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Cavities and the Demographic Performance of Tropical Rainforest Trees

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ABSTRACT

In tropical forests, trees often have damage in the form of visible cavities. However, the impacts of these cavities on tropical tree growth and survival are unknown, despite potential implications for the global carbon cycle. Here, we integrate 10 years of forest dynamics data with a survey of cavity presence on 25,450 rainforest trees (> 5 cm in diameter) in the 20 ha Xishuangbanna plot in southern China. We found that cavities negatively impacted tree growth, but not survival, with the growth of smaller trees more negatively affected by cavities. Variation in the impact of cavities was not explained by functional traits related to species life history strategy (specific leaf area, wood density, seed mass, leaf %N, leaf %P). These results suggest that cavities may affect both the compositional and carbon dynamics of tropical forests, but further research is needed to determine what drives variation amongst tree species in cavity impact.

1 | Introduction

Tropical rainforests store roughly 46% of the world's terrestrial carbon pool (Soepadmo 1993) and make a substantial contribution to the global carbon cycle (Mitchard 2018; Pan et al. 2011). Numerous factors, including light, canopy position, stand density, climate variability, physiological and anatomical differences and others, regulate demographic rates across tropical tree species (Condit et al. 1996; Comita and Engelbrecht 2009; Eck et al. 2019; Rüger et al. 2011). Identifying the importance of each of these variables for tree growth and survival rates is critical as demographic differences scale up to dictate tropical forest dynamics, which in turn affect carbon dynamics, thereby impacting the global carbon cycle (e.g., Zuleta et al. 2023).

A potential factor impacting large tropical trees is the presence of tree cavities. Specifically, rates of externally visible trunk cavities are typically greater than 25% of the individuals with diameters greater than 60 cm in a tropical forest (e.g., Liu et al. 2018). The density and distribution of visible or open cavity trees in forest ecosystems are considered to be essential for the survival and dispersal of fauna that depend on cavities for breeding and shelter (Aitken and Martin 2007; Boyle et al. 2008; Zheng et al. 2009) which has wider implications for the conservation of biodiversity and forest management. To date, the majority of research on cavities has been conducted in temperate forests in order to disentangle the impacts of visible cavities on the diversity and richness of fauna that depend on cavities (Edworthy and Martin 2014; Remm and Lõhmus 2011; Zheng et al. 2009). Only

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five forests in tropical Asia have been studied extensively with respect to tree cavities (Boyle et al. 2008), and no long-term tree growth data have been linked to the presence of cavities in tropical forests.

The aims of the tree cavity research that does exist have varied from latitudinal comparisons to whether the traits of trees are related to cavity presence or formation. For example, Boyle et al. (2008) proposed a higher incidence of cavities from the poles to the tropics, where the prevalence of cavities is influenced by local terrain, species, tree size, stand density and crown positions (Fan et al. 2003; Liu et al. 2018; Remm and Lõhmus 2011; Zheng et al. 2009). The high number and density of cavities in tropical forests are thought to be related to a higher incidence of dead branches in live trees or branches that have diameters that are more suitable for cavity formation and increased susceptibility to disease in tropical trees (Boyle et al. 2008). Research on tree cavities has also indicated that the probability of cavity presence increases with trunk diameter (Lindenmayer et al. 1993; Liu et al. 2018; Zheng et al. 2009) as the size of the cavity increases with tree age (Lindenmayer et al. 1993). Additional work has shown that wood density is related to the likelihood of cavities (Dix et al. 1995), as it influences selections made by excavators (Zahner et al. 2012) and fungal activities are facilitated by the availability of oxygen and moisture in the wood (Dix et al. 1995).

The properties of tree cavities are dynamic, changing over time in tandem with the growth of the affected tree. For example, visible cavity sizes in living trees show a positive correlation with stem radial growth rates, where cavity sizes increase in depth by 0.84 cm year^{-1} in growing trees compared to 0.14 cm year^{-1} in dead trees (Zheng et al. 2016). However, the degree to which this occurs in other forests is unknown due to a lack of studies quantifying cavity size and radial growth for many individuals through time. Furthermore, entrance diameter, followed by vertical and horizontal depth of cavity expansion rates, both rise as cavities age in a tropical forest (Edworthy and Martin 2014), with tropical forests experiencing eight times greater vertical expansion than radial expansion (Zheng et al. 2016). Thus, not only does the probability of having a visible cavity increase with size, but the cavity itself continues to grow as the tree grows.

Cavity damage to the tree may reduce the transport of water and carbohydrates and increase the susceptibility of the affected individuals to pathogenic fungi and trunk mechanical failure. Thus, it should be expected that trees with cavities may experience lower growth and survival rates than trees without cavities. An alternative perspective was presented by Janzen (1976) who proposed that the presence of cavities provided an opportunity for perching and roosting of vertebrates. These vertebrates were more likely to defecate in these locations and thereby fertilise the soil surrounding the individual tree. This could lead to an increase in the performance of a tree with a cavity. It is worth noting that the Janzen (1976) hypothesis was focused on externally visible cavities and was not focused on internal heart rot, where no clear cavity is visible (Janzen, pers. comm.). Nevertheless, empirical knowledge on visible cavity impacts on demographic rates across tropical tree species is limited.

Beyond the general predicted impacts of cavities on tropical tree growth and survival, it is known that rates of cavity formation vary by species (i.e., Liu et al. 2018). It is possible that the sensitivity of tree species to the presence of cavities varies, and this variation may be predicted on the basis of the functional strategy of the species. Tree species vary along a spectrum from acquisitive to conservative functional strategies (Wright et al. 2010; Sterck et al. 2011; Worthy and Swenson 2019). Acquisitive species have faster resource acquisition rates, faster growth and lower survival rates. Traits associated with acquisitive species are low wood density, small seed size, higher specific leaf area and high leaf nutrient content. Conservative species have slower resource acquisition rates, slower growth and higher survival rates. These species have high wood density, large seeds, low specific leaf area and low leaf nutrient content (Wright et al. 2004; Chave et al. 2009). A hypothesised relationship between functional strategies and sensitivity to cavities is that trees with acquisitive strategies may be more susceptible to heart rot fungi and branch breakage (e.g., due to their lighter wood) and require more water transport for photosynthesis, whereas conservative species can withstand the negative impacts of cavities. An alternative hypothesis is that acquisitive species may be able to simply withstand cavities through rapid resource acquisition and growth, and conservative species may not be able to mitigate the impacts of cavities due to their slower rates of resource acquisition. Lastly, we may expect that the impact of functional strategies on the sensitivity of growth and survival rates of trees may interact with tree size. Specifically, larger trees with acquisitive strategies may be less likely to survive when experiencing a cavity, as they are likely closer to the safety margin for trunk mechanics (Figure 1).

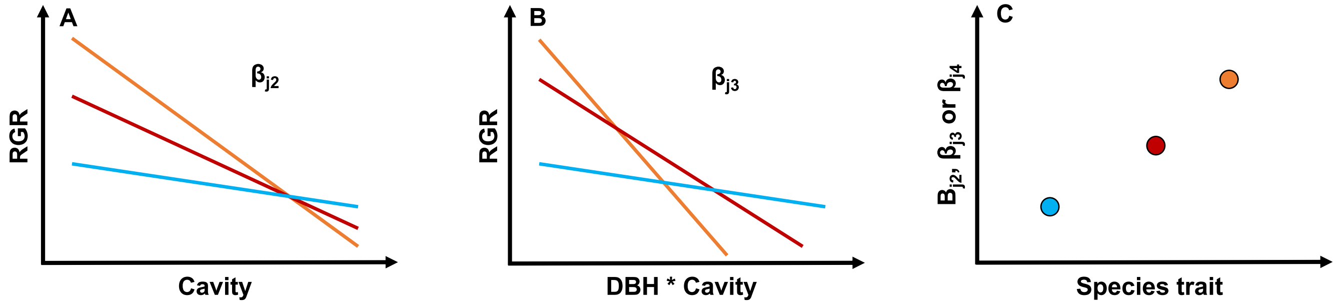

FIGURE 1 | A conceptual figure showing the expected relationships between performance (here growth), the presence of a cavity (Panel A; parameter β_{j2}) and the interaction between DBH and cavities (Panel B; parameter β_{j3}). Here, species-level random effects are modelled for the cavity and DBH*cavity parameters. Species-level functional trait data can be correlated with the species-level parameter estimates (Panel C) by randomly drawing from the posterior distributions of those parameter estimates (see Methods).

In this study, we utilise a large data set that facilitates the linkage between the presence of tree cavities and their growth and survival rates. Specifically, 25,450 individual trees were inspected for cavities in a tropical forest in China, and their growth and survival rates were recorded over 10 years. The three main questions we address are: (i) Does the presence of cavities impact individual tree growth, and does this change with size?; (ii) Does the presence of cavities impact individual tree survival, and does this change with size? and (iii) Are there species-specific differences in growth and survival sensitivity to cavities and are acquisitive or conservative individual trees species more sensitive?

2 | Methods

2.1 | Study Location

The 20 ha Xishuangbanna Forest Dynamic plot (XFDP), which is located in China near the northern limit of the tropics (21°36′42″ N–21°36′58″ N, 101°34′26″ E–101°34′47″ E), served as the site for our study. The conservation of biodiversity is given priority in this region of the world (Myers et al. 2000). This forest, which is a tropical seasonal rainforest, contains 468 species of trees. The region has a mean annual temperature of 21°C and receives 1532 mm of precipitation (Lan et al. 2011). After the wet season, which lasts from May to October, the dry season lasts from November to April, with an average precipitation of 282 mm during this time (Zhu et al. 2006). The plot, which measures 400 m by 500 m, was divided into 2000 subplots, each measuring 10 m by 10 m and standing between 710 and 866 m above sea level ($n=2000$). All free-standing stems in the XFDP with a diameter greater than 1 cm at 130 cm above the ground (dbh) were tagged, identified as to species, mapped and measured in 2007 ($n=95{,}629$) and 2017 ($n=96{,}419$).

2.2 | Tree Cavity Survey

This study utilises tree cavity survey data collected by coauthors in 2010 and are described in Liu et al. (2018). Here, we briefly describe the methodology used in that work. First, it is important to note that the study only considers visible cavities on the tree. Thus, any heart rot in trees that was not associated with a visible cavity was not considered, and this undoubtedly introduced error into our analyses. In this study, every living individual in the forest dynamics plot with a diameter at breast height (dbh) equal to or greater than 5 cm was inspected for the presence of a cavity utilising a combination of binoculars, ladders and rope climbing (< 500 trees). As rope climbing requires substantial effort, it was only used on very large individuals where the bole could not be clearly seen via binoculars on the ground or via a ladder. Ideally, we would climb every one of the thousands of trees in the forest, but this is not feasible, would risk damaging individuals in a long-term plot, and poses an increased safety risk. Thus, a second caveat of our approach is that we undoubtedly missed some visible cavities in our survey. A cavity tree was defined as a tree containing at least one visible cavity with a minimum diameter of 2 cm and a depth that appeared to be greater than 2 cm. This definition follows that used in previous work (Fan et al. 2003; Koch 2008). A total of 27,745 individual trees from the 386 species had at least one individual with a dbh greater than or equal to 5 cm. A total of 1725 trees (6.22%) were determined to have visible cavities given our criteria (Liu et al. 2018). The percentage of trees with cavities increases with size class. For example, 2.84% of all trees have a cavity, while 26.84% of trees with a dbh of at least 60 cm have a cavity (Liu et al. 2018).

2.3 | Functional Traits

Our previous work has collected functional trait data that were utilised in this study (Yang et al. 2018). We were interested in utilising trait data that are believed to represent where a species falls along a life history continuum characterised by acquisitive (i.e., fast) to conservative (i.e., slow) trait syndromes. The traits we measured were specific leaf area (SLA), wood density, seed mass, leaf %N and leaf %P. All traits were measured on at least 3 individuals per species using globally standardised protocols (Perez-Harguindeguy et al. 2016). The individuals measured occurred within the forest dynamics plot or were located in the forest immediately surrounding the plot. Leaf traits were measured on fully expanded and hardened canopy leaves. Species mean trait values were calculated and z-scaled for downstream analyses. Acquisitive trait values are high SLA, low wood density, low seed mass, high leaf %N and high leaf %P. Conservative trait values are the reverse of the acquisitive trends.

2.4 | Models of Tree Growth Rates

Tree relative growth rates were calculated for individuals from 2007 to 2017 where only species with 30 or more individuals were included. There are obvious sources of error that were removed from the dataset prior to analysis. These include instances where the height at which the diameter was recorded changed between censuses and using the approach of Condit et al. (2004) that removes extremely high or low dbh (i.e., four standard deviations from the mean) values compared to the prior census. Next, we modelled tree relative growth rates as a function of the dbh in the first census, the presence or absence of a cavity, and the interaction of the variables using a hierarchical Bayesian approach. The form of these models was:

$$\begin{aligned}\mu_{i,j} = \alpha + \alpha_j + \beta_{j1}{}^{*}\ \log\left(\mathrm{DBH}_i\right) + \beta_{j2}{}^{*}\ \mathrm{Cavity}_{i,j} \\ + \beta_{j3}{}^{*}\ \log\left(\mathrm{DBH}_{i,j}\right)^{*}\ \mathrm{Cavity}_{i,j} + z_k\end{aligned} \tag{1}$$

where $\mu_{i,j}$ is the expected log relative growth rate of individual i in species j, α is a global intercept, α_j is a species-specific intercept for species j and β_{j1} is the slope relating log(DBH) to RGR for species j. The parameters β_{j2} and β_{j3} are the slope parameters for species j for $\mathrm{Cavity}_{i,j}$ and the interaction between dbh and $\mathrm{Cavity}_{i,j}$, respectively. Finally, we included the z_k parameter, which is a random effect for each 20 × 20 m quadrat k. We utilised a Mantel correlogram to quantify the scale of spatial autocorrelation in the dataset, and it was on a scale less than 20 × 20 m (10.6 m). We, therefore, used this quadrat scale to account for potential spatial autocorrelation. In these models, the $\mu_{i,j}$ was normally distributed, and the slope parameters had weak normal priors, as described in Appendix S1. The models were run in STAN (Stan Development Team 2018) via the *rethinking* R package version 2.4 (McElreath 2023) run on R version 4.4.1 (R Core Team 2024). We considered models with a

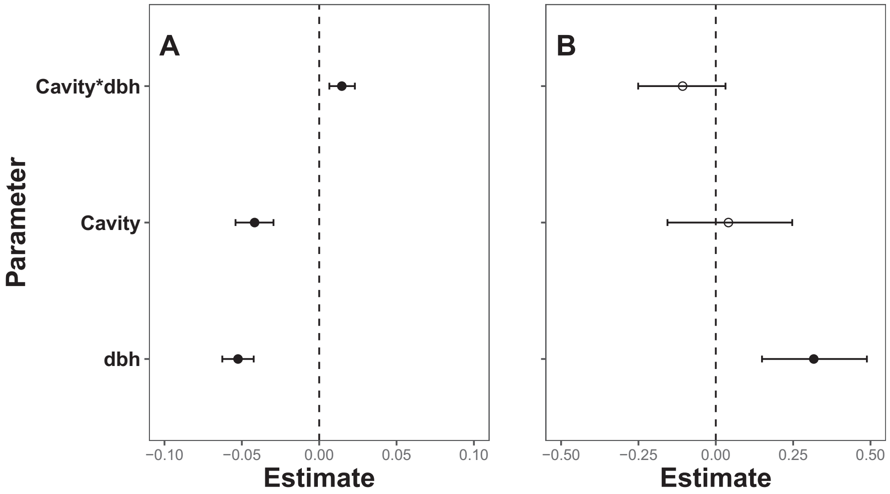

FIGURE 2 | Model parameter estimates for relative growth rate (A) and survival (B). The point indicates the mean of the posterior distribution and the bars indicate the 95% credible interval. Open circles indicate the 95% credible interval includes zero and fill circles indicate that it does not. The dbh, Cavity and dbh*Cavity parameters are β_1, β_{j2} and β_{j3} and in Equations (1) and (2).

quadratic term for dbh, but these models failed to adequately converge and were no longer explored.

2.5 | Models of Tree Survival Rates

We modelled individual tree survival from 2007 to 2017 using a hierarchical Bayesian approach where only species with 30 or more individuals were included. We assumed tree survival had a binomial distribution and was linearly related to DBH in the first census of an interval, the presence or absence of a cavity and the interaction of these two variables. The form of the model was:

$$\begin{aligned}\operatorname{logit}\left(p_{i,j}\right) &= \alpha + \alpha_j + \beta_{j1}{}^{*}\ \log\left(\mathrm{DBH}\right)_i + \beta_{j2}{}^{*}\ \mathrm{Cavity}_{i,j} \\ &+ \beta_{j3}{}^{*}\ \log\left(\mathrm{DBH}_{i,j}\right)^{*}\ \mathrm{Cavity}_{i,j} + z_k\end{aligned} \tag{2}$$

where logit($p_{i,j}$) is the logit transformation of the survival (1) or death (0) of individual i. The α is a global intercept, α_j is a species-specific intercept for species j and β_{j1} is a slope relating log(DBH) to survival for species j. The parameters β_{j2} and β_{j3} are the slope parameters for species j for Cavity$_{i,j}$ and the interaction between dbh and Cavity$_{i,j}$, respectively. All slope parameters each had weak normal priors as described in Appendix S1. Again, we included the z_k parameter as a random effect for each 20 × 20 m quadrat k to account for potential spatial autocorrelation, which tends to occur within this spatial proximity (Liu et al. 2018). These models were also implemented in STAN (Stan Development Team 2018) using the *rethinking* R package version 2.4 (McElreath 2023) run on R version 4.4.1 (R Core Team 2024). The full specification for both models and the code is available in Appendix S1. We also considered models with a quadratic term for dbh, but these models failed to adequately converge.

2.6 | Functional Traits & Demographic Rate Model Parameters

Next, we sought to address the question of whether functional traits at the species level were related to growth and survival rates in general and to the responses to the presence of a cavity. This was accomplished by first sampling from the species-specific posterior distributions of the α_j, β_{j2}, and β_{j3} model parameters, respectively, in the growth and survival models for both census intervals 10,000 times (e.g., Iida et al. 2016). In other words, we sampled the species-specific intercept and slopes from their respective posterior distributions. Then, for each sample, we used a Kendall's correlation analysis to correlate species-level trait values with the sampled intercept or slope value. This was repeated for all 10,000 samples of the posterior distributions and resulted in a distribution of 10,000 Kendall's Tau coefficients from which we report the median Tau value and the 95% credible interval.

3 | Results

3.1 | Models of Cavities and Tree Growth

We modelled tree relative growth rate (RGR) as a function of dbh, cavity presence and the interaction term during each census interval. Across all species, the RGR of trees declined with dbh and was negatively impacted by the presence of cavities (Figure 2A). There was also a significant positive interaction between cavities and dbh on tree growth. Thus, growth in smaller trees was more negatively impacted by the presence of cavities as compared to larger trees (Figure 2A). Figures of the posterior predictive distributions binned by dbh without and with cavities are presented in the supplemental material (Figure S5). The posterior checks indicated that the model was able to capture size-dependent changes in growth such that an alternative model (e.g., one with a quadratic term associated with dbh) was not needed.

3.2 | Models of Cavities and Tree Survival

A total of 3413 of the 25,450 individual trees studied (13.41%) died over the 10 years studied. We investigated the impact of dbh, cavities and their interaction on tree survival (Equation 2). We found no relationship between any of the independent variables

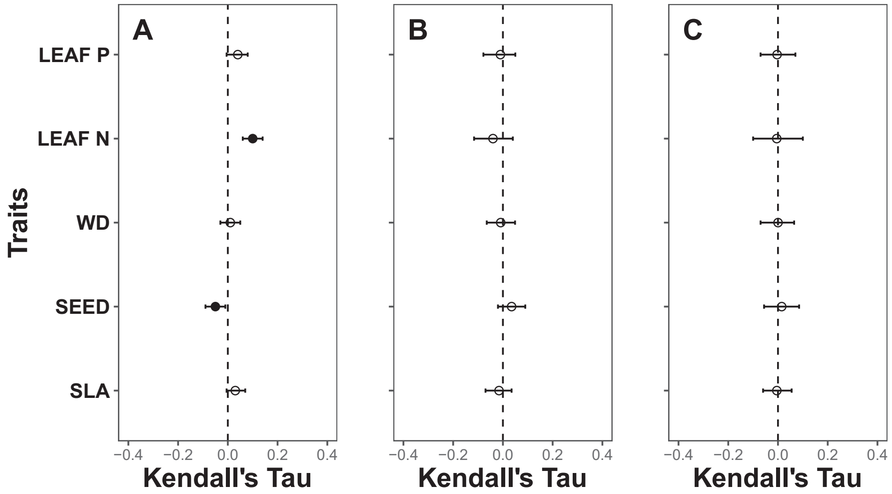

FIGURE 3 | The correlation between functional traits and the posterior distribution of growth model parameters. The point is the mean of 10,000 Kendall's Tau values and the bars are the 95% credible intervals. Open circles indicate the bars overlap with zero and the closed circles indicate they do not. Panel A are the correlations between the intercept (α_j). Panel B are the correlations for the cavity parameter (β_{j2}). Panel C are the correlations for the DBH*cavity parameter (β_{j3}). Leaf N, leaf %N; Leaf P, leaf % P; SEED, seed mass (g); SLA, specific leaf area (cm^2/g); WD, wood density (g/cm^3).

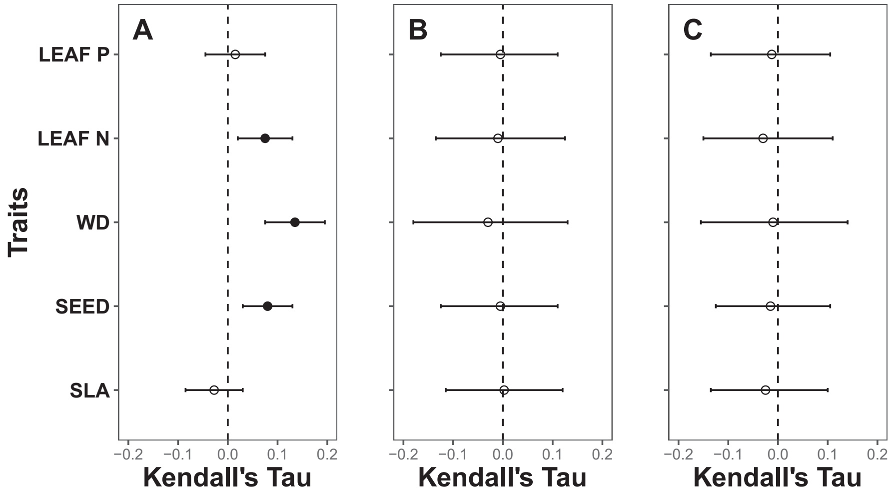

FIGURE 4 | The correlation between functional traits and the posterior distribution of survival model parameters. The point is the mean of 10,000 Kendall's Tau values and the bars are the 95% credible intervals. Open circles indicate the bars overlap with zero and the closed circles indicate they do not. Panel A are the correlations between the intercept (α_j). Panel B are the correlations for the cavity parameter (β_{j2}). Panel C are the correlations for the DBH*cavity parameter (β_{j3}). Leaf N, leaf %N; Leaf P, leaf %P; SEED, seed mass (g); SLA, specific leaf area (cm^2/g); WD, wood density (g/cm^3).

and survival (Figure 2B). Indeed, survival was not consistently related to dbh using either linear or quadratic relationships. Thus, other variables outside of cavities and size are stronger drivers of survival in the forest studied. The posterior predictive checks binned by dbh for trees without and with cavities are presented in the supplemental material (Figure S6).

3.3 | Functional Trait Correlations of Growth and Survival Model Parameters

The growth and survival modelling frameworks utilised in this study include species-level random effects on the intercept (α_j), cavity (β_{j2}) and dbh*cavity (β_{j3}) parameters. There was variation amongst these species-specific parameter estimates (Figures S1–S4). We were first interested in whether species-specific RGR and survival rates (i.e., α_j) were correlated with functional traits. We found that RGR was higher in species with higher leaf N and species with lower seed mass (Figure 3). Thus, some acquisitive trait strategies, but not all (i.e., no relationship with low wood density, high leaf P or high SLA) tended to be correlated with faster RGR at the species level. Survival was higher in species with higher wood density, higher seed mass and higher leaf N (Figure 4). The increase in survival in species with higher wood density and higher seed mass (i.e., conservative strategies) was anticipated, but increased survival in species with higher leaf N (i.e., an acquisitive strategy) was not.

Next, we investigated whether species-specific sensitivity to cavities (i.e., β_{j2}) was correlated with their functional trait values. We found that there was no relationship between any of the traits measured and their observed changes in sensitivity to cavities in either census interval for RGR (Figure 3) or survival (Figure 4). Thus, while we found that species, on average, experience significant changes in their RGR or survival rates when they have visible cavities, this was not related to the functional traits measured.

Finally, we investigated whether the sensitivity of species to visible cavities was related to their trait values via correlating traits with the posterior distribution of the interaction parameters (i.e., β_{j3}). We found that the functional traits in this study were unrelated to these parameters (Figures 3 and 4). Here, we highlight the potential for shrinkage in these models, particularly when considering dbh. Thus, the lack of evidence for species-level interaction terms and their correlations with the functional traits measured in this study may be due to low sample sizes for rare species across the dbh range.

4 | Discussion

The presence of tree cavities is frequently found in tropical tree communities, particularly in large trees (Heineman et al. 2015; Lindenmayer et al. 2012; Liu et al. 2018). Here, using a survey of cavity presence and absence from 25,450 trees in a long-term forest dynamics plot, we quantified the linkage between cavities and tree growth and survival rates and how these linkages are influenced by tree diameter and functional strategies. We show that trees with cavities have lower growth rates, and this effect is exacerbated in smaller trees (Figure 2). Conversely, the presence of tree cavities was not linked to survival rates (Figure 2). Finally, species-level variation in relative growth rates (RGR) and survival rates was predicted by only some of the functional traits measured in this study (Figures 3 and 4), but the sensitivity of individual species (i.e., the magnitude of impact of cavities on RGR or survival rate) was not related to these traits. In the following, we discuss these results and their implications in detail.

4.1 | Impact of Cavities on Growth and Survival Rates in a Tropical Rain Forest

We conducted a quantitative assessment of how cavities influence the relative growth and survival rates in a tropical rainforest trees in a forest dynamics plot. A total of 25,450 living trees were inspected. The results from our regression models uncovered that RGR is negatively impacted by the presence of cavities, and this negative effect was magnified in smaller trees (Figure 2). Lastly, we show that RGR declined in larger trees, which is known generally in the forestry literature (e.g., Lindenmayer et al. 1993). We have previously shown that larger trees tend to have a higher frequency of cavity presence (Liu et al. 2018). Taken together, the presence of cavities had a negative impact on tree RGR in this tropical rainforest study and may have an under-appreciated impact on the carbon dynamics of tropical forests (e.g., Heineman et al. 2015; Zuleta et al. 2023). Survival rates in trees were no different in trees with or without cavities. Combined, the results show that cavities had a negative impact on tree RGR and no impact on tree survival. Thus, the results reject an expectation arising from Janzen (1976) who suggested tree cavities promote the recruitment of nutrients that should be expected to improve tree performance.

4.2 | Interspecific Sensitivity to Cavities and Functional Strategies

The regression models used in this study had species-level random effects on the intercept, on the term relating cavities to tree performance, and the interaction term for dbh and cavity presence. We hypothesised that interspecific variation in RGR and survival and their sensitivity to cavities was likely to be linked to where species fall along a continuum of conservative to acquisitive functional strategies defined on the basis of functional traits. The RGR and survival rate results both indicate that some traits are related to species differences (i.e., model intercepts) in these rates. Specifically, high RGR is correlated with higher leaf nitrogen and lower seed mass. These are both trait strategies associated with acquisitive strategies. However, it is noteworthy that leaf P, wood density and SLA had no impact on RGR. Thus, acquisitive values for only two of the five traits were related to RGR (Figure 3A). The species-level survival intercept was positively related to leaf N, wood density and seed mass. Higher (i.e., conservative) values of wood density and seed mass are expected to be related to survival (e.g., Wright et al. 2010), but higher leaf N (i.e., acquisitive) values are not. Furthermore, leaf P and SLA were not related to survival. Thus, the trait correlations did not neatly fit the expectations between high survival and conservative trait values (Figure 4A).

The functional traits studied were not related to inter-specific differences in the RGR and survival rate sensitivities to cavities (i.e., the slopes) in the models. We also did not find any trait relationships with the interaction terms in the models (Figures 3 and 4). Thus, while some trait differences are related to RGR and survival rates, the degree to which RGR or survival changes when there is a cavity does not appear to be linked to the traits measured. There are multiple potential reasons for this outcome. One possibility is that the traits measured are simply not the right traits (Yang et al. 2018; Swenson and Rubio 2025). For example, more information about canopy allometry may be more predictive as it would be more directly related to the mechanical challenges a tree with a cavity may be experiencing. Second, while we may be measuring the right traits, and there is some reason to believe this given their correlations with the intercept parameters, we may need to have individual-level information for stronger models. Third, the commonness of rarity in communities and, particularly, in diverse tropical communities may have resulted in an inability to detect true species differences. However, we note that such differences could be detected in the intercepts and their correlations with traits are functionally expected. Lastly, the challenge of conducting cavity surveys of all individuals in a forest certainly introduces error. We most likely did not observe all visible cavities; differences in cavity size and age are important, and non-visible cavities and rot are important.

5 | Conclusions

Here, we have leveraged a unique large-scale survey of external tree cavities in a tropical forest dynamics plot to demonstrate the linkages between cavities and tree performance. We demonstrate that cavities have negative impacts on tree RGR, particularly in smaller trees, but no impact on survival. These negative impacts on growth have several important implications for our understanding of forest dynamics and carbon. For example, previous work has highlighted that above-ground biomass estimates based upon allometric equations utilising dbh data are likely to overestimate biomass and, therefore, carbon due to the high frequency of cavities that are not typically considered (Chave et al. 2014; Heineman et al. 2015; Marra et al. 2018; Zuleta et al. 2023). Thus, cavities likely have profound impacts on not only the compositional dynamics of forests but also their carbon dynamics, and these impacts have yet to be well studied or incorporated into forest models (e.g., Zuleta et al. 2023). The present work takes an important step in this regard by uncovering the linkages between tree cavities and performance.

Author Contributions

D.D., S.J.W., J.-Y.L. and N.G.S. designed the study; J.-Y.L., Z.Z., M.C. and J.Y. collected the data; D.D., S.J.W. and N.G.S. analysed the data; D.D. wrote the manuscript with contributions from all co-authors.

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Data Availability Statement

The individual growth, survival and cavity data and the species-level functional trait data are in a Dryad repository that is made public upon acceptance here: https://doi.org/10.5061/dryad.dz08kps7h. The code for running the models in this paper is in Appendix S1 via Zenodo here: https://doi.org/10.5281/zenodo.14719740.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.