

Survival, growth, and functional traits of tropical wet forest tree seedlings across an experimental soil moisture gradient in Puerto Rico

Journal:	<i>Ecology and Evolution</i>
Manuscript ID	Draft
Wiley - Manuscript type:	Research Article
Date Submitted by the Author:	n/a
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Category:	Community Ecology
Habitat:	Terrestrial
Organism:	Plants
Approach:	Ecological Experiment
Abstract:	<p>Droughts are predicted to become more frequent and intense in many tropical regions, which may cause shifts in plant community composition. Especially in diverse tropical communities, understanding how traits mediate demographic responses to drought can help provide more general insight into the effects of climate change on these ecosystems. To understand tropical tree responses to reduced soil moisture, we grew seedlings of eight species across an experimental gradient of soil moisture at the Luquillo Experimental Forest, Puerto Rico. We quantified survival and growth over an eight-month period and characterized demographic responses in terms of tolerance to low soil moisture (higher rates of survival and growth under low soil moisture conditions) and sensitivity to variation in soil moisture (more pronounced changes in demographic rates). We then compared demographic responses with inter-specific variation in a suite of 11 functional traits, measured on individuals surviving the experiment. Lower soil moisture was associated with reduced survival and growth, but traits mediated species-specific responses. Species with relatively conservative traits, like high leaf mass per area, had higher survival at low soil moisture whereas species with more extensive root systems were more sensitive to soil moisture, in that they exhibited more pronounced changes in growth across the experimental soil moisture gradient. Our results suggest that increasing</p>

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	drought will favor species with more conservative traits that confer greater survival in low soil moisture conditions.

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Manuscripts

Dear Editor,

We are happy to submit our manuscript ("*Survival, growth, and traits of tropical wet forest tree seedlings across an experimental soil moisture gradient in Puerto Rico*") to be considered for publication in *Ecology and Evolution*.

We believe our study is ideally suited for *Ecology and Evolution* because we use an experimental approach to assess demographic responses across species under a plausible scenario of climate change. Our experiment provides an important foundation for understanding longer-term demographic responses to drought at our study area, the Luquillo Long-Term Ecological Research site. Specifically, we grew seedlings of eight species across an experimental gradient of soil moisture and quantified survival and growth over an eight-month period. We compared demographic responses with inter-specific variation in a suite of 11 functional traits commonly associated with resource strategies and drought tolerance. Species varied considerably in their average demographic rates and responses to variation in soil moisture, and some of these responses were related to species traits. For example, species with relatively conservative resource traits (e.g., high leaf mass per area), had higher survival at low soil moisture while species with more extensive root systems were more sensitive to soil moisture. Overall, our results suggest that increasing drought will favor species with more conservative traits that confer greater survival in low soil moisture conditions.

Thank you for considering our work for publication and please do not hesitate to contact us with any questions.

Sincerely,
Robert Muscarella, on behalf of co-authors
Plant Ecology and Evolution
Uppsala University

Survival, growth, and functional traits of tropical wet forest tree seedlings across an experimental soil moisture gradient in Puerto Rico

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Running title: *Seedling response to soil moisture gradient*

21 Abstract

22 Droughts are predicted to become more frequent and intense in many tropical regions, which
23 may cause shifts in plant community composition. Especially in diverse tropical communities,
24 understanding how traits mediate demographic responses to drought can help provide more
25 general insight into the effects of climate change on these ecosystems. To understand tropical
26 tree responses to reduced soil moisture, we grew seedlings of eight species across an
27 experimental gradient of soil moisture at the Luquillo Experimental Forest, Puerto Rico. We
28 quantified survival and growth over an eight-month period and characterized demographic
29 responses in terms of tolerance to low soil moisture (higher rates of survival and growth under
30 low soil moisture conditions) and sensitivity to variation in soil moisture (more pronounced
31 changes in demographic rates). We then compared demographic responses with inter-specific
32 variation in a suite of 11 functional traits, measured on individuals surviving the experiment.
33 Lower soil moisture was associated with reduced survival and growth, but traits mediated
34 species-specific responses. Species with relatively conservative traits, like high leaf mass per
35 area, had higher survival at low soil moisture whereas species with more extensive root systems
36 were more sensitive to soil moisture, in that they exhibited more pronounced changes in growth
37 across the experimental soil moisture gradient. Our results suggest that increasing drought will
38 favor species with more conservative traits that confer greater survival in low soil moisture
39 conditions.

40 **Key words:** *Drought tolerance, drought sensitivity, acquisitive, conservative, Puerto Rico*

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1. INTRODUCTION

Even under moderate scenarios of climate warming, precipitation in many tropical regions is projected to decline and become more variable in the coming decades (Feng et al., 2013; Lehner et al., 2017; Pendergrass & Hartmann, 2014). The Caribbean, for example, is expected to face a 5-50% reduction in rainfall by 2100 (Herrera & Ault, 2017; Mote et al., 2017; Ramseyer et al., 2019; Taylor et al., 2018). These changes will influence vegetation through combined impacts of warming and drying of the air and soil. Different species are, however, likely to have different responses to the impacts of climate change (McDowell et al., 2018; Poorter & Markesteijn, 2008; Smith-Martin et al., 2022a). As a result, forecasting the consequences of altered precipitation regimes on tropical forest ecosystems requires a solid understanding of how diverse species will respond to novel conditions (Comita & Engelbrecht, 2014; Meir et al., 2015).

One challenge for understanding how different species will respond to drought is the variety of ways to characterize demographic responses (Figure 1). For example, species may differ in their ability to survive or grow under extremely low resource conditions (e.g., periods of very dry soil) (Tilman, 1982). Species could also differ in the degree to which their demographic rates are sensitive to variation in environmental conditions. More specifically, the relative magnitude by which a given demographic rate varies across a relevant range of environmental stress can be used to characterize species responses (Engelbrecht et al., 2007). Additionally, demographic responses may manifest differently for different vital rates (i.e. demographic compensation) (e.g., Yang et al., 2022), making it critical to evaluate multiple demographic rates for a more complete picture of responses to environmental variation. Overall, a solid understanding of species responses to environmental change requires a comprehensive evaluation of responses for multiple demographic rates.

Diverse responses of tropical trees to drought should be linked, at least in part, to traits that reflect their resource strategies (O'Brien et al., 2017; Oliveira et al., 2021; Paz et al., 2015; Smith-Martin et al., 2022a). For example, species with relatively 'acquisitive' traits (e.g., lower wood density, leaf mass per area [LMA], and root tissue density) tend to maximize growth rates by producing 'cheap' tissues (i.e., low carbon investment) with efficient hydraulic architectures (Castro-Díez et al., 1998; Gilbert et al., 2006; Markesteijn, Poorter, Bongers, et al., 2011; Markesteijn, Poorter, Paz, et al., 2011; van Gelder et al., 2006). While these characteristics may enable a rapid demographic response to changes in resource availability (i.e., greater sensitivity), efficient hydraulic systems also tend to be more susceptible to drought-induced mortality (i.e., less tolerant) (Castro-Díez et al., 1998; Mantova et al., 2021; Niinemets & Valladares, 2006; Smith-Martin et al., 2022a; van Gelder et al., 2006). In contrast, species with relatively 'conservative' functional strategies (e.g., higher wood density, LMA, and root tissue density) tend to exhibit lower maximum growth rates but greater survival during low resource conditions, including drought (Gilbert et al., 2006; Markesteijn, Poorter, Bongers, et al., 2011; Markesteijn, Poorter, Paz, et al., 2011). In other words, species with more conservative traits may be better able to tolerate dry conditions (drought resistance) whereas species with more acquisitive traits may be more sensitive (or responsive) to shifts in water availability. Overall, increasing drought frequency and severity is likely to select for species with relatively conservative functional strategies due to a combined effects of higher sensitivity of acquisitive species and greater tolerance of conservative species (Bartlett et al., 2019; Duque et al., 2015; Esquivel-Muelbert et al., 2018).

The selective pressure exerted by altered precipitation regimes on community composition may be particularly strong for early life stages of trees. Specifically, the seedling

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3 87 life stage represents a major recruitment bottleneck and seedling survival rates can influence
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5 88 future tree community composition (Grime, 1979; Poorter, 2007). Additionally, because of their
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8 89 shallow root systems, seedlings can be particularly strongly affected by drought (Comita &
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10 90 Engelbrecht, 2014; Harrison & LaForgia, 2019; Uriarte et al., 2018; Wright & Westoby, 1999).
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12 91 Seedling traits related to drought response may, therefore, play a particularly important role in
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15 92 determining how drought conditions impact the future composition of tropical forests.

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17 93 To address these issues, we evaluated responses of wet tropical forest seedlings to
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19 94 variation in soil moisture using an eight-month seedling transplant experiment, where eight
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21 95 common tree species that spanned a broad range of life-history strategies were subjected to an
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24 96 experimental gradient of soil moisture via rainfall manipulation. We monitored seedling growth
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26 97 and survival for the duration of the experiment and then correlated metrics of demographic
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28 98 performance with a suite of functional traits to better understand how traits mediate demographic
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31 99 response to drought conditions. We addressed the following questions:

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33 100 **How do species vary in terms of their demographic performance across an**
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35 101 **experimental soil moisture gradient? And, is variation in demographic rates related to**
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38 102 **species functional traits?** We expected species to vary considerably with respect to survival and
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40 103 growth responses along the soil moisture gradient based on their different life-history strategies
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42 104 and successional associations. We expected species with relatively conservative traits (e.g., low
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44 105 LMA, wood density, and root tissue density) to have higher overall survival and lower overall
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46 106 growth compared to species with more acquisitive traits. Along the soil moisture gradient, we
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48 107 expect species with relatively conservative traits to exhibit higher tolerance to drought (i.e.,
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51 108 higher rates of survival and growth under low soil moisture conditions) compared to species with
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54 109 relatively acquisitive traits (Table S1). At the same time, we expected species with relatively

110 acquisitive traits to exhibit higher sensitivity to soil moisture variation (i.e., more pronounced
 111 changes in demographic rates) compared to species with more conservative traits (Hiromi et al.,
 112 2012; Markesteijn, Poorter, Bongers, et al., 2011; Markesteijn, Poorter, Paz, et al., 2011; Poorter
 113 & Markesteijn, 2008).

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115 2. METHODS

116 *Study site*

117 The experiment was conducted at the El Verde Research Area, within the Luquillo Experimental
 118 Forest (LEF), Puerto Rico (18°32'N, 65°81'W). The LEF is classified as subtropical wet montane
 119 forest with a mean annual rainfall of 3500 mm (± 725 sd) and mean temperature of 23°C (Daly et
 120 al., 2003; Ewel & Whitmore, 1973; Thompson et al., 2002). Rainfall is aseasonal, with no month
 121 typically receiving <200 mm. Rainless periods of ~1 week are common (once per year, on
 122 average) while longer droughts (>2 weeks) have historically occurred every few years (Scatena
 123 et al., 2012). The dominant soil types in the LEF are Zarzal, a deep and well-drained oxisol, and
 124 Cristal, a deep but poorly drained ultisol (Mount & Lynn, 2004). The area comprises both
 125 primary and secondary forests that have been free from human disturbance since the 1940s
 126 (Thompson et al., 2002).

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128 *Experimental set-up and plot physical conditions*

129 We collected seeds of eight woody species (seven trees and one palm; Table S2) that were
 130 fruiting between Dec 2018 – Mar 2019. These species represent a range of life-history strategies
 131 and account for about 44% of the total individuals >1 cm DBH in the nearby 16-ha Luquillo
 132 Forest Dynamics Plot (Thompson et al., 2002). Seeds were cleaned, spread on local soil in

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horticultural trays, and then covered with a thin layer of the same soil. Trays were placed under shade cloth and watered daily until seedling emergence. Within a week of emergence, individuals were transplanted to pots (ca. 10 cm diameter, 12 cm deep) and placed under shade cloth.

We set up our experiment along the top of two ridges within 1 km of El Verde Field Station. Ridge tops were selected to minimize water flow into the plots and to maximize drought stress (O’Connell et al., 2018). In May 2019, we established sixty seedling plots (30 drought and 30 control, randomly assigned), where sixteen seedlings (2 per species) were transplanted randomly in a 4 × 4 grid with 10 cm between each seedling (Figure S1). Individual seedlings were randomly assigned to plots and locations within the grid. After a 3-week acclimation period, we constructed rain-out shelters directly over each grid of seedlings using PVC frames with a 1.2 m × 1.2 m SUNTUF® corrugated polycarbonate roof (Palram Industries Ltd. Kutztown, PA, USA) and a PVC gutter on the downslope side (Figure S1). For drought plots, precipitation from the gutter ran into a hose directed away from the plot. For control plots, precipitation runoff from the roof was collected in a 5-gallon bucket and poured back onto the seedlings using a watering can within ~24 hours of each rain event during the experiment. We dug trenches on the upslope edge of droughted plots and buried a small (~13 cm wide) strip of polycarbonate corrugated roof panel approximately 10 cm deep, leaving a 3 cm lip above ground to prevent downslope water flow. A sham trenching was performed for control shelters. We scrubbed roofs with a soft brush as needed to prevent algae and lichen growth which could reduce light.

In each plot, we measured volumetric soil water content at 0-12 cm (hereafter soil moisture) depth every two weeks using a handheld probe (Campbell Scientific HS2 system,

Queensland, Australia). Four measurements were taken at the corners of the seedling grid. Because measured values of soil moisture in plots spanned a continuum, we treated soil moisture as a continuous variable in analyses rather than a binary treatment effect (although we summarize treatment effects on soil moisture in Figure S2). To validate that the soil moisture conditions reflect a gradient of drought stress from the plant perspective, we used a stable carbon isotope analysis of leaf tissues (Cernusak et al., 2013) to assess the degree of integrated drought stress experienced by seedlings in our experiment (see details in Table S3).

We measured canopy openness for each plot using a spherical densiometer (Forestry Suppliers, Jackson, MS) at the end of the experiment. Two observers recorded densiometer measurements above the center of each shelter and these were averaged. To determine if shelters altered the temperature experienced by seedlings, we placed temperature loggers (DS1921G ThermoChron iButton, Maxim/Dallas Semiconductor Corp., USA) in plastic bags and hung them 5 cm from the soil surface in the center of 8 randomly chosen shelters as well as 2 m from the shelters. Loggers recorded temperature hourly over 3 days (7/31/2020-8/2/2020). We compared average hourly temperature between sheltered and adjacent un-sheltered areas using a paired t-test.

Seedling demography and functional traits

For each seedling, we recorded total initial leaf area (cm²), monitored survival weekly, and measured the length of all leaves monthly. We then estimated total leaf area (and leaf area growth) using species-specific leaf length-leaf area relationships from data collected on shade house grown seedlings (Table S3).

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At the end of the experiment, all surviving seedlings were harvested to measure a suite of functional traits. Seedlings were excavated, keeping their root systems intact, and rinsed with water. We immediately measured maximum root length, basal diameter (cm), and leaf thickness (mm). We then sectioned seedlings by organ (i.e., leaves, and roots), which were weighed for fresh mass and then scanned (CanoScan Lide 400) to estimate leaf area (cm²) and several root traits (*see below*). All parts were dried at 70°C until constant mass (for ≥72 hours) before recording dry mass. Total area of fresh leaves was determined with ImageJ (Schneider et al., 2012). Root system scans were edited by hand to improve their contrast and then we used WinRHIZO (2012 version, Regent Instrument, Quebec, Canada) to measure root system morphology. In total, we quantified the following 11 traits for each surviving seedling: leaf area (cm²), leaf mass per area (LMA; kg m⁻²), leaf thickness (mm), leaf dry matter content (%), root:shoot mass ratio (%), specific root length (SRL, cm g⁻¹), root tissue density (RTD, g cm⁻³), total root system length (cm), average root system diameter (mm), maximum rooting depth (cm), and number of root tips. We log transformed all traits (except LDMC) comply with normality assumptions prior to analyses.

To directly assess the effect of the experimental treatments on seedling physiological performance, we measured leaf intrinsic water-use efficiency (iWUE) using carbon (C) isotopes (methods supplement).

Several traits were strongly correlated (Table S4) and therefore we used Principal Component Analysis (PCA) to reduce the dimensionality of the trait data and explore the extent to which multivariate phenotypes were correlated with demographic responses to the soil moisture gradient. Using log-transformed variables, we first fit a PCA using the ‘prcomp’ function in R v 4.2.0 (R Development Core Team, 2020). Then, to clarify the relationships

among the included traits, we performed a varimax rotation on the first and second PCA axes. In subsequent analyses, we used values along the rotated component (RC) axes to reflect multivariate phenotypes in addition to the univariate trait values.

Data analysis

We used separate modeling approaches to characterize species-specific variation in survival and growth across the experimental soil moisture gradient. For survival, we fit species-specific mixed effects Cox proportional-hazards models using the R-packages ‘survival’ and ‘coxme’ (Therneau, 2020a, 2020b). Specifically, the ‘surv’ function was used to create a survival object, which contained the survival census data and was used as the response variable in a mixed linear model. We then fit a mixed effects Cox model using the ‘coxme’ function for survival of seedling i in plot p over census interval t using the form:

$$Survival_{ip}(t) \sim survival_0(t) \times \exp(moisture_p + canopy_p + leaf\ area_i + \epsilon_p) \quad [\text{Eqn. 1}]$$

where $survival_0$ signifies the seedlings status (alive or dead) at time, t , moisture is the grand mean of soil moisture in plot, p , canopy is the plot-level canopy openness (densiometer) measurement, leaf area is the total leaf area of the individual seedling when the experiment began (used as a predictor to account for variation in initial seedling size), and ϵ_p is the plot random effect.

For growth, we used the R-package ‘lme4’ to fit linear mixed models (LMMs) (Bates et al., 2013) with daily leaf area growth rate ($\text{cm}^2 \text{ day}^{-1}$) of individual seedlings between each census interval as the response variable. Daily growth of individual i in plot p takes the form:

$$Growth_{ip} \sim moisture_p + canopy_p + leaf\ area_{ip} + \epsilon_p + U_i \quad [\text{Eqn. 2}]$$

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3 223 where moisture, canopy, and leaf area are as described above, ϵ_p is a random effect of plot, and
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5 224 U_i is an individual random effect to account for repeated measurements. For both survival and
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8 225 growth models, we considered an interaction term between soil moisture and canopy openness
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10 226 but this did not improve model fit so we excluded it from the final models.
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12 227 Based on the fitted models, we define two complementary metrics which quantitatively
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14 228 describe variation in two vital rates (survival and growth) across the experimental gradient of soil
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17 229 moisture. First, we define ‘sensitivity’ to soil moisture variation as the change in a predicted
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19 230 demographic rate (survival or growth) across the relevant range of soil moisture in our
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21 231 experiment. Specifically, we calculated the difference between predicted survival and growth at
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23 232 the 10 and 90 percentile values of observed soil moisture from our plots (corresponding to 13.5%
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26 233 and 39.1% soil moisture, respectively) for each species. Based on this calculation, species with
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28 234 higher ‘sensitivity’ display a greater change in a given vital rate per unit change in soil moisture
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30 235 across the main range of our experimental gradient. Second, we define ‘tolerance’ to low soil
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32 236 moisture as the predicted vital rate (survival or growth) at the lower 10 percentile value of
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34 237 observed soil moisture (i.e., 13.5%, while holding other covariates at their mean values). To
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37 238 evaluate the relationship between seedling traits and demographic performance, we used linear
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39 239 regression to relate species mean values (as well as multivariate trait axes) with the sensitivity
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41 240 and tolerance metrics for both survival and growth.
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47 242 **3. RESULTS**
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49 243 Across the plots, average soil moisture calculated over the duration of the experiment ranged
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51 244 from 9-49% (median $27.8 \pm \text{SD } 8.4$) (Figure S2). The rank order of plots in terms of soil
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54 245 moisture was consistent and highly correlated with the minimum soil moisture per plot
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(Pearson's $r=0.7$, $p<0.01$). Canopy openness values ranged from 2-20% (median $9.1 \pm \text{sd } 3.5$); these were not significantly correlated with soil moisture (Pearson's $r = -0.17$, $p=0.18$). There was no significant difference in average hourly temperature measured in sheltered and adjacent un-sheltered areas ($t=-1.25$, $df=14$, $p=0.23$). Four of six species tested (except *P. montana* and *T. balsamifera* showed a negative correlation between intrinsic water-use efficiency (iWUE) and soil moisture (Figure S3, Table S4), suggesting that lower soil moisture indeed led to more integrated drought stress during the experiment.

Seedling demographic responses

Species varied considerably in their survival; four had >80% overall survival (*G. guidonia*, *I. laurina*, *T. balsamifera*, and *M. bidentata*), while two had <20% overall survival (*C. schreberiana* and *U. baccifera*) (Figure 2A; Figure S4). Survival generally increased with soil moisture, but the effect varied substantially among species, with significant positive effects for half of the species. Survival was negatively associated with canopy openness for four species, positively associated with starting size for one species (*Urera baccifera*), and negatively associated with starting size for two species (*Guarea guidonia* and *Prestoea acuminata* var. *montana*) (Table S7).

Species also varied substantially in their growth rates along the soil moisture gradient (Figure 2B; Figure S5). For example, among seedlings that survived until the end of the experiment, total leaf area growth ranged from -1.32 to $4.16 \text{ mm}^2 \text{ day}^{-1}$ (-3.02 to 9.53 cm^2 total), with negative leaf area growth indicating leaf loss through herbivory or senescence possibly due to water stress. As with survival, leaf area growth rates were generally positively correlated with soil moisture, although the effect was significant for only six of the eight species. Most species

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3 269 were predicted to have negative leaf area growth rates in plots with soil moisture less than ~20%.
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5 270 Leaf area growth was positively associated with canopy openness for two species and negatively
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8 271 associated with starting size for all species (Table S8).
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12 273 *Trait-mediated demographic responses*
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14 274 Functional traits varied extensively both among and within species. The varimax-rotated PCA
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17 275 revealed a separation among species that was broadly consistent with an acquisitive-to-
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19 276 conservative spectrum of multivariate phenotypes (Figure 3; Table S6). Rotated component 1
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21 277 (RC1) explained 32% of the total trait variation and primarily represented an axis of carbon
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23 278 investment in leaf and root tissues (i.e., higher values of LDMC, LMA, RTD, and lower values
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26 279 of SRL). Rotated component 2 (RC2) explained an additional 32% of the variation and reflected
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28 280 increasing investment in belowground tissue (i.e., larger total root system length, more root tips,
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31 281 and a higher root-to-shoot ratio).
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33 282 Species average survival was positively correlated with RC axis 1 (Pearson's $r=0.79$,
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35 283 $p=0.02$), as well as five individual traits (high LMA, leaf thickness, LDMC, RTD, and total root
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38 284 system length), indicating that species with more conservative trait values (greater resource
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40 285 investment in leaf and root tissue) tended to have higher overall survival (Table S9). Average
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42 286 growth rates were positively correlated with RC axis 2 (Pearson's $r=0.76$, $p=0.03$) and three
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44 287 individual traits (total root system length, rooting depth, and the number of root tips), reflecting
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47 288 higher overall growth rates for species with more extensive root systems (Table S9).
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49 289 We found several significant associations between traits and our metrics of sensitivity
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51 290 and tolerance (Figure 4). Here we highlight results for multivariate trait axes, but we provide full
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54 291 results in Table S9. Sensitivity of growth to variation in soil moisture (i.e., difference in
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predicted growth at the 90 and 10 percentile values of observed soil moisture) was positively correlated with RC2 ($r=0.84$, $p=0.01$) and three individual root traits (total length, depth and number of tips), which together reflect a more pronounced responses for species with larger root systems. Sensitivity of survival was not significantly correlated with either of the RC axes nor any of the individual traits.

Survival tolerance to low soil moisture (i.e., survival predicted at the lower 10 percentile of observed soil moisture) was positively related to RC1 ($r=0.85$, $p=0.01$), as well as three leaf traits (leaf area, LMA and LDMC) and one root trait (RTD) and negatively correlated with one root trait (SRL), overall suggesting that species with relatively conservative traits had higher survival under low soil moisture conditions. Tolerance of growth to low soil moisture conditions was negatively related with RC2 ($r=-0.87$, $p=0.01$) and three individual root traits (total length, depth and number of tips), indicating that species with smaller root systems had relatively higher predicted growth rates in low soil moisture conditions.

4. DISCUSSION

We used a seedling transplant experiment in an aseasonal subtropical forest to relate demographic responses along a soil moisture gradient with a suite of above- and below-ground traits. The experiment was conducted roughly one year after a major hurricane affected the site and light availability at the forest floor was ~9% canopy openness (Comita et al., 2010; Uriarte et al., 2018). Our key findings show that species-specific survival and growth responses were related to traits such that: (1) species with conservative leaf and root functional traits had higher average survival, as well as higher survival in low soil moisture conditions (i.e., high tolerance) compared to species with more acquisitive traits; (2) species with more extensive root systems

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5 316 gradient (i.e., high sensitivity). Overall, our results suggest that if, as predicted, low soil moisture
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7 317 events become more common in the Luquillo Mountains, seedlings with more conservative
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9 318 resource-acquisition strategies may be favored (potentially through relaxed CNDD effects -
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11 319 Lebrija-Trejos et al., 2023; Uriarte et al., 2018) through differential rates of survival and growth.
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13 320 Nonetheless, other sources of environmental heterogeneity and disturbance regimes will remain
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15 321 critically important for selecting which species recruit into which microsites based on nutrient
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17 322 and light availability.
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26 324 *Trait-mediated demographic response to soil moisture gradient*
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28 325 A major focus of trait-based ecology has been on using plant traits to explain demographic
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30 326 responses to environmental heterogeneity, including drought (Comita & Engelbrecht, 2014;
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32 327 Harrison & LaForgia, 2019; Hiromi et al., 2012; Markesteijn, Poorter, Paz, et al., 2011; e.g.,
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34 328 Poorter & Markesteijn, 2008). In the context of tropical tree seedlings, this work has provided
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36 329 some general insights but few studies have linked trait variation with demographic responses
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38 330 along continuous gradients of soil moisture (but see Engelbrecht & Kursar, 2003). Moreover,
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40 331 relatively few studies have investigated extensive suites of both above- and below-ground traits
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42 332 to identify which specific traits (or multivariate phenotypes) are most strongly linked with
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44 333 demographic response to soil drought.

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47 334 In our study, species were roughly arranged along a multivariate trait axis (RC1), with
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49 335 more conservative species having higher carbon investment in leaf and root tissue (de la Riva et
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51 336 al., 2016; Eldhuset et al., 2013; Köcher et al., 2012). As hypothesized, we found a positive
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54 337 correlation between species-mean position along RC1 and species average survival as well as
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survival tolerance to low soil moisture, indicating that species with more conservative traits tended to be more tolerant to drought stress. Specifically, tougher leaves and roots appeared to confer greater tolerance of low soil moisture, which is generally consistent with several other studies (de la Riva et al., 2016; Niinemets, 2001; Tng et al., 2018).

The second multivariate trait axis in our study (RC2) reflected investment in below-ground tissue, with higher values associated with longer root systems, more root tips, and higher root-to-shoot dry mass ratio. Species with higher values of RC2 were more tolerant to low soil moisture in terms of growth, indicating that species with more extensive rooting systems had relatively higher predicted growth rates under low soil moisture conditions. Species with more extensive rooting systems (higher values of RC2) were also more sensitive to variation in soil moisture in terms of growth.

In this study, we focused on trait-mediated responses to a soil moisture gradient for seedlings because they can be particularly sensitive to drought due to limited root systems and also because of the logistic limitation involved with conducting transplant experiments with larger plants. Nonetheless, understanding overall effects of drought on tropical forest communities will require greater integration with data from different life stages. For example, Visser *et al.* (2016) reported ontogenetic shifts in the relationships between functional traits and vital rates for tropical trees suggesting that different traits may be more or less important at different life stages. While we lack data on hydraulic vulnerability of adult trees for most of the species in our experiment, our results are generally consistent with recent work on adult trees in the LEF (Smith-Martin et al., 2022a, 2022b), which showed relationships between drought vulnerability and tree species with different successional associations. Specifically, early successional species (typically with more acquisitive traits) were less drought tolerant than late

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successional species. Our seedling results combined with recent data from later life cycle stages will hopefully prove useful in parameterizing ecosystem demographic models, which previously suggested that increasing drought could cause the LEF to transition from a carbon sink to a carbon source (Feng et al., 2018).

The timing of our study relative to recent hurricane disturbance also needs to be noted. The study began just over a year after Hurricane María affected the site, the strongest storm to affect the area in 89 years (Uriarte et al., 2019). Previous studies have shown the importance of temporal and spatial variation in light availability in the understory in determining seedling fate (Comita & Hubbell, 2009; Uriarte et al., 2018). For example, Comita *et al.* (2010) documented how light availability varied after Hurricane Georges (1998) and how this temporal variation influenced overall seedling survival and the way in which it interacted, at times, with biotic factors such as the density of con- and heterospecific seedlings to determine survival. Thus, disturbance history provides important context for interpreting the results of the experiment (Zimmerman et al., 2021).

Conclusions

Our results suggest that more frequent and intense droughts in the Luquillo Mountains of Puerto Rico are likely to favor species and individuals within the tree seedling community with more conservative functional strategies. Ultimately, these changes have the potential to alter ecosystem processes (e.g., carbon cycling) (Feng et al., 2018) as well as responses to future disturbances (Smith-Martin et al., 2022a). Developing a further understanding of the implications of our results will require considering the effects of variability in soil moisture at other life stages and other disturbances, which may have synergistic impacts with drought.

384

385 Acknowledgements

386 Research was funded by an NSF-ROA for DM awarded to LTER grant DEB-1831952, a grant
387 from the Swedish Research Council, Vetenskapsrådet (2019-03758 to RM), and support from the
388 Swedish Phytogeographical Society to RL and RM. Support was also provided by the University
389 of Puerto Rico and the International Institute for Tropical Forestry. Assistance with field work
390 was provided by Kara Eckert, Zeke Zeff, Jamaris Torres Diaz, and Yosselin Aparicio. We thank
391 Jon Karr at the Duke Environmental Isotope Lab for his laboratory assistance running leaf tissue
392 samples.

393

394 Author Contributions

395 DM, MU, JKZ and RM conceived and designed the experiment. DM, RM, JAH, RL, JKZ and
396 CRV performed the experiment. DM, JAH, RM and RL analyzed the data. DM, JAH, RM, RL,
397 CRV and MU wrote the manuscript; all authors provided editorial advice.

398

399 Data availability statement

400 All data associated with this manuscript are available on Github at
401 https://github.com/bobmuscarella/Luquillo_LTER_Seedling_Drought_Experiment.

402

403 Conflict of interest

404 The corresponding author confirms on behalf of all authors that there have been no involvements
405 that might raise the question of bias in the work reported or in the conclusions, implications, or
406 opinions stated.

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408 **Figure legends**

409 **Figure 1.** Schematic diagram illustrating metrics of survival tolerance and sensitivity to soil
410 moisture. The two curves show predicted survival as a function of soil moisture for two
411 hypothetical species. We calculated 'tolerance' to low soil moisture as the predicted probability
412 of survival at the value of soil moisture corresponding to the lower 10th percentile value in our
413 experimental dataset. We calculated 'sensitivity' as the difference in predicted probability of
414 survival between the 90th and 10th percentile values of soil moisture in our experimental dataset.
415 In our experiment, the 10th and 90th percentile values of soil moisture correspond to 13.5% and
416 39.1%, respectively. In the diagram, the red curve represents a species with relatively high
417 tolerance and low sensitivity to low soil moisture. The blue curve, in contrast, represents a
418 species with a relatively low tolerance and high sensitivity to low soil moisture.

420 **Figure 2.** A) Predicted model fits for survival for eight seedling species across the
421 experimentally-induced soil moisture gradient. Solid lines show model fits where soil moisture
422 had a statistically-significant effect on survival, whereas dashed lines show fits with non-
423 significant soil-moisture effects. The point where lines cross the left-most vertical line represents
424 "tolerance", i.e., survival at low 10%-ile of soil moisture measurements; "sensitivity" is based on
425 the difference in predicted survival at the 90%- and 10%-iles of soil moisture observations. B)
426 Predicted model fits for leaf area growth in relation to soil moisture. The gray area indicates
427 negative leaf area growth rates (leaf area decrease) by species. Solid lines represent statistically-
428 significant slopes.

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Figure 3. Varimax-rotated Principal Component Analysis of functional traits for all surviving individual seedlings. A) Variable ordination biplot, showing the functional trait space condensed to two ordination axes. Grey points show positions of individual seedlings. B) Position of seedlings within two-dimensional functional trait space; individuals colored by species. Diamond points show mean position in ordination space across individuals of each species.

Figure 4. Bivariate correlations between demographic metrics (tolerance and sensitivity of survival and growth) and the first two RC axes of the trait ordination. See main text and Figure 1 legend for definitions of the tolerance and sensitivity metrics. Solid lines represent statistically significant ($p < 0.05$) correlations.

Figure 1.

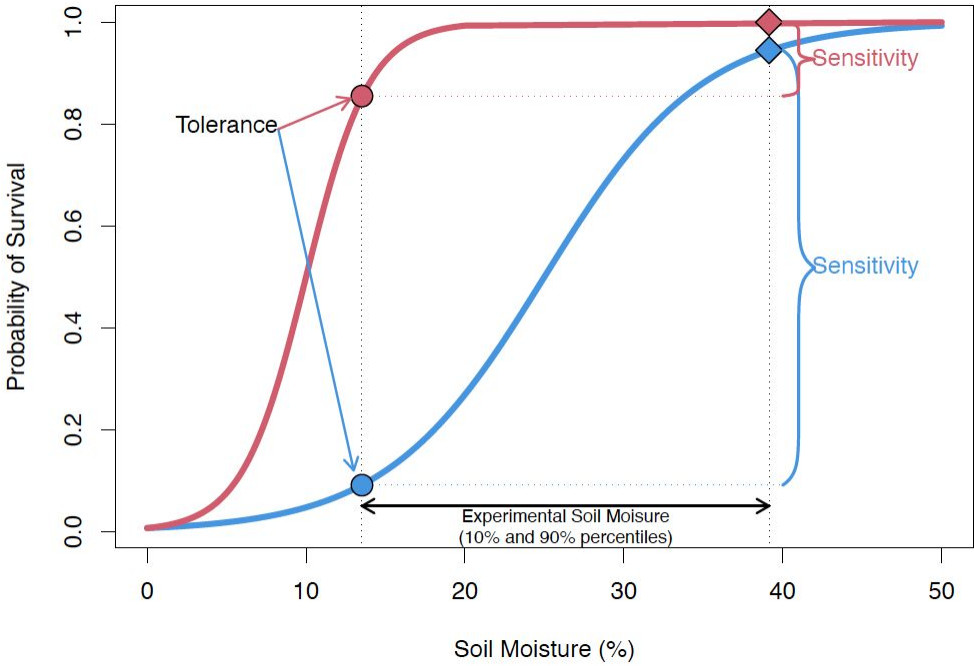


Figure 2.

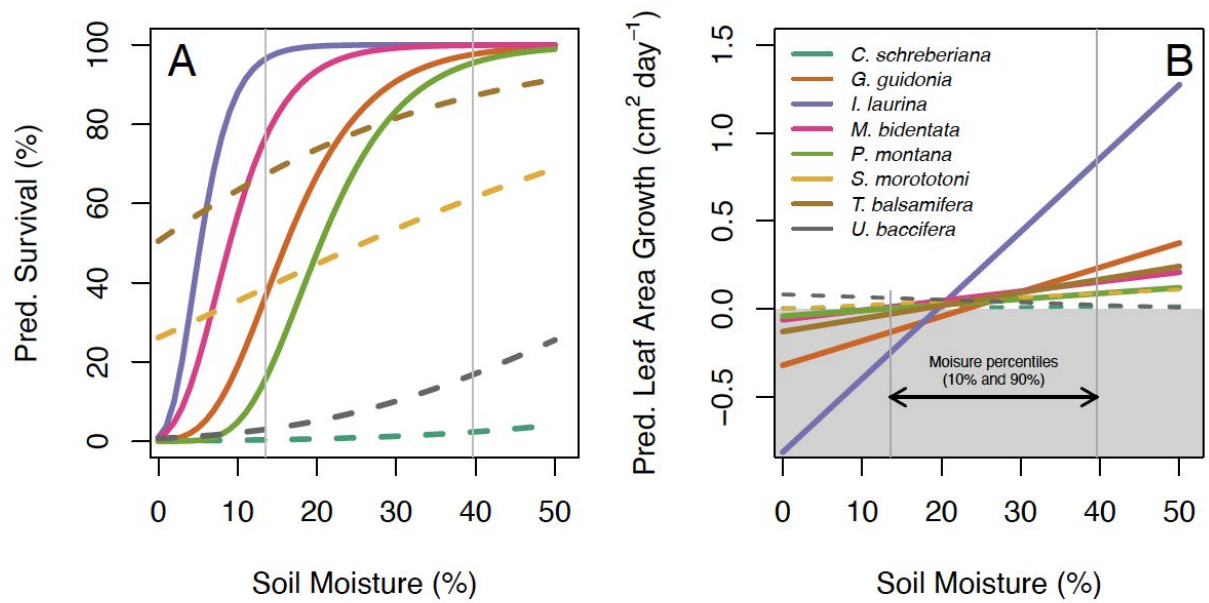
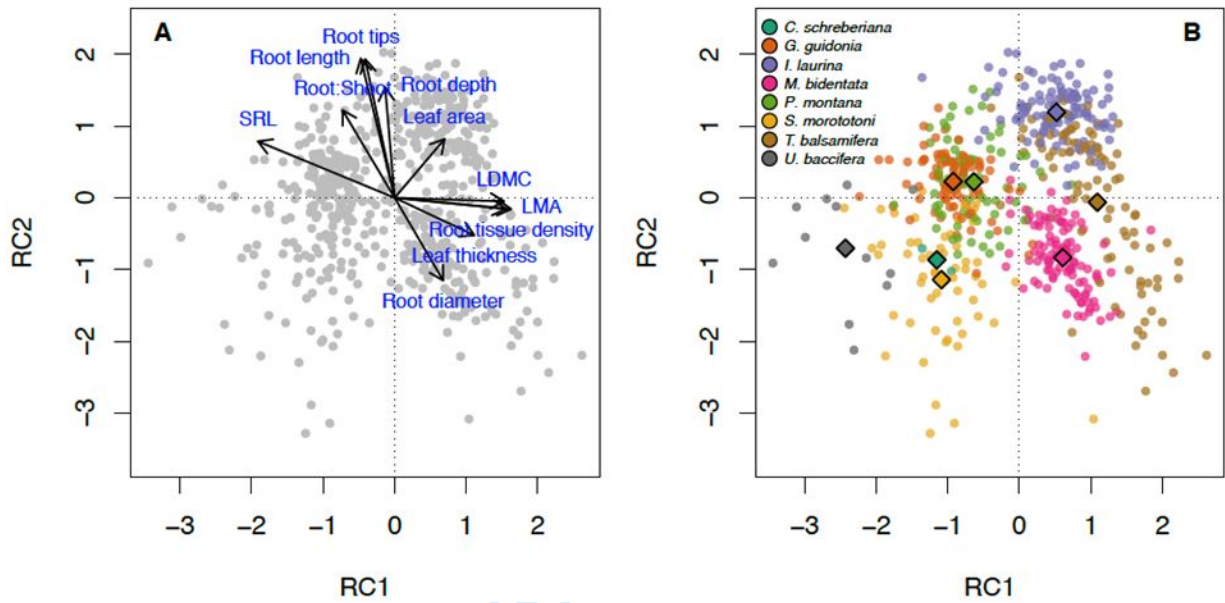
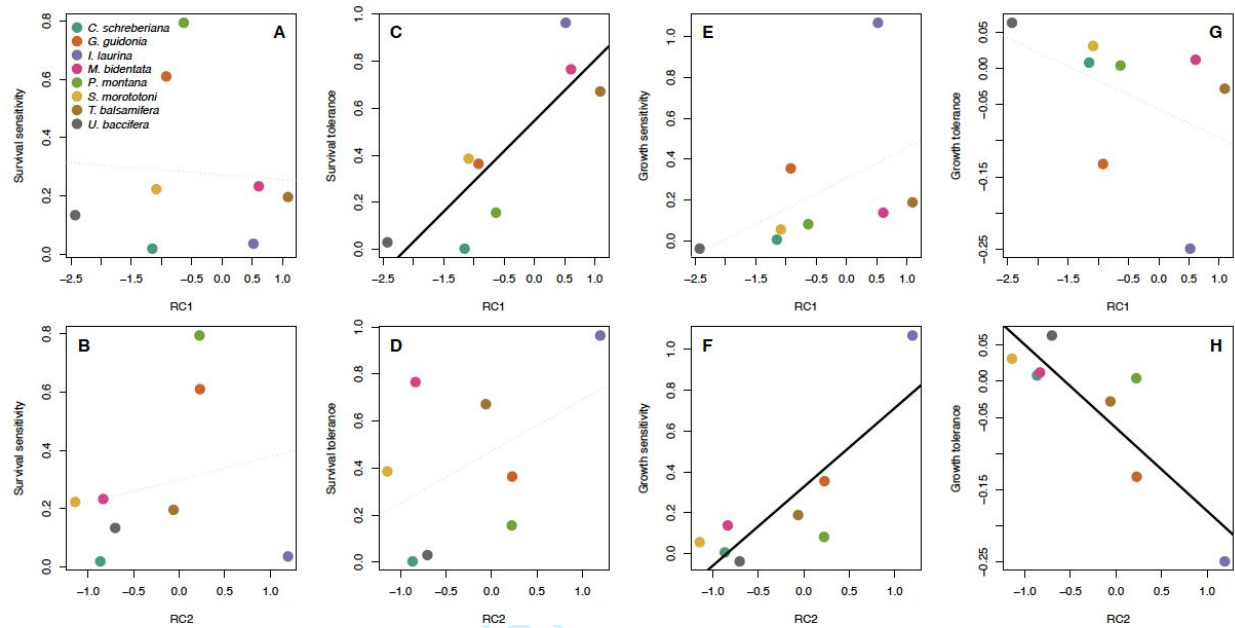


Figure 3.



450 **Figure 4.**

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