HAL
open science

From seedlings to adults: Linking survival and leaf functional traits over ontogeny

María Natalia Umaña, Jessica Needham, Claire Fortunel

▶ To cite this version:

HAL Id: hal-04814108

https://hal.inrae.fr/hal-04814108v1

Submitted on 2 Dec 2024

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

From seedlings to adults: Linking survival and leaf functional traits over ontogeny

María Natalia Umaña[1] ⬤ | **Jessica Needham**[2] | **Claire Fortunel**[3] ⬤

[1]Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan, USA

[2]Climate and Ecosystem Sciences Division, Lawrence Berkeley National Laboratory, Berkeley, California, USA

[3]AMAP (Botanique et Modélisation de l'Architecture des Plantes et des Végétations), Université de Montpellier, CIRAD, CNRS, INRAE, IRD, Montpellier, France

Correspondence
María Natalia Umaña
Email: maumana@gmail.com

Abstract

As long-lived tropical trees grow into the multi-layered canopy and face different environmental conditions, the relationships between leaf traits and whole-plant survival can vary over ontogeny. We tested the strength and direction of the relationships between leaf traits and long-term survival data across life stages for woody species from a subtropical forest in Puerto Rico. Trait–survival relationships were largely consistent across ontogeny with conservative traits leading to higher survival rates. The stage-specific relationship R^2 increased by up to one order of magnitude compared to studies not considering ontogenetic trait variations. Stage-specific traits were significant predictors of their corresponding stage-specific survival: Seedlings traits were better predictors of seedling survival than adult traits, and adult traits were better predictors of maximum adult survival than seedling traits. Our results suggest that stage-specific leaf traits reflect different strategies over ontogeny and can substantially improve predictability of survival models in tropical forests.

KEYWORDS
demography, forest dynamics plot, leaf economics traits, long-term tree surveys, Puerto Rico, seedling plots

INTRODUCTION

Plant functional traits have been widely recognized as a powerful tool for gaining a mechanistic, generalizable understanding of ecology, including mechanisms underlying species interactions, community structure, and ecosystem functioning (McGill et al., 2006; Reich, 2014; Violle et al., 2007). Trait-based approaches have mainly focused on species-level differences using species averaged values in comparative studied, often overlooking the role of intraspecific trait variation (Kraft et al., 2008; Reich et al., 1997). In particular, trait-based approaches often assume that the effects of traits on performance remain consistent over time and independent of the ontogenetic

stage at which the relationship is evaluated. However, there is mounting evidence for the role of intraspecific trait variation in ecological processes (Bolnick et al., 2011; Umaña et al., 2018), especially for long-lived organisms such as trees, which undergo substantial morphological, structural, and physiological changes over their life cycle (Barton, 2023; Fortunel et al., 2020, Barton & Boege, 2017). Furthermore, demographic rates in trees also vary with ontogeny (Hérault et al., 2011; King, 2011) and the traits that optimize demography might differ across trees' life cycle and in some cases exhibit rank reversals (Pu et al., 2020; Visser et al., 2016, Lasky et al., 2015). Therefore, identifying deviations from the trait–performance relationships linked to trait variation over ontogeny is necessary to understand stage-specific behaviors that should be accounted for to improve predictability of the trait framework.

Trait shifts over ontogeny can be the result of shifts in allocation patterns or changes in environmental conditions that occur over trees' life cycle (Barton, 2023; Pigliucci, 2001). These trait changes may subsequently affect the relationships with performance over tree's ontogeny (Visser et al., 2016). For instance, specific leaf area—SLA, the area deployed for light interception by unit dry mass—is typically weakly related to adult tree survival but has been suggested to better predict survival at the seedling stage (Kitajima, 1994). This discrepancy in the role of SLA on demographic rates across developmental stages is attributed to variation in resource allocation with size (Falster et al., 2011; King, 2011), where larger trees invest more in structural tissues relative to photosynthetic tissues than seedlings (King, 2011). As a result, the relationship between light-related leaf traits and whole-plant performance (e.g., survival) may be stronger in earlier ontogenetic stages than in adult trees. In other cases, ontogenetic changes in traits may result from shifts in local conditions, such as increases in light availability and/or hypothesized decreases in herbivore pressure as trees age, which results in leaves that are more conservative in carbon processing—according to leaf economics spectrum (LES) (Wright et al., 2004)—and less defended (Boege et al., 2007). These leaf trait shifts can enhance trees' resource acquisition (e.g., carbon processing) for the stage-specific local conditions and subsequently increase performance. Regardless of the underlying sources causing trait variation, these changes may affect trait–performance relationships over ontogeny and traits at a particular stage may be better predictors of demography at that stage than at other stages. To disentangle the complex interplay between tree traits, ontogeny, and performance requires stage-specific trait information.

One further limitation when assessing the relationships between traits and performance is that trees exhibit important ontogenetic changes in their demographic rates (King et al., 2006). Tree survival typically follows a hump-shape

pattern as trees increase in size (often used as a proxy of ontogeny), with lower survival rates in young and older trees (King et al., 2006; Ryan & Yoder, 1997). Earlier studies have used species mean rates to assess the trait–demography relationships (Martínez-Vilalta et al., 2010), but this approach overlooks potential inconsistencies in these relationships across trees' life cycle (Chen et al., 2018; Lasky et al., 2015). To address this limitation, recent studies have developed approaches that account for size-dependent mortality asymmetries, providing promising avenues for building an integrated and compelling demographic framework for studying demography in forest communities (Needham et al., 2018, 2022). For example, Needham et al. (2018) examined size-dependent survival for tree species that moved beyond mean population parameters and accounts explicitly for individual heterogeneity across developmental stages in demography.

In this study, we sought to bridge survival rates and leaf traits over ontogeny for trees occurring in a species-rich community in a subtropical forest in Puerto Rico. We compiled long-term census data from tree and seedling communities and measured leaf traits for seedlings and trees (Thompson et al., 2002; Umaña et al., 2015, 2016; Uriarte et al., 2005, 2009). We focused on four leaf traits capturing photosynthetic and structural functions that have shown weak relationships with tree survival (Wright et al., 2010; Visser et al., 2016) and wide intraspecific variation (Fortunel et al., 2020; Siefert et al., 2015). Specifically, we ask: (1) Does the directionality of the relationships between leaf traits and survival remain consistent throughout ontogeny? (2) Is the stage-specific trait–survival relationship stronger when traits are measured at the matching stage? We hypothesize that the direction of the relationship between traits and survival rates will remain consistent throughout ontogeny, with leaves with acquisitive LES traits (e.g., high SLA) and lower investment in structural tissues (e.g., low leaf C content) showing higher survival rates. However, we expect that the strength of the relationship will vary depending on the trees' developmental stage. For instance, the leaf trait–survival relationship will be stronger during the seedling stage due to a higher allocation of resources to photosynthetic tissues. Additionally, we predict that the relationship will be stronger when considering trait and survival rates at the same developmental stage, such as seedling trait and seedling survival or adult traits and adult survival.

METHODS

Study site

The study was performed at the 16-ha Luquillo Forest Dynamics Plot (LFDP) located in a subtropical wet

forest in the northeastern part of Puerto Rico (Thompson et al., 2002). The mean annual rainfall is 3500 mm/year, the mean temperature is 25°C, and the elevation of the LFDP ranges between 333 and 428 m above sea level. The forest harbors around 143 tree species and is dominated by the palm *Prestoea acuminata* and the tabonuco tree (*Dacryodes excelsa*) (Thompson et al., 2002). The forest composition is the result of human and natural disturbance; the hurricanes that are most relevant for the data used are hurricane Hugo (category 3, 1989) and hurricane George (category 3, 1998) (Thompson et al., 2002; Zimmerman et al., 1994).

Tree and seedling censuses

All woody stems ≥1 cm in dbh (≥1 cm at 1.3 m) (except for lianas) present in the LFDP were tagged, mapped, and species-identified (Thompson et al., 2002; Zimmerman, 2021). Status (alive or dead) and diameter were recorded in 2000, 2005, 2011, and 2016. All free standing seedlings <1 cm in diameter were monitored across 150 seedling plots (2 × 1 m) (Uriarte et al., 2005). Seedling censuses were conducted in 2000, 2004, and annually from 2007 to 2016, and all surveys were used to estimate species seedling survival. For further details, see Appendix S1: Section S1, Table S1 (data available at: Luquillo long term ecological research [LTER] data, Zimmerman, 2021).

Functional traits

Four leaf traits were collected related to light acquisition—representing the LES and structure (Poorter & Rozendaal, 2008; Wright et al., 2004)—for seedlings and adult species: leaf area (LA, in square meters), leaf percentage carbon (%C), leaf percentage nitrogen (%N), and SLA (in square centimeters per gram) (Umaña et al., 2015, 2016; Uriarte et al., 2009). For further details, see Appendix S1: Section S1; Swenson & Umana, 2015).

Analyses

Survival rates

To estimate species mean seedling survival, we fit a linear mixed effect model across all species in which seedling survival (0 = dead, 1 = alive) of seedling i of species s was modeled as a function of initial seedling height as a fixed effect to account for size-dependent mortality. Plot ID and species were included as intercept-specific random effects to account for variation in survival across plots and species. The model equation was: $S \sim \text{height} + (1|\text{species}) + (\text{plot})$. From the model fit, we extracted the intercept values that represent species mean seedling survival rates for subsequent analysis (Umaña et al., 2023). For this analysis, we used the function "lmer" in "lme4" package in R (Bates et al., 2015).

To estimate species juvenile (JS) and maximum survival (MS), we modeled size-dependent survival of individual i of species s with logistic functions that capture the hump-shaped survival of most species, that is, the decrease in survival at small and at very large sizes (Needham et al., 2018, 2022). To obtain robust estimates of survival, we only used species with more than 200 individuals and excluded the palm *P. acuminata* that lacks radial growth. The selected species represented 31 species and 68% of the total basal area including palms and 88% excluding palms. From the model fit, we obtained species survival probability at 1 cm dbh (JS) and MS per census interval, subsequently averaged across all censuses. We used Bayesian Markov Chain Monte Carlo (MCMC) with the "rstan" package in R (Goodrich et al., 2020), and we ran three chains with 2500 iterations per species. For further details, see Appendix S1: Section S1; Umaña et al. (2023).

Relationships between demography and functional traits

To examine the relationship between traits and demography, we fit linear models for each combination of (1) developmental stage for leaf trait measurements (seedlings or adults) and (2) survival rates (seedling, JS, or MS), representing a total of 24 models. Given that multiple statistical tests may increase the probability of type I error, we performed a Benjamini–Hochberg false discovery rate test (Benjaminit & Hochberg, 1995; Verhoeven et al., 2005). We log-transformed LA and SLA to reduce skewness and used the function "lm" in R to fit the models (R Development Core Team, 2017). The models using JS and MS included 25 species, while the models for seedling survival included 34 species. The variation in species number was due to differences in availability of demographic and trait data at the different developmental stages. The species used in the analyses are included in Appendix S1: Table S1. Furthermore, we examined the pairwise relationships between survival rates at each stage to ensure the consistency in species ranking across ontogeny.

RESULTS

Overview

Mean LA was smaller in seedlings than adults, while mean SLA and leaf carbon content (LCC) were larger in

seedlings than adults, and leaf nitrogen content (LNC) was not significantly different between the two stages (Table 1). Leaf trait correlations between seedlings and adults were always positive and significant, except for LCC (Appendix S1: Table S2). Survival rates increased through developmental stages across all species: mean seedling survival was 0.76, mean JS was 0.87, and mean MS was 0.97 (Appendix S1: Table S3). Survival rates at the seedling stage were significantly and positively related to JS but not related to MS. JS and MS were significantly and positively related (Appendix S1: Table S4).

Relationship between traits and survival over ontogeny

We found that leaf traits measured in adults captured JS and MS rates, but not seedling survival rates. Specifically, maximum tree survival rates declined for species with high SLA (Figure 1; Appendix S1: Table S5; $R^2 = 0.26$). JS decreased for species with high LNC (Figure 1; Appendix S1: Table S5; $R^2 = 0.37$). In addition, leaf traits measured in seedlings captured seedling and JS rates, but not MS rates. In particular, JS decreased for species with high SLA (Figure 1; Appendix S1: Table S5; $R^2 = 0.22$). Seedling survival declined for species with low LCC and high SLA (Figure 1; Appendix S1: Table S5; $R^2 = 0.15$, 0.11, respectively).

DISCUSSION

A key assumption of the trait framework is that functional traits should be tightly linked to demographic performance (Arnold, 1983; Violle et al., 2007). However, earlier studies have shown that this relationship is significant, but weak for leaf traits (Yang et al., 2018). In this study, we tackled one of the potential reasons that may weaken relationships between traits and performance: intraspecific trait and demographic variation over ontogeny. We show that stage-specific leaf traits better predict survival at that stage, and that the strength of these relationships is often higher than previously reported in tropical forests. These results have implications for improving predictability of communities by accounting for stage-dependent variations in traits and demography. Below we discuss our results in more detail.

Our results show that the predictive power and significance of the trait–survival relationships improve when combining traits and demographic rates measured at the same ontogenetic stage. Adult traits were significantly related to MS, seedling traits were significantly related to seedling survival, and both stage-specific traits were related to JS (Figure 1). These results agree with the idea that trait–survival relationships are sensitive to both the variation in demography over ontogeny (Visser et al., 2016) and to the variation in traits across trees' life cycle. One reason explaining the stronger correspondence between traits and survival at the same life stage is that individual traits are optimized for the specific environmental context of that stage. For example, leaf traits exhibited more conservative values at the adult stage than at the seedling stage (Table 1). These more conservative values are often observed in leaves that are fully exposed to direct sunlight (Niinemets & Kull, 1994), which are the prevalent conditions in the forest canopy (Chazdon & Fetcher, 1984). In the canopy, trees can invest in more costly leaves with longer return on investment as they have full access to light (Wright et al., 2004). This co-variation between light conditions and leaf traits may also explain why JS rates were explained by both seedling and adult traits, as juveniles reach the mid-canopy and have intermediate access to light compared to seedlings and adults.

By comparing the explanatory power from this study with earlier studies, we noticed a substantial increase in the strength of the relationships between leaf mass per area (LMA, the inverse of SLA) and seedling survival rates when using stage-specific traits. The coefficient of determination (R^2) increased by up to one order of magnitude from $R^2 = 0.02$ in Visser et al. (2016) and $R^2 = 0.01$ in this study

TABLE 1 Trait mean, ranges and Wilcoxon signed ranked test for seedlings and adults of tree species present at the Luquillo Forest Dynamics Plot in Puerto Rico.

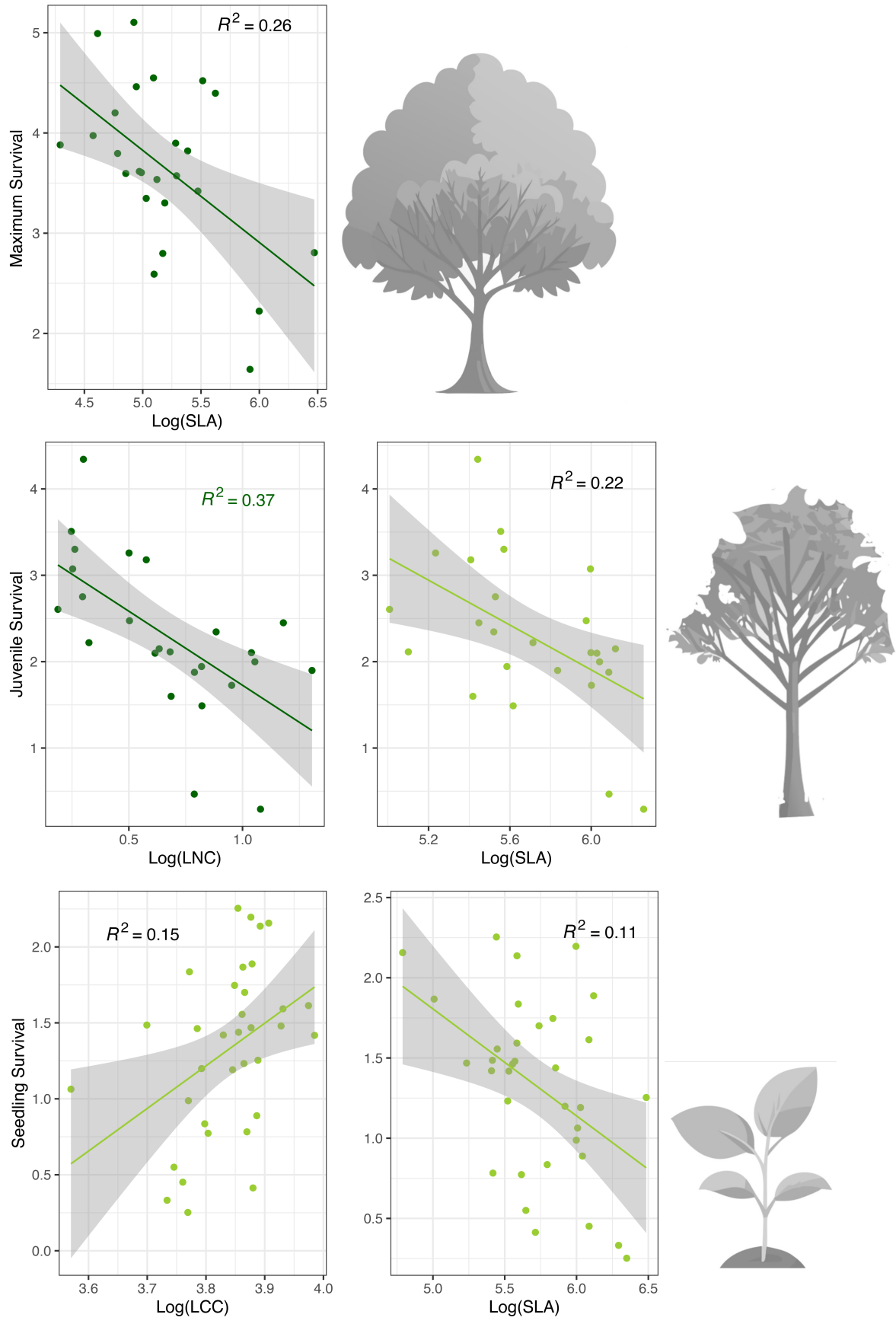| Trait	Abbreviation (units)	Adults			Seedlings			Wilcoxon test	
		Min	**Mean**	**Max**	**Min**	**Mean**	**Max**	**W**	**p-value**
Leaf area	LA (cm^2)	14.03	270.82	2407.06	0.33	11.47	35	103	<0.001
Leaf carbon content	LCC (%)	37.31	45.61	49.83	35.52	46.54	53.78	147	0.03
Leaf nitrogen content	LNC (%)	1.2	2.05	3.69	1.33	2.59	4.91	163	0.08
Specific leaf area	SLA (cm^2/g)	73.17	200	346.39	120.14	332.66	655.43	103	<0.001

FIGURE 1   Legend on next page.

using adult traits to $R^2 = 0.11$ when using seedling traits. Similarly, the relationships between LMA (SLA, in this study) and adult survival showed an increase in R^2 compared to reported in previous tropical studies, but in a lesser extent ($R^2_{\text{This study}} = 0.26$ vs. $R^2_{\text{Visser et al. 2016}} = 0.24$, and $R^2_{\text{Wright et al. 2010}} = 0.17$). The strongest relationship found in this study was between leaf nitrogen measured for adults and JS. Leaf nitrogen has been less studied than SLA (Fortunel et al., 2020; Messier et al., 2017; Umaña & Swenson, 2019), and to our knowledge, no studies have examined its relationships with survival across ontogeny. However, we showed that this trait had a prevalent role explaining survival rates at all stages (yet not significant for seedlings after Benjamini–Hochberg correction), likely due to its key role in synthetizing amino acids which are part of Rubisco and ultimately influencing the efficiency of carbon dioxide fixation. Our findings corroborate the role of leaf economics traits on tree survival and highlight the relevance of measuring traits and demography at the same ontogenetic stage to improve survival models. Importantly, differential responses between seedlings and adults or juveniles to environmental changes have strong implications for understanding the future of tropical forests.

Our results further showed that the strength of trait–performance relationships varied across life stages and was stronger at the juvenile stage. This finding is consistent with previous studies that have shown that traits are better predictors of juvenile tree survival than MS rates (Wright et al., 2010). This variation of trait effects on survival over ontogeny has been attributed to increasing requirements for mechanical and hydraulic support that occur as trees grow in size (King, 2011) where the effect of photosynthetic traits such as SLA or LNC on demography tends to dissipate (Falster et al., 2011). In line with this explanation, previous studies have reported that crown architecture and size play a larger role than SLA in predicting adult tree performance (Sterck et al., 2011). Furthermore, an additional factor contributing to weaker trait–survival relationships for adults is the challenge for obtaining good estimates of MS due to low samples sizes in tropical forests, which leads to greater uncertainty associated with survival rate estimations for larger individuals.

At the seedling stage, we observed the weakest relationships between leaf traits and survival compared to juveniles and adults ($R^2_{\text{seedlings}} = 0.08–0.17$ vs. $R^2_{\text{adults and juveniles}} = $

0.12–0.36). These results contrast with theory suggesting that smaller individuals should show stronger trait–demographic relationship (King, 2011). Also, previous studies have reported that, at the seedling stage, SLA tends to be a strong predictor of growth for seedlings (Lambers & Poorter, 1992; Wright & Westoby, 1999). One possible explanation for this inconsistency is that previous studies recorded seedling growth under more favorable conditions of light than those experienced by the seedlings in our study, which were growing in dark forest understories. Moreover, seedling performance can be strongly impacted by cotyledons and seed mass (Metz et al., 2023; Wright & Westoby, 1999), which may have played a significant role influencing survival at this very early stage.

Our findings corroborate previous trends showing that species with conservative leaf traits, characterized by low SLA and low LNC, exhibit higher survival rates and this trend remains consistent throughout different life stages. Conservative leaves have longer leaf lifespan but require a greater investment of dry mass per unit of LA (i.e., low SLA) (Reich et al., 1992; Wright et al., 2004). Consequently, these species typically exhibit slower carbon-based metabolism, resulting in slow growth and high survival rates (Lambers & Poorter, 1992). In seedlings, we also found that LCC impacted survival rates, with higher carbon content associated with increased survival. This suggests that increasing carbon content at early life stages may be an effective strategy for enhancing seedling survival by tolerating herbivores, as previous studies have shown that leaves with lower carbon content tends to be more susceptible to physical damage and insect attack (Alvarez-Clare & Kitajima, 2007).

CONCLUSION

A key step in building a solid predictive trait framework for forest communities requires the understanding of how demography varies over time and how traits impact performance over different life stages (Laughlin et al., 2020). We show that functional strategies for seedlings and adults are consistently linked to tree demography across different life stages, with leaf acquisitive traits aligned with low survival rates, yet stage-specific traits tend to be more strongly and significantly related to

FIGURE 1 Significant relationships (after Benjamini–Hochberg false discovery rate correction) between leaf traits and survival over ontogeny. Light green points and lines represent relationships using seedling trait data and dark green points and lines represent relationships using adult trait data. Shaded area represents the 95% CIs. See Appendix S1: Table S2 for details on slope coefficients and Table 1 for abbreviations and units. Illustrations by María Natalia Umaña.

the same stage survival. This study represents an effort for bridging traits and survival across life stages and underscores the need for incorporating stage-specific traits and demography to improve predictability of communities.

DATA AVAILABILITY STATEMENT

Adult censuses data (Zimmerman, 2021) are available in the Environmental Data Initiative's data portal at https://doi.org/10.6073/pasta/f0b8285061bcf65193d0a312585b5f21. Seedling censuses data (Zimmerman, 2018) are available in the Environmental Data Initiative's data portal at https://doi.org/10.6073/pasta/45e4817e74b51b9533b1bd4115415569. Adult trait data (Swenson & Umana, 2015) are available in Dryad at https://doi.org/10.5061/dryad.j2r53. Seedling trait data (Umaña et al., 2021) are available in Dryad at https://doi.org/10.5061/dryad.sqv9s4n29.

ORCID

María Natalia Umaña https://orcid.org/0000-0001-5876-7720

Claire Fortunel https://orcid.org/0000-0002-8367-1605

REFERENCES

Alvarez-Clare, S., and K. Kitajima. 2007. "Physical Defence Traits Enhance Seedling Survival of Neotropical Tree Species." *Functional Ecology* 21: 1044–54.

Arnold, S. J. 1983. "Morphology, Performance and Fitness." *American Zoology* 361: 347–361.

Barton, K. E. 2023. "The Ontogenetic Dimension of Plant Functional Ecology." *Functional Ecology* 38: 98–113.

Barton, K. E., and K. Boege. 2017. "Future Directions in the Ontogeny of Plant Defence: Understanding the Evolutionary Causes and Consequences." *Ecology Letters* 20: 403–411.

Bates, D., M. Maechler, B. M. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67, no.1: 1–48. https://doi.org/10.18637/jss.v067.i01

Benjaminit, Y., and Y. Hochberg. 1995. "Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing." *Journal of the Royal statistical society: series B (Methodological)* 57(1): 289–300.

Boege, K., R. Dirzo, D. Siemens, and P. Brown. 2007. "Ontogenetic Switches from Plant Resistance to Tolerance: Minimizing Costs with Age?" *Ecology Letters* 10: 177–187.

Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. W. Rudolf, S. J. Schreiber, M. C. Urban, and D. A. Vasseur. 2011. "Why Intraspecific Trait Variation Matters in Community Ecology." *Trends in Ecology & Evolution* 26: 183–192.

Chazdon, R. L., and N. Fetcher. 1984. "Light Environments of Tropical Forests." In *Physiological Ecology of Plants of the Wet Tropics*, edited by E. Medina, H. A. Mooney, and C. Vázquez-Yánes, 27–36. Netherlands: Springer.

Chen, Y., M. N. Umaña, M. Uriarte, and S. Yu. 2018. "Abundance-Dependent Effects of Neighbourhood Dissimilarity and Growth Rank Reversal in a Neotropical Forest." *Proceedings of the Royal Society B* 285: 20172878.

Falster, D. S., Å. Brännström, U. Dieckmann, and M. Westoby. 2011. "Influence of Four Major Plant Traits on Average Height, Leaf-Area Cover, Net Primary Productivity, and Biomass Density in Single-Species Forests: A Theoretical Investigation." *Journal of Ecology* 99: 148–164.

Fortunel, C., C. Stahl, P. Heuret, E. Nicolini, and C. Baraloto. 2020. "Disentangling the Effects of Environment and Ontogeny on Tree Functional Dimensions for Congeneric Species in Tropical Forests." *New Phytologist* 226: 385–395.

Goodrich, B., S. Weber, and D. Lee. 2020. "Package 'rstan' the R Interface to Stan. R Package Version 2.21.2."

Hérault, B., B. Bachelot, L. Poorter, V. Rossi, F. Bongers, J. Chave, C. E. T. Paine, F. Wagner, and C. Baraloto. 2011. "Functional Traits Shape Ontogenetic Growth Trajectories of Rain Forest Tree Species." *Journal of Ecology* 99: 1431–40.

King, D. A. 2011. "Size-Related Changes in Tree Proportions and their Potential Influence on the Course of Height Growth." In

Size-and Age-Related Changes in Tree Structure and Function, edited by F. Meinzer, B. Lachenbruch, and T. Dawson, 165–192. New York: Springer.

King, D. A., S. J. Davies, and N. S. Md. Noor. 2006. "Growth and Mortality Are Related to Adult Tree Size in a Malaysian Mixed Dipterocarp Forest." *Forest Ecology and Management* 223: 152–58.

Kitajima, K. 1994. "Relative Importance of Photosynthetic Traits and Allocation Patterns as Correlates of Seedling Shade Tolerance of 13 Tropical Ttees." *Ecology* 98: 419–428.

Kraft, N. J. B. B., R. Valencia, D. D. Ackerly, A. Forest, R. Valencia, and D. D. Ackerly. 2008. "Functional Traits and Niche-Based Tree Community Assembly in an Amazonian Forest." *Science* 322: 10–13.

Lambers, H., and H. Poorter. 1992. "Inherent Variation in Growth Rate between Higher Plants: A Search for Physiological Causes and Ecological Consequences." *Advances in Ecological Research* 23: 187–261.

Lasky, J. R., B. Bachelot, R. Muscarella, N. Schwartz, J. Forero-Montaña, C. J. Nytch, N. G. Swenson, et al. 2015. "Ontogenetic Shifts in Trait-Mediated Mechanisms of Plant Community Assembly." *Ecology* 96: 2157–69.

Laughlin, D. C., J. R. Gremer, P. B. Adler, R. M. Mitchell, and M. M. Moore. 2020. "The Net Effect of Functional Traits on Fitness." *Trends in Ecology & Evolution* 35: 1037–47.

Martínez-Vilalta, J., M. Mencuccini, J. Vayreda, and J. Retana. 2010. "Interspecific Variation in Functional Traits, Not Climatic Differences among Species Ranges, Determines Demographic Rates across 44 Temperate and Mediterranean Tree Species." *Journal of Ecology* 98: 1462–75.

McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. "Rebuilding Community Ecology from Functional Traits." *Trends in Ecology & Evolution* 21: 178–185.

Messier, J., B. J. Mcgill, B. J. Enquist, and M. J. Lechowicz. 2017. "Trait Variation and Integration across Scales: Is the Leaf Economic Spectrum Present at Local Scales?" *Ecography* 40: 685–697.

Metz, M., S. J. Wright, J. K. Zimmerman, A. Hernández, S. M. Smith, N. G. Swenson, M. N. Umaña, et al. 2023. "Functional Traits of Young Seedlings Predict Trade-Offs in Seedling Performance in Three Neotropical Forests." *Journal of Ecology* 111: 2568–82.

Needham, J., C. Merow, C.-H. Chang-Yang, H. Caswell, and S. M. McMahon. 2018. "Inferring Forest Fate from Demographic Data: From Vital Rates to Population Dynamic Models." *Proceedings of the Royal Society B: Biological Sciences* 285: 20172050.

Needham, J. F., D. J. Johnson, K. J. Anderson-Teixeira, N. Bourg, S. Bunyavejchewin, N. Butt, M. Cao, et al. 2022. "Demographic Composition, Not Demographic Diversity, Predicts Biomass and Turnover across Temperate and Tropical Forests." *Global Change Biology* 28: 2895–2909.

Niinemets, U., and K. Kull. 1994. "Leaf Weight per Area and Leaf Size of 85 Estonian Woody Species in Relation to Shade Tolerance and Light Availability." *Forest Ecology and Management* 7: 1–10.

Pigliucci, M. 2001. *Phenotypic Plasticity: Beyond Nature and Nurture*. Baltimore, MD: Johns Hopkins University Press.

Poorter, L., and D. M. A. Rozendaal. 2008. "Leaf Size and Leaf Display of Thirty-Eight Tropical Tree Species." *Oecologia* 158: 35–46.

Pu, X., M. N. Umaña, and G. Jin. 2020. "Trait-Mediated Neighbor Effects on Plant Survival Depend on Life Stages and Stage-Specific Traits in a Temperate Forest." *Forest Ecology and Management* 472: 118250.

R Development Core Team. 2017. *R: A Language and Environment for Statistical Computing R Development Core Team*. Vienna: R Foundation for Statistical Computing.

Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1992. "Leaf Life-Span in Relation to Leaf, Plant, and Stand Characteristics Among Diverse Ecosystems." *Ecological Monographs* 62: 365–392.

Reich, P. B. 2014. "The World-Wide 'Fast – Slow' Plant Economics Spectrum: A Traits Manifesto." *Journal of Ecology* 102: 275–301.

Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1997. "From Tropics to Tundra: Global Convergence in Plant Functioning." *Ecology* 94: 13730–34.

Ryan, M. G., and B. J. Yoder. 1997. "Hydraulic Limits to Tree Height and Tree Growth: What Keeps Trees from Growing beyond a Certain Height?" *BioScience* 47: 235–242.

Siefert, A., C. Violle, L. Chalmandrier, C. H. Albert, A. Taudiere, A. Fajardo, L. W. Aarssen, et al. 2015. "A Global Meta-Analysis of the Relative Extent of Intraspecific Trait Variation in Plant Communities." *Ecology Letters* 18: 1406–19.

Sterck, F., L. Markesteijn, F. Schieving, and L. Poorter. 2011. "Functional Traits Determine Trade-Offs and Niches in a Tropical Forest Community." *Proceedings of the National Academy of Sciences of the United States of America* 108: 20627–32.

Swenson, N. G., and M. N. Umana. 2015. "Data From: Interspecific Functional Convergence and Divergence and Intraspecific Negative Density Dependence Underlie the Seed-to-Seedling Transition in Tropical Trees." Dryad. Dataset. https://doi.org/10.5061/dryad.j2r53.

Thompson, J., N. Brokaw, J. K. Zimmerman, R. B. Waide, E. M. Everham, III, D. J. Lodge, C. M. Taylor, D. García-Montiel, and M. Fluet. 2002. "Land Use History, Environment, and Tree Composition in a Tropical Forest." *Ecological Applications* 12: 1344–63.

Umaña, M. N., J. Forero-Montaña, R. Muscarella, C. J. Nytch, J. Thompson, M. Uriarte, J. Zimmerman, and N. G. Swenson. 2016. "Interspecific Functional Convergence and Divergence and Intraspecific Negative Density Dependence Underlie the Seed-to-Seedling Transition in Tropical Trees." *The American Naturalist* 187: 99–109.

Umaña, M. N., C. Zhang, M. Cao, L. Lin, and N. G. Swenson. 2015. "Commonness, Rarity, and Intraspecific Variation in Traits and Performance in Tropical Tree Seedlings." *Ecology Letters* 18: 1329–37.

Umaña, M. N., E. F. Zipkin, C. Zhang, M. Cao, L. Lin, and N. G. Swenson. 2018. "Individual-Level Trait Variation and Negative Density Dependence Affects Growth in Tropical Tree Seedlings." *Journal of Ecology* 206: 2446–55.

Umaña, M. N., G. Arellano, N. Swenson, and J. Zambrano. 2021. "Tree Seedling Trait Optimization and Growth in Response to Local-Scale Soil and Light Variability [Dataset]." Dryad. https://doi.org/10.5061/dryad.sqv9s4n29.

Umaña, M. N., J. Needham, J. Forero-Montaña, C. J. Nytch, N. G. Swenson, J. Thompson, M. Uriarte, and J. K. Zimmerman. 2023. "Demographic Trade-Offs and Functional Shifts in a Hurricane-Impacted Tropical Forest." *Annals of Botany* 131: 1051–69.

Umaña, M. N., and N. G. Swenson. 2019. "Does Trait Variation within Broadly Distributed Species Mirror Patterns across Species? A Case Study in Puerto Rico." *Ecology* 100: e02745.

Uriarte, M., C. D. Canham, J. Thompson, J. K. Zimmerman, L. Murphy, A. M. Sabat, N. Fetcher, and B. L. Haines. 2009. "Natural Disturbance and Human Land Use as Determinants of Tropical Forest Dynamics: Results from a Forest Simulator." *Ecological Monographs* 79: 423–443.

Uriarte, M., S. P. Hubbell, R. John, R. Condit, and C. D. Canham. 2005. "Neighbourhood Effects on Sapling Growth and Survival in a Neotropical Forest and the Ecological Equivalence Hypothesis." In *Biotic Interactions in the Tropics: Their Role in the Maintenance of Species Diversity*, edited by D. Burslem, M. Pinard, and S. Hartley, 89–106. Cambridge: Cambridge University Press.

Verhoeven, K. J. F., K. L. Simonsen, and L. M. McIntyre. 2005. "Implementing False Discovery Rate Control: Increasing Your Power." *Oikos* 108: 643–47.

Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. "Let the Concept of Trait be Functional!" *Oikos* 116: 882–892.

Visser, M. D., M. Bruijning, S. J. Wright, E. Muller-Landau, H. C. Jongejans, L. S. Comita, and H. de Kroon. 2016. "Functional Traits as Predictors of Vital Rates across the Life-Cycle of Tropical Trees." *Functional Ecology* 30: 168–180.

Wright, S. J., K. Kitajima, N. J. B. Kraft, P. B. Reich, I. J. Wright, D. E. Bunker, R. Condit, et al. 2010. "Functional Traits and the Growth-Mortality Trade-Off in Tropical Trees." *Ecology* 91: 3664–74.

Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, et al. 2004. "The Worldwide Leaf Economics Spectrum." *Nature* 428: 821–27.

Wright, I. J., and M. Westoby. 1999. "Differences in Seedling Growth Behaviour among Species: Trait Correlations across Species, and Trait Shifts along Nutrient Compared to Rainfall Gradients." *Journal of Ecology* 87: 85–97.

Yang, J., M. Cao, and N. G. Swenson. 2018. "Why Functional Traits Do Not Predict Tree Demographic Rates." *Trends in Ecology & Evolution* 33: 326–336.

Zimmerman, J. 2018. "LFDP Phenology Plot Seedlings-16 ha Plot ver 5347491." Environmental Data Initiative. https://doi.org/10.6073/pasta/45e4817e74b51b9533b1bd4115415569.

Zimmerman, J. 2021. "Census of Species, Diameter and Location at the Luquillo Forest Dynamics Plot (LFDP), Puerto Rico ver 1545979." Environmental Data Initiative. https://doi.org/10.6073/pasta/f0b8285061bcf65193d0a312585b5f2.

Zimmerman, J. K., E. M. Everham, R. B. Waide, D. J. Lodge, C. M. Taylor, and N. V. L. Brokaw. 1994. "Responses of Tree Species to Hurricane Winds in Subtropical Wet Forest in Puerto Rico – Implications for Tropical Tree Life-Histories." *Journal of Ecology* 82: 911–922.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Umaña, María Natalia, Jessica Needham, and Claire Fortunel. 2024. "From Seedlings to Adults: Linking Survival and Leaf Functional Traits over Ontogeny." *Ecology* e4469. https://doi.org/10.1002/ecy.4469