveys indicating that most understory herbaceous plants in these forests are > 0.5 m in height, we focused on herbaceous plants within this size range. We counted all individual native herbaceous understory plants in each plot, excluding vines and epiphytes not rooted in the soil. We

also tallied all woody saplings ≥1 cm to ≤ 5 cm DBH (diameter at breast height, measured at 1.3 m). In a marked 2 × 2 m subplot at the center of each plot, we counted all woody seedlings (≥ 10 cm and DBH < 1 cm). Each plot was then randomly assigned to either a *Z. spectabile* "removal" treatment or a "no management" (control) treatment (n = 6 per forest type). All understory vegetation measurements were repeated in June 2020, one year after the initial survey and the *Z. spectabile* removal treatment application.

Land managers reported that cutting *Z. spectabile* aboveground biomass alone led to rapid resprouting, while common herbicides such as glyphosate were ineffective. They also noted that removing belowground biomass was prohibitively labor—and cost—intensive and caused excessive disturbance to the forest understory. Based on these observations, we developed a removal treatment adapted from methods used to control the related invasive species *H. gardnerianum* in Hawaii and New Zealand (Anderson & Gardner, 1999; Harris et al., 1996; Minden et al., 2010). All *Z. spectabile* stems were cut at ground level to expose rhizomes, and metsulfuron-methyl (Escort©, DuPont, Wilmington, DE) was applied by hand with a 100 ml syringe to minimize damage to non-target vegetation. Seedlings (small individuals arising from seed with stems < 0.25 m long) that could be removed without disturbing the soil were hand-weeded, and all aboveground biomass from cut and weeded plants was removed from each plot. Seedlings (< 0.25 m) and small and large stems (0.25-1 m and > 1 m, respectively) were separated; fresh weights were recorded, and subsamples from each size class were oven-dried to estimate total aboveground dry biomass. Dry biomass totals were divided by the number of individuals in each class to calculate mean aboveground dry biomass, which was then used to non-destructively estimate *Z. spectabile* biomass in the "no-management" plots.

Data analysis: All analyses were conducted in R version 4.3.2 (R Core Team, 2023). Linear mixed-effects models were performed using the lmer() function from the lme4 package (Bates et al., 2015); when necessary, data were transformed using log(x + 1) to meet model assumptions. All other statistical analyses were performed using base R functions. The mean and standard error of the mean (1 SE) are reported throughout.

Patterns of invasion and reproduction: We compared *Z. spectabile* stem (≥ 1 m) and inflorescence densities between primary and secondary forests (n = 7) using paired t-tests. Germination rates were compared among primary forest, secondary forest, and open pasture (n = 10 per habitat) using a one-way Kruskal–Wallis test, as data did not meet normality assumptions. When significant differences were found, Dunn's post hoc tests with Holm correction were applied for pairwise comparisons.

Effects of invasion on tree seed germination and seedling survival and growth: To evaluate treatment effects on seed germination, seedling survival, and growth, we used separate one-way randomized complete block ANOVAs followed by post-hoc pairwise Tukey's HSD test for each response variable; treatment was treated as the fixed factor and block as the random factor.

Effects of management intervention on *Z. spectabile* and understory vegetation: Preliminary analyses using both *Z. spectabile* stem density and estimated aboveground biomass as indicators of invasion level yielded consistently similar results. Therefore, we report only the results based on estimated aboveground biomass. Using measurements collected in all plots (n = 24) prior to implementing the removal treatment, we explored the relationship between *Z. spectabile* biomass and forest characteristics (% canopy openness, basal area, and % soil moisture) using Pearson's correlations. To assess initial differences between primary and secondary forests, we compared % canopy openness, basal area, % soil moisture, and understory vegetation structure using

two-sample t-tests (n = 12 per forest type). We also evaluated relationships between *Z. spectabile* aboveground biomass and understory vegetation (density of native herbaceous plants, woody seedlings and woody saplings) within each forest type separately using simple linear regression (n = 12 per treatment group). To assess the effects of the *Z. spectabile* removal treatment on understory vegetation, we fitted separate linear mixed-effects models (LMMs) for the primary and secondary forests. Each model included time (pre-treatment vs. one-year post-treatment), treatment, and their interaction (time × treatment) as fixed effects, with plot included as a random effect to account for paired observations over time (n = 6 per treatment).

RESULTS

Patterns of invasion and reproduction: Despite *Z. spectabile* having been introduced to the edges of the adjacent secondary and primary forests at the same time ~ 30 years prior, our survey in 2017 showed significantly higher densities of stems (≥ 1 m length) in the secondary forest compared to the primary forest (n = 7) (t_6 = -2.47, p = 0.048). Similarly, the density of inflorescences was three-fold higher in secondary than primary forest (t_6 = -2.94, p = 0.026) (Fig. 2).

Our test of vegetative reproduction through sprouting from nodal segments showed a mean of 5.8 ± 0.3 clonal sprouts per mature stem (1.0-1.5 m in length) and a mean of 0.4 ± 0.01 of nodes producing sprouts over a six-month period (n = 20). All cut stems placed on the forest floor produced at least three sprouts each, resulting in 100 % sprouting success (Fig. 1C).

The mean number of seeds per mature inflorescence was 64.3 ± 7.9, although this one-time sample is likely an underestimate of total seed production since fruit formation occurs sequentially over several months beginning at the basal bracts of the inflorescence (Rezende et al., 2020). A simple extrapolation — multiplying mean seeds per inflorescence by mean inflorescences per hectare — yields

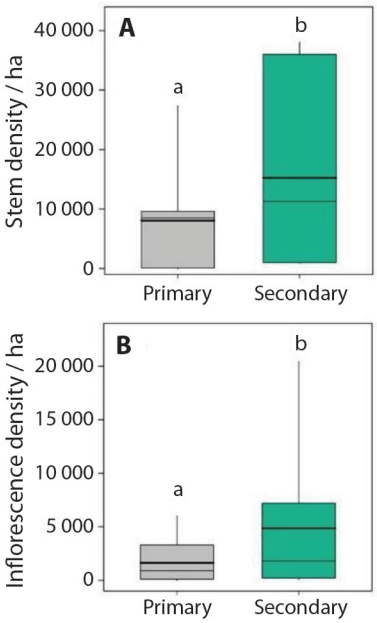

Fig. 2. A. Stem density of *Z. spectabile* in paired primary and secondary plots (n = 7). **B.** Inflorescence density of *Z. spectabile* in paired primary and secondary plots (n = 7). Boxes show the median (bold line) and mean (lighter line). Different letters indicate significant differences between forest types (p < 0.05).

an estimated 104 717 *Z. spectabile* seeds/ha in primary forest and 312 314 seeds/ha in secondary forest at the time of sampling. Seed germination was significantly lower in fallow pasture (0.03 ± 0.02) compared to secondary forest (0.47 ± 0.11) and primary forest (0.58 ± 0.09), which showed similarly higher levels (H_2 = 14.8, p = 0.001).

Effects of invasion on tree seedling germination, survival, and growth: Seed germination and seedling survival did not differ significantly for any of the four tree species sown into invaded, removal, or non-invaded treatments (n = 10) ($F_{2,27}$ < 1.2, p > 0.05) in all cases (SMF 1).

Effects of management intervention on *Z. spectabile* and understory vegetation: Baseline measurements of forest characteristics (% canopy openness, basal area, and % soil

Table 1
Comparison of forest characteristics and understory plants between the primary and 30-year-old secondary forests prior to implementing *Z. spectabile* removal.

Native community metric	Primary forest	Secondary forest	Test statistic *	p value
% Canopy cover	18.7 ± 2.7	23.5 ± 2.4	t = -1.312	0.331
% Soil moisture	40 ± 1.1	30.5 ± 1.0	t = 0.994	0.824
Tree basal area (m^2/ha)	594.0 ± 54	563.8 ± 53	t = 0.528	0.581
Z. spectabile aboveground dry biomass (kg/m^2)	0.029 ± 0.0	0.08 ± 0.0	(z = 3.646)	**0.001**
Woody sapling density (stems/m^2)	0.13 ± 0.2	0.6 ± 0.0	(z = -2.254)	**0.024**
Woody seedling density (stems/m^2)	0.66 ± 0.6	0.61 ± 0.1	t = 0.563	0.579
Herb density (individuals/ m^2)	1.5 ± 0.1	1.04 ± 0.1	t = 2.597	0.616

Values are means ± 1 SE. Test statistics are for two-sample t-tests or Mann-Whitney U (in parenthesis). Control treatments (n = 12).

moisture) did not differ significantly between primary and secondary forests, and aboveground *Z. spectabile* biomass was not significantly correlated with any of the measured forest characteristics (SMT 1). However, some patterns in understory vegetation differed between forest types. Consistent with results from our initial survey (conducted in the same forests but different plots), *Z. spectabile* aboveground biomass was nearly three times greater in the secondary than in the primary forest (Table 1). Sapling density was significantly higher in the primary forest, while herbaceous plants and woody seedlings occurred at similar densities across forest types (Table 1). Interestingly, in secondary forest plots, woody seedling density was negatively correlated with *Z. spectabile* aboveground biomass ($F_{1,22}$ = 7.1, p = 0.014, R^2 = 0.209); no other understory vegetation metrics were significantly associated with *Z. spectabile* biomass in either forest type ($F_{1,22}$ < 1.1, p > 0.315 in all cases).

One year after implementing the removal treatment, *Z. spectabile* biomass in primary forest removal plots remained below pre-treatment levels, while biomass increased significantly in the no-management plots, as shown by a significant time × treatment interaction ($F_{1,10}$ = 9.3, p = 0.012, Fig. 3A). In the secondary forest plots, we also found a strong time × treatment interaction ($F_{1,10}$ = 13.2, p = 0.005): *Z. spectabile* biomass was significantly reduced by the removal treatment, whereas it remained stable over time in the no-management plots. However, *Z. spectabile* rapidly re-invaded the removal plots in both forest types, despite the substantial physical removal of aboveground biomass (~ 0.33 kg m^{-2} fresh weight primary forest and ~ 1.1 kg m^{-2} in secondary forest) and the application of herbicide. This re-invasion is illustrated by the fact that the secondary forest removal plots reached approximately 0.03 kg m^{-2} of dry biomass comparable to levels observed in unmanaged primary forest plots (Fig. 3A, Fig. 3B). Full statistical results for all *Z. spectabile* responses are provided in SMT 2.

Understory vegetation composition changed over time with modest effects of *Z. spectabile* removal treatment. In primary forest, woody seedling density increased over time across all plots ($F_{1,10}$ = 13.39, p = 0.003) but neither the treatment ($F_{1,10}$ = 1.3, p = 0.275) nor the treatment × time interaction ($F_{1,10}$ = 0.267, p = 0.617) were significant (Fig. 3G). Understory woody sapling and herb densities did not change over time or due to treatment in primary forest (Fig. 2C, Fig. 2E). In secondary forest, woody sapling density increased slightly over time in all plots ($F_{1,10}$ = 6.86, p = 0.026) but not in response to treatment ($F_{1,10}$ = 0.34, p = 0.857) or the treatment × time interaction ($F_{1,10}$ = 0.711, p = 0.419) (Fig. 3D). Understory herb density increased over time in all plots ($F_{1,10}$ = 5.7, p = 0.037) and significantly in response to *Z. spectabile* removal ($F_{1,10}$ = 5.4, p = 0.043), but there was no significant treatment × time

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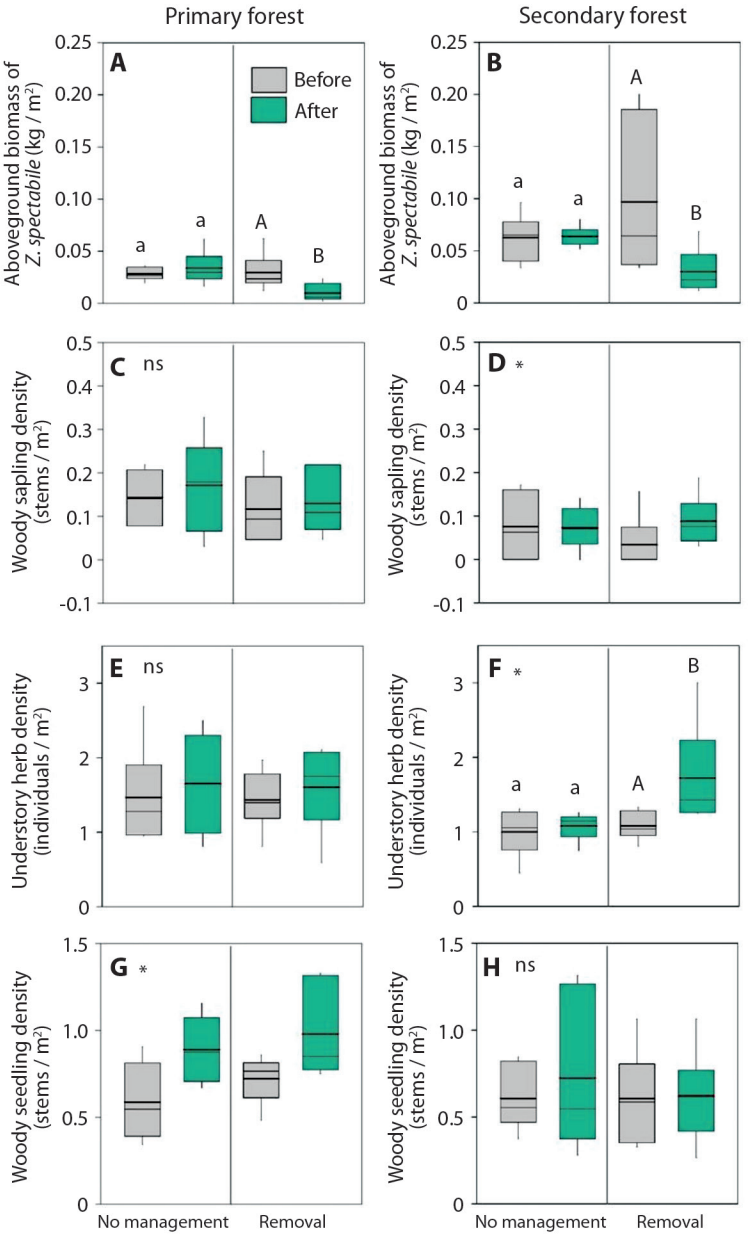

Fig. 3. Understory vegetation metrics measured before and one year after two treatments in primary and 30-year-old secondary forests. Treatments were: No Management — Z. *spectabile* left intact; and Removal — all aboveground Z. *spectabile* biomass removed, followed by herbicide application to the rhizomes. A–B. Aboveground biomass of Z. *spectabile*. C–D. Aboveground sapling density. E–F. Understory herb density. G–H. Woody seedling density. Boxes show the median (bold line) and mean (lighter line). Different letters indicate significant differences between treatments ($p < 0.05$); bars sharing the same letter are not significantly different. Asterisks (*) denote significant changes over time within a treatment.

interaction ($F_{1,10}$ = 2.6, p = 0.138) (Fig. 3F). Woody seedling density in secondary forest showed no significant changes over time or in response to treatment. Statistical results for all understory vegetation responses are included in SMT 2.

DISCUSSION

This study provides the first baseline data on the invasion, effects, and management of *Z. spectabile* in the tropical forest understories of Central America (Chacón-Madrigal et al., 2022; Rojas-Sandoval et al., 2023). Our findings reveal several key insights about *Z. spectabile* invasion patterns, reproductive capacity, effects on understory forest vegetation, and potential control. First, *Z. spectabile* stem and inflorescence density and aboveground biomass were significantly higher in secondary forests, suggesting greater invasion susceptibility in regenerating forests. Second, prolific nodal sprouting, high seed production and germination rates, resistance to chemical control, and rapid regrowth after removal of aboveground biomass all indicate strong invasive potential and the substantial challenge of controlling this exotic species. Finally, while aboveground biomass removal followed by herbicide application temporarily reduced invasion levels, we observed limited responses in native understory vegetation within the first year. However, negative correlations between *Z. spectabile* aboveground biomass and woody seedling density in secondary forest, coupled with increased herbaceous understory plant density in removal plots suggest potential impacts on forest succession and understory plant communities. Our results underscore the need for longer-term studies of impacts of invasion on understory vegetation, as well as potential belowground competition. Given the labor-intensive nature of removal and the limited effectiveness of herbicide, improved management strategies are urgently needed.

We observed significantly greater *Z. spectabile* invasion in 30-year-old secondary forest compared to primary forest, despite similar canopy openness, basal area, and soil moisture across sites. Aboveground biomass and inflorescence density were more than three-fold greater in secondary forest, suggesting that forest successional stage strongly influences invasion dynamics. Early—to mid—successional forests often exhibit reduced structural and compositional complexity and increased understory light availability-factors that favor invasive species establishment and spread (Anderson, 2007; Waddell et al., 2020; Walker & Chapin, 1987). In our study region, *Z. spectabile* has been documented in disturbed habitats ranging from home gardens and agroforestry systems to restored forests 1-18 years post-planting (Pardo, Cole, & Holl unpublished data). These patterns, along with horticultural recommendations for planting in partial to deep shade (Whistler, 2000), suggest that canopy cover facilitates establishment. Introduced pasture grasses and ruderal herbs—the most widespread invasive plants in Latin America (Rojas-Sandoval et al., 2023)—are typically suppressed by increased canopy cover (Holl et al., 2018; Zahawi et al., 2013), but shade-tolerant invasives pose new challenges to natural and assisted forest recovery (Padmanaba & Corlett, 2014). Disturbance, fragmentation, and land-use change have increased vulnerability even in mature forests (Fine, 2002; Martin et al., 2009), and with over 30 % of Latin America's tropical forest cover in some stage of succession (Chazdon et al., 2016), the risk of establishment and persistence of shade-tolerant invaders like *Z. spectabile* is high.

Our results, along with observations in other ecosystems (e.g., interactions with generalist pollinators and seed dispersers: Sakai et al. (2013) show that *Z. spectabile* possesses multiple traits that support rapid invasion and persistence in tropical forest ecosystems (Colautti et al., 2006; Nathan et al., 2008; Pyšek et al., 2020). *Z. spectabile* demonstrated prolific vegetative reproduction in our trials, with 100 % of aboveground cut stems producing nodal sprouts and > 35 % of initial aboveground biomass regrowing from rhizomes one year after control attempts in both forest types.

Seed production was also substantial, with ~ 205 000 seeds/ha recorded in invaded forests, and high germination rates observed in both primary and secondary forests. The high density of seedlings, presumably originating from dispersed seeds, along with high germination rates in both primary and secondary forests, indicates strong seed viability. The small seed mass, along with *Z. spectabile*'s rapid spread and establishment in forested environments, but not in open pasture, suggests that conditions in the understory, rather than dispersal limitation, drive establishment patterns within landscapes where *Z. spectabile* has been introduced.

The effects of *Z. spectabile* on understory vegetation observed in this study were mixed. In the secondary forest, we found a significant negative correlation between *Z. spectabile* aboveground biomass and woody seedling density, suggesting that high invasion levels may suppress seedling establishment (although based on this correlation we cannot rule out the alternative hypothesis that *Z. spectabile* is able to invade faster into areas with low seedling density). We also recorded a positive response of native herbaceous plant abundance within removal plots, indicating potential release from belowground or light competition. However, removal of *Z. spectabile* biomass followed by herbicide application did not lead to a measurable short-term increase in native woody seedling or sapling abundance in either forest type. Moreover, we did not find any differences in sown seed germination, seedling survival or growth in invaded, non-invaded or *Z. spectabile* removal plots within the first year for four tree species. This lack of immediate response is not unexpected, as growth of many woody species is limited by overstory light competition as has been well demonstrated by gap phase dynamics (e.g., Denslow, 1987; Martínez-Ramos et al., 1989). Woody species may respond more gradually to moderate changes in light conditions in the understory or to reduced competition, whether above or below ground, from *Z. spectabile*, than the one-year timespan of our field experiments.

This study did not compare understory plant communities between invaded and uninvaded forests, which may limit our ability to detect invasion-related impacts. The secondary forest examined was likely invaded within the first decade of post-agricultural regeneration, meaning understory communities in both forest types may have been shaped by nearly 30 years of *Z. spectabile* presence. Previous research shows that native vegetation often recovers slowly after invasive species removal due to legacy effects such as recruitment bottlenecks (Cole et al., 2012; Flory & Clay, 2009) or persistent environmental changes (Ehrenfeld et al., 2001; Kourtev et al., 2002). In Hawaiian montane wet forests, for example, removal of *H. gardnerianum* led to minimal native woody seedling growth after one year (Cole et al., 2021) and limited understory recovery even after six years (Minden et al., 2010). A global meta-analysis of invasive plant control studies further indicates that native vegetation recovery is typically slow and often unsuccessful when reinvasion occurs (Kettenring & Adams, 2011). Our results suggest that *Z. spectabile* may alter successional trajectories by reducing native woody seedling and herbaceous plant abundance, particularly in regenerating forests. These findings highlight the importance of long-term monitoring, comparisons with uninvaded sites, and ongoing control efforts to support forest understory recovery.

Controlling *Z. spectabile* on an ongoing basis to allow for understory recovery presents significant challenges. In our study, we found that the simplest method—cutting aboveground stems and leaving them on site—stimulated prolific nodal sprouting from cut stems and rapid regrowth from rhizomes left in the soil. A local alternative of excavating rhizomes and burying all biomass deep enough to prevent sprouting is considered excessively disruptive and costly by land managers. For example, at invasion levels similar to the sites at LLFS, above-ground fresh biomass alone ranged from 1 500 to > 20 000 kg per ha. Our more targeted strategy—removing aboveground biomass followed by spot herbicide application to exposed

rhizomes—aligns with common control protocols for invasive gingers in other tropical forests (Loh et al., 2014). Although not compared to just manual cutting of aboveground biomass, this method was only partially effective, with rapid biomass recovery within the first year, indicating the need for more intensive or repeated treatments. *H. gardnerianum*, a related shade-tolerant invasive ginger, is often managed through repeated cutting and herbicide application (Loh et al., 2014) but appears to exhibit far less nodal sprouting than *Z. spectabile*, potentially making it more responsive to these methods.

Our findings underscore the need for continued monitoring and research on the effects of *Z. spectabile* invasion into tropical forests. Despite evidence that *Z. spectabile*—along with many other introduced species—poses a significant invasion risk across Central America, herbarium records and systematic monitoring remain sparse throughout much of the region (Chacón-Madrigal et al., 2022; Rojas-Sandoval et al., 2023). Future studies should span multiple years and assess both above and below ground competition with understories plant communities. Control methods also warrant further investigation: on-site composting of cut biomass under black plastic, sustained manual removal on an annual basis, and targeted herbicide application may all represent viable strategies. The labor-intensive nature of *Z. spectabile* management, and its potential to impact native forests, highlights the need for scalable, cost-effective control approaches. Equally important are public education initiatives and policy interventions aimed at preventing further introductions and limiting the spread of this and other high-risk plant species.

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See supplementary material
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