Interactive effects of fallow age and Chromolaena odorata invasion on tree regeneration in Central African agricultural landscapes

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Abstract

Natural regeneration of trees outside forests (TOF) is a key process sustaining biodiversity and ecosystem functions in tropical agricultural landscapes, yet it is increasingly shaped by interactions between succession and biological invasion. This study quantified the combined effects of fallow age and *Chromolaena odorata* cover on tree regeneration in agricultural fallows of Mongala Province (Democratic Republic of the Congo). Seedling inventories were conducted around 300 seed trees across gradients of fallow age (0–3, 3–6, > 6 years) and invasion intensity (0–25% to > 75% cover). Seedling density, spatial patterns, and size structure were analysed using zero-inflated negative binomial models. Seedling density declined significantly with increasing *C. odorata* cover, particularly in early fallows, where predicted densities decreased from 1051 to 270 ind. ha^{-1} (≈ 74% reduction). This effect weakened along the successional gradient and became negligible in older fallows, indicating a strong interaction between succession and invasion. Invasion effects were non-linear, with sharp declines occurring beyond intermediate levels of cover, suggesting threshold responses and increased probability of recruitment failure. Species responses varied markedly: *Erythrophleum suaveolens* and *Pycnanthus angolensis* showed strong declines, whereas *Petersianthus macrocarpus* increased under high invasion, indicating species-specific ecological filtering. Invasion also reduced spatial heterogeneity and limited progression to larger seedling size classes. These findings highlight that regeneration is governed by context-dependent interactions between succession and invasion intensity, with early fallows representing both a window of opportunity and a phase of high vulnerability. Accounting for non-linear invasion effects is critical for understanding forest recovery and designing targeted management strategies in tropical agricultural landscapes.

1. Introduction

Across tropical Africa, agricultural expansion and shifting cultivation have profoundly transformed forest landscapes, resulting in extensive mosaics of croplands, fallows, and remnant tree cover (Curtis et al. 2018; Mpanda et al. 2021). In these human-modified systems, trees outside forests (TOF) play a crucial ecological and socio-economic role by maintaining biodiversity, supporting ecosystem services, and contributing to forest recovery processes (FAO 2016; Zomer et al. 2016). In particular, natural regeneration within agricultural fallows represents a major pathway for the persistence and renewal of woody species in landscapes where access to intact forests is increasingly limited (Curtis et al. 2018; Loubota Panzou et al. 2024).

Natural regeneration in fallow systems is shaped by multiple interacting drivers, including land-use history, successional stage, seed availability, and biotic interactions (Chazdon et al. 2009; Mwampamba and Schwartz 2011). Among these factors, fallow age is widely recognised as a key determinant of regeneration dynamics, as it influences light availability, soil conditions, and vegetation structure (Chazdon 2014; Poorter et al. 2021). Early successional stages may favour seedling establishment due to higher light availability, whereas later stages may enhance survival through improved microclimatic buffering and soil development. However, the relationship between fallow age and regeneration is often

non-linear and species-dependent, reflecting differences in ecological strategies among tree species (Poorter et al. 2019; Rozendaal et al. 2019).

In tropical agricultural landscapes, these successional processes are increasingly altered by invasive plant species (Pyšek et al. 2020). Among them, *Chromolaena odorata* (L.) R.M. King & H. Rob. is one of the most aggressive invasive shrubs in tropical Africa and is now widespread in post-cultivation fallows (Rai and Singh 2024). Its rapid growth, dense canopy, and potential allelopathic effects can reduce light availability, limit seedling establishment, and modify competitive interactions (Kato-Noguchi and Kato 2023; Juru et al. 2024). While *C. odorata* is often associated with reduced tree regeneration, its effects are not uniformly negative. In some contexts, dense shrub cover may alter competitive dynamics or microenvironmental conditions in ways that influence seedling recruitment differently across species and successional stages (Gbètoho et al. 2018; Hardy et al. 2025).

Despite increasing attention to the role of TOF in landscape resilience, the combined effects of fallow age and invasive shrub cover on tree regeneration remain insufficiently understood, particularly in Central African agricultural systems (Reed et al. 2016; Chazdon et al. 2020). Most studies have examined these drivers independently, overlooking potential interactions between successional stage and invasion intensity. In addition, species-specific responses to these interacting factors remain poorly documented, limiting our ability to predict regeneration trajectories and design context-adapted management strategies.

In the Democratic Republic of Congo (DRC), and particularly in Mongala Province, shifting cultivation dominates rural land use and generates extensive networks of agricultural fallows where TOF constitute the main source of natural forest regeneration (FAO 2016; Loubota Panzou et al. 2024). These landscapes provide an appropriate context for analysing how regeneration patterns vary across successional stages and invasion gradients. In such systems, understanding both the magnitude and variability of regeneration responses is essential for informing sustainable land management and restoration-oriented practices.

Against this background, this study investigates the natural regeneration of five dominant TOF species (*Petersianthus macrocarpus* (P. Beauv.) Liben, *Pycnanthus angolensis* (Welw.) Warb., *Ricinodendron heudelotii* (Baill.) Heckel, *Erythrophleum suaveolens* (Guill. & Perr.) Brenan, and *Piptadeniastrum africanum* (Hook.f.) Brenan) across agricultural fallows differing in age and *C. odorata* cover in Mongala Province, Democratic Republic of the Congo. Specifically, we aimed to: (i) quantify the effects of fallow age and invasion level on seedling density; (ii) assess whether the effect of *C. odorata* varies across successional stages; (iii) analyse species-specific responses to these interacting drivers; and (iv) evaluate how these factors influence the spatial and structural patterns of regeneration.

We hypothesised that: (1) seedling density decreases with increasing *C. odorata* cover;

(2) this negative effect is strongest in early fallows and weakens with increasing fallow age; (3) species exhibit contrasting responses to invasion and succession; and (4) both spatial patterns of recruitment

and seedling size structure are jointly influenced by distance from seed trees, fallow age, and invasion level.

By explicitly testing these hypotheses, this study provides a quantitative assessment of how successional dynamics and biological invasion interact to shape tree regeneration in fallow-based tropical landscapes, and contributes to a better understanding of forest recovery processes outside forests.

2. Materials and methods

2.1. Study area

The study was conducted in Mongala Province, located in the north-western part of the Democratic Republic of the Congo within the central Congo Basin (Fig. 1). The province is characterised by lowland tropical landscapes dominated by moist evergreen and semi-evergreen forests interspersed with agricultural fields and fallows resulting from shifting cultivation.

The climate is humid tropical, with relatively stable high temperatures throughout the year and mean annual rainfall generally exceeding 1,500 mm (Azenge et al. 2025). Rainfall is distributed across a long rainy season and a shorter dry season, creating favourable conditions for continuous plant growth and rapid vegetation recovery following agricultural abandonment.

Vegetation is largely composed of dense tropical rainforest formations, although extensive areas have been converted into agricultural mosaics. Shifting cultivation is the dominant land-use system, with fields typically cultivated for one to two years before being abandoned to fallow. Fallow duration varies widely, resulting in a heterogeneous patchwork of fallows of different ages that constitute key sites for the regeneration of trees outside forests.

Soils are predominantly highly weathered tropical soils with low to moderate fertility. Repeated cultivation can further reduce nutrient availability, making fallow periods essential for restoring soil structure and fertility. However, vegetation recovery during fallow stages is often constrained by competition with herbaceous and shrub species, particularly invasive plants (Diyarzola and Bernard 2024).

C. odorata is among the most widespread invasive species in agricultural fallows of Mongala Province, where it forms dense shrub layers in recently abandoned fields.

2.2. Data collection

Natural regeneration of TOF was assessed through a field-based seedling inventory conducted in agricultural fallows across Mongala Province, (DRC). The study focused on five dominant TOF species

(*P. macrocarpus*, *P. angolensis*, *R. heudelotii*, *E. suaveolens* and *P. africanum*) and aimed to quantify how regeneration varies across gradients of fallow age, *C. odorata* cover, and distance from seed trees.

The sampling design was structured to capture variability in both successional stage and invasion intensity while ensuring spatial representativeness. Fifteen villages were selected across the three administrative territories of Mongala Province to reflect the range of agroecological and land-use conditions in the study area. Within each village, agricultural fallows were identified in collaboration with local farmers to determine fallow age and recent land-use history.

Fallow age was classified into three categories (0–3 years, 3–6 years and > 6 years), representing early, intermediate and advanced stages of post-cultivation succession. The cover of *C. odorata* was visually estimated around each seed tree and assigned to four ordinal classes (C1: 0–25%, C2: 25–50%, C3: 50–75% and C4: >75%), capturing increasing levels of invasion.

For each of the five species, 60 mature seed trees were selected as focal sampling units, resulting in a total of 300 seed trees. Seed trees were distributed across fallow age classes and invasion levels to ensure that all combinations of successional stage and *C. odorata* cover were represented at the landscape scale. While minor imbalances occurred at the village level due to local availability constraints, the overall design remained well balanced across treatments.

Around each seed tree, seedling abundance was assessed using four rectangular transects oriented along the cardinal directions. Each transect was 40 m long and 3 m wide, corresponding to the average radius of cultivated fields, and was subdivided into eight segments of 5 m. This design allowed the spatial distribution of seedlings to be captured along a gradient of distance from the seed tree while standardising sampling effort across sites.

All seedlings encountered within transects were counted and assigned to one of three height classes (0–30 cm, 30–50 cm and > 50 cm), providing information on both recruitment and size structure. Seedling counts were subsequently aggregated at the seed-tree level prior to statistical analysis, so that each seed tree represented an independent sampling unit associated with a specific combination of fallow age, invasion level and local environmental conditions. This aggregation reduced the risk of pseudoreplication associated with multiple transects and ensured consistency with the analytical framework used in the study.

2.3. Data processing and analysis

2.3.1. Data preparation

All statistical analyses were conducted using the R statistical environment (R version 4.5.3; R Core Team, 2025). The dataset comprised seedling counts recorded around individual seed trees across combinations of fallow age, *C. odorata* cover, species identity, and distance from the seed tree.

Seedling density was expressed as the number of individuals per hectare (ind. ha^{-1}). Total seedling density was calculated as the sum of individuals across all height classes. Additional variables described seedling structure by three height classes (0–30 cm, 30–50 cm, and > 50 cm).

Explanatory variables were defined as follows:

- **Fallow age**: three ordered classes (0–3 years, 3–6 years, > 6 years);
- **C. odorata cover**: four ordered levels (C1: 0–25%, C2: 25–50%, C3: 50–75%, C4: >75%);
- **Species**: five focal tree species (*E. suaveolens*, *P. macrocarpus*, *R. heudelotii*, *P. angolensis*, and *P. africanum*).

Distance from the seed tree was treated as a continuous variable.

Prior to analysis, data were checked for consistency, missing values, and outliers. Distributions of response variables were examined using histograms and boxplots (see Figure S1). Seedling density exhibited strong right-skewness, high variance, and a large proportion of zero counts, indicating overdispersion and zero inflation typical of ecological count data.

2.3.2. Modelling of seedling density

To analyse the effects of fallow age, *C. odorata* cover, species identity, and distance on seedling density, we fitted zero-inflated negative binomial (ZINB) models using the *glmmTMB* package. This modelling framework was selected to simultaneously account for: (i) overdispersion in count data, and (ii) excess zeros arising from ecological processes such as recruitment failure.

The final model structure was:

$$\text{Seedling density} \sim \text{species} \times \text{fallow age} \times \text{cover} + \text{ns}(\text{distance}, \text{df} = 3)$$

with a zero-inflation component specified as:

$$\text{Zero inflation} \sim \text{fallow age} + \text{cover}$$

Distance from the seed tree was modelled using a natural spline (df = 3) to capture non-linear spatial patterns of seed dispersal and establishment.

Model coefficients were interpreted on the log scale and exponentiated to obtain rate ratios. Estimated marginal means (EMMs) and associated confidence intervals were computed using the *emmeans* package and used to generate predicted response curves and interaction plots.

Pairwise comparisons among *C. odorata* cover levels within each fallow age class and species were performed using Tukey-adjusted contrasts to control for multiple testing. Results were presented as:

- a simplified summary table in the main text (Table 2), and

- a full set of contrasts in the Supplementary Material (Table S2).

2.3.3. Spatial patterns of seedling recruitment

Spatial variation in seedling density relative to distance from the seed tree was analysed within the ZINB modelling framework described above. The inclusion of a spline function of distance allowed flexible modelling of non-linear dispersal and establishment patterns.

Predicted seedling densities were generated across continuous gradients of distance and invasion levels for each fallow age class and species. These predictions were visualised using heatmaps, facilitating the interpretation of interactions between spatial processes, successional stage, and invasion intensity.

2.3.4. Analysis of seedling size structure

To characterise regeneration dynamics beyond total density, seedling populations were analysed by height class.

Relative proportions of each size class were calculated as:

$$p_i = \frac{\text{density of size class } i}{\text{total seedling density}}$$

Variation in size-class composition across fallow age and invasion gradients was analysed descriptively and visualised using stacked bar charts. In addition, ternary plots were used to represent the relative contribution of each size class across environmental gradients, providing an integrated view of regeneration structure (Fig. S5).

2.3.5. Model diagnostics and validation

Model adequacy was assessed using simulation-based diagnostics implemented in the *DHARMa* package. Diagnostic procedures included tests of residual uniformity, dispersion, zero inflation, and outliers.

Results indicated that the zero-inflated negative binomial model adequately captured the excess of zero observations (zero-inflation test: non-significant) and did not exhibit problematic outliers. Although dispersion and uniformity tests indicated statistically significant deviations, visual inspection of residual plots suggested only moderate departures from model assumptions, which are common in large ecological count datasets.

Diagnostic results supported the adequacy of the model despite minor deviations typical of large ecological datasets (Fig. S2, Fig. S3; Text S2).

2.3.6. Data visualisation

All figures were produced using the *ggplot2* package, with additional extensions (*ggdist*, *patchwork*, and *ggtern*) for advanced visualisation. Figures were designed to maximise interpretability and facilitate comparison across species, fallow age classes, invasion levels, and spatial gradients.

3. Results

3.1. Dataset structure and distribution of observations

The dataset followed a fully balanced factorial design combining fallow age (0–3, 3–6, > 6 years), Chromolaena odorata cover (C1-C4), and five tree species, resulting in an equal number of observations per treatment combination (n = 160). This balanced structure ensured robust estimation of main and interaction effects while minimising potential biases associated with unequal sampling effort (Fig. 2).

3.2. Effects of fallow age and invasion level on total seedling density

Seedling density varied markedly across both fallow age and Chromolaena odorata cover gradients (Table 1; Fig. 3). The zero-inflated negative binomial (ZINB) model revealed significant effects of fallow age, invasion level, and their interaction (all $p < 0.001$), indicating that the impact of invasion depends strongly on successional stage.

Predicted seedling densities declined sharply with increasing invasion intensity, particularly in early fallows (0–3 years). Model-based estimates showed a decrease from 1051 ind. ha^{-1} under low invasion (C1) to 270 ind. ha^{-1} under high invasion (C4), corresponding to a reduction of approximately 74%. This strong decline was consistent across descriptive statistics, which showed a reduction in mean density from 1343 to 203 ind. ha^{-1} across the same gradient.

Table 1
Descriptive statistics of seedling density (individuals ha⁻¹) across fallow age and *Chromolaena odorata* cover gradients.

Fallow age	*C. odorata* cover	n	Mean	SD	Median	Q1	Q3	Min	Max
0–3 years	C1	800	1343	1185	1270	197	2235	0	5264
	C2	800	771	673	646	192	1192	0	3394
	C3	800	324	240	304	117	488	0	1565
	C4	800	203	208	162	0	291	0	1279
3–6 years	C1	800	932	867	772	168	1524	0	6141
	C2	800	803	774	586	201	1210	0	3749
	C3	800	621	772	324	100	757	0	3542
	C4	800	668	832	242	91	1060	0	3481
> 6 years	C1	800	758	704	496	194	1222	0	3226
	C2	800	760	651	590	266	1092	0	2811
	C3	800	706	659	539	134	1070	0	3077
	C4	800	753	701	615	94	1244	0	2779

In intermediate fallows (3–6 years), invasion effects remained significant but were less pronounced, with predicted densities declining from 784 ind. ha⁻¹ (C1) to 454 ind. ha⁻¹ (C4), representing a reduction of approximately 42%. In contrast, in older fallows (> 6 years), predicted densities were relatively stable across invasion levels (698–760 ind. ha⁻¹), indicating a marked attenuation of invasion effects.

The zero-inflation component of the model further indicated that the probability of structural zeros increased under high invasion levels and in early fallows, suggesting that invasion not only reduces seedling density but also increases the likelihood of recruitment failure.

3.3. Species-specific responses to fallow age and invasion gradients

Species responses to invasion and succession varied significantly, as indicated by a strong three-way interaction between species, fallow age, and invasion level ($p < 0.001$). Predicted marginal means revealed contrasting response patterns among species (Fig. 4; Table S4).

E. suaveolens exhibited the strongest negative response to invasion, with predicted densities declining from 1454 ind. ha⁻¹ under low invasion (C1) to 149 ind. ha⁻¹ under high invasion (C4) in early fallows, corresponding to a reduction of approximately 90%. Similarly, Pycnanthus angolensis showed pronounced declines across invasion gradients, particularly in early and intermediate fallows.

P. africanum showed a moderate response, with significant declines under high invasion in early and intermediate fallows, but weaker and non-significant responses in older fallows.

In contrast, *P. macrocarpus* exhibited a positive response to invasion, with predicted densities increasing from 203 ind. ha^{-1} (C1) to 396 ind. ha^{-1} (C4) in early fallows, and up to 1090 ind. ha^{-1} under high invasion in older fallows, representing more than a fourfold increase.

R. heudelotii showed relatively stable responses across invasion gradients, particularly in intermediate and older fallows, where differences among invasion levels were small and non-significant.

These results indicate that *C. odorata* acts as a strong ecological filter, suppressing regeneration in some species while favouring others, thereby generating substantial interspecific variability in regeneration dynamics.

3.4. Spatial patterns of seedling recruitment

Seedling density decreased non-linearly with increasing distance from seed trees, as captured by the spline term included in the ZINB model (Fig. 6). This decline was steepest in early fallows, indicating strong dispersal limitation during initial successional stages.

Predicted densities were highest near seed trees and declined rapidly within the first tens of metres, after which the decline became more gradual. In intermediate and older fallows, spatial gradients were less pronounced, suggesting more diffuse recruitment patterns.

Invasion intensity significantly modified these spatial patterns. High *C. odorata* cover reduced seedling density across all distances and flattened spatial gradients, resulting in more homogeneous distributions (Fig. 7). This indicates that invasion weakens distance-dependent recruitment processes and reduces spatial heterogeneity in seedling establishment.

Overall, these results demonstrate that regeneration patterns are jointly structured by dispersal limitation and environmental filtering, with invasion affecting both the magnitude and spatial configuration of recruitment.

3.5. Changes in regeneration structure across invasion gradients

Seedling size structure varied systematically across invasion gradients and fallow age classes (Fig. 8). Across all conditions, the smallest size class (0–30 cm) dominated seedling populations.

However, the proportion of larger seedlings (> 50 cm) declined consistently with increasing invasion intensity. Under high invasion levels (C3-C4), the relative contribution of larger size classes was substantially reduced compared to low invasion conditions, indicating a shift towards younger developmental stages.

This pattern suggests that *C. odorata* not only limits seedling recruitment but also constrains growth and progression to later developmental stages, potentially affecting long-term regeneration trajectories.

3.6. Pairwise comparisons of invasion effects

Pairwise comparisons based on estimated marginal means confirmed significant differences in seedling density across invasion levels for most species (Table 2; Table S2). High invasion levels (C3 and C4) were generally associated with significantly lower seedling densities compared to low invasion (C1), particularly in early fallows.

For example, in Erythrophleum suaveolens, rate ratios decreased from 0.53 (C2 vs C1) to 0.06 (C4 vs C1) in early fallows, indicating a progressive and substantial decline in seedling density with increasing invasion intensity.

Table 2
Pairwise comparisons of seedling density across invasion levels within fallow age classes (rate ratios from negative binomial models).

Species	Fallow age	C2 vs C1	C3 vs C1	C4 vs C1
E. suaveolens	0–3 years	0.53***	0.22***	0.06***
	3–6 years	0.60***	0.30***	0.12***
	> 6 years	0.70***	0.39***	0.15***
P. africanum	0–3 years	0.73*	0.28***	0.19***
	3–6 years	0.81 ns	0.21***	0.17***
	> 6 years	0.91 ns	0.61***	0.63***
P. angolensis	0–3 years	0.50***	0.16***	0.13***
	3–6 years	0.76 ns	0.26***	0.16***
	> 6 years	0.92 ns	1.00 ns	0.97 ns
P. macrocarpus	0–3 years	1.44 ns	3.36***	2.60***
	3–6 years	1.51*	3.72***	7.32***
	> 6 years	3.76***	5.15***	8.51***
R. heudelotii	0–3 years	0.52***	0.13***	0.08***
	3–6 years	1.00 ns	1.04 ns	1.07 ns
	> 6 years	1.07 ns	1.00 ns	1.01 ns

Note: *Values represent rate ratios relative to low invasion (C1). Values < 1 indicate a decrease in seedling density, whereas values > 1 indicate an increase. Significance levels: *** p < 0.001; * p < 0.05; ns = not significant.*

In contrast, *P. macrocarpus* showed the opposite pattern, with rate ratios exceeding 1 under moderate to high invasion levels and reaching up to 8.51 in older fallows, indicating a strong positive response to invasion.

Other species, such as *R. heudelotii*, showed no significant differences among invasion levels in intermediate and older fallows, confirming species-specific variability in sensitivity to invasion.

Overall, these pairwise comparisons reinforce the results of the main model and highlight the contrasting responses of species to invasion across successional stages.

4. Discussion

4.1. Successional stage as a major driver of regeneration dynamics

This study demonstrates that fallow age is a major determinant of tree regeneration dynamics in Central African agricultural landscapes, but its effect is strongly contingent on invasion intensity. While seedling density was highest in early fallows under low invasion (≈ 1050 ind. ha^{-1}), this advantage was rapidly eroded under high *C. odorata* cover, with densities declining to ≈ 270 ind. ha^{-1}, representing a reduction of more than 70%.

This result refines the classical view that early successional stages favour regeneration due to higher light availability and reduced structural competition (Poorter et al. 2021). Our findings show that this advantage is conditional, and can be overridden by strong competitive exclusion from invasive species.

In contrast, older fallows (> 6 years) maintained relatively stable regeneration levels across invasion gradients (≈ 700–760 ind. ha^{-1}), suggesting that successional development buffers the negative effects of invasion. This pattern indicates that regeneration dynamics are not simply driven by successional stage, but by interactions between succession and biotic filtering processes.

These findings support a more nuanced view of succession, where early stages represent both a window of opportunity for recruitment and a period of high vulnerability to invasion, while later stages provide greater ecological resistance to competitive exclusion, consistent with increasing biotic resistance and structural complexity along successional gradients (Chazdon et al. 2020; Poorter et al. 2021).

4.2. Strong but non-linear effects of *Chromolaena odorata* on regeneration

The results provide strong evidence that increasing *C. odorata* cover reduces seedling density, but this effect is clearly non-linear and threshold-dependent. Across species, major declines occurred primarily between low (C1) and high invasion levels (C3-C4), with reductions exceeding 70–90% in early fallows for several species.

This pattern suggests the existence of ecological thresholds, beyond which invasion shifts from a moderate influence to a dominant limiting factor for regeneration. Below these thresholds, regeneration may still occur, albeit at reduced levels; above them, dense shrub cover likely imposes severe constraints through light limitation, space pre-emption, and possibly allelopathic effects (Kato-Noguchi and Kato 2023).

Importantly, the zero-inflation component of the model showed that invasion increased the probability of structural zeros, particularly in early fallows. This indicates that invasion does not merely reduce seedling abundance but also increases the likelihood of complete recruitment failure, a critical but often overlooked mechanism in regeneration studies.

These results extend previous findings by demonstrating that invasion impacts are not gradual but may involve non-linear transitions in regeneration success, reinforcing the need to explicitly account for invasion intensity rather than presence alone, as ecological impacts of invasive species are often strongly dependent on their abundance and may exhibit threshold responses (Gbètoho et al. 2018; Pyšek et al. 2020).

4.3. Interactive effects of succession and invasion: a context-dependent process

A central contribution of this study is the demonstration that the impact of *C. odorata* is strongly modulated by successional stage. The negative effects of invasion were most pronounced in early fallows, where density reductions exceeded 70%, but became negligible in older fallows.

This interaction highlights that early successional stages constitute a critical ecological bottleneck, where recruitment is both highly active and highly sensitive to environmental filtering. In such conditions, invasive shrubs can effectively suppress regeneration and potentially alter successional trajectories.

In contrast, the reduced impact of invasion in older fallows suggests that increasing vegetation complexity, canopy development, and microclimatic buffering enhance ecosystem resistance to invasion. This aligns with the concept of biotic resistance, whereby more developed plant communities limit the establishment and impact of invasive species (Chazdon et al. 2020).

Overall, these findings demonstrate that invasion effects cannot be generalised across successional gradients, but instead emerge from dynamic interactions between ecosystem development and competitive processes.

4.4. Species-specific responses and ecological filtering

The strong interspecific variation observed in this study confirms that *C. odorata* acts as a selective ecological filter shaping regeneration patterns. Species such as *E. suaveolens* experienced drastic declines (> 90%) under high invasion in early fallows, whereas *P. macrocarpus* showed a marked increase in density, with values exceeding four times those observed under low invasion.

These contrasting responses suggest that invasion favours species with traits adapted to shaded and competitive environments, while excluding more light-demanding or competition-sensitive species. This pattern is consistent with trait-based community assembly theory, where environmental filters select species according to functional traits (Funk et al. 2008; Kraft et al. 2015).

The relatively stable response of *R. heudelotii* across invasion gradients further illustrates that some species may be tolerant to a wide range of environmental conditions, contributing to their persistence in disturbed landscapes.

Such species-specific responses have important implications for long-term forest composition. By selectively favouring certain species, invasion may lead to functional and compositional shifts, potentially reducing diversity and altering ecosystem functioning even when overall seedling abundance remains high.

4.5. Spatial constraints on regeneration and their interaction with invasion

The observed decline in seedling density with increasing distance from seed trees confirms the central role of dispersal limitation in structuring regeneration patterns. This effect was particularly strong in early fallows, where recruitment was highly concentrated near seed sources, indicating limited dispersal distances and strong spatial clustering.

However, invasion significantly modified these spatial dynamics. High *C. odorata* cover reduced seedling density across all distances and flattened spatial gradients, leading to more homogeneous distributions. This suggests that invasion weakens distance-dependent recruitment processes, likely by imposing strong environmental constraints that override dispersal-driven patterns.

These findings highlight the joint role of dispersal limitation and environmental filtering in shaping regeneration, and demonstrate that invasive species can alter not only the magnitude but also the spatial structure of recruitment.

Such alterations in spatial patterns may have cascading effects on community assembly and spatial heterogeneity, which are key components of ecosystem resilience and biodiversity maintenance.

4.6. Implications for regeneration dynamics and management

The results of this study have important implications for the management of agricultural fallows and forest restoration in Central Africa.

First, the high regeneration potential observed in early fallows under low invasion confirms their importance as key regeneration niches. However, the strong decline in seedling density under high

invasion (up to 70–90%) indicates that these systems are highly vulnerable to competitive exclusion during early successional stages.

Second, the identification of strong invasion effects in early fallows suggests that management interventions should prioritise early-stage control of *C. odorata*, before dense stands become established. Preventing invasion during this critical window is likely to be more effective than attempting to restore regeneration after invasion thresholds have been exceeded.

Third, the marked species-specific responses observed highlight the need for context-dependent management strategies. While some species are strongly suppressed by invasion, others may tolerate or even benefit from altered environmental conditions. Management approaches should therefore consider species traits and ecological strategies rather than applying uniform interventions.

Finally, the observed effects of invasion on both spatial patterns and size structure indicate that invasion can influence not only recruitment but also subsequent growth and community development. This underscores the importance of integrating multiple dimensions of regeneration (density, structure, spatial patterns) in restoration planning.

5. Conclusion

This study provides a robust quantitative assessment of how successional dynamics and biological invasion jointly shape tree regeneration in agricultural fallows of Central Africa. By integrating field data with zero-inflated modelling approaches, we demonstrate that fallow age and *Chromolaena odorata* cover interact strongly to determine not only seedling density, but also the spatial structure and developmental trajectory of regeneration.

Our results show that early fallows constitute a critical phase for regeneration, characterised by high recruitment potential under low invasion but also high vulnerability to competitive exclusion. Under high invasion levels, seedling density declined by more than 70%, and the probability of recruitment failure increased substantially, highlighting the sensitivity of early successional stages to biotic constraints. In contrast, older fallows exhibited more stable regeneration across invasion gradients, suggesting increasing ecological resistance with successional development.

Importantly, the effects of *C. odorata* were not gradual but strongly non-linear, with marked declines in regeneration occurring beyond intermediate levels of invasion. This threshold-like behaviour indicates that invasion intensity is a key determinant of ecological impact and should be explicitly considered when assessing regeneration processes and designing management interventions.

The study further reveals pronounced species-specific responses to invasion. While several species experienced strong declines in seedling density under high invasion, others showed neutral or even positive responses, indicating that invasion acts as a selective ecological filter shaping regeneration trajectories and potentially altering long-term community composition.

Beyond overall density patterns, invasion was also found to modify spatial recruitment processes and seedling size structure, reducing distance-dependent gradients and limiting the progression of seedlings to larger size classes. These findings demonstrate that invasion affects multiple dimensions of regeneration, with potential cascading effects on forest structure and recovery dynamics.

From a management perspective, our results emphasise the importance of early intervention. Preventing the establishment of dense Chromolaena odorata stands during early successional stages appears critical to maintaining regeneration potential. At the same time, the strong interspecific variability observed suggests that management strategies should be adapted to ecological context and species-specific responses rather than relying on uniform control approaches.

Overall, this study highlights that regeneration in human-modified tropical landscapes is governed by complex and context-dependent interactions between succession, invasion intensity, dispersal processes, and species traits. By demonstrating the importance of non-linear invasion effects and successional context, it contributes to a more mechanistic understanding of forest recovery processes outside forests and provides a foundation for more targeted and effective restoration strategies.

Declarations

Author Contribution

Jean Pierre Azenge conceptualised the study, designed the methodology, coordinated all research data collection and analysis interpretation, and drafted the manuscript. Paxie W. Chirwa and Justin N'Dja Kassi provided crucial academic supervision throughout the study, offering substantial intellectual inputs and critical revisions to the manuscript. All authors critically reviewed and approved the final version of the manuscript submitted for publication.

6. Acknowledgements

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Figures

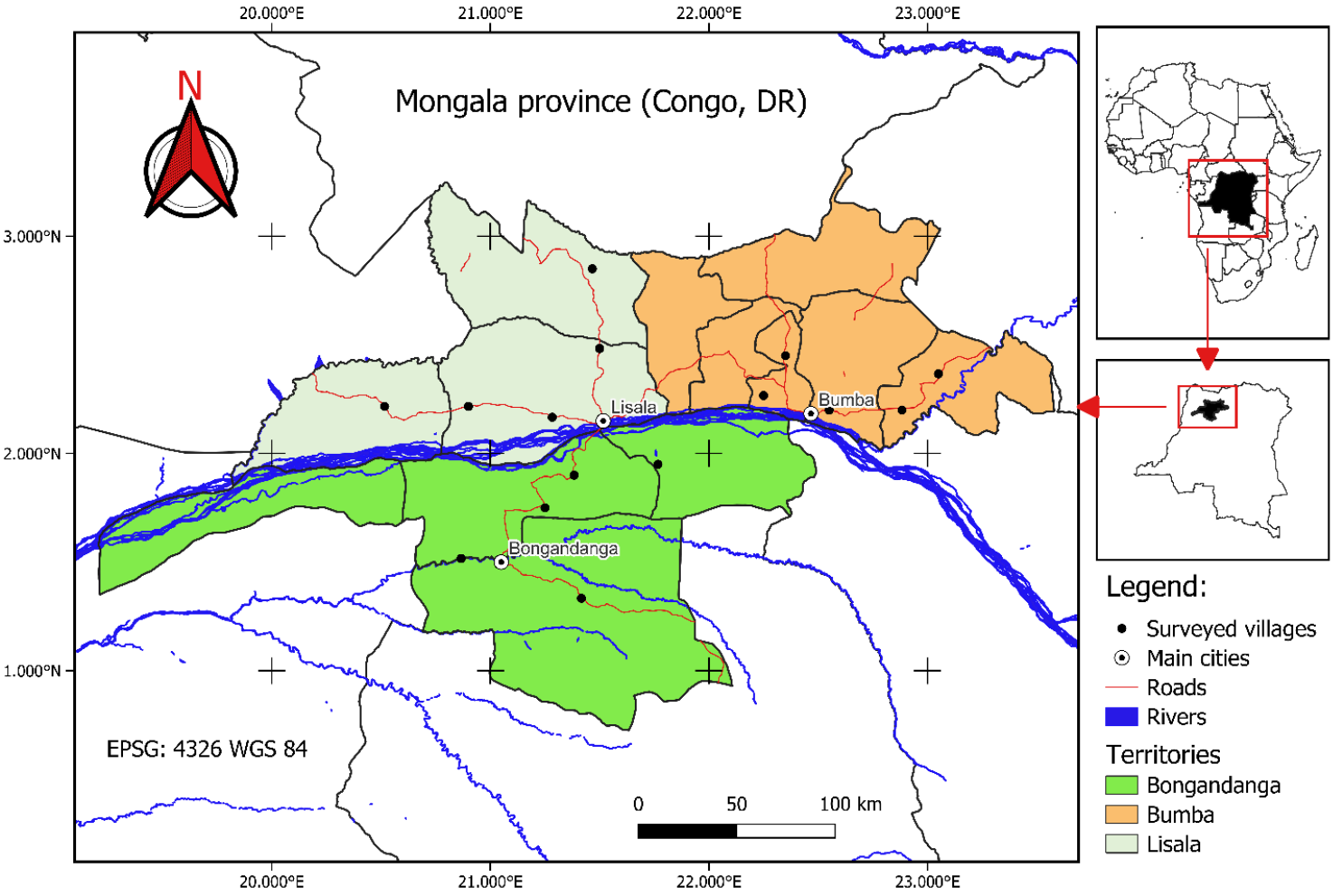

Figure 1

Location of surveyed villages and regeneration inventory sites in Mongala Province, Democratic Republic of the Congo.

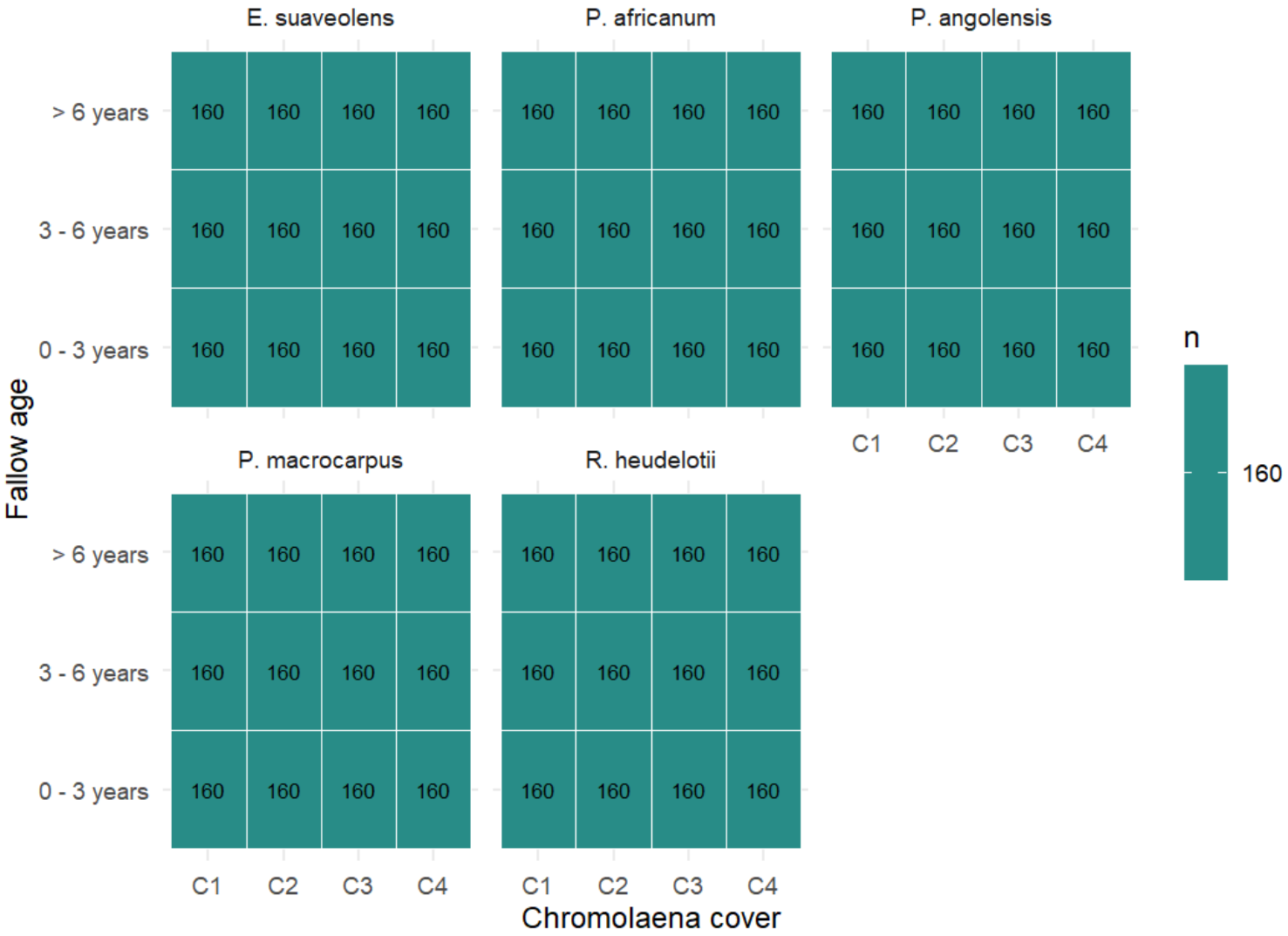

Figure 2

Heatmap of sample size distribution across species, fallow age classes, and Chromolaena odorata cover levels.

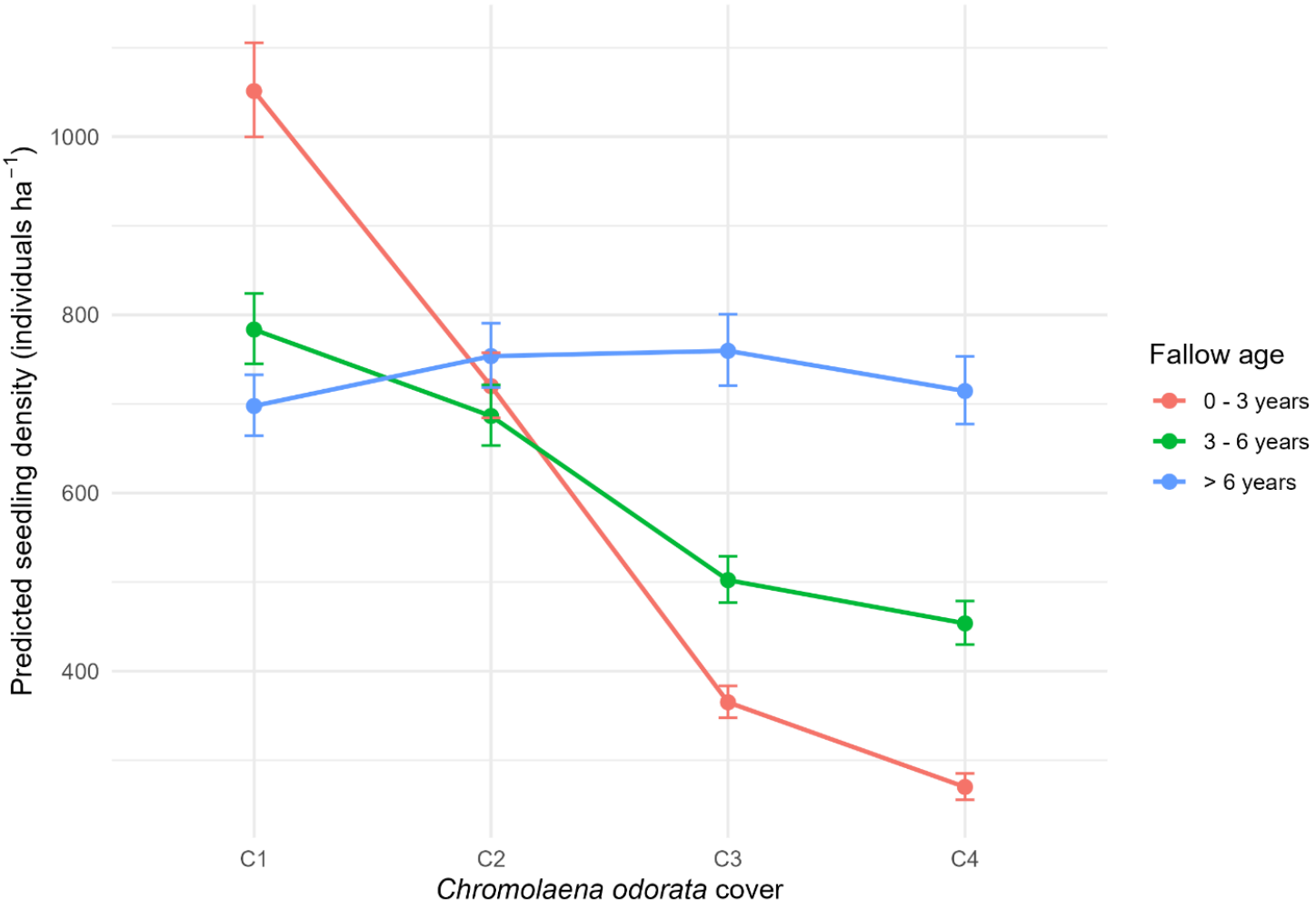

Figure 3

Predicted seedling density across Chromolaena odorata cover levels and fallow age classes based on zero-inflated negative binomial models (mean ± 95% confidence intervals).

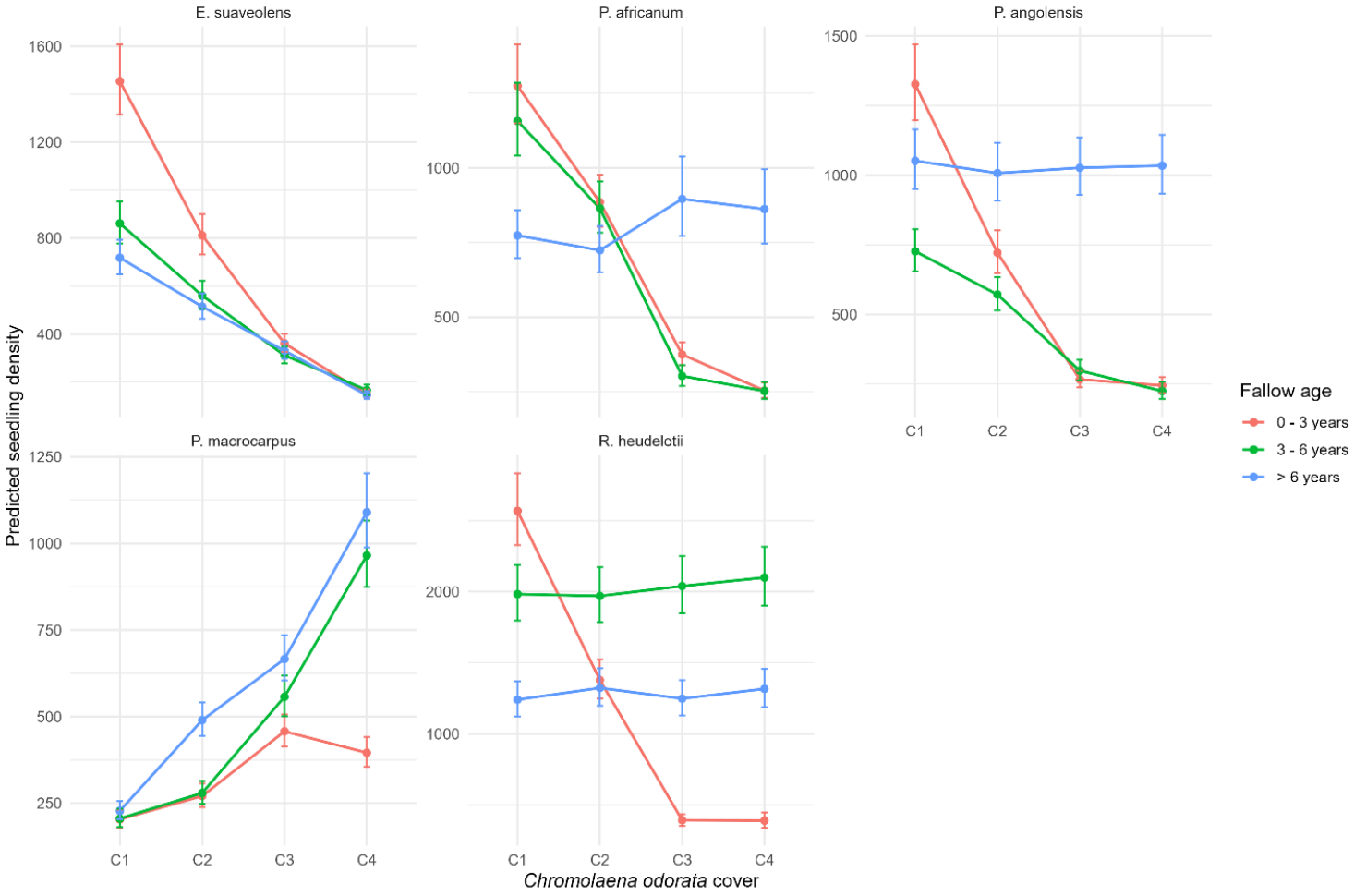

Figure 4

Species-specific predicted seedling density across Chromolaena odorata cover levels and fallow age classes derived from zero-inflated negative binomial models (mean ± 95% confidence intervals).

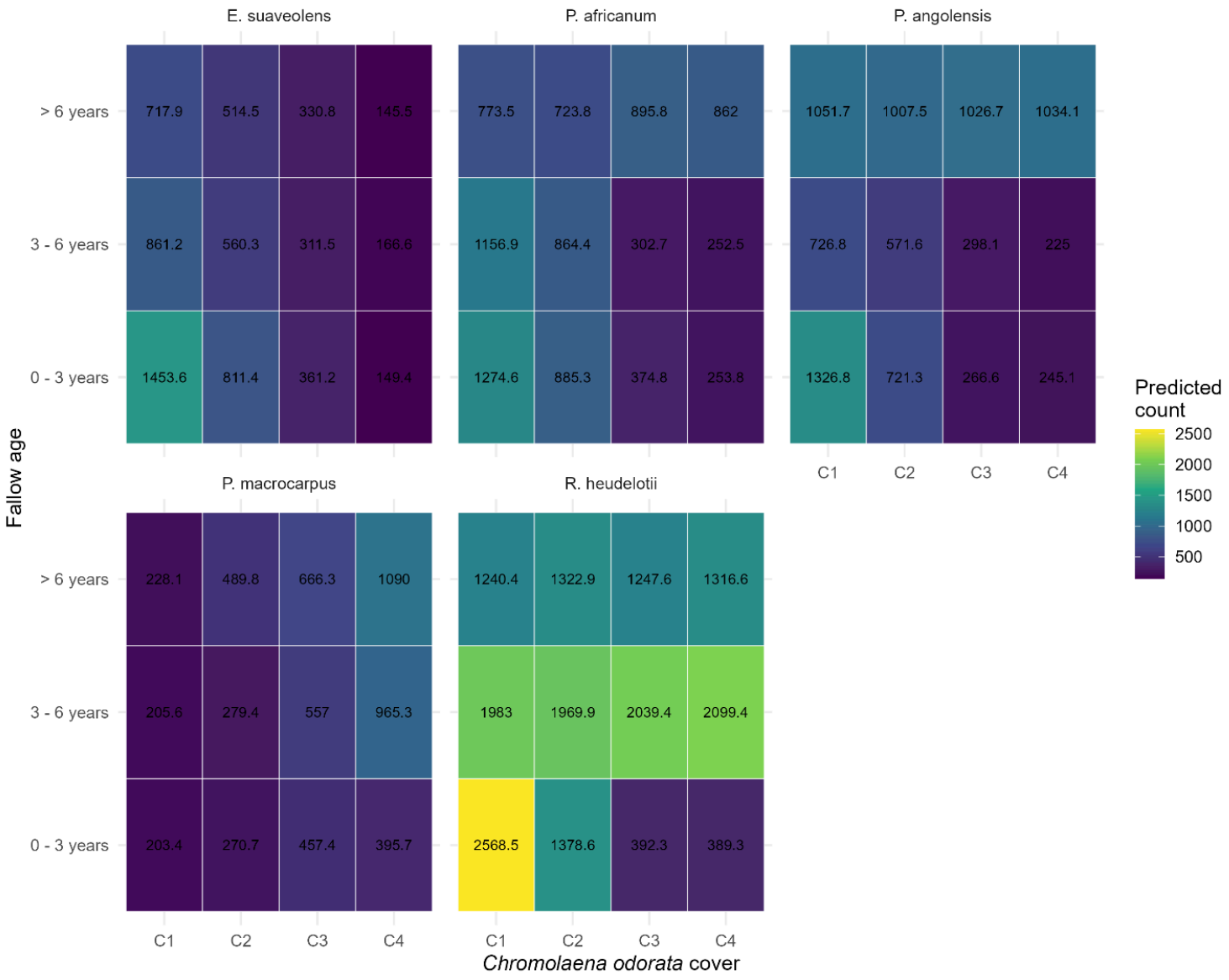

Figure 5

Heatmaps of predicted seedling density across fallow age and Chromolaena odorata cover levels for each species based on ZINB model predictions.

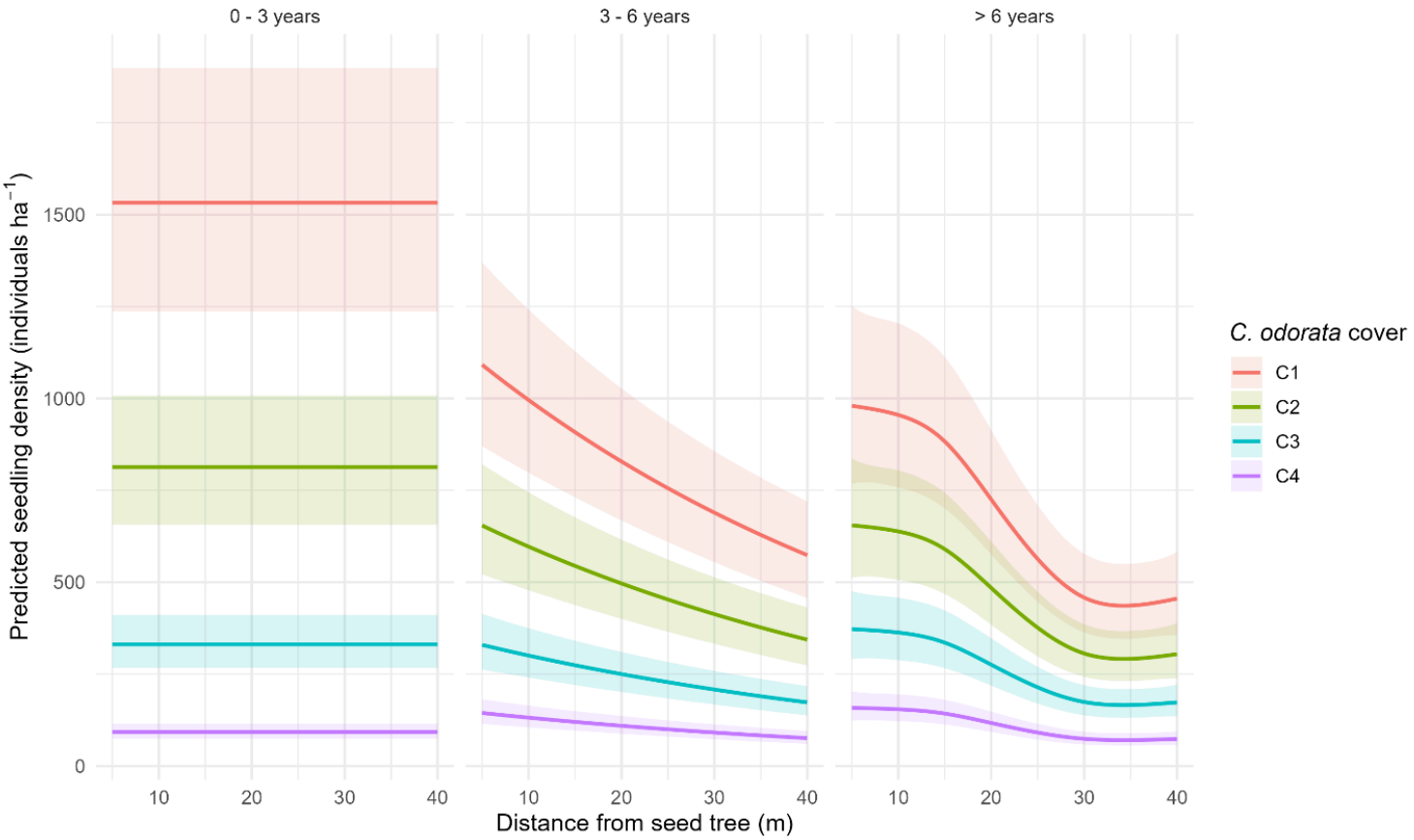

Figure 6

Predicted relationship between seedling density and distance from seed tree across fallow age classes and Chromolaena odorata cover levels based on ZINB models with spline functions (mean ± 95% confidence intervals).

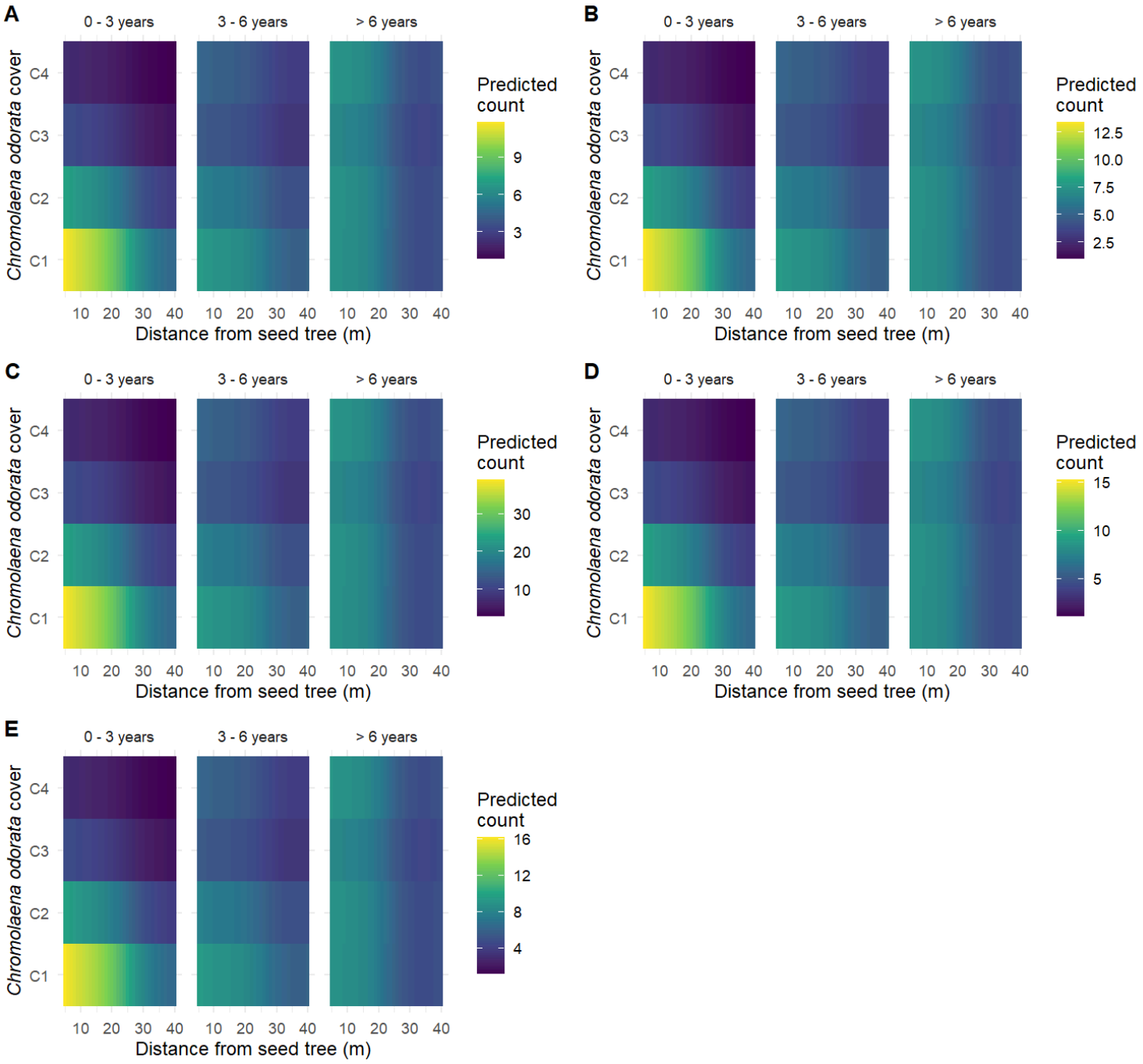

Figure 7

Predicted seedling density as a function of distance from seed tree and Chromolaena odorata cover across fallow age classes and species. Panels represent individual species (A: Erythrophleum suaveolens, B: Petersianthus macrocarpus, C: Ricinodendron heudelotii, D: Piptadeniastrum africanum, E: Pycnanthus angolensis).

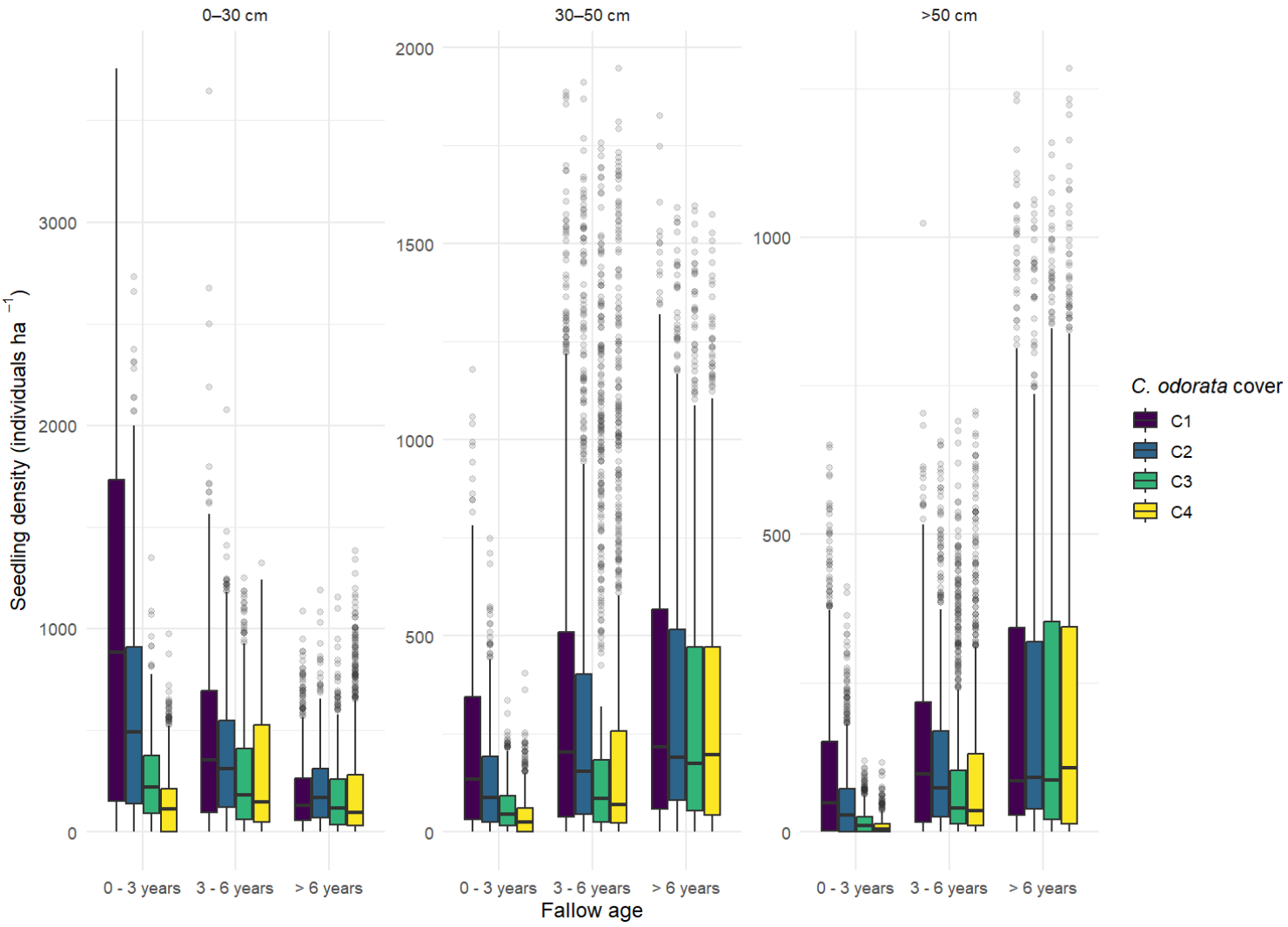

Figure 8

Relative composition of seedling height classes across fallow age and Chromolaena odorata cover levels, showing dominance of early-stage seedlings and reduced proportion of taller individuals under high invasion.

Supplementary Files

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- SupplementarymaterialAzengeetal23032026.docx